Elasmobranchs in UK seas: prioritising vulnerability and addressing life history data gaps to inform assessment and management

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Abstract

Elasmobranchs straddle commercial and biodiversity (conservation) interests. Their biological vulnerability has led to patterns of stock depletions and regional extirpations following commercial exploitation. Proactive management through pragmatic and timely measures are required to promote sustainable exploitation and conserve depleted species - both central tenets of the UK Shark, Skate and Ray Conservation Plan (analogous to a National Plan of Action (NPOA) for Sharks). The current thesis provides a framework for evidence-based decisions to be made under NPOAs, with case-studies providing new biological data to inform assessments and management advice in support of sustainable exploitation.

The UK-NPOA omits a number of elasmobranchs and does not prioritise species or actions. This thesis considers *all* UK elasmobranchs using data-limited methods to provide an impartial, evidence-based prioritisation of species of interest for subsequent research. Research and management needs are further prioritised using a semi-quantitative Productivity Susceptibility Analysis (PSA) to rank relative vulnerabilities of elasmobranchs that may interact with otter trawl and gillnet fisheries in the Celtic Sea. These approaches will be of wider applicability, particularly for developing countries where data are most limited.

The approaches guide the selection of three commercially exploited species as case studies: starry smooth-hound *Mustelus asterias*, shagreen ray *Leucoraja fullonica* and sandy ray *Leucoraja circularis*. Supplementation of fishery-independent surveys with additional specimens provided a standardised approach to collecting quantitative maturity data, which in turn informs assessment and management advice. Results have already been incorporated into ICES Expert Group assessments and advice. All three species are vulnerable to over-exploitation. A maximum landing length of ca. 100 cm for starry smooth-hound would protect the large, fecund females. Both *Leucoraja* species are listed as Threatened by IUCN and with the presentation of the first available estimates of maturity which highlight their biological vulnerability, restrictions on landings are recommended.

Declaration

I certify that this dissertation has not been submitted previously as part of the requirements for another degree and that it is the result of my own independent work, except where work which has formed part of jointly-authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated below and acknowledged in the statement preceding the Chapter. I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others.

The work presented in Chapter 2 was previously reported (non-peer reviewed and not in public domain) as a section of a Cefas project report (2019) entitled “Elasmobranch Longline Surveys in Inshore Ecosystems (ELSIE)” by McCully Phillips, S. R. (the candidate), Maia, C., Silva, J., Neville, S. and Ellis, J. R. (secondary supervisor). The candidate was the principle investigator for this project and consequently responsible for project design, leading the analyses and writing the final report. C. Maia and J. Silva were project staff responsible for assisting with other sections of the final project report not related to the prioritisation Chapter. S. Neville was the project manager responsible for communications with the customer, overall fiscal responsibility and reviewing the final report for content and completeness. The work was undertaken under the supervision of Dr. J. Ellis who reviewed the project concept, design, analyses and text prior to submission to the customer.

The work presented in Chapter 3 was previously published in Fisheries Research in 2015 as “Having confidence in productivity susceptibility analyses: A method for underpinning scientific advice on skate stocks?” by McCully Phillips, S. R. (the candidate), Scott, F. and Ellis, J. R. (secondary supervisor). The study was conceived by the candidate and I was responsible for the project design, data collection, leading the writing of the manuscript and production of Tables and Figures 3 and 4. I developed the concept of using independent experts and confidence scoring as a tool and provided the input data to Dr. F. Scott for modelling. Dr. Scott wrote the R-scripts and produced Figures 1–2 and 5–8. This work was undertaken under the supervision of Dr. J. Ellis. All authors provided critical feedback and helped shape the research, analysis and manuscript.

The work presented in Chapter 4 was previously published in 2012 in the ICES Journal of Marine Science as "Lengths at maturity and conversion factors for skates (Rajidae) around the British Isles, with an analysis of data in the literature" by McCully, S. R. (the candidate), Scott, F. and Ellis, J. R. (secondary supervisor). The candidate was responsible for data collection and collation, analysis, interpretation, leading the authorship and production of Table 14–Table 17. Dr. F. Scott was responsible for the R-code modelling the maturity ogives and subsequent production of Figure 9–Figure 11. This work was undertaken under the supervision of Dr. J. Ellis who was also involved in data collection, reviewing literature and collated material for Table 19 and Table 20, and commented on and contributed to the interpretation and text. Whilst the underlying data included data collected by the candidate and Dr. J. Ellis during fishery-independent trawl surveys and other field studies, further maturity data were collected by other Cefas sea-going staff on annual trawl surveys.

The work presented in Chapter 5 was previously published in 2015 in the Journal of Fish Biology as "Reproductive characteristics and life-history relationships of starry smooth-hound *Mustelus asterias* in British waters" by McCully Phillips, S. R. (the candidate) and Ellis, J. R. (secondary supervisor). The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures 2–11. This work was undertaken under the supervision of Dr. J. Ellis who also produced Figure 1, was involved in data collection, commenting on and contributing to the interpretation and text.

An early draft of the work presented in Chapter 6 was previously presented to the ICES Working Group for Elasmobranch Fishes (WGEF) as a working document (non-peer reviewed and not freely available) in 2018, entitled "*Leucoraja fullonica* and *Leucoraja circularis* in the Northeast Atlantic" by McCully Phillips, S. R. (the candidate) and Ellis, J. R. (secondary supervisor). The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures. This work was undertaken under the supervision of Dr. J. Ellis who was also involved in data collection and commenting on the text. Sample collection was courtesy of scientists onboard fisheries-independent surveys – primarily the Spanish Porcupine Bank Survey (conducted by Instituto Español de Oceanografía, IEO, Spain) and the French Southern Atlantic Bottom Trawl Survey (EVHOE; conducted by L'Institut Français de Recherche pour l'Exploitation de la Mer, IFREMER, France). Dissections were assisted by lead scientists (among others) at both institutes, namely Dr. Cristina Rodríguez-Cabello (IEO, Santander, Spain) and Dr. Pascal Lorance (IFREMER, Nantes, France).

The work presented in Chapter 7 was previously published in 2020 in the Journal of Fish Biology as “Diet composition of starry smooth-hound *Mustelus asterias* and methodological considerations for assessing the trophic level of predatory fish” by McCully Phillips S. R. (the candidate), Grant, A. (primary supervisor) and Ellis, J. R. (secondary supervisor). The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures. This work was undertaken under the supervision of Prof. A. Grant and Dr. J. Ellis who provided critical feedback and helped shape the research, analysis and manuscript. Dr. Ellis was also involved in data collection and lead the review of literature and production of Supplementary Tables 1 and 2.

The views and opinions expressed in this thesis are those of the author and do not necessarily reflect the opinions of Cefas.

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Each published paper specifically acknowledges the vast number of individuals who contributed, either through reviewing text, assisting with dissections or through the collection of samples (follow doi link at start of Chapters 3–5 and 7), so these are not going to be repeated here. That is apart from reiterating a huge thank you to the numerous SIC's, scientists, crews and commercial fishermen involved in the retention of cadavers in support of this work and the staff and students who assisted with the dissections along the way –

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List of Acronyms

%0	Frequency of occurrence (in dietary studies)
%N	Percentage by numbers (in dietary studies)
%P	Percentage by fullness and points (in dietary studies)
ABC	Acceptable Biological Catch
AIC	Akaike information criterion
B	Levins' measure of niche breadth
BTS	Beam trawl survey
CFP	Common Fisheries Policy
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMS	Convention on the Conservation of Migratory Species of Wild Animals
CPC	Cumulative Prey Curve
CPUE	Catch Per Unit Effort
D	Disc width
DATRAS	ICES Database of Trawl Surveys
DCF	European Data Collection Framework
DEFRA	Department for Environment, Food and Rural Affairs
DLS	Data Limited Stock
EAF	Ecosystem Approach to Fisheries
EBFM	Ecosystem-based Fisheries Management
EC	European Commission
ERA	Ecological Risk Assessment
EU	European Union
EVHOE	EValuation Halieutique Ouest de l'Europe (French Southern Atlantic Bottom Trawl Survey)
FAO	Food and Agriculture Organization of the United Nations
F_O	Ovarian fecundity
FSP	Fishery Science Partnership
F_U	Uterine fecundity
GES	Good Environmental Status
GFS	Groundfish survey
GLM	Generalised Linear Model
GOV	Grand Ouverture Verticale Trawl

GSI	Gonado-somatic index (gonad weight as a percentage of total weight)
HSI	Hepato-somatic index (liver weight as a percentage of total weight)
IBTS	International Bottom Trawl Survey
ICCAT	International Commission for the Conservation of Atlantic Tunas
ICES	International Council for the Exploration of the Sea
IFCA	Inshore Fisheries and Conservation Authorities
iFISH	UK database for commercial landings of fish and shellfish
I_G	Gonado-somatic index (see GSI)
I_H	Hepato-somatic index (see GSI)
IPCC	Intergovernmental Panel on Climate Change
IPOA	International Plan of Action
IRI	Index of relative importance
IUCN	International Union for Conservation of Nature
$L\infty$	Theoretical length that a fish would reach if they grew indefinitely
L_{100}	(Total) Length at 100% maturity
L_{50}	(Total) Length at 50% maturity
L_{IC}	Inner clasper length
$\mathrm{L_{max}}$	Maximum total length
L_{OC}	Outer clasper length
L_T	Total length
M	Fishing mortality
M_E	Eviscerated (gutted) mass
M_G	Mass of gonads
M_L	Mass of liver
MLL	Maximum Landing Length
MLS	Minimum Landing Size
MMO	Marine Management Organisation
MSFD	Marine Strategy Framework Directive
MSY	Maximum Sustainable Yield
M_T	Total mass
NOAA	National Oceanic and Atmospheric Administration (USA)
NPOA	National Plan of Action
OFL	Over Fishing Limit
OSPAR	Convention for the Protection of the Marine Environment of the North-East Atlantic
PA	Precautionary Approach

PHHT	Portuguese high headline trawl
PoA	Plan of Action
PSA	Productivity Susceptibility Analysis
r^2	square of the correlation coefficient, *r*
RV	Research Vessel
TAC	Total Allowable Catch
TL	Trophic level
UNCLOS	United Nations Convention for the Law of the Sea
UNEP	United Nations Environment Programme
W	Weight (see also M_T, total mass)
WCA	Wildlife and Countryside Act
WGEF	(ICES) Working Group for Elasmobranch Fishes
WKLIFE	(ICES) Workshop on the Development of Assessments based on LIFE history traits and Exploitation Characteristics
WSSD	World Summit on Sustainable Development

Chapter 1

Introduction

1 Introduction

1.1 Fisheries

Fish constitute a vital and key natural resource, in terms of nutrition, as well as supporting income, employment, trade and recreation, and are of importance to both developed and developing countries alike. Over time, the reliance on marine capture production has increased in response to global population from around 20 million tonnes (t) in 1950 to around 80 million t by the early 1990s (FAO, 2018). Since this time, however, it has remained relatively stable, possibly as a result of the boom in aquaculture, which was negligible in 1950 and grown to provide around 80 million t by 2016 (FAO, 2018). In 2016, 8.3 million t of marine capture production were attributed to the Northeast Atlantic, of which the UK reported 0.7 million t (FAO, 2018). Globally, elasmobranchs comprise a small proportion of marine capture production, at around 0.7–0.9 million t (1990–2016; Musick and Musick, 2011; FAO, 2018) with a value estimated around US$1 billion (Dent and Clarke, 2015). The relative importance of elasmobranch capture production to the UK is examined in more detail in Section 1.1.2.

1.1.1 UK fisheries

The development of UK fisheries and the relative importance of different species have evolved historically and geographically over the longer term in relation to a variety of factors. For instance, during the early part of the 1900s oily fish (e.g. herring, *Clupea harengus*) were the main commercially exploited fish, as they could be smoked or pickled, allowing for better shelf life and for transport from coasts to inland areas. Following the improvement of transport and development of refrigeration there was a shift to exploit 'white fish' such as whiting *Merlangius merlangus*, cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. The industrial developments also extended to fishing vessels, as sail gave way to steam which gave way to diesel powered vessels, and more powerful vessels able to use larger and heavier gears, such as twin-beam trawling. These steps resulted in improved efficiency and the exploitation of fishing grounds further afield (e.g. Engelhard, 2008). These factors also opened up foreign markets to UK fisheries, who could tranship catch, land into foreign ports or export fish. Exports of elasmobranchs were economically valuable to the UK in the 1980s, with around 6 500 t exported in 1988, of which nearly 6 000 t comprised of spurdog *Squalus acanthias* which was primarily exported to France and Italy (Vannuccini, 1999). However, this market declined over the following decade to just over 600 t by 1998, worth US $1.9 million (Vannuccini, 1999).

Advances in fishing gear and ships electronics also played a role in the changing face of UK fisheries, with the advent of monofilament line in the 1950s which was strong, flexible and relatively cheap, and the use of plotters and echosounders facilitating fishing on more grounds. This was a leap forward in terms of catchability yet coupled with improved catches of target species, there were also large increases in the bycatch of elasmobranchs. With the rapid expansion of fishers and vessels exploiting unmanaged fish stocks, overcapacity became an issue along with declining catch rates. This common issue in the European seas of the Northeast Atlantic led to the development of the Common Fisheries Policy (CFP) with regulations (2141/70 and 2142/70) dating back to 1970 (EEC 1970a,b) which aimed to ensure that fisheries were sustainable environmentally, economically and socially, although it was not until 1983 that total allowable catches (TACs) and quotas were brought in as measures (reviewed by Holden, 1994 and more recently by Lado, 2016).

1.1.2 Contemporary elasmobranch fisheries globally and in UK seas

Sharks, skates and rays, collectively termed elasmobranchs (Class Chondrichthyes; Subclass Elasmobranchii), are taken in targeted and mixed commercial and recreational fisheries worldwide, as target and/or bycatch species. The importance of elasmobranchs in global capture fisheries has been relatively small and stable in recent years (total annual catch of between 0.7 and 0.8 million t from 2005–2016) when compared to, for example, pelagic teleosts which had capture productions of up to 3.2 million t combined in 2018 (FAO, 2018). Whilst this is to be expected, given the low productivity and life history of elasmobranchs (Section 1.2) in comparison to the highly productive pelagic teleosts, it requires close monitoring to ensure sustainability.

In 2018, the reported landings of all skates and rays into the UK by UK-registered vessels was 2 900 t worth £3.6 million (with a further 600 t worth £0.3 million landed into UK ports by foreign vessels), while dogfish landings totalled 2 100 t worth £0.7 (with an additional 100 t landed into the UK by foreign vessels; MMO, 2018). In comparison to the top five finfish landed in the UK in 2018 (Table 1), this is minor in terms of volume (<1% of finfish landings), yet given the generic grouping of landings, this could potentially be major for some depleted or patchily distributed skate, ray or dogfish species, when these removals are considered as a proportion relative to stock size.

Table 1: Top five finfish species and elasmobranch landings into the UK by UK vessels 2014–2018 (shark landings negligible and included in 'other' category). Data from MMO, 2018.

	Quantity (thousand tonnes)				
	2014	2015	2016	2017	2018
Mackerel	126.2	94.8	103.9	95.5	80.9
Herring	38.3	38.6	40.5	44.9	49.1
Haddock	35.4	32.4	33.1	33.5	35.2
Cod	14.0	15.4	20.7	21.6	24.6
Blue whiting	9.7	12.1	11.9	13.1	20.0
Total finfish	306.3	274.8	302.6	297.6	304.7
Skates and rays (% of total finfish catch)	2.4 (0.78)	2.4 (0.87)	2.4 (0.79)	2.4 (0.81)	2.9 (0.95)
Dogfish (% of total finfish catch)	0.7 (0.23)	1.6 (0.58)	1.7 (0.56)	1.5 (0.50)	2.1 (0.69)

1.1.3 Historic elasmobranch fisheries

Traditionally in the UK, elasmobranchs were considered as 'second-class' fish with reports from the 1800s documenting the lack of demand for these species. Steven (1932) detailed the early skate and ray fishery with comments from Colonel Montague in 1809 reporting the 'immense quantities' landed in Devon which were primarily used for baiting crab pots or eaten by fishermen's families during times of scarcity, "*but were never exposed for sale*". In fact, during this era, dogfish, skates and rays were known as 'rabble-fish' (as being rejected from the market; Couch, 1862). However, shortly after this time a limited market developed for skates and rays with Day (1880–1884) reporting that "*much of this rabble-fish going to Billingsgate and other large inland markets*". The market for this complex remained limited until the late 1800s and the turn of the 20th century when a defined fishery was documented (Steven, 1932). Landings of skates and rays were in the region of 18–21 000 tonnes between 1906 and 1913 and in the post-war period landings increased steadily to an average of ca. 21 000 tonnes until 1930 (Steven, 1932). After the Second World War, landings were around 20 000 tonnes and have been declining steadily since 1958 to the historically low level of less than 5 000 tonnes since 2005 (Ellis *et al.*, 2010). The recent reduction in landings is also a consequence of restrictive management in the form of quotas which have been in place since 1999 in the North Sea and 2008 in other areas, in response to concerns over stock status (Section 1.5.2).

Spurdog was previously considered a pest bycatch species in herring fisheries in the 1800s, as the schooling nature of this species meant a large catch of 'dogs' would result in net damage as well as their predation on commercial species (ICES, 2011). Analogous to skates and rays, the value of this species was recognised and a targeted fishery was initiated in the early 1900s, with the wide-ranging nature of this species resulting in targeted fisheries operating across the shelf seas of the northern parts of the Northeast Atlantic. The fishery in the Northeast Atlantic grew steadily exceeding 20 000 t by 1950, peaking at >62 000 t in 1963 where after it remained around 40–50 000 t until the 1980s, when declines followed until restrictive management action in 2008 (Section 1.5.2; ICES, 2019).

Other commercially important elasmobranch fisheries historically operating in the UK have included pelagic sharks, in particular porbeagle *Lamna nasus* (Gauld, 1989) and, basking shark *Cetorhinus maximus* (Parker and Stott, 1965; Kunzlik, 1988) and deep-water sharks to the west of the British Isles (ICES, 2011). However, this range of species are not covered in this thesis as restrictive management is currently in place prohibiting landings (CEC, 2018; 2019) due to the stocks being considered depleted.

1.1.4 Summary

Contemporary elasmobranch fisheries in UK waters have been centred around skates and rays and several dogfish species. Given the historic pattern of exploitation followed by depletion that is seen for several elasmobranchs, it is important that lessons are learned; that research and budgets are prioritised to support sustainable exploitation, with management action taken prior to over-exploitation. The first step in such a goal is a comprehensive understanding of the species encountered in UK waters. Although various accounts have provided such overviews (e.g. Wheeler, 1992; Wheeler *et al*., 2004; Fowler *et al*., 2004) updated accounts are necessary to reflect the dynamism of the marine environment. Such an updated review of elasmobranchs encountered in UK waters is provided in Chapter 2, where an unbiased approach to prioritising all elasmobranch species is developed, thus providing a sound evidence base for subsequent research. One main fishing area and the primary métiers catching elasmobranchs were assessed further in Chapter 3, using a semi-quantitative Productivity Susceptibility Analysis (PSA). These approaches informed on the main species in need of enhanced research (Chapters 4–6).

1.2 Elasmobranch life history

The life history strategy of elasmobranchs, characterised by their longevity, slow growth, late age and large size of sexual maturity, protracted gestation and breeding cycles and low fecundity, has been well documented for nearly 50-years (e.g. Holden, 1973, 1974; Hoenig and Gruber, 1990; Stevens *et al*., 2000). These biological traits make elasmobranchs particularly vulnerable to over-exploitation and less resilient to density-dependent changes, especially during eras of intense fishing pressure and habitat alteration (Snelson *et al*., 2008). Such vulnerabilities were identified as early as the 1970s (Holden 1973, 1974) following the peak of the spurdog fishery and during the expansion of UK fisheries for pelagic sharks and deep-water fisheries. Despite early warnings, management action lagged behind science with continued exploitation on some of the larger-bodied more vulnerable species, leading to well-documented declines and localised extirpations of, for example, common skate *Dipturus batis* complex from the Irish Sea (Brander, 1981), white skate *Rostroraja alba* (Dulvy *et al*., 2000) and angel shark *Squatina squatina* (Rogers and Ellis, 2000) in European seas. Similar examples are documented for other parts of the world, such as the barndoor skate *Dipturus laevis* (Casey and Myers, 1998). Whilst sustainable harvesting of some elasmobranch species is possible (Holden, 1973; Walker, 1998; Simpfendorfer, 1999; Prince, 2005), it does require close monitoring and management.

Nowadays, elasmobranchs are a compelling mega-faunal taxa which receive much media attention. Numerous accounts in high impact journals have highlighted declines, although the magnitude of some purported declines in some of these studies (e.g. Baum *et al*., 2003; Baum and Myers, 2004) have subsequently been challenged by the wider scientific community. These papers claimed collapses in shark populations in the Northwest Atlantic, with declines of large shark populations estimated at >60% to >99%. These studies were rebutted (Burgess *et al*., 2005) stating that the data analysed were limited and inadequate to assess all species, while some other data (including those used in national stock assessments) were excluded. These purported declines can have large influences on conservation listings, subsequent management actions and, consequently, the economic viability of some fisheries. For instance, the evidence of declines and subsequent analyses and assessments presented within CITES listing proposals for some elasmobranch species (e.g. silky shark *Carcharhinus falciformis* and bigeye thresher shark *Alopias superciliosus*) has been the subject of debate (Friedman *et al*., 2020).

There is a clear need to balance the prevention of future species loss (both regional and global), by taking the precautionary approach (Section 1.5.4), whilst avoiding 'dogma' which can lead to popular misperception. For example, Chapter 4 summarises the importance of accurate data use, by challenging the purported reduction in the length at maturity of thornback ray *Raja clavata* as a consequence of fishing pressure (Nottage and Perkins, 1983; Whittamore and McCarthy, 2005). Indeed, several purported reductions in length at maturity are likely to be an artefact of methodological differences (Chapter 4; McCully *et al*., 2012).

Robust evidence-based approaches are necessary to avoid hasty and disproportionate management action (e.g. Friedman *et al*., 2020). This thesis makes a contribution towards a sound evidence base for identifying stocks of concern (Chapters 2–3) and relevant input data (Chapters 4–6) to support sustainable commercial elasmobranch fisheries.

Given the importance of robust biological understanding, several life history parameters are yet to be elucidated for many elasmobranch species. The importance of each parameter for demographic modelling and stock assessments varies. Length/age at maturity and fecundity (as collected in Chapters 4–6) are fundamental, while trophic level (Chapter 7) is desirable, especially for those ecosystem models using food-web and trophic links (e.g. Araújo *et al*., 2005; Mackinson and Daskalov, 2007). For stocks where biological data are extremely limited, PSAs can provide a useful tool whereby exact parameterisation of biological traits are not required as grouped ranges are employed to determine 'high' 'medium' and 'low' productivity. This method can also allow for 'educated guesses' in the most data-limited situations based on analogy with similar species (McCully Phillips *et al*., 2015; Chapter 3).

1.3 Role of elasmobranchs in the ecosystem

Elasmobranchs have important roles to play in the ecosystem, from maintaining biodiversity (as some of the more vulnerable marine species) to assuming the role as higher trophic level (and sometimes apex) predators within marine ecosystems, which may help maintain structure and function.

Some of these roles correspond to the central principles of the Marine Strategy Framework Directive (MSFD; European Commission 2008/56/EC: Section 1.4.1), which aims to achieve Good Environmental Status (GES) through 11 descriptors. The main descriptors for which elasmobranchs are important elements of include:

D1) the maintenance of biodiversity

D3) healthy populations of commercial fish species (Section 1.5.2)

D4) elements of food webs to ensure long-term abundance and reproduction

D9) contaminants in seafood are below safe levels; and to a lesser extent

D6) the sea floor integrity ensures functioning of the ecosystem

In terms of biodiversity (Descriptor 1), extant elasmobranchs comprise over 500 species of shark (from nine orders, 34 families and 107 genera; Ebert *et al*., 2013) and 633 valid named species of ray[1] (from 26 families, with a further 50 species undescribed but known to exist; Last *et al*., 2016; Weigmann, 2016) worldwide, with the number of described species still increasing. Elasmobranchs are widely distributed and utilise a vast number of habitats, with shark species richness and endemicity being highest on continental shelves (Lucifora *et al*., 2011). With the UK surrounded by continental shelf seas, shark diversity is considered moderate, exceeding that of open oceans but less than the diversity seen at mid-latitudes (Lucifora *et al*., 2011). However, the number of skates exploiting this ecosystem is more diverse. Chapter 2 provides an updated species list for elasmobranchs occurring around the British Isles, with 72 species identified representing eight orders and 23 families. Species richness can be a misleading indicator of ecological importance however, whereby individual species may have unique ecological roles and different functions are fulfilled by a few species; indeed, areas with moderate species richness have been identified as having high functional richness (Lucifora *et al*., 2011).

Genetic diversity in elasmobranchs is also an important consideration in the maintenance of biodiversity (hence its incorporation as a parameter into the PSA Chapter 3), as taxa with low rates of speciation may be more prone to extinction (Heard and Mooers, 2000). For biodiversity targets like the MSFD, monotypic families should be considered of great importance in the maintenance of phylogenetic diversity (Vézquez and Gittleman, 1998).

In many ecosystems, elasmobranchs are vulnerable to over-exploitation (Section 1.2) and the presence of them as higher predators within an ecosystem is considered a sign of ecosystem health. The reduction in elasmobranch populations, through direct and indirect influences, can lead to direct effects such as altered size structures within populations (e.g. Walker and Heessen, 1996), as well as changes in biological parameters such as the length at maturity (e.g. Sosebee, 2005) and fecundity (e.g. Holden and Meadows, 1962) in response to decreased abundance.

Any significant change in abundance may also lead to indirect effects such as alterations in trophic interactions and community composition (Steven *et al*., 2000), thus a consideration in Descriptor 4 of the MSFD. Despite elasmobranchs occupying roles near the top of food chains, often species are combined into a single category within multispecies and ecosystem modelling (e.g. ‘sharks’ as used by Araújo *et al*., 2005; Mackinson and Daskalov, 2007) yet

[1] Including freshwater and euryhaline species

large intra- and inter-specific variation in feeding strategies is exhibited within this taxa. The diverse feeding modes and prey species consumed by 'sharks' (Frazzetta, 1994), along with any individual changes in species abundance are not reflected in such models. Yet often this is as a consequence of limited data (e.g. on dietary composition), which can be difficult to obtain from 'shark' species in particular (and costly in those cases where genetic techniques are required to identify prey). However, as computing power and modelling capabilities improve so do the number of ecosystem species and linkages that can be represented, yet this requires data on relevant size- and species-specific dietary data (as collected in Chapter 7).

The comprehension of predator-prey interactions and diet composition provides a platform from which contaminant studies can also be considered (MSFD Descriptor 9). Given the susceptibility of elasmobranchs to the bioaccumulation of contaminants as a consequence of their longevity, and also the biomagnification of contaminants though their high trophic level, the consideration of contaminants is pertinent to this taxon. There are several documented cases of elasmobranch meat (and fins) containing mercury levels that are considered unsafe for human consumption (e.g. Pethybridge *et al*., 2010; Nicolaus *et al*., 2017). The bioaccumulation of contaminants is not only of consideration for piscivorous predators, but also a consideration for elasmobranch species foraging on benthic invertebrates such as crustaceans (Chapter 7) where the chemical composition of the sea-floor is altered through the sequestering of contaminants, and this is then reflected through the food chain (Descriptor 6).

1.4 Management and conservation of elasmobranchs

The high commercial value of some elasmobranch species coupled with biological vulnerability and a history of extirpations (Section 1.2) means that elasmobranchs straddle both commercial and conservation interests and legislations. The first fishing regulation introduced in the UK for an elasmobranch species was a Total Allowable Catch (TAC) for skates and rays in the North Sea in 1999 (Section 1.5.2) and the first conservation regulation was the listing of basking shark on the Wildlife and Countryside Act (WCA) in 1998 (Section 1.4.1). Therefore, the introduction of legislation and management measures has been a slow process, considering the early warnings of UK government scientists (Holden, 1973, 1974). This has likely been a result of various factors, including data deficiencies, such as the lack of species-specific landings data until 2008 for skates and rays, identification and reporting problems and inconsistencies coupled with their capture in mixed fisheries which makes management measures complex. However, as the timeline of regulations set out in Section 1.4.1 shows, there has been a sharp move since the turn of the 21st century to take a more precautionary approach and afford protection through national and international measures to vulnerable species, often based on limited data and expert judgement. Current legislation and conservation measures related to elasmobranch species of the UK are summarised in Appendix I which covers both national and international measures.

1.4.1 Nature conservation and legislation

Elasmobranchs have received increased attention from nature conservation organisations and conventions following some well-documented declines (Section 1.2) and although many of these Acts and Conventions have existed for decades it is only in the recent history that elasmobranchs have been proposed for listing and, if accepted, listed.

One of the earliest conventions considering marine conservation in the Northeast Atlantic was the Oslo/Paris Convention for the Protection of the Marine Environment (OSPAR) which was initiated in 1972, under which 15 governments and the EU cooperate. Whilst this resolution was initially focussed on marine pollution, it diversified into considering biodiversity and ecosystem health in 1998. Subsequently, the OSPAR list of 'threatened and declining species' was initiated. Several elasmobranch species were listed in 2008, including basking shark, white skate, angel shark, common skate complex, porbeagle and spurdog (in all OSPAR regions in which they occur) and spotted ray *Raja montagui* (in the Greater North Sea), as well as three species of deep-water shark (see Appendix I). This instrument is not, however, legally binding and Member States are not obliged to act on recommendations limiting its effectiveness.

The Convention on the Conservation of Migratory Species of Wild Animals (CMS) was initiated in 1979 following the establishment of the United Nations Environment Programme (UNEP). CMS is an environmental treaty listing species on Appendix I (species threatened with extinction) or II (species would benefit from international cooperation from Range States), but solely focussing on migratory animals and their habitats. This focus on migratory species provides a means by which wide-ranging species which traverse management bodies and different national legislations, can be afforded protection throughout their range as some agreements under CMS are legally binding, making this treaty a valuable and effective piece of legislation for many species. The first elasmobranch to be listed was the whale shark *Rhincodon typus* under Appendix II in 1999 and, as of 2020, 37 elasmobranch species are now listed (see Appendix I), of which 22 are on Appendix I. Seven CMS-listed species occur in UK waters: spurdog, angel- porbeagle- basking- shortfin mako- *Isurus oxyrinchus* and common thresher shark *Alopias vulpinus*, and tope *Galeorhinus galeus*, with some others occurring as vagrants.

In 1981, the Wildlife and Countryside Act (WCA) was passed as an Act of Parliament in the UK in order to comply with the European Directive 2009/147 on the conservation of wild birds. This Act is legally binding and has developed over time with the addition of other taxa. In 1998, basking shark was the first elasmobranch protected by this law, which was followed by the addition of limited protection for angel shark in 2008 superseded by full protection in 2011 along with white skate. This national legislation is reserved for the most depleted of species and although only three elasmobranchs are protected under it, it provides the highest level of protection making it an offense to kill or injure, capture, possess or keep, transport or sell (and in the case of basking shark, also disturb, and damage a place of shelter) these species, making it a straightforward and effective instrument.

Other national legislation pertaining to elasmobranchs in the UK includes the Tope (Prohibition of Fishing) Order 2008, whereby fishing for tope by any method other than by rod and line is prohibited, and a maximum of 45 kg per day liveweight is allowed to be retained for bycatch. In coastal waters, regional bylaws by two of the ten English Inshore Fisheries and Conservation Authorities (IFCAs) have a minimum landing size (MLS) for skates and rays, set at 40 cm between the tips of the wings by the Southern IFCA and 45 cm by the former Cumbria Sea Fisheries Committee District (under the North Western IFCA jurisdiction). These measures are of limited utility in the conservation of skates and rays as these wing widths (even the larger MLS of 45 cm), when converted to total length (see Chapter 4) are largely below the length at maturity for most coastal skate species, except for *Raja montagui* (spotted ray), thus only protecting juveniles. The smaller-bodied species such as *Leucoraja naevus* (cuckoo ray) and *Amblyraja radiata* (starry ray), for which such MLS measures would benefit mature fish, occur further offshore than the IFCA jurisdiction allows. In relation to other elasmobranchs, the Eastern IFCA has prohibited the landing of tope.

Basking shark were also the first elasmobranch species to receive international trade protection under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2003. This inter-governmental agreement entered into force 1975 to ensure that international trade in specimens of wild animals (and plants) does not threaten their survival, thus making this instrument exceptional in protecting threatened species from harvest to support international demand. Contracting Parties are legally bound to implement the Convention by ensuring domestic legislation is in place to support international trade limitations or prohibitions on listed species. However, it is this implementation where CITES has shortcomings, with many countries lacking the domestic legislation and/or effective governance to support such listings. Furthermore, this Convention does not afford any protection to species traded domestically. Both factors may limit its effectiveness, particularly in some developing countries. As of 2019 there are 46 elasmobranch species listed in Appendix I (international trade prohibited except under exceptional circumstance) or II (international trade strictly controlled by conditions).

The EU MSFD was adopted in 2008 with the aim of achieving GES by 2020 in the European marine environment, with each Member State being responsible for developing a strategy for its marine waters. GES is informed by 11 descriptors (Section 1.3) enshrining the ecosystem approach (Section 1.5.4) to human activities into a legislative framework. This is the first EU legislative instrument related to the protection of marine biodiversity, of which elasmobranchs may be considered a key component in the maintenance of biodiversity (Section 1.3).

In Scotland, a Statutory Instrument called 'The Sharks, Skates and Rays (Prohibition of Fishing, Trans-shipment and Landing) Order' was implemented in 2012. This legislation prohibits the landing of tope altogether, but also prohibits the landing of 19 different elasmobranch species (see Appendix I) from capture in rod and line and hand-line fisheries. Such a strong stance in protecting elasmobranch species from recreational fisheries is unique in the UK.

One of the main criteria used by conservation Conventions, Acts and treaties in assessing the status of a species and their treat of extinction is the ability to measure, observe or infer a decline in numbers or distribution. Assessing the status of marine species has always proved problematic, but for many species of elasmobranchs the development of assessment tools, methods and models has lagged behind that of traditional fisheries science (Section 1.5).

1.4.2 Non-legislative conservation and assessment

Established in 1964, The International Union for Conservation of Nature (IUCN) was one of the first conservation bodies to assess global species status and biodiversity, through their Red List of Threatened Species. At the end of 2019, over 112 000 species had been assessed, along with the first complete assessment of European marine fishes published in 2015 (Nieto *et al*., 2015), noting that diadromous species were addressed in an analogous report on freshwater fish.

Each species is assessed on their extinction risk (based on: range, population trends, habitat and ecology, threats and many other parameters) and are categorised as Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), with those species assessed as VU, EN and CR collectively termed ‘Threatened’ species.

In the 2015 review (Nieto *et al*., 2015), the most threatened species class were chondrichthyans (sharks, skates, rays and chimeras), with 40.4% considered ‘Threatened’; all 15 CR European marine fish species and 15 of the 22 EN species were elasmobranchs. The IUCN is not a legally binding instrument but is important in its provision of comprehensive species assessments on the global and regional scale. The process employs experts from around the world to assess species in dedicated taxon-based workshops. However, the large number of assessors required has drawn some criticism of the subjective nature in which evidence can be used (see Coelho *et al*., 2019 and references therein). Conversely this mechanism has resulted in the assessment of all (known) elasmobranchs providing an indication of status relative to one another while also highlighting not only those under greatest threat, but importantly also those species that were Data Deficient and thus where efforts needs to be focussed. This objective directly complements the semi-quantitative assessments undertaken in Chapters 2–3.

Between 1995 and 1999 a UK list of Priority Habitats and Species was created to identify the most threatened species and where conservation action was needed under the UK Biodiversity Action Plan (UK BAP). This list was revised in 2007 and included 14 elasmobranchs found in UK waters (see Appendix I). However, devolution of the nations and domestic drivers led to a new set of ‘Priority Lists’ set at the country-level. Therefore, for England, the Species of Principal Importance list was created under Section 41 of Natural Environment and Rural Communities (NERC) Act of 2006. There are 12 of the same elasmobranchs listed on this (see Appendix I), as appeared on the UK list, but notably with angel shark (IUCN listed CR) and *Leucoraja circularis* (sandy ray; IUCN listed EN) removed in the English list. The Northern Irish, Welsh and Scottish lists are also shown in Appendix I and show only subtle differences from the original UK version and each other. Such lists do not provide any species protection so are of limited utility beyond listing species of conservation interest, yet with two of the most threatened species missing from the English list, yet other species such as *Raja undulata* (undulate ray; IUCN listed NT) which have a TAC and are commercially harvested listed, these lists warrant further examination and possible revision.

1.4.3 Plans of Action

The emergence of several depleted elasmobranch stocks worldwide through a lack of management led to the first main resolution pertaining directly to sustainable management of shark fisheries and shark conservation: the International Plan of Action for sharks (IPOA-Sharks; FAO, 1999). Although the plan of action was voluntary, it was encouraged that all concerned States (both Members and non-members of FAO) should implement it. It covered all targeted and non-target catches of Chondrichthyes, advising member States to adopt national plans by 2001.

EC member states agreed that, due to the CFP, a single action plan for EC countries would be more appropriate. Fowler *et al*. (2004) drafted a shark action plan, with an overall objective "*to ensure the conservation and management of sharks, skates, rays and chimaeras occurring in the European waters of the UK and taken in target and incidental fisheries by the UK fleet*", although it was not adopted as a National Plan of Action (NPOA).

In 2009, an EU action plan (COM, 2009) for sharks was released and adopted. The overarching general objectives were "*to deepen knowledge both of shark fisheries and of shark species and their role in the ecosystem*", and "*to ensure that directed fisheries for shark are sustainable and that by-catches of shark resulting from other fisheries are properly regulated*". This was subsequently followed by the release of the Defra Shark, Skate and Ray Conservation Plan (Defra, 2011, 2013) which aims to "*manage elasmobranch stocks sustainably".*

The present study is in support of some of the central principals of the Plan. Chapters 2–3 address the outcome pertaining to ensuring that "*action is taken to protect and restore those species most at risk"* (Defra, 2011) by assessing all elasmobranchs in UK waters to determine which species are most at risk, while highlighting species which are currently unmanaged yet potentially vulnerable. The collection and analysis of key biological parameters in Chapters 4–6 support the outcome aiming to improve "*knowledge on elasmobranch fisheries and species….through better data collection and scientific research"* (Defra, 2011) so that appropriate ecological information can be "*used to more effectively manage elasmobranchs"* (Defra, 2011).

1.5 Fisheries management and assessment of elasmobranchs

1.5.1 Fisheries management overview

Scientific fishery assessment originated in the Northeast Atlantic and the management of fisheries are considered some of the most elaborate worldwide, yet despite the substantial human and financial investments in fishery management, many commercial fish resources here are fully exploited, overexploited, or depleted (Maguire, 2005).

The performance of the UK and other European countries in their compliance to the FAO (UN) Code of Conduct for Responsible Fisheries (1995) was found to be lacking when assessed (Pitcher *et al*., 2008). Despite the code being in place for 12 years, the UK achieved a poor overall compliance. Some plausible rationales included "*fishery management has not been properly implemented, scientific assessments have not been sufficiently reliable, decision makers have set TACs above the advice, fishers have caught more than the TAC, and that enforcement of the regulations and of the TACs has been ineffectual"* (Maguire, 2005).

The main challenge that underpins all fisheries management is how to get a reliable estimate of abundance. This is particularly problematic for elasmobranchs, which are commonly landed as bycatch, were not historically reported to species level (thus time-series of landings data are short) and, for several taxa, are commonly misidentified. Trends in biomass, numbers at age, and spawning stock biomass are commonly gained from fishery-independent surveys. However, in the Northeast Atlantic no such dedicated surveys for elasmobranchs exist, although data for many smaller species (catsharks, dogfish, skates and rays) are collected from demersal trawl surveys. The data arising from these surveys are potentially subject to some bias, as the survey design is traditionally aimed at targeting finfish (Rago, 2005). Another potential source of inaccuracy results from the aggregating nature of some elasmobranchs, which could increase the uncertainty of population estimates.

1.5.2 Fisheries and elasmobranch assessment within the ICES community

As detailed in Section 1.1.1, straddling fish stocks in European waters have been managed as a shared resource under the CFP since 1970, with quotas for the main commercial species being introduced since 1983. The European Commission proposes catch limits, based on scientific advice which is primarily provided by the International Council for the Exploration of the Sea (ICES). This intergovernmental marine science organisation was established in 1902 with the UK being one of the first member countries. Expert groups coordinated by ICES meet annually to conduct analyses that underpin scientific advice; one such group is the

Working Group for Elasmobranch Fishes (WGEF). This group is "*responsible for providing assessments and advice on the state of the stocks of sharks, skates, and rays throughout the ICES area*" (www.ices.dk). This group originated from a study group which first met in 1989, but issues with data inconsistencies and limitations hampered assessments, until 2002 when the first exploratory elasmobranchs assessments were undertaken. Assessments for commercially exploited teleosts were based on fishery-independent trawl surveys, which were designed to target commercial species. Whilst elasmobranchs are generally 'bycatch' species, these data were sufficient to perform trend-based assessments for some of the more common species in some areas (e.g. thornback ray in the North Sea). For some of the more offshore or depleted species (e.g. porbeagle and angel shark) fishery-independent survey data are not informative. Currently, ICES provide advice for 55 elasmobranch stocks, with this advice either biennial (commercial stocks) or quadrennial (species without fishing opportunities), and data-limited assessments (Section 1.5.3) are conducted on each stock.

A TAC was first established for skates and ray in the North Sea in 1999; it was set at 6 060 t and subsequently decreased most years to its lowest level of 1 313 t by 2016. However, prior to 2008 the TAC was higher than reported landings therefore quota management has only been restrictive for this stock for a decade (ICES, 2019). A similar picture is seen with spurdog, with quotas (9 470 t) being introduced on this stock in 2000, rapidly being reduced to zero by 2010 – a clear demonstration of fisheries management lagging behind science, noting the forewarnings of over-exploitation on this stock by Holden during the late 1960s and early 1970s (Holden, 1973, 1974). Alternative management measures have been introduced for some elasmobranch species, including maximum landing length (MLL) for spurdog (2009–2010) and porbeagle shark (2009), and bycatch allowances (e.g. spurdog 2007–2008). In cases of recognised depletion, several species of elasmobranch have been included on the EU prohibited species list (e.g. basking and angel shark) which prohibits fishing for, retaining on board, transhipping, landing, storing, selling, displaying or offering for sale.

1.5.3 Data-limited stocks

Data-limited fisheries can be defined as "*stocks that are not fully evaluated in relation to primary stock status and fishing mortality management reference points, are a significant feature of [European] fisheries*" (Le Quesne *et al*., 2013); with approximately half of all landings from waters under European management being considered data-limited. However, the issue of data-limitation spans fisheries all over the world (Pilling *et al*., 2008), particularly elasmobranch fisheries, deep-water and straddling stocks. In these cases, there may be little or no information available to set initial catches, assess stock status or estimate reference points, through a lack of reported or biological data (Shotton, 2005). A number of approaches to the management of data-limited stocks have been undertaken worldwide (reviewed in Pilling *et al*., 2008 and Dowling *et al*., 2019), dependent upon the level and quality of the data availability, and the aims of management.

The poor performance of failing to meet fisheries targets within Europe and the policy requirements for sustainable fisheries exploitation, catalysed the development and implementation of the Data-Limited Stock (DLS) approach within the ICES community. Of the more than 200 stocks for which ICES provided advice, over 60% did not have population estimates that would allow catch options to be derived using the existing Maximum Sustainable Yield (MSY; Section 1.5.4) framework (ICES 2012a). Consequently, the Workshop on the Development of Assessments based on LIFE history traits and Exploitation Characteristics (WKLIFE) was established in 2012. This Expert Group developed a framework working towards the provision of quantitative advice for all stocks (ICES, 2012b). The DLS approach categorised stocks into six categories from the data-rich with quantitative assessments (Category 1) down to the most data-limited bycatch stocks or those with negligible landings (Category 6) with assessment methods proposed under each category (ICES, 2012b).

Most elasmobranchs assessed by ICES WGEF fall under Category 3 (where fishery-independent survey data are available), Category 5 (where landings data are available) or Category 6 (negligible landings and stocks caught in minor amounts as bycatch). The WKLIFE group continue to test and refine assessment methods to the present day. However, given the magnitude of the task the focus has often been data driven (e.g. by testing methods using a ‘data-rich’ elasmobranch) rather than by examining species requirements (e.g. by testing on a highly vulnerable stock with only problematic landings data) with no prioritisation considered. Chapter 2 provides an evidence base for prioritising a large number of elasmobranch species, while Chapter 3 provides a semi-quantitative assessment of elasmobranchs caught in fisheries. Both chapters contribute to determining where assessment and management action should be focussed. The data collected in Chapters 4–6 provides key parameters with which demographic models can be populated using data collected on fishery-independent surveys as a platform of opportunity thus making better use of existing data collection.

1.5.4 Fisheries targets

The precautionary approach and an ecosystem approach to fisheries management were some of the earliest strategies adopted for assessment and management where data are limited or highly uncertain. Almost all fisheries are unselective multispecies affairs even when they target particular species (e.g. shrimp trawl fisheries) (Dulvy *et al.*, 2003). Consequently, fisheries science has increasingly moved towards adopting an ecosystem-based approach to fishery management (EBFM or EAF) in response to addressing the effects on all species, target or non-target, as well as on the wider environment and ecosystem (e.g. benthic communities). EBFM essentially reverses the order of management priorities so that management starts with the ecosystem rather than a target species and aims to sustain healthy marine ecosystems and the fisheries they support (Pikitch *et al.*, 2004). When considering that elasmobranchs are often the higher trophic level predators in an ecosystem, overfishing and depletion of predators has the potential to induce changes across all trophic levels in the ecosystem, thus highlighting the importance of an EBFM stance where fisheries management in relation to elasmobranchs is concerned.

Management according to the Precautionary Approach (PA) exercises prudent foresight to avoid unacceptable or undesirable situations. It takes into account that changes in fisheries systems are only slowly reversible, difficult to control, not well understood, and subject to change in the environment and human values (FAO, 1996). This precautionary approach to fisheries management was adopted in 1996 and highlights the need to control access to the fishery early, before problems appear, or if already overexploited to act immediately to limit the fishery, setting caps on increases in fishing capacity and mortality rate. There are elasmobranch fisheries that fall into both categories.

The adoption of this measure in the Northeast Atlantic was slow, despite the UK government listing the "*consistent application of the precautionary principle*" (Defra, 2009) as one of its marine objectives. One problem in European implementation of this approach has been the lack of formal consideration of uncertainty based upon limit and target reference points and control rules, a necessary tool of fisheries management (Caddy and Mahon, 1995). Target reference points express an optimal biomass, maximum catch or benefit in relation to risk, while limit reference points identify levels of biomass or fishing that may trigger dangerous and unwanted consequences such as stock collapse, or adverse impacts on species linked to the fishery through the food web (Pitcher *et al*., 2008). They have applications to all fisheries, even those that are data-limited (Caddy, 1998), however data-limited fisheries limit reference points are of particular importance, especially when applying the precautionary approach.

A widely used target reference point is Maximum Sustainable Yield (MSY), which is theoretically the largest average catch that can be sustainably harvested from a stock under existing environmental conditions, over an indefinite timeframe, maintaining maximum replacement rates. The concept was developed in the early 1930's (Russell, 1931; Hjort *et al*., 1933; Graham, 1935), and was subsequently adopted in fisheries management due to its simple nature and its ability to provide a management goal quickly and with ease. In 1982, the United Nations Convention on the Law of the Sea (UNCLOS) agreement incorporated MSY into its provisions, thus ensuring its integration into national and international fisheries acts and laws (Mace, 2001). In 2002, the World Summit on Sustainable Development (WSSD; COFI, 2003) committed signatories to maintain or restore stocks to MSY '*where possible'* by 2015. However, at an early stage it was highlighted that most stocks assessed by ICES did not have the necessary information and estimates to implement a precautionary control rule (Cadrin and Pastoors, 2008). As data-limited approaches developed in response and ICES formalised a framework (see Section 1.5.3) the situation improved quickly and the percentage of stocks where fishing mortality did not exceed the fishing mortality at MSY increased from 34% in 2003 to 60% in 2015 in the Northeast Atlantic (FAO, 2018). The slow implementation and limited success of formalised fisheries management goals has in part been due to the vast number of stocks, many of which can be considered data-limited. Therefore, a consistent approach to assessing risk can be used to determine where action is most needed (Chapters 2–3).

1.6 Questions to address and aims of the study

The repetitive pattern of stock depletions and, in some cases, regional extirpations following rapidly from commercial exploitation of elasmobranchs is the main driver for proactive management with which pragmatic and timely management measures should be considered prior to overfishing and stock collapse.

The current thesis supports such targets through prioritising species for research. Initially, this has been conducted by a qualitative assessment in Chapter 2 which has been developed to consider all species, including the most data-limited, thus providing an unbiased evidence base upon which species and research can be prioritised and where national plans could usefully focus attention. Following this broad assessment to identify priority species, a more quantitative approach, such as a Productivity Susceptibility Analysis (PSA) as used in Chapter 3, can be used to examine vulnerabilities at a finer scale (e.g for specific fisheries) and identify key data gaps hampering quantitative assessment. The relative vulnerabilities of the members of the skate complex currently managed under the generic skate TAC were identified, which then allows managers to focus attention and undertake proactive research on the most vulnerable species. Species identified in Chapters 2 and 3 as high priority are then subject to more detailed study in Chapters 4–7 to address some of the life-history data gaps. Chapter 4 provides length at maturity estimates and conversion factors for UK skate species, parameters which are essential to any demographic assessment. Chapters 5 and 7 provide biological and dietary information on starry smooth-hound, which was the highest ranking (Chapter 2), commercially exploited elasmobranch species that is not currently afforded any species-specific management measures (e.g. not subject to any catch limits or size restrictions). Chapter 6 focusses on the occurrence, biology and ecology of shagreen and sandy ray - both species managed as part of the generic 'skate and ray' TAC and thus commercially exploited. This is despite the IUCN Red List assessments for sandy and shagreen ray being Endangered and Vulnerable, respectively. Given that the life-history of both these 'Threatened' skates is largely unknown, with limited published information to date on either species in the Northeast Atlantic, Chapter 6 provides key data which can inform management. These case studies therefore populate important data gaps for some priority and vulnerable elasmobranch species of the UK with recommendations made regarding management option in Chapter 8.

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Chapter 2

UK elasmobranchs and prioritisation of research effort

2 UK elasmobranchs and prioritisation of research efforts

This Chapter was based on the following output:

McCully Phillips, S. R., Maia, C., Silva, J., Neville, S. and Ellis, J. R. (2019). Elasmobranch Longline Surveys in Inshore Ecosystems (ELSIE). Cefas Project Report C7770; 105 pp.

The candidate was the principle investigator for this project and consequently responsible for project design, leading the analyses and writing the final report. C. Maia and J. Silva were project staff responsible for assisting with other sections of the final project report not related to the prioritisation Chapter. S. Neville was the project manager responsible for communications with the customer, overall fiscal responsibility and reviewing the final report for content and completeness. The work was undertaken under the supervision of Dr. J. Ellis as the lead elasmobranch advisor at Cefas, who reviewed the project concept, design, analyses and text prior to submission to the customer.

Only the section of the report relating to the prioritisation method was used within this Chapter, and minor updates to the introduction and discussion have been made to incorporate relevant recent literature.

2.1 Introduction

The need for the development of national and/or regional plans of action for sharks (FAO, 1999) has mandated countries to address the conservation and sustainable exploitation of elasmobranchs, as also indicated in the subsequent EU action plan (COM, 2009) and UK Shark, Skate and Ray Conservation Plan (Defra, 2011; see Section 1.4.3). The first step in any plan needs to be an understanding of which species occur in the area of interest, whether this is national waters or regional seas.

The known global diversity of elasmobranch species (Section 1.3) is increasing yearly through the discovery of new species (e.g. four new species in the genus *Hemiscyllium*; Dudgeon *et al*., 2020), taxonomic revisions (e.g. *Carcharhinus obsolerus*; White *et al*., 2019 and *Dipturus intermedius*; Last *et al*., 2016) and as a result of speciation (e.g. family: Orectolobidae; Corrigan and Beheregaray, 2009). Recent advances in genetics has enabled various cryptic species to be better defined (e.g. Naylor *et al*., 2012).

There can also be temporal changes in species distributions, which can lead to a species exploiting different habitats if their environment becomes more favourable (e.g. changes in water temperature) or conversely reduced by habitat loss, anthropogenic impacts or climate change (Sguotti *et al*., 2016). Furthermore, species may make longer migrations or change migration paths making use of waters of different jurisdictions. In each case, a firm understanding of the species utilising national waters is paramount in the implementation of any plan of action, and prioritisation of subsequent research efforts.

Several taxonomic lists for elasmobranchs occurring around the British Isles are available (Wheeler, 1992; Edwards and Davis, 1997; Wheeler *et al*., 2004; Fowler *et al*., 2004; George, 2009). However, given the recent changes in the taxonomy and range extensions of some species, an updated list of elasmobranch[2] species (Ellis and McCully, 2013) was used in this study. This list documents 72 species from eight orders and 23 families (Table 6).

The next step in the implementation of any national plan is to evaluate the importance of national waters to each species. If the time spent and/or spatial extent of a species in the area is limited, or utilisation is minimal or questionable, then the consideration of further work may be limited. In contrast, if a species is endemic to the area, or has a discrete breeding population (or stock) in national waters, then such species should be given more careful and detailed consideration. These results need to be viewed in parallel with the commercial and conservational importance of a species.

Species of conservation importance need consideration in order to safeguard against extirpation and extinction in support of the maintenance of biodiversity and ecosystem structure, while meeting environmental targets (Section 1.3). A documented or assessed reduction in abundance and/or species range commonly forms the foundation for the designation as a species of conservation importance, from which incorporation into legislative protection often follows (Section 1.4).

Biological vulnerability can be inferred from life history traits, in particular maximum size (Jennings *et al*., 1998, 1999; Dulvy *et al*., 2000; Dulvy and Reynolds, 2002). This life history parameter also tends to correlate to a large size/late age at maturity and, in relation to elasmobranchs, low fecundity and the periodicity of reproduction (as viviparous species tend to reproduce less frequently). Indeed, life history parameters can be used to prioritise species

[2] The original paper listed all chondrichthyans (sharks, skates, rays and chimaeras), however for the purpose of this thesis, only elasmobranchs are considered. Species based on questionable records, from adjacent waters or from specimens washed ashore in neighbouring areas were also excluded.

for conservation where few other data are available (Jennings *et al*., 1998, 1999; Reynolds *et al*., 2001). The utility of 'classes' and grouping life history data also allows for some uncertainty in estimates, while supporting the principle that conspecifics with a similar body size will likely exhibit similar life history strategies and thus vulnerability. Reproductive mode is another life history parameter that may relate to biological vulnerability and extinction risk (García *et al*., 2008).

Consideration also needs to be given to whether a species is important for national fisheries and, therefore, important for meeting sustainable exploitation goals. Commercially important fish stocks have traditionally been the focus of decades of research given the economic importance (e.g. herring *Clupea harengus* which largely shaped fisheries science at the turn of the twentieth century (Went, 1972)), while 'second class' fish such as elasmobranchs received limited attention until the late 20th century. The overall importance of elasmobranchs in the British Isles in terms of commercial landings (tonnes) and value is proportionally very low (<2% in 2018; Section 1.1.3), however elasmobranchs can be very important for inshore artisanal fleets in some local fisheries (e.g. thornback ray in longline and net fisheries in the outer Thames; Ellis *et al*., 2008). Supporting these fisheries whilst ensuring sustainable exploitation of exploited stocks requires scientific research to ensure the empirical data for the parameterisation of models are sufficiently robust for stock assessments.

The need to prioritise species to study is fundamental both worldwide and around the British Isles, given the diversity of elasmobranchs encountered but limited research resources which have competing demands from commercially important teleosts and shellfish and other marine taxa of conservation concern (e.g. seabirds and cetaceans). In order to assess and triage a large number of species rapidly, methods requiring limited data or easily estimated parameters are required (Dulvy *et al*., 2004). This broadscale data-limited prioritisation exercise requires limited empirical data yet has the ability to focus national research priorities by assessing the commercial, conservation and ecological importance of a range of species in British waters.

2.2 Materials and methods

In order to prioritise the elasmobranch fishes of the British Isles, as listed originally by Ellis and McCully (2013), all elasmobranch species were scored under the following four categories:

1. Conservation interest
2. Commercial importance
3. Importance of UK to the species range
4. Biological vulnerability

2.2.1 Conservation interest

This parameter was ranked according to European International Union for Conservation of Nature (IUCN) listings (Nieto *et al.*, 2015), and also as to whether the species was listed for legal protection on the UK Wildlife and Countryside Act and/or listed on Appendix I or II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The scores allocated for these criteria (Table 2) could range from 0–15, as the three parameters were summed.

Table 2: Scores applied to elasmobranch fishes in relation to conservation interest.

IUCN Listing	Score
Critically Endangered (CR)	5
Endangered (EN)	4
Vulnerable (VU)	3
Data Deficient (DD)	2
Near Threatened (NT)	1
Least Concern (LC)	0
Not Evaluated (NE)	1

UK Wildlife and Countryside Act	Score
Listed	+5
Not listed	0

CITES	Score
Listed	+5
Not listed	0

2.2.2 Commercial importance

This was scored according to (i) International Council for the Exploration of the Sea (ICES) landings data (based on data provided for the 10-year period 2008–2017, only using data from FAO area 27 (the Northeast Atlantic)), and (ii) market value for the UK fishery in terms of the value of fish (value (£) per kg), as reported to the Marine Management Organisation (MMO) and stored in the iFish database, between 2005 and 2017 (MMO, 2018). The data used for the former were the ICES Working Group for Elasmobranch Fishes (WGEF) 'cleaned' official landings data (i.e. national data reported to ICES are examined by the national delegate (and other experts) and erroneous data are assigned to either their correct category, a generic group, or excluded. These data are then used in assessments and reports, e.g. ICES, 2019). The scores allocated for these two criteria (Table 3) ranged from 1–5 (magnitude of landings) and 1–3 (value of fish), with the two scores multiplied to give totals of 1–15.

It should be noted that some species (e.g. porbeagle, tope and spurdog) have been subject to very restrictive fisheries management since 2008–2009 so have limited landings, which would result in their 'commercial importance' not scoring as high as they would have historically.

Table 3: Scores applied to elasmobranch fishes in relation to commercial importance.

Commercial (FAO) landings (t)	Score
>3 000	5
>500	4
>100	3
>15	2
<15	1

Value to UK	£ per kg	Score
High	>1.5	3
Medium	1–1.5	2
Low	<1	1

2.2.3 Biological vulnerability

This was scored by maximum body length (scored from 1–5) and reproductive mode (scored as 1–3), as outlined in Table 4. Values were multiplied to create the overall score of biological vulnerability ranged from 1 (e.g. blue pygmy skate) to 15 (e.g. porbeagle).

Table 4: Scores applied to elasmobranch fishes in relation to biological vulnerability.

Maximum length (cm)	Score
200+	5
150–199	4
100–149	3
50–99	2
<50	1

Reproductive mode	Score
Viviparous (Fecundity <10 pups per reproductive episode)	3
Viviparous (Fecundity >10 pups per reproductive episode)	2
Oviparous	1

2.2.4 Importance of UK waters to the stock range

This was scored according to the importance of the Northeast Atlantic to the species and by their occurrence in waters around the British Isles (Table 5). For the former, species were identified as (a) cosmopolitan (i.e. occurring in the Atlantic and the Indian and/or Pacific basins); (b) occurring in the wider Atlantic (i.e. they also occurred in the western North Atlantic and/or South Atlantic) and (c) occurring in the eastern North Atlantic (which could include the Mediterranean and parts of north-western Africa). Sources of reference material for this score included Ebert *et al*. (2013), Last *et al*. (2016) and IUCN Red List reports (https://www.iucnredlist.org/), as well as prior knowledge.

Species were subsequently scored as either (a) absent from the British Isles (i.e. those species which occur in waters adjacent to the British Isles, but have not been reported from the area), (b) occasional vagrants have been reported, (c) regular visitor, (d) present around the British Isles, but this area was only the fringe of the distribution, (e) present and widely distributed around the British Isles and (f) present and (probably) breeds in British waters (the term 'breeding' used to highlight whether the species had mating, egg-laying/parturition or nursery grounds in the area), or with discrete stocks in the area. A combination of expert knowledge, Heessen *et al*. (2015) and IUCN Red List reports (https://www.iucnredlist.org/) were used to score this attribute. Values of these two parameters were multiplied to give scores between 0 and 15.

Table 5: Scores applied to elasmobranch fishes in relation to importance of UK waters to the stock range.

Global distribution	Score
NE Atlantic only	3
Wider Atlantic	2
Cosmopolitan	1

UK Distribution	Score
British waters has ecologically important breeding sites and/or discrete stocks	5
Present around the British Isles	4
Present in British seas, but only the fringe of the distribution	3
Regular visitor to British seas	2
Occasional vagrants reported	1
Absent, no authenticated records in British seas	0

2.2.5 Overall ranking process

Conservation importance (0–15), biological vulnerability (1–15) and commercial importance (1–15) were summed, and this was then multiplied by the importance of this species to the UK (0–15). This approach prevented those species that have not been officially reported from around the British Isles from attaining a high score, but would allow them to rank higher if the distribution of the species was found to extend to UK seas at some point in the future. This approach gave final scores (out of a maximum of 675), to allow species to be prioritised impartially (Table 6). The current status of fisheries advice, in relation to advice given by either ICES or the International Commission for the Conservation of Atlantic Tunas (ICCAT), was also listed for reference.

2.2.6 Provision of advice by ICES and ICCAT

Although this was not scored or used in the prioritisation process, it was included in the prioritisation tables (Table 6–Table 8) to identify those species for which the ability to provide advice has been hampered by a lack of data. Where advice is not provided, this is a good indication of data deficiencies, a lack of presence in trawl surveys (so no stock size indicator), limited catch/landings records, or that this stock is rare in wider European waters. Each species was listed as having:

- SA – advice based on a quantitative stock assessment
- ST – advice based on survey trends (usually fishery-independent trawl surveys)
- QA – qualitative assessment only, given limited signal from survey trends or other data sources (e.g. landings data)
- NA – no assessment possible

Furthermore, the existence of fisheries management applied to each species is ultimately considered by categorising species as:

- TAC – managed under the quota system
- Pro – prohibited species under the EU fishing opportunity guidelines (within the main range area, not fringes of distribution)
- NA – no current management through quota or EU prohibited species list

This is documented for those species (Table 8) to assist interpretation and help identify where important species are not subject to species-specific management measures.

2.3 Results

The prioritisation process identified 16 species that scored ≥150 (Table 7) and these species were considered further in terms of data availability and data gaps (Table 7 and Table 8). Of these 16 species, the main group were skates (flapper skate *Dipturus intermedius*, common blue skate *Dipturus batis*, sandy ray *Leucoraja circularis*, blonde ray *Raja brachyura*, small-eyed ray *Raja microocellata*, shagreen ray *Leucoraja fullonica*, Norwegian skate *Dipturus nidarosiensis*, cuckoo ray *Leucoraja naevus*, spotted ray *Raja montagui*, white skate *Rostroraja alba* and undulate ray *Raja undulata*), with the highest-ranking sharks and dogfish including angel shark, *Squatina squatina*, starry smooth-hound *Mustelus asterias*, porbeagle shark *Lamna nasus*, black-mouth dogfish *Galeus melastomus* and greater-spotted dogfish *Scyliorhinus stellaris*.

Of these top ranking 16 species, five are currently prohibited to be fished for or landed in EU waters (since 2015), while eight are managed under the generic 'skates and rays' TAC. The remaining three species are currently not subject to any species-specific management measures in EU waters. The five top-ranking species have no quantitative stock assessments. The conservation scores for the top ranking 16 species ranged from 0–10 with no species scoring the maximum 15 (as none of these are listed on both the WCA and CITES). The highest scoring species were angel shark, porbeagle and white skate, while cuckoo ray, spotted ray and black-mouth dogfish scored zero, as they are classified as 'least concern' by the IUCN. Biological vulnerability scores ranged from 2–15, with angel shark and porbeagle receiving the maximum score of 15. The remaining 14 species all scored ≤6 primarily due to their oviparous nature and/or smaller maximum lengths. The biological knowledge for the top ranking species shown in Table 8 highlights the lack of available data for many important parameters. Overall, most parameters were deemed 'limited' (e.g. some information may be available from other geographic location), while data was completely 'unavailable' for fifteen parameter/species combinations. The best-known parameter was length/weight conversion factors, with robust information available for 10 of the 16 species and only unavailable for two (sandy ray and Norwegian skate). The 'least' known parameters overall were age and growth and fecundity, with each having six species for which data were unavailable.

Three species (Norwegian skate, blonde ray and small-eyed ray) all managed under the generic skates and ray TAC[3], scored the top mark of 15 for commercial importance, with a range of 2 (angel shark) to 15.

The importance of UK waters to the species ranged from 8 (white skate) to the maximum 15, with 13 species attaining the maximum score. The three species for which these waters were not deemed the highest importance were porbeagle (cosmopolitan distribution with breeding population within UK waters), Norwegian skate (Northeast Atlantic distribution with fringe of population within UK waters) and white skate (present in the wider Atlantic and in UK waters).

Seven species have sufficient representation in trawl surveys to provide data for assessment and advice (Table 7). The remaining nine species are present only as isolated records or limited catches from which a time-series cannot be used.

[3] A separate TAC is applied to small-eyed ray in European Union waters of ICES divisions 7.f and g (Bristol Channel and Celtic Sea) and in European Union waters of ICES area 4 (North Sea) it must be released unharmed (CEC, 2020). Norwegian skate are prohibited to be fished for in European Union waters of ICES subarea 6 and divisions 7.a-c and 7.e–h and 7.k (western waters of British Isles; CEC, 2020).

Table 6: Prioritisation of 72 elasmobranch fishes occurring around the British Isles and adjacent waters, listed in taxonomic order.

Taxonomic Rank[4]	Scientific name	Common name	Conservation importance	Biological vulnerability	Commercial importance	Importance of UK	Final score	ICES / ICCAT advice
1	*Hexanchus griseus*	Bluntnose six-gill shark	0	10	1	3	33	NA
2	*Heptranchius perlo*	Sharpnose seven-gill shark	2	6	3	3	33	NA
3	*Chlamydoselachus anguineus*	Frilled shark	0	15	1	3	48	NA
4	*Isurus oxyrinchus*	Shortfin mako	7	10	15	2	64	SA
5	*Lamna nasus*	Porbeagle shark	10	15	12	5	185	SA
6	*Cetorhinus maximus*	Basking shark	14	15	2	4	124	QA
7	*Alopias superciliosus*	Big-eye thresher shark	9	15	6	1	30	NA
8	*Alopias vulpinus*	Thresher shark	9	15	9	4	132	NA
9	*Apristurus aphyodes*	White ghost catshark	0	2	1	9	27	NA
10	*Apristurus laurussonii*	Iceland catshark	0	2	3	6	30	NA
11	*Apristurus manis*	Ghost catshark	0	2	1	6	18	NA
12	*Apristurus melanoasper*	Black roughscale catshark	0	2	1	3	9	NA
13	*Apristurus microps*	Smalleye catshark	0	2	1	6	18	NA
14	*Galeus melastomus*	Black-mouth dogfish	0	2	8	15	150	ST
15	*Galeus murinus*	Mouse catshark	0	2	4	9	54	NA
16	*Scyliorhinus canicula*	Lesser-spotted dogfish	0	2	5	15	105	ST
17	*Scyliorhinus stellaris*	Greater-spotted dogfish	1	4	5	15	150	ST
18	*Pseudotriakis microdon*	False catshark	2	15	1	3	54	NA
19	*Mustelus asterias*	Starry smooth-hound	1	6	10	15	255	ST
20	*Mustelus mustelus*	Smooth-hound	3	8	1	0	0	NA
21	*Galeorhinus galeus*	Tope shark	3	10	5	5	90	QA
22	*Prionace glauca*	Blue shark	1	10	5	4	64	SA
23	*Sphyrna zygaena*	Smooth hammerhead	7	10	1	1	18	NA
24	*Dalatias licha*	Kitefin shark	4	8	1	3	39	NA
25	*Centroscyllium fabricii*	Black dogfish	0	4	6	6	60	NA
26	*Etmopterus princeps*	Great lantern shark	0	4	3	6	42	NA
27	*Etmopterus spinax*	Velvet belly	1	2	6	6	54	NA
28	*Centroscymnus coelolepis*	Portuguese dogfish	4	6	4	3	42	QA
29	*Centroselachus crepidater*	Longnose velvet dogfish	0	6	3	3	27	NA
30	*Scymnodon ringens*	Knifetooth dogfish	0	9	2	9	99	NA
31	*Somniosus microcephalus*	Greenland shark	1	15	3	6	114	NA
32	*Oxynotus centrina*	Angular roughshark	3	8	1	6	72	NA
33	*Oxynotus paradoxus*	Sailfin roughshark	2	6	1	9	81	NA
34	*Centrophorus squamosus*	Leafscale gulper shark	4	9	12	3	75	QA

[4] The higher taxonomic ordering and ranking of Eschemeyer (2012) was followed by Ellis and McCully (2013).

Taxonomic Rank[4]	Scientific name	Common name	Conservation importance	Biological vulnerability	Commercial importance	Importance of UK	Final score	ICES / ICCAT advice
35	*Deania calcea*	Birdbeak dogfish	4	6	2	3	36	NA
36	*Deania hystricosa*	Rough longnose dogfish	2	6	1	3	27	NA
37	*Squalus acanthias*	Spurdog	4	6	10	5	100	SA
38	*Centrophorus uyato*	Little gulper shark	3	6	1	3	30	NA
39	*Echinorhinus brucus*	Bramble shark	4	10	1	3	45	NA
40	*Squatina squatina*	Angel shark	10	15	2	15	405	QA
41	*Tetronarce nobiliana*	Common electric ray	0	8	1	4	36	NA
42	*Torpedo marmorata*	Marbled electric ray	0	4	9	9	117	NA
43	*Bathyraja pallida*	Pale ray	0	4	2	9	54	NA
44	*Bathyraja richardsoni*	Richardson's ray	0	4	2	3	18	NA
45	*Bathyraja spinicauda*	Spinytail ray	0	4	2	6	36	NA
46	*Bathyraja* sp.		1	1	2	6	24	NA
47	*Amblyraja hyperborea*	Arctic skate	0	2	6	6	48	NA
48	*Amblyraja jenseni*	Jensen's skate	0	2	2	6	24	NA
49	*Amblyraja radiata*	Starry ray	0	2	10	10	120	ST
50	*Dipturus batis*	Common blue skate	5	4	10	15	285	QA
51	*Dipturus intermedius*	Flapper skate	5	5	10	15	300	QA
52	*Dipturus nidarosiensis*	Norwegian skate	1	5	15	9	189	NA
53	*Dipturus oxyrinchus*	Long-nose skate	1	4	8	9	117	NA
54	*Leucoraja circularis*	Sandy ray	4	3	12	15	285	QA
55	*Leucoraja fullonica*	Shagreen ray	3	3	8	15	210	QA
56	*Leucoraja naevus*	Cuckoo ray	0	2	10	15	180	ST
57	*Malacoraja kreffti*	Krefft's ray	0	2	2	9	36	NA
58	*Malacoraja spinacidermis*	Soft skate (or prickled skate)	0	2	2	6	24	NA
59	*Neoraja caerulea*	Blue pygmy skate	0	1	2	9	27	NA
60	*Raja brachyura*	Blonde ray	1	3	15	15	285	QA
61	*Raja clavata*	Thornback ray	1	3	10	10	140	ST
62	*Raja microocellata*	Small-eyed ray	1	2	15	15	270	ST
63	*Raja montagui*	Spotted ray	0	2	10	15	180	ST
64	*Raja undulata*	Undulate ray	1	3	6	15	150	ST
65	*Rajella bathyphila*	Deepwater ray	0	2	2	6	24	NA
66	*Rajella bigelowi*	Bigelow's ray	0	2	2	6	24	NA
67	*Rajella kukujevi*	Mid-Atlantic skate	0	2	2	6	24	NA
68	*Rajella fyllae*	Round skate	0	2	2	6	24	NA
69	*Rostroraja alba*	White skate	10	5	6	8	168	QA
70	*Dasyatis pastinaca*	Common stingray	3	6	6	8	120	NA
71	*Pteroplatytrygon violacea*	Pelagic stingray	0	6	2	1	8	NA
72	*Myliobatis aquila*	Common eagle ray	3	6	6	4	60	NA

Table 7: Priority species in order of highest scoring (only those scoring ≥150 are shown).

Priority Rank	Scientific name	IUCN Listing (Regional, if not, global)	Wildlife and Countryside Act	CITES (App 1 or 2)	Global distribution	Importance of UK waters	Reproductive mode	Maximum length (cm)	Commercial importance (t)	Value to UK	Sampled in existing trawl surveys	ICES / ICCAT advice	Conservation importance (0–15)	Biological vulnerability (1–15)	Commercial importance (0–15)	Importance of UK (0–15)	Final score (0–675)
1	*Squatina squatina*	Critically Endangered	Yes	No	NE Atlantic	Breeding	Viv <10	250	<15	Medium	Isolated records	NA	10	15	2	15	405
2	*Dipturus intermedius*	Critically Endangered	No	No	NE Atlantic	Breeding	Ovip	250	>3000	Medium	Survey data limited	QA	5	5	10	15	300
3	*Dipturus batis*	Critically Endangered	No	No	NE Atlantic	Breeding	Ovip	150	>3000	Medium	Survey data limited	QA	5	4	10	15	285
4	*Leucoraja circularis*	Endangered	No	No	NE Atlantic	Breeding	Ovip	120	>500	High	Survey data limited	QA	4	3	12	15	285
5	*Raja brachyura*	Near Threatened	No	No	NE Atlantic	Breeding	Ovip	120	>3000	High	Survey data limited	QA	1	3	15	15	285
6	*Raja microocellata*	Near Threatened	No	No	NE Atlantic	Breeding	Ovip	91	>3000	High	Data for advice	ST	1	2	15	15	270
7	*Mustelus asterias*	Near Threatened	No	No	NE Atlantic	Breeding	Viv >10	140	>3000	Medium	Data for advice	ST	1	6	10	15	255
8	*Leucoraja fullonica*	Vulnerable	No	No	NE Atlantic	Breeding	Ovip	120[5]	>500	Medium	Survey data limited	QA	3	3	8	15	210
9	*Dipturus nidarosiensis*	Near Threatened	No	No	NE Atlantic	Fringe	Ovip	200	>3000	High	Isolated records	NA	1	5	15	9	189
10	*Lamna nasus*	Critically Endangered	No	Yes	Cosmopolitan	Breeding	Viv <10	370	>500	High	Isolated records	SA	10	15	12	5	185
11	*Leucoraja naevus*	Least Concern	No	No	NE Atlantic	Breeding	Ovip	72	>3000	Medium	Data for advice	ST	0	2	10	15	180
12	*Raja montagui*	Least Concern	No	No	NE Atlantic	Breeding	Ovip	72	>3000	Medium	Data for advice	ST	0	2	10	15	180
13	*Rostroraja alba*	Critically Endangered	Yes	No	Wider Atlantic	Present	Ovip	200	>100	Medium	Isolated records	NA	10	5	6	8	168
14	*Galeus melastomus*	Least Concern	No	No	NE Atlantic	Breeding	Ovip	90	>500	Medium	Data for advice	ST	0	2	8	15	150
15	*Scyliorhinus stellaris*	Near Threatened	No	No	NE Atlantic	Breeding	Ovip	162[6]	>3000	Low	Data for advice	QA	1	4	5	15	150
16	*Raja undulata*	Near Threatened	No	No	NE Atlantic	Breeding	Ovip	114	>100	Medium	Data for advice	ST	1	3	6	15	150

[5] 100cm commonly referred to as maximum length (Stehmann and Bürkel, 1984; and personally observed; Chapter 6), but early indications are that a larger maximum size estimated at ca. 120cm is more likely.
[6] This value has been taken from Quéro (1984) but most recent surveys and studies (Silva *et al*., 2013; ICES, 2019) have indicated lengths of up to ca. 130cm.

Table 8: Overview of data available for priority species, indicating whether data are available (✓), limited (~) or absent (x).

Priority Rank	Scientific name	Common name	Sampled in existing trawl surveys	ICES / ICCAT advice	Fisheries Management	Life History				New data from existing UK surveys?
						Age/Growth	Age/Size at Maturity	Fecundity	Length-weight	
1	*Squatina squatina*	Angel shark	Isolated records	NA	Pro	×	~	✓	~	×
2	*Dipturus intermedius*	Flapper skate	Survey data limited	QA	Pro	~	~	×	~	~
3	*Dipturus batis*	Common blue skate	Survey data limited	QA	Pro	~	~	×	✓	~
4	*Leucoraja circularis*	Sandy ray	Survey data limited	QA	TAC	×	~	×	×	×
5	*Raja brachyura*	Blonde ray	Survey data limited	QA	TAC	~	~	~	✓	~
6	*Raja microocellata*	Small-eyed ray	Data for advice	ST	TAC	~	~	~	✓	~
7	*Mustelus asterias*	Starry smooth-hound	Data for advice	ST	NA	✓	✓	✓	✓	✓
8	*Leucoraja fullonica*	Shagreen ray	Survey data limited	QA	TAC	×	~	×	✓	~
9	*Dipturus nidarosiensis*	Norwegian skate	Isolated records	NA	TAC	×	×	×	×	×
10	*Lamna nasus*	Porbeagle shark	Isolated records	SA	Pro	✓	✓	✓	✓	×
11	*Leucoraja naevus*	Cuckoo ray	Data for advice	ST	TAC	✓	✓	✓	✓	✓
12	*Raja montagui*	Spotted ray	Data for advice	ST	TAC	✓	✓	~	✓	✓
13	*Rostroraja alba*	White skate	Isolated records	NA	Pro	~	~	×	~	×
14	*Galeus melastomus*	Black-mouth dogfish	Data for advice	ST	NA	×	~	~	~	×
15	*Scyliorhinus stellaris*	Greater-spotted dogfish	Data for advice	ST	NA	×	~	~	✓	~
16	*Raja undulata*	Undulate ray	Data for advice	ST	TAC	~	~	~	✓	~

2.4 Discussion

The highest ranking three species (angel shark, flapper and common blue skate) from this prioritisation can all be considered species of 'conservation concern' (along with porbeagle and white skate). The IUCN listings are an informative metric when considering conservation importance given that all 72 species considered have been assessed by the IUCN so receive an equitable score. The additional parameters of being listed under the WCA and CITES are also applicable to all species however very few are currently listed, and these lists are reserved for species considered in need of the highest level of protection. Consideration of including the Convention of Migratory Species (CMS) list as an additional parameter was given, however discounted as it would bias results to those species which undertake migrations, as it does not consider non-migratory species.

Angel shark were the top-ranking species due to a high conservation score ('Critically Endangered' IUCN listing, and listed on the WCA) compounded by the low fecundity of this species (Tortonese, 1956) and its importance to the UK (with discrete breeding population(s) assumed). Although once widespread across the waters of the British Isles (Roux, 1984) the presence of this species has declined dramatically (Rogers and Ellis, 2000; Shepherd *et al*., 2019) following historic exploitation, recreational angling, bycatch and habitat loss; with extirpations reported from parts of its former range (ICES, 2019). This species has a very localised and fragmented distribution, with known contracted populations in Cardigan Bay, Wales (Hiddink *et al*., 2019) and Tralee Bay, Ireland (Shepherd *et al*., 2019) that may have limited connectivity to other stocks in the NE Atlantic and Mediterranean. Trawl records of incidental capture of juveniles in Cardigan Bay indicates this to be a breeding area (Cefas, *unpublished data*). There are no indicators of stock size and very limited biological knowledge (Table 8). Given the depleted abundance (Rogers and Ellis 2000; Shephard *et al*., 2019) restricted distribution and cryptic nature, existing trawl surveys are not able to provide any appropriate data for monitoring or assessment of this species.

The two species in the "common skate complex" (flapper and common blue skate) were next highest ranking. They are currently prohibited from fishing opportunities (CEC, 2020) thus affording them the highest level of protection. Their large body size makes them vulnerable to overfishing (Jennings *et al*., 1998, 1999; Dulvy *et al*., 2000; Dulvy and Reynolds, 2002) as demonstrated by their documented extirpation from the Irish Sea following commercial exploitation (Brander, 1981). However, in the last 5-years, a small but steady increase in common blue skate (juveniles) have been seen in fishery-independent surveys operating in the western Channel (ICES Division 7.e; Silva *et al*., 2018) and flapper skate are now observed (in very low numbers) in the North Sea International Bottom Trawl Survey (IBTS) again, after several years of absence (ICES, 2019).

Sandy and blonde rays were the next highest scoring priority species. Both are large-bodied skates (ca. 120 cm total length) that are not sampled effectively in fishery-independent surveys, primarily due to poor geographic overlap with important habitats. Sandy ray was ranked of higher conservation importance, while blonde ray has a greater market value. Sandy ray is a more offshore species, inhabiting deeper waters of the continental shelf, upper slope and offshore banks, while blonde ray is more of a coastal, shallow water species, and so may have a greater exposure to fishing activities. Biological knowledge of sandy ray is extremely limited (Table 8) and should be a priority going forward (Chapter 6; McCully Phillips and Ellis, 2018). Given the high commercial value of blonde ray, it is surprising that some key biological parameters (e.g. reliable age and growth estimates, and fecundity) are still largely unelucidated for British waters. The same parallels can be drawn to small-eyed ray, which although not widespread around the British Isles, is locally abundant in the Bristol Channel, yet biological data for this stock are limited (e.g. Ryland and Ajayi, 1984). This species does however have a stock size indicator, due to the overlap of a beam trawl survey with its main habitat. However, as beam trawls select for small-bodied specimens (Silva *et al*., 2012) biological data for larger (possibly mature) specimens is limited to support the derivation of robust maturity ogives.

Starry smooth-hound is a more wide-ranging species, being encountered around the British Isles and taken in a range of surveys thus providing a stock-size indicator for assessment purposes. Biological data were largely lacking until the work of Farrell *et al*. (2010a, b), however these studies were based on specimens from a restricted geographic area and contained a limited number of larger (mature) fish. Given the high-ranking position (seventh place) of this species, increased commercial landings and a lack of any formal management, a good understanding of the biology and ecology is imperative (Chapter 5; McCully and Ellis, 2015). The catch rates of starry smooth-hounds in fishery-independent surveys has also been increasing in recent years, thus providing an opportunity for biological data collection. There are behavioural (e.g. aggregating nature and seasonal presence) and morphological (e.g. medium-sized dogfish) parallels between starry smooth-hound and spurdog therefore pragmatic action and data collection while numbers appear abundant may inform proactive management measures and prevent future stock collapse scenarios.

Shagreen ray is a data-limited species also managed under the generic skate and ray TAC. Similar to sandy ray, it is a larger-bodied offshore skate species that is caught in lower numbers during fishery-independent trawl surveys, and ICES have been unable to provide a stock-size indicator to monitor temporal trends. Biological knowledge is also very limited, and data collection a priority for this species (Chapter 6; McCully Phillips and Ellis, 2018).

The other eight species scoring between 150–189 range from porbeagle shark which has a cosmopolitan distribution, well understood biology (Francis *et al*., 2008) and breeds in British waters to the lesser-known Norwegian skate with very limited biological data (Stehmann *et al*., 2015) but is only present in British waters at the fringe of its distribution.

The occurrence, distribution and importance of UK waters to a species are factors which should be considered as any part of a Plan of Action (PoA). Although the Defra Shark, Skate and Ray Conservation Plan (Defra, 2011) is a high-level document addressing the overarching aim of '*sustainable elasmobranch fisheries*' through key objectives, it does not consider which species occur in national waters nor prioritise the actions or species which need addressing in order to achieve the aim. National PoAs have been adopted by most of the top shark fishing nations – considered to be the 26 countries responsible for 84% of landings 2000–2009: with the UK ranking 19th (FAO, 2019). Australia ranked in 23rd place and was one of the first countries to adopt a comprehensive PoA in 2004 (DAFF, 2004). The background section within 'the need for a PoA' details the number (n = 178) of chondrichthyan species caught in national waters and further lists the 60 species that are designated as "*of concern*" through IUCN criteria and national catch statistics. This starting point then provided the evidence base for the subsequent 18 'issues' to address within the Plan. Shark-plan 2 (DAFF, 2012) then takes the 'issues' determining actions under each and prioritising them in terms of importance and setting time limits on actions. These Plans demonstrate the importance of both a clear understanding of species of occurrence and concern within national waters as a baseline, and the need for prioritising species and actions within such Plans, as addressed in this Chapter.

The lack of life history parameters for many of the most important species to UK waters is remarkable (Table 8), with much of the limited knowledge relating to different stock units. Although this can be used as a proxy in terms of quantifying parameters, as McCully *et al*. (2012; Chapter 3.3.1) highlighted, there can be significant differences in key life history parameters such as length at maturity between stock units which would require distinct management measures to ensure sustainable exploitation at a regional level. The overall lack of data on age and growth of the top-ranking elasmobranch species was anticipated, given the many technical challenges associated with providing robust estimates for these parameters (reviewed by Goldman, 2005). However, accurate estimates of these parameters are essential for successful fisheries management in terms of providing estimates of natural mortality, longevity and hence supporting sustainable exploitation (Goldman, 2005). Fecundity data are also lacking for most species – another important parameter in demographic modelling especially when related to maternal total length and density dependence (e.g. De Oliveira *et al*., 2013).

As demonstrated in Table 8, the lack of biological data for many species can often hamper stock assessments, therefore, the approach taken in this Chapter was deliberately as qualitative as possible, in order to allow <u>all</u> species to be included in this baseline assessment. Such an approach can be adopted widely and used in a variety of areas where only rudimentary data are available (e.g. developing countries). Many approaches that require more quantitative data are also available (reviewed by Walker *et al*., 2014) with a semi-quantitative approach taken in Chapter 3.

The outcome of this research and approach will encourage proactive research rather than supporting reactive work once a risk or decline has been identified, which from past experience may not be detected until decades after the event (e.g. common skate complex, Brander, 1981) and could result in regional extirpation and stock levels too low to hamper population recovery.

2.5 Summary conclusion

- This method has the ability to triage a large number of elasmobranch species occurring in national waters using limited data. Such work needs to be done on an appropriate geographic scale to harmonise with the objectives of the study – in this case to identify the most important species around the British Isles for increased research to support sustainable exploitation.
- The top three ranking species (angel shark, flapper skate and common blue skate) are all subject to a zero TAC at the current time (CEC, 2020), thus affording them high levels of protection and measures to reduce fishing mortality. Therefore, in line with the impartiality of the prioritisation, the next ranking species were considered.
- The decision was taken to focus research priorities on skate species managed under the generic TAC as these comprised 50% of the top ranking (n = 16) species (Chapter

4); sandy and shagreen ray as two of the potentially most vulnerable skate species exploited within this complex which have almost no biological information and are rarely encountered in surveys (Chapter 6), and finally starry smooth-hound, as the highest ranking species with no management in place (Chapter 5).

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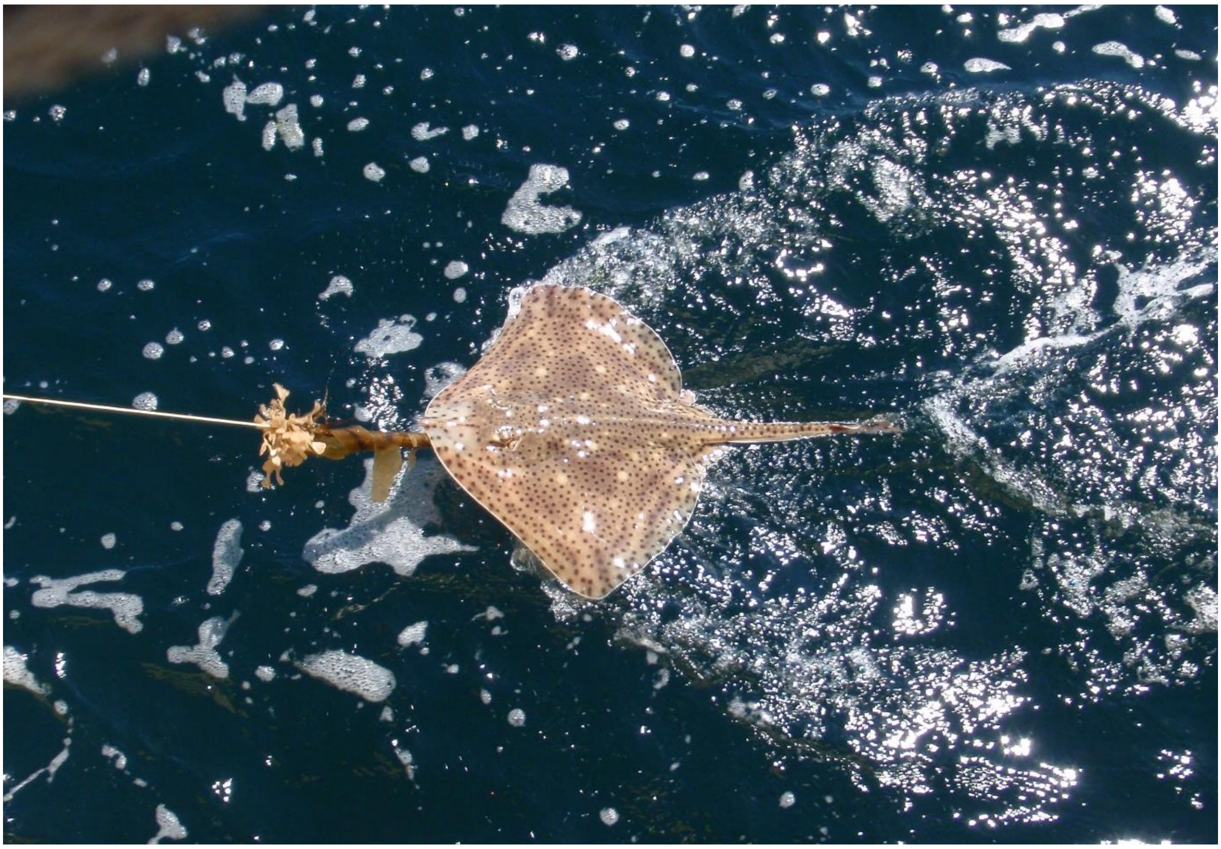
Chapter 3



Productivity susceptibility analyses of UK skate stocks

3 Productivity susceptibility analyses of UK skate stocks

This Chapter was based on the following publication:

McCully Phillips, S. R., Scott, F. and Ellis, J. R. (2015). Having confidence in productivity susceptibility analyses: A method for underpinning scientific advice on skate stocks? *Fisheries Research*, **171**, 87–100.

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The study was conceived by the candidate and I was responsible for the project design, data collection, leading the writing of the manuscript and production of Tables and Figures 3 and 4. I developed the concept of using independent experts and confidence scoring as a tool and provided the input data to Dr. F. Scott for modelling. Dr. Scott wrote the R-scripts and produced Figures 1–2 and 5–8. This work was undertaken under the supervision of Dr. J. Ellis. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Minor updates to the introduction and discussion have been made to incorporate relevant recent literature.

3.1 Abstract

National and European shark conservation plans aim to manage elasmobranch stocks sustainably. However, uncertainties and deficiencies with available data hamper traditional, quantitative assessment methods of stock status to inform those plans, and thus effective management. The International Council for the Exploration of the Sea (ICES) Expert Groups have explored a range of data deficient assessment methods that may be used to support management advice, including Productivity Susceptibility Analysis (PSA). This method was applied to the demersal elasmobranch fauna (21 species) of the Celtic Sea to explore how such approaches could inform the management of skates (Rajidae). This species complex is an important catch component for demersal trawl and gillnet fisheries and is currently managed under a mixed species Total Allowable Catch (TAC). PSAs were conducted on both of these fisheries, by four experts from three countries to introduce independence, and to quantify the range in perceptions of each stock. Confidence scoring of attributes was incorporated and probability distributions generated to model uncertainty in the expert responses to susceptibility attributes. Results showed that three shark species (tope *Galeorhinus galeus*; angel shark *Squatina squatina* and spurdog *Squalus acanthias*) were the most vulnerable species in both fisheries (a consequence of their life history strategy and

large size), followed by two skates (otter trawl) and three skates (gillnet). All of these species have some form of restrictive management in place such as a prohibited listing status, or minor bycatch allowance to allow for stock rebuilding. Blonde ray *Raja brachyura* was ranked as the next most vulnerable member of the commercially exploited skate complex. This adaptation of the PSA approach enabled skate species of higher and lower risk to be ranked and thus inform where management efforts should be focussed, whilst giving a novel consideration to uncertainty through canvassing expert opinion.

3.2 Introduction

In European waters, scientific agencies have only been able to assess the size of fish stocks, fishing mortality rates and catch levels for just over one third of commercial stocks (e.g. COM (2009a) 224, Annex II). This is often because scientific advice and assessments are hampered by inaccurate commercial data (e.g. landings, discards and effort), limited biological knowledge (e.g. age and growth, natural mortality and reproductive output), or limitations of fishery-independent survey data. For example, fishery-independent surveys were designed to monitor stocks of commercially important roundfish and flatfish, thus the fishing gears used, seasons and areas sampled are sub-optimal for capture of many elasmobranch species. Some groups of fish that are not assessed currently (e.g. because they are deemed of less commercial importance in overall landings) can be highly susceptible to the impacts of fishing and there is an increased focus to consider and advise on such species under the ecosystem approach to fisheries management (EU, 2013). The UK's 'Shark, Skate and Ray Conservation Plan' (Defra, 2011) aims: "*To manage elasmobranch stocks sustainably so that depleted stocks recover and that those faring better are fished sustainably*", yet to progress towards such targets for data deficient species, despite the inherent uncertainties, novel and robust assessment and management procedures are required.

Following the United Nations Code of Conduct for Responsible Fisheries (FAO, 1995), the "*best scientific evidence available*" should be used to evaluate the state of any fisheries to support decisions, while the precautionary approach to fisheries management requires a formal consideration of uncertainty. In order to address such principles, various risk-based approaches have been considered for data-limited, multi-species scenarios. These include Ecological Risk Assessments (ERAs), which attempt to evaluate the vulnerability of a species or stock to overfishing based on its biological sensitivity or productivity, and its susceptibility to the main fisheries operating over their geographic range.

Within an ERA framework a hierarchical approach may be taken to evaluate the effects of fishing. The approach moves from a largely qualitative analysis of risk that can involve stakeholder judgement (level one), through a semi-quantitative approach (e.g. Productivity Susceptibility Analysis (PSA), level two) to a fully quantitative approach (level three), which requires appropriate data to be available (Hobday *et al*., 2011). In this way, the vulnerability of a species to a fishery (and fishing gear) is assessed (Fletcher, 2005; Griffiths *et al*., 2006). ERA approaches have expanded from single species applications to help implement the ecosystem-based approach for fisheries management (Smith *et al*., 2007; Zhou *et al*., 2009), allowing rapid assessment of the potential species at risk within an ecosystem to particular fisheries and gears, including within multispecies fisheries (Stobutzki *et al*., 2002; Hobday *et al*., 2011).

Elasmobranchs are generally considered as vulnerable to over-fishing (Ellis *et al*., 2008 and references cited therein), as they are often long-lived, slow growing and of low fecundity. While there are or have been some directed fisheries for these species in the Northeast Atlantic, many of these species represent 'bycatch', a proportion of which is retained. The commercial importance of the various species, which is related to the market value, size and condition of individual fish, and technical regulations (e.g. quota availability and minimum landing sizes) influences discard/retention patterns in commercial fisheries (Silva *et al*., 2012). There is frequently limited information on the biology of many elasmobranch species, in particular key Northeast Atlantic skate species, and on their interactions with commercial gears and discard survival rates. As a result, analytical assessments have been possible for only a few elasmobranch species. In fact, ICES (The International Council for the Exploration of the Sea) has only benchmarked[7] one elasmobranch assessment – spurdog *Squalus acanthias* (De Oliveria *et al*., 2013); with management advice for other species based primarily on temporal trends in relative abundance from scientific trawl surveys. Nevertheless, given the requirements for precautionary management, and the introduction of the European Commission's Community Plan of Action for sharks (COM, 2009b), there is an increasing need to provide some form of advice for a wider group of elasmobranch species.

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[7] An intense process for evaluating the current data and assessment methodology. The aim of a benchmark is consensus agreement on an assessment methodology that is to be used in future update assessments, laid down in a stock annex. The result will be the 'best available' method on which ICES advice can be based on (ICES website – 21 February 2013).

‘Semi-quantitative’ PSAs have been considered for elasmobranch species around the world (reviewed by Gallagher *et al*., 2012, listed by Hordyk and Carruthers, 2018). These applications have included pelagic elasmobranchs in the Atlantic (Simpfendorfer *et al*., 2008; Cortés *et al*., 2010; Arrizabalaga *et al*., 2011) and Pacific Oceans (Griffiths *et al*. 2017), artisanal fisheries along Pacific (Furlong-Estrada *et al*., 2017; Clarke *et al*., 2018) and Indian Ocean coastlines (Temple *et al*., 2019) and deep-water fisheries to the west of the British Isles (Watling *et al*., 2011; Dransfeld *et al*., 2013). These examples vary both in the number and range of taxa through to their methodological interpretation of a PSA. Similarly, the extent to which expert opinion is canvassed, and the method by which this is achieved (blind scoring or through consultation) varies, as does the consideration of uncertainty in such scores. The importance of quantifying uncertainty and canvassing expert opinion to improve decision making was emphasized by Aspinall (2010). While this variability implies that a ‘one size fits all’ approach may not be operationally optimal, some level of testing and standardisation is required to allow direct comparison, and to incorporate the PSA method into the provision of management advice.

The level to which PSAs may feed into management measures varies, but as a minimum they can help identify the most vulnerable species within a fishery, and thus where future management efforts and advice should be directed. They may also have a role in exploring the efficacy of management options designed to reduce the susceptibility of species of concern. The advantages of any management measures, however, would be specific to the fishery examined and could also depend on factors such as the fixed biological characteristics of the most vulnerable species, political drivers, data availability, industry compliance and feasibility.

Until 2012, assessing and advising on stocks of uncertain status and limited data was not achievable within ICES through their traditional frameworks. ICES provides advice for over 200 stocks, yet ICES (2012a) determined that 122 did not have population estimates from which catch options could be derived using the traditional MSY framework, and are therefore considered “data-limited” (ICES 2012b). Given the drive to provide and implement some form of quantitative management advice for increasing numbers of stocks, ICES developed a framework of data-limited approaches in 2012 (ICES 2012a, c). Within this framework there are six categories of data deficiency, with associated methodological recommendations made at each level, with PSA’s recommended for both category five (‘data-poor stocks’) and six (‘negligible landings stocks and stocks caught in minor amounts as bycatch’) stocks (ICES 2012c). However, this approach can also be applied across the board to include data-rich stocks, as a means to identify the relative vulnerability of species to fisheries, and to distinguish species of high and low risk. Some data-limited methods by their nature adopt a precautionary approach, where decreasing information increases the margin of precaution, thus moving the stock in the direction of sustainable exploitation, whilst having due regard for the species' biological characteristics and uncertainty in the information (ICES 2012b).

Two ICES expert groups investigated the application of PSAs in their 2013 meetings (ICES 2013a, b); including demersal elasmobranchs in the Celtic Sea, which were considered a category six stock (ICES 2012c). In this paper we undertake a level two PSA (Hobday *et al*., 2011), with emphasis on the skate complex of the Celtic Sea, in order to evaluate the utility of the PSA approach to multi-species fisheries management, whilst incorporating expert scoring and probability modelling of uncertainties.

3.3 Materials and Methods

3.3.1 PSA framework and attributes

To evaluate the skate complex of the Celtic Sea, an existing PSA framework was updated, based upon biological productivity characteristics and their susceptibility to the fisheries that catch them. The NOAA toolbox (http://nft.nefsc.noaa.gov/index.html) PSA framework (Patrick *et al*., 2009) was used to assess nine data-limited rajid stocks (for which ICES provides advice) from the Celtic Sea ecoregion in two demersal fisheries (otter trawl and gillnet[8]), with an additional four prohibited skates and eight other elasmobranch taxa included for comparison. These additional species, for which greater information were available, were used for 'ground-truthing'.

As per Patrick *et al*. (2009), vulnerability was assumed to be influenced by two components: the productivity or biological sensitivity of the stock (related to its biological characteristics) and its fisheries susceptibility (related to the likely impact of the specific fishery/gear on the stock). Each of these components comprised a number of different traits or factors.

Several different attributes and approaches were examined throughout the PSA process. After consultation with fisheries managers and biologists in the ICES community, it was decided to form this PSA on the criteria used in the NOAA toolbox (Patrick *et al*., 2009) as a baseline, whilst also recognising that each application of a PSA may require modification to

[8] 'Gillnet' fishery relates to gillnet, trammel net and tangle nets (i.e. monofilament gears)

improve the relevance to particular stocks and management areas. Therefore, the attributes used were modified slightly to better address some of the biological characteristics more specific to elasmobranchs. Twelve productivity attributes were employed in this PSA (Table 9). Two of these attributes (measured fecundity and breeding strategy) were modified from the default NOAA toolbox, to better distinguish between the life history strategies of elasmobranchs. Two new attributes (breeding cycle and genetic distinctness) were also added to the assessment.

Table 9: Productivity attributes used in the PSA. Those in normal font were as per the NOAA PSA framework (Patrick *et al*., 2009), modified attributes are shown in **bold** and additional attributes shown in ***bold italics***.

Productivity Attributes	Low (1)	Moderate (2)	High (3)
r	<0.16	0.5–0.16	>0.5
Maximum age	>30 years	10–30 years	<10 Years
Maximum size	>150 cm	60–150 cm	<60 cm
von Bertalanffy growth coefficient (k)	<0.15	0.15–0.25	>0.25
Estimated natural mortality	<0.20	0.20–0.40	>0.40
Measured fecundity	**<10**	**10–100**	**>100**
Breeding strategy	**Live bearer**	**Demersal egg layer**	**Broadcast spawner**
Breeding cycle (female)	***Bi / Triennial***	***Annual cycle with a seasonal peak***	***Annual cycle with protracted breeding season or with multiple broods per year***
Recruitment pattern	Infrequent recruitment success (<10% of year classes are successful)	Moderately frequent recruitment success (between 10% and 75% of year classes are successful)	Highly frequent recruitment success (>75% of year classes are successful)
Age at maturity	>4 years	2–4 years	<2 years
Mean trophic level	>3.5	2.5–3.5	<2.5
Genetic distinctness	***In this region, this species is the only one in its family***	***In this region, this species is the only one in its genus***	***In this region, this species is one of several in its genus***

Similarly, the majority of susceptibility attributes within the NOAA PSA approach were used. Thirteen attributes were included (Table 10), of which three (fishery importance, management applicable and monitoring (or assessment) of status) were added attributes. These three attributes, which were considered discrete issues, were used to replace the single 'management strategy' attribute used in the NOAA toolbox. Another attribute ('fishing rate relative to M') was excluded, as this is unknown for all species included in this assessment. A small modification was made to 'value of fishery' to remove the actual dollar or retention values and make the scoring more qualitative in terms of desirability without giving exact monetary definitions. Given the international fishing occurring in these waters, and that experts from three different countries contributed their scores, a common currency was not available or suitable in this case.

Table 10: Susceptibility attributes used in the PSA. Those in normal font are as per the NOAA PSA framework (Patrick *et al*., 2009), modified attributes are shown in **bold** and additional attributes shown in ***bold italics***.

Susceptibility Attributes	Low (1)	Moderate (2)	High (3)
Fishery	***Non-commercial species in this fishery***	***Important bycatch in mixed fisheries and/or targeted in seasonal/localised fisheries***	***Important target fisheries operate or have operated in recent times (for this métier)***
Management applicable	***Landings or catches strictly regulated for much of the stock area***	***Landings or catches partly regulated for the stock area***	***No management measures for the species/species-complex***
Monitoring (or assessment) of stocks	***Appropriate monitoring to inform on stock status***	***Limited data can inform on trends in catches or landings***	***Insufficient data to evaluate status***
Areal overlap	<25% of stock occurs in the area fished	Between 25% and 50% of the stock occurs in the area fished	>50% of stock occurs in the area fished
Geographic distribution	Continuous: stock is distributed in >50% of the range of the fishery	Restricted: stock is distributed in 25% to 50% of the range of the fishery	Fragmented: stock is distributed in <25% of the range of the fishery
Vertical overlap	<25% of stock occurs in the depths fished	Between 25% and 50% of the stock occurs in the depths fished	>50% of stock occurs in the depths fished
Biomass of spawners (SSB) or other proxies	B is >40% of B0 (or maximum observed from time series of biomass estimates)	B is between 25% and 40% of B0 (or maximum observed from time series of biomass estimates)	B is <25% of B0 (or maximum observed from time series of biomass estimates)
Seasonal migrations	Seasonal migrations decrease overlap with the fishery	Seasonal migrations do not substantially affect the overlap with the fishery	Seasonal migrations increase overlap with the fishery
Schooling/aggregation and other behavioural responses	Behavioural responses decrease the catchability of the gear	Behavioural responses do not substantially affect the catchability of the gear	Behavioural responses increase the catchability of the gear [i.e., hyperstability of CPUE with schooling behaviour]
Morphology affecting capture	Species shows low selectivity to the fishing gear.	Species shows moderate selectivity to the fishing gear.	Species shows high selectivity to the fishing gear.
Survival after capture and release	Probability of survival >67%	Probability of survival ≥33% and ≤67%	Probability of survival <33%
Desirability/value of the fishery	**Stock is not highly valued or desired by the fishery**	**Stock is moderately valued or desired by the fishery**	**Stock is highly valued or desired by the fishery**
Fishery impact to EFH or habitat in general for non-targets	Adverse effects absent, minimal or temporary	Adverse effects more than minimal or temporary but are mitigated	Adverse effects more than minimal or temporary and are not mitigated

Each individual biological productivity or susceptibility attribute was given a score of between 0–3 for each species (with bridging values of 1.5 and 2.5 permitted). Each attribute was also given a 'weight' (i.e. how much consideration is given to this attribute in the assessment). Following Patrick *et al*. (2009), the default score was two (where each attribute would be given equal importance), with a range of zero (i.e. excluded from the assessment) to four (of greatest importance). The weights assigned to each attribute remained constant across all species within an assessment and for each fishery assessed. The attribute score multiplied by the weight gives the 'weighted attribute score'. Furthermore, for each attribute scored per species, the 'data quality' was also scored between one and five (Table 11).

Table 11: Data Quality Scores (adapted from Patrick *et al*., 2009).

Data Quality Score	Description
1	**Best data**: Information based on collected data for the stock and area of interest that is both established and substantial.
2	**Adequate data**: Information with limited coverage and corroboration, or not wholly reliable.
3	**Limited data:** Estimates with high variation and limited confidence or based on similar taxa.
4	**Very limited data:** Expert opinion or based on general literature review from wide range of species, or from outside study area.
5	**No data:** No information to base score on.

3.3.2 Incorporating expert judgement

Given that biological productivity does not change between fisheries and that these attributes are less subjective, the authors scored these attributes based on literature and expert opinion, and they were not sent out to the national experts to score independently. However, to ensure accuracy, these scores were verified by an internationally renowned European expert for elasmobranch biology (with over 30 years of experience), and consensus achieved.

Four national experts (from three European countries, with between six and 20 years in elasmobranch research) scored the susceptibility attributes. Experts scored 13 attributes for the 21 species in both the demersal otter trawl and gillnet fleets. They also provided a data quality score and assigned weightings (between zero and four, the higher the score, the more 'weight' that attribute carries within the assessment) that they believed appropriate to each of the 13 attributes. Weightings were assigned to attributes using the modal values attained, and did not change between species within a gear, or between the two gears themselves.

3.3.3 Incorporating confidence

The NOAA PSA includes a 'Data Quality' score, which implies the overall quality of the data or belief in the score rather than the actual type of data used in the analysis (Patrick *et al.*, 2010). This results in five tiers, ranging from the best data (or high belief in the score) to no data (or little belief in the score) (Patrick *et al.*, 2010). In this study, the authors wanted to tease apart the two elements, and score the quality of the data (giving the 'Data Quality' score) independently from the confidence of each expert in the score they assigned to the attributes (giving an additional 'Confidence' score). Given the geographic spread and varying levels of fishery knowledge of the experts involved, we wanted to capture this information, whereby an expert can be more confident in a score than available data would suggest, and vice versa. Therefore, as an alternative, a 'Confidence Score' (adopted from the Intergovernmental Panel on Climate Change, IPCC 2005) was added. These had the values: low, medium, high, very high, which represented a degree of confidence of being correct as 0.2, 0.5, 0.8 and 0.9 respectively (Table 12). Each susceptibility attribute for each species was given an individual confidence score by all assessors for each gear type (Figure 1).

Table 12: Confidence Scoring (adapted from IPCC, 2005). 'Very Low' score omitted, as assessors would not score a species or an attribute they had such low confidence in.

Terminology	Degree of confidence in being correct
Low	About 2 out of 10 chance of being correct
Medium	About 5 out of 10 chance of being correct
High	About 8 out of 10 chance of being correct
Very high	About 9 out of 10 chance of being correct

The confidence scores were used to model the susceptibility attribute scores as beta probability distributions (Holt *et al.*, 2014). The susceptibility scores were rescaled from their original values to between 0 and 1 (i.e. scores of 1, 1.5, 2, 2.5 and 3 were rescaled to 0.167, 0.333, 0.5, 0.667 and 0.833). These rescaled attribute scores were used as the modes of the distributions. The confidence scores (0.2, 0.5, 0.8 and 0.9, see Table 12) were used as the area under the probability distribution function (pdf) in the range around the mode ± 1/12 (the distance between modes divided by 2), i.e. when sampling a value from the distribution, the more confident the expert is, the more likely the value will be closer to the mode (the rescaled attribute score) (Figure 2). A distribution was generated for all of the 20 combinations of susceptibility attribute score and confidence level.

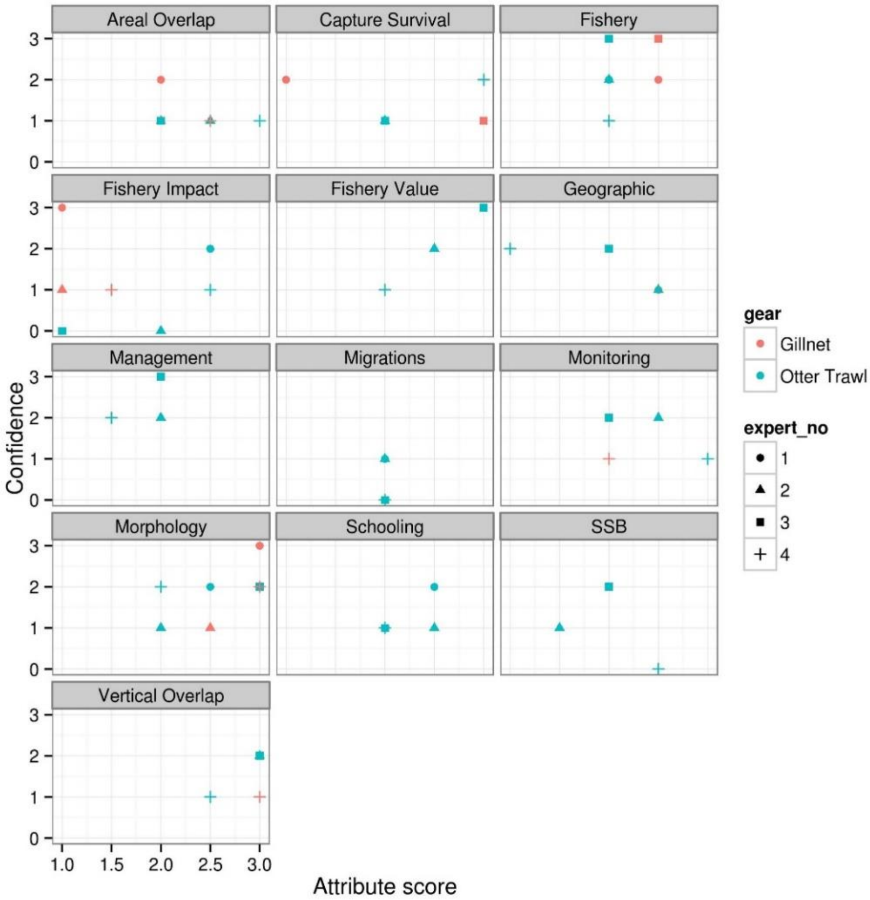

Figure 1: Example confidence and susceptibility attribute scores by expert for blonde ray.

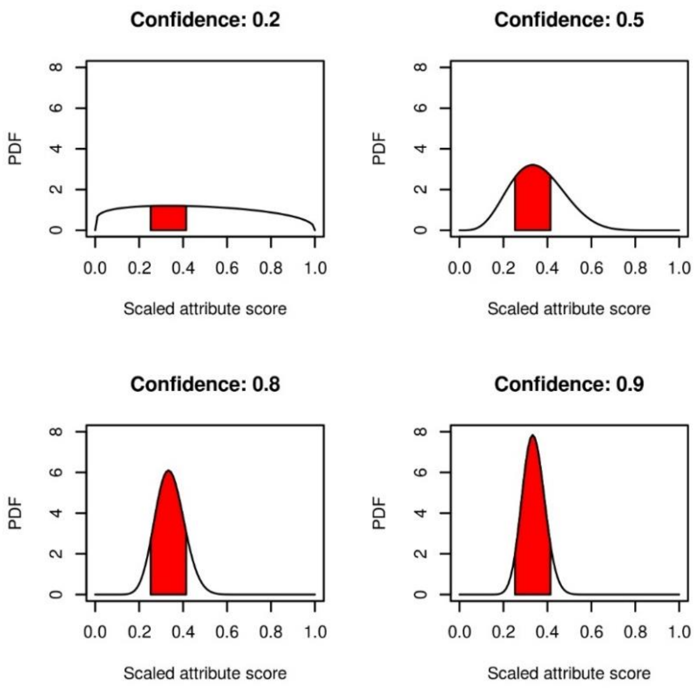

Figure 2: Beta distribution for attribute score of 1.5 (mode = 0.33). The coloured region shows the area of probability distribution that contains the attribute score. As confidence increases, the distribution tightens around the mode.

3.3.4 Modelling confidence of expert responses

The weightings (0-4) assigned to each attribute were incorporated with the susceptibility attribute distributions to generate distributions for the weighted susceptibility scores by species and gear. This was carried out by calculating the weighted susceptibility (sum (weight * score) / sum (weight)) value for each expert, then averaging across experts to get the 'final' weighted susceptibility distribution.

This followed the method employed by Uusitalo *et al*. (2005) who noted: "*the probability distributions of the experts were combined by simple average since there is evidence that simple combinational methods outperform group judgements* (Gigone and Hastie, 1997) *compared with more complex combinational rules* (Clemen and Winkler, 1999)". By treating the expert's probabilities equally and symmetrically, they can also be considered exchangeable (Clemen and Winkler, 1999). This method allowed examination of how the weighted susceptibility scores differed between experts.

For each species and gear combination, 500 samples were taken from each individual attribute distribution of each expert. These were rescaled back to the original attribute score range (0–3) and used to calculate 500 weighted susceptibility scores by each expert. These were then averaged across experts to give a distribution of weighted susceptibility. Each expert was given equal weight in the analysis.

3.3.5 Combining weighted susceptibility and productivity scores

The weighted productivity score was combined with our samples from the weighted susceptibility score to calculate the overall PSA (i.e. vulnerability) score. This vulnerability score (v) is defined as the Euclidean distance of the weighted productivity (p) and weighted susceptibility (s) scores from the origin on the scatter plot (i.e. 3.0, 1.0) using the equation:

$$v = \sqrt{(p-3)^2} + (s-1)^2$$

(Patrick *et al*., 2009; 2010).

The vulnerability scores were input into the NOAA toolbox PSA spreadsheet, to give the final PSA scatter plots, where productivity scores are plotted (x-axis) in reverse (3 to 1) against susceptibility scores (y-axis), allowing the most vulnerable species (i.e. low productivity and high susceptibility) to be identified in the top right hand corner of the plot.

3.4 Results

3.4.1 PSA rankings

The relative vulnerabilities (final PSA score) of all species considered were ranked in terms of most to least vulnerable in relation to gillnet (Table 13, Figure 3) and otter trawl fisheries (Table 13, Figure 4). In the gillnet fishery, the most vulnerable species was tope *Galeorhinus galeus* (score of 2.00), which was followed closely by five other species, all of which are currently designated as prohibited or zero TAC in the Celtic Seas ecoregion. Given the rationale of this study to look at species contained within the mixed 'skate and ray' TAC, the most vulnerable member of this complex was blonde ray *Raja brachyura*, ranking eighth most vulnerable, with a vulnerability score of 1.75. Blonde ray was followed by two large-bodied *Dipturus* species (long-nose skate *D. oxyrinchus* and Norwegian skate *D. nidarosiensis*) – both deeper water species for which knowledge of their biology is limited. Results in the otter trawl fishery were broadly similar, with angel shark *Squatina squatina* ranking as the most vulnerable (1.98), followed by tope and then three prohibited or zero TAC species (spurdog, white skate *Rostroraja alba* and flapper skate *Dipturus intermedius*), with blonde ray again deemed to be the most vulnerable member of the mixed skate TAC complex (1.74) for this gear.

The data quality score for biological productivity (which is the same over both gears) ranged from low (e.g. angel shark) to high. Spurdog was the only species that achieved a 'high' data quality score for productivity (and the only species to have a robust quantitative stock assessment). Nine species scored 'low' and eleven scored as 'medium' data quality. Within fisheries susceptibility, all species in both fisheries achieved a data quality score of 'medium'. The expert scores for productivity varied very little, and consensus was achieved easily. The range of scores for fisheries susceptibility also varied relatively little, and the only attribute where a 'high' and 'low' score was achieved simultaneously was for 'Desirability/value of the fishery', which was simply a misinterpretation of prohibited/zero TAC species (and a lack of clear scoring instructions for this attribute, under changing management regimes) and was quickly rectified following a clarification by the lead author.

Table 13: Results of the PSA vulnerabilities and overall rankings for elasmobranchs in the Gillnet and Otter Trawl fisheries in the Celtic Sea.

Species	FAO Code	Both Gears Productivity		Otter Trawl Susceptibility		Gillnet Susceptibility		Otter Trawl Vulnerability		Gillnet Vulnerability	
		Attribute Score	Data Quality Score	Attribute Score	Data Quality Score	Attribute Score	Data Quality Score	Score	Rank	Score	Rank
Tope (*Galeorhinus galeus*)	GAG	1.33	2.88	2.07	2.85	2.11	2.80	1.98	2	2.00	1
Angel shark (*Squatina squatina*)	AGN	1.29	3.82	2.00	3.22	1.97	3.07	1.98	1	1.97	2
Spurdog (*Squalus acanthias*)	DGS	1.39	1.97	2.06	2.00	2.12	1.94	1.93	3	1.96	3
White skate (*Rostroraja alba*)	RJA	1.52	3.55	2.10	3.37	2.16	3.48	1.85	4	1.88	4
Flapper skate (*Dipturus intermedius*)	RJB1[9]	1.50	2.79	2.06	2.98	2.12	2.98	1.83	5	1.87	5
Electric ray (*Torpedo nobiliana*)	TTO	1.48	4.06	1.93	3.00	1.95	3.06	1.78	6	1.79	7
Common blue skate (*Dipturus batis*)	RJB2	1.65	2.94	2.13	2.77	2.18	2.72	1.76	7	1.79	6
Blonde ray (*Raja brachyura*)	RJH	1.76	3.03	2.22	2.61	2.24	2.63	1.74	8	1.75	8
Long-nosed skate (*Dipturus oxyrinchus*)	RJO	1.71	4.00	2.16	3.32	2.14	3.31	1.73	9	1.72	10
Norwegian skate (*Dipturus nidarosiensis*)	JAD	1.65	3.88	2.04	3.35	2.10	3.36	1.70	10	1.74	9
Starry smooth-hound (*Mustelus asterias*)	SDS	1.70	2.91	2.10	2.42	2.12	2.45	1.70	11	1.72	11
Shagreen ray (*Leucoraja fullonica*)	RJF	1.77	3.76	2.14	2.91	2.19	2.86	1.67	12	1.71	12
Sandy ray (*Leucoraja circularis*)	RJI	1.77	3.76	2.12	3.42	2.14	3.47	1.66	13	1.68	13
Small-eyed ray (*Raja microocellata*)	RJE	1.80	3.03	2.10	2.56	2.12	2.60	1.63	14	1.64	15
Marbled electric ray (*Torpedo marmorata*)	TTR	1.67	3.82	1.93	3.02	1.95	3.09	1.63	15	1.64	16
Undulate ray (*Raja undulata*)	RJU	1.86	2.88	2.12	2.84	2.19	2.78	1.60	17	1.65	14
Thornback ray (*Raja clavata*)	RJC	1.89	2.24	2.18	2.44	2.11	2.44	1.61	16	1.56	17
Spotted ray (*Raja montagui*)	RJM	1.98	2.55	2.10	2.55	2.10	2.56	1.50	18	1.50	18
Cuckoo ray (*Leucoraja naevus*)	RJN	1.98	2.42	2.06	2.46	2.07	2.51	1.46	19	1.48	19
Greater-spotted dogfish (*Scyliorhinus stellaris*)	SYT	1.98	3.88	1.92	2.80	1.90	2.79	1.37	20	1.35	20
Lesser-spotted dogfish (*Scyliorhinus canicula*)	SYC	2.09	2.67	1.91	2.03	1.82	2.02	1.29	21	1.22	21

[9] Since this work was undertaken and published, the FAO have recently introduced a new code for *Dipturus intermedius* (DRJ), with *Dipturus batis* remaining as RJB.

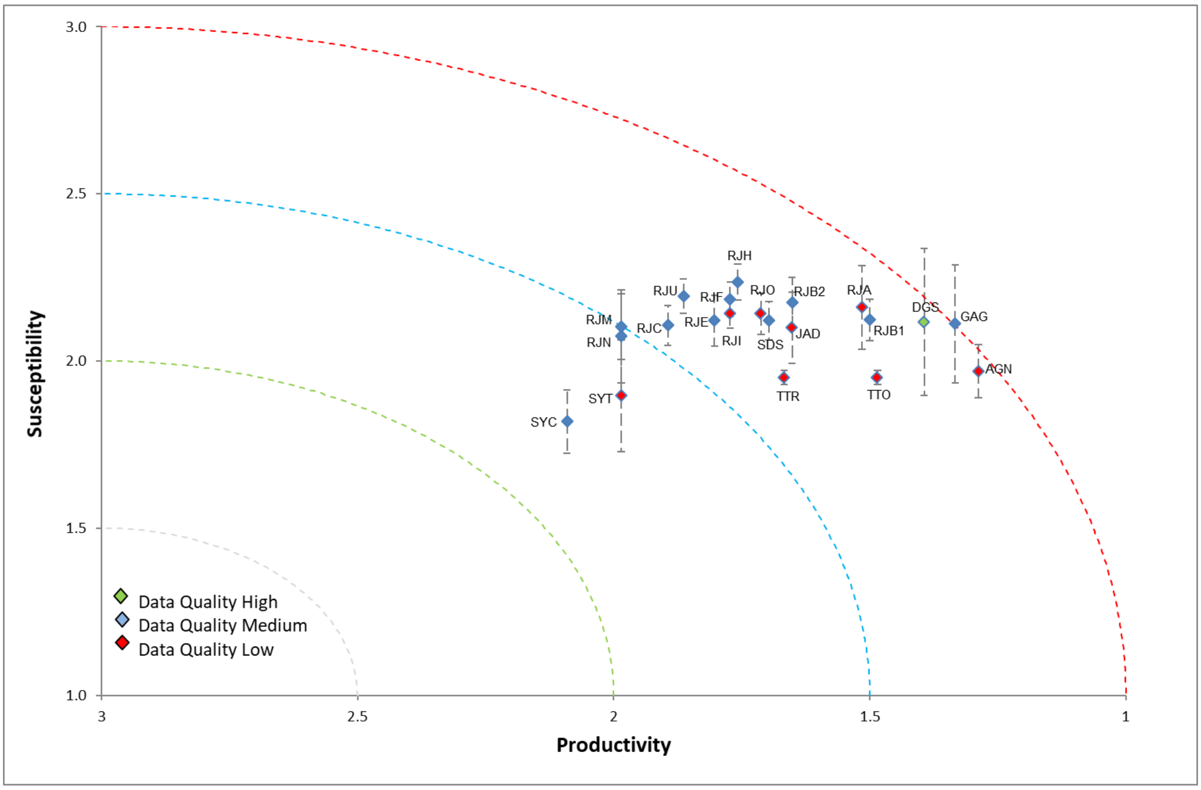

Figure 3: PSA plot of vulnerabilities for Celtic Sea skates (and other elasmobranchs) in the demersal gillnet fishery. See Table 13 for species codes.

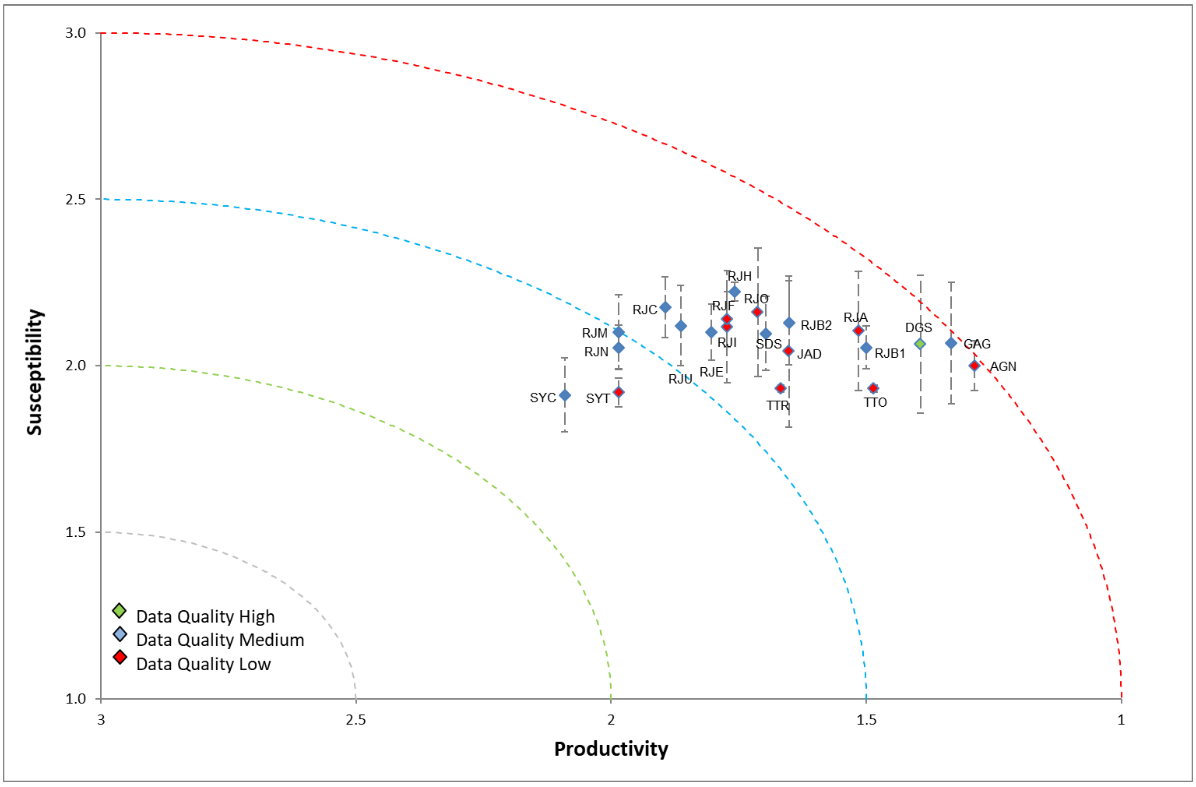

Figure 4: PSA plot of vulnerabilities for Celtic Sea skates (and other elasmobranchs) in the demersal otter trawl fishery. See Table 13 for species codes.

3.4.2 Modelling confidence of expert responses

The beta distributions resulting from the attribute score and confidence, for each species by expert and gear were plotted to examine the spread of these data. Example distributions for three contrasting species (blonde ray; lesser-spotted dogfish *Scyliorhinus canicula* and angel shark) are shown (Figure 5). Where only two or three distributions are evident, more than one expert gave the same combination of attribute and confidence score.

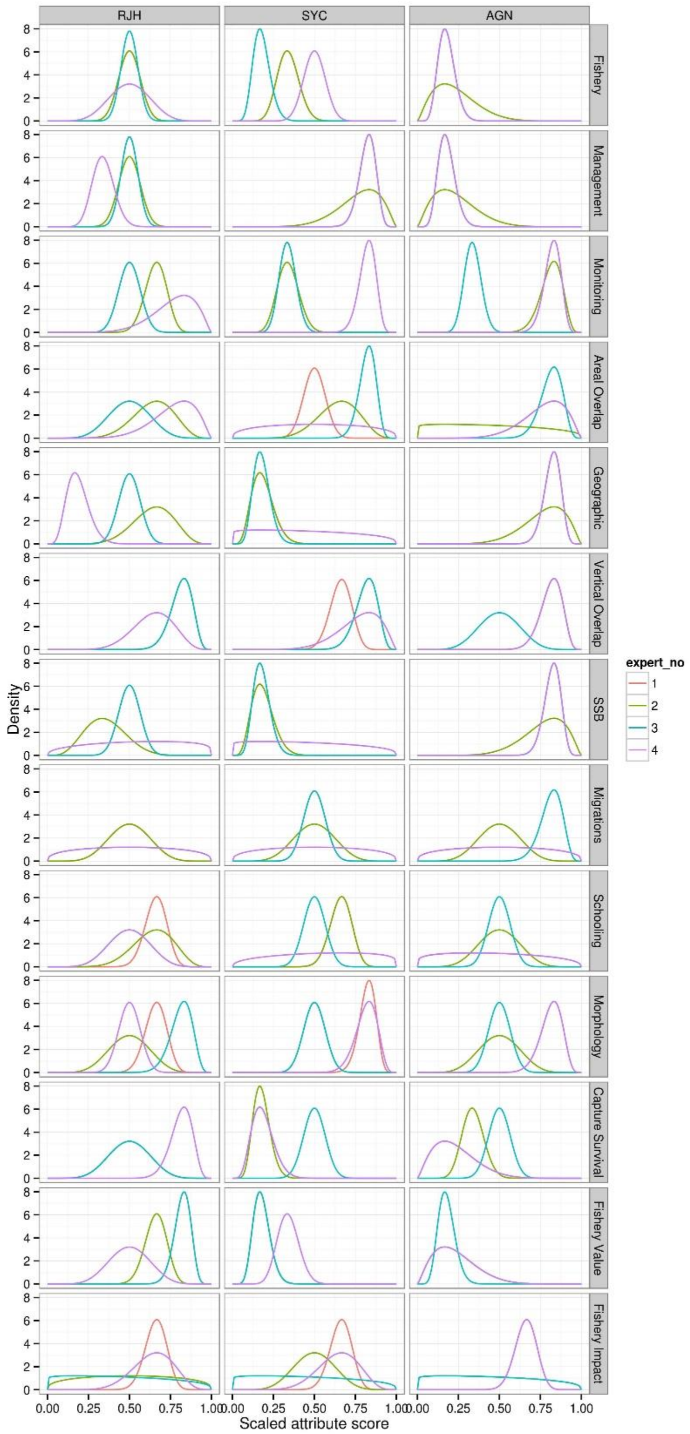

Figure 5: Beta distributions for the attribute susceptibility score for three example species, blonde ray (RJH), lesser-spotted dogfish (SYC) angel shark (AGN), given by experts in relation to otter trawl fisheries.

In some cases the agreement was very high, for example blonde ray 'fishery' attribute, where all experts concluded the same attribute score, but with slightly different levels of confidence, but in other cases, like the 'monitoring' attribute, the experts returned a spread of attribute scores.

Further examination of these data was undertaken by plotting the distributions for the weighted susceptibility scores by species and gear (Figure 6 and Figure 7), to see how these scores differed between experts. Trends in scores could be identified across experts, for example expert four had the lowest confidence in their scores for all species and both fisheries assessed, while expert one was usually more confident in their scores. Trends in confidence also varied within individual experts depending upon the species – for example expert one was more confident in relation to spurdog (DGS, in Figure 6), but very unsure of the susceptibility scores for Norwegian skate (JAD) in both fisheries.

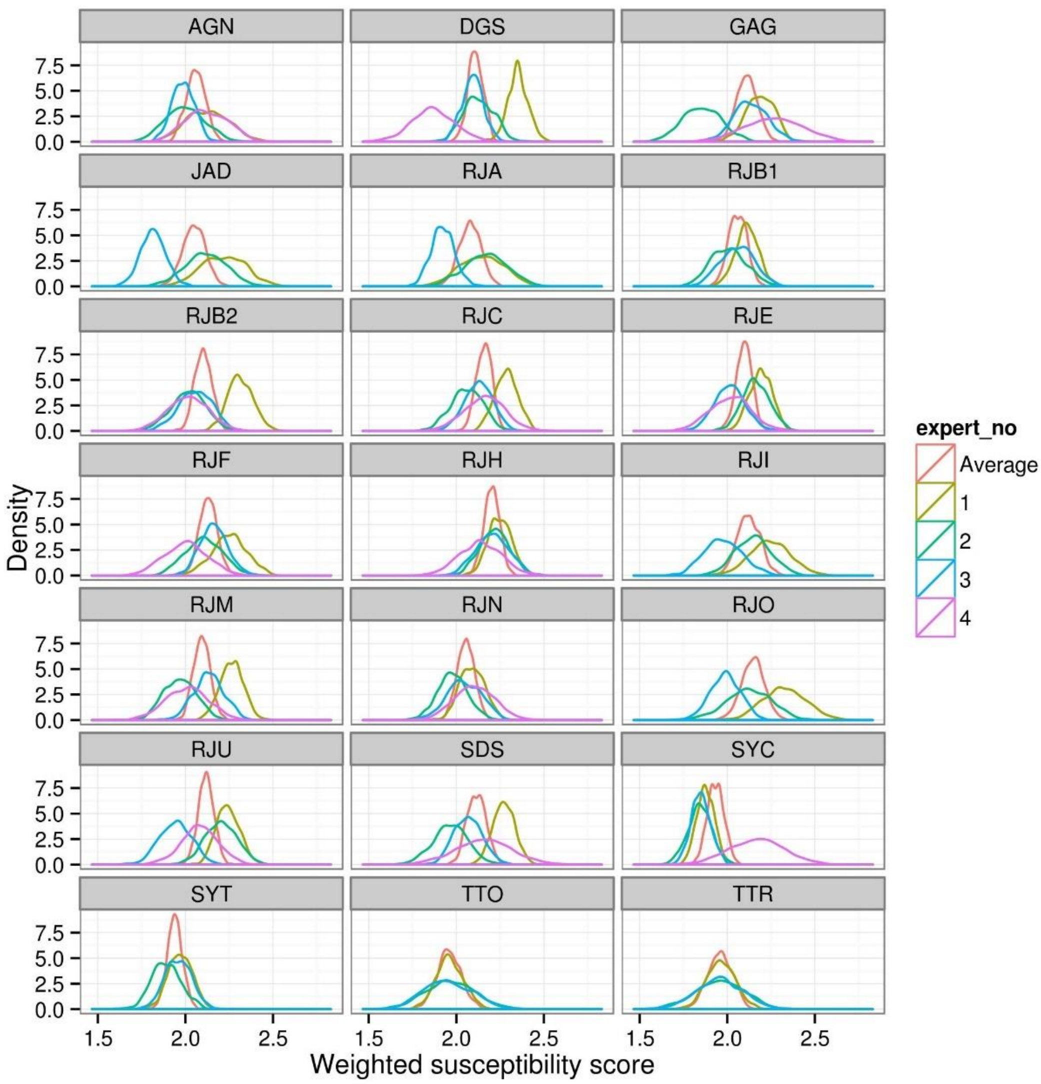

Figure 6: Distribution of the weighted susceptibility scores by expert and averaged across experts for elasmobranchs taken in otter trawl fisheries. See Table 13 for species codes.

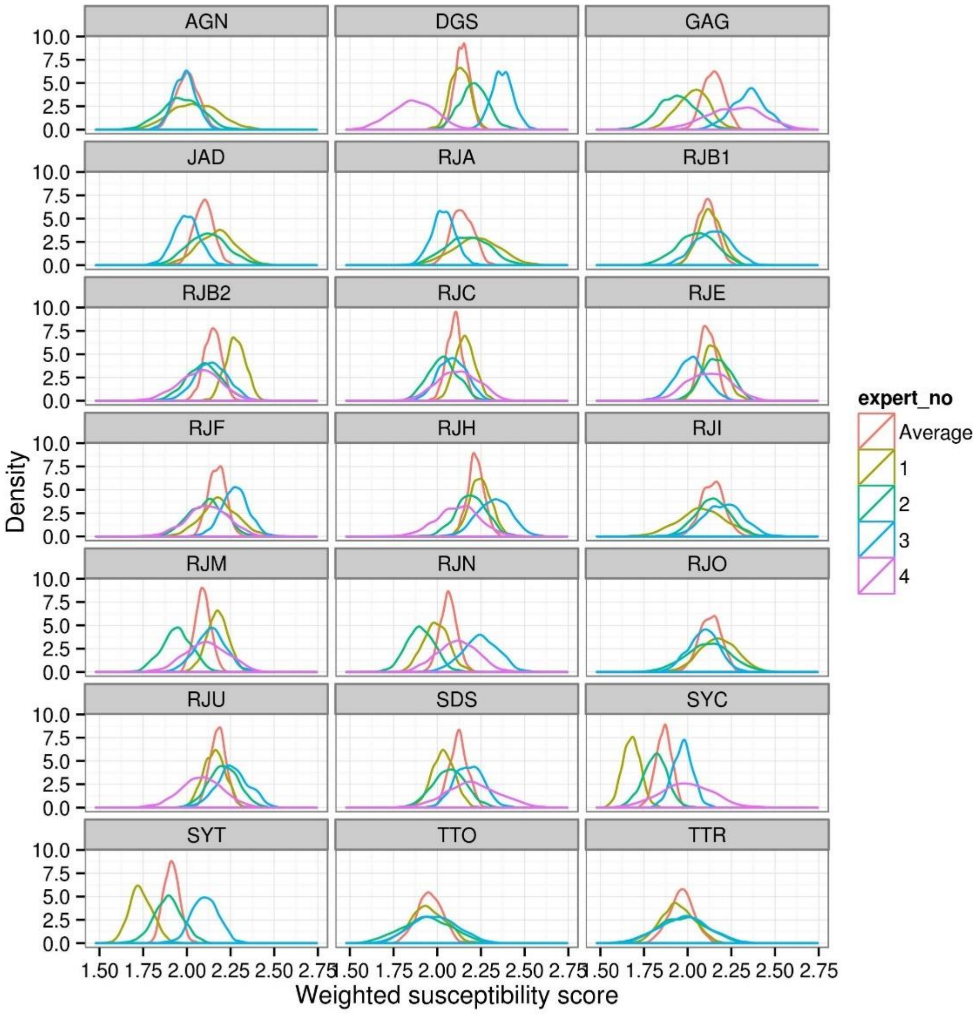

Figure 7: Distribution of the weighted susceptibility scores by expert and averaged across experts for elasmobranchs taken in gillnet fisheries. See Table 13 for species codes.

There was a striking resemblance between both fisheries assessed, with the average probability distributions (Figure 8) mirroring each other. While some species were considered more susceptible in gillnet fisheries than otter trawl fisheries, and vice versa, the actual probability curves were almost identical in most cases. Fifteen of the 21 species assessed were considered more vulnerable in gillnet fisheries than otter trawl, however in five of these cases, the vulnerability score was just 0.01 more. Five species were considered to be more vulnerable in otter trawl fisheries, including three species of shark (lesser- and greater-spotted dogfish *Scyliorhinus stellaris* and angel shark). The largest variation in vulnerability score received between the two fisheries was lesser-spotted dogfish (SYC), which was the most biologically productive species in this assessment and ranked least vulnerable overall in both fisheries. The most commercially important skate for the UK, in terms of quantities landed, is thornback ray *Raja clavata* (RJC), which was considered to be more vulnerable in otter trawls than gillnets.

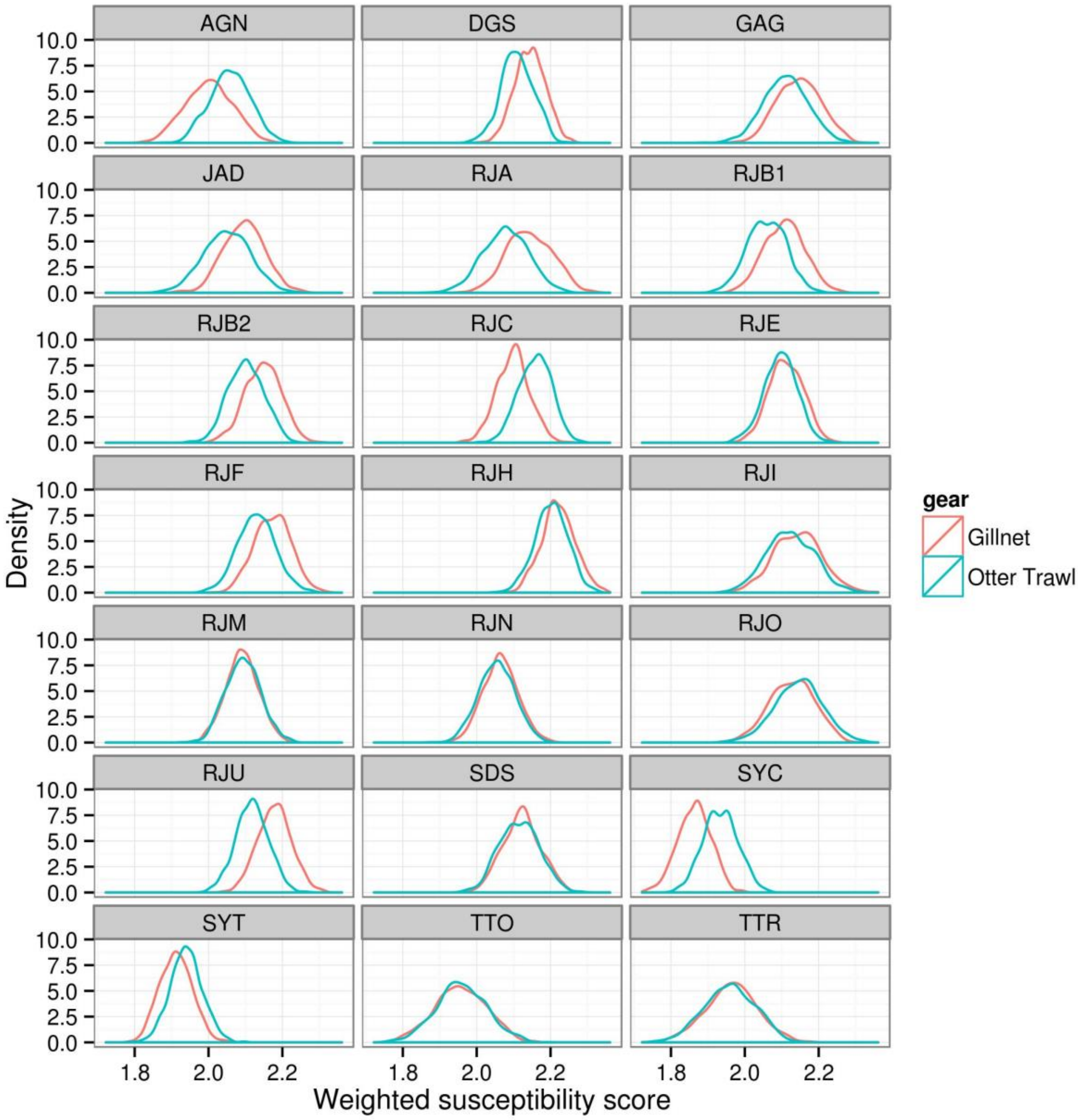

Figure 8: Distribution of the averaged weighted susceptibility scores in otter trawl and gillnet fisheries. See Table 13 for species codes.

3.5 Discussion

3.5.1 PSA rankings

This assessment was conducted primarily to assess the relative vulnerabilities of the various skates, caught in mixed fisheries, currently managed under a common TAC in the Celtic Seas ecoregion. The inclusion of other elasmobranchs allowed comparison to be drawn between six different families of elasmobranch, thereby allowing slightly different life histories to be included. A previous study (McCully *et al*., 2012) investigated whether data-rich teleosts with quantitative stock assessments could be used to 'ground-truth' the elasmobranch results. Those results, however, were inconclusive, with elasmobranchs clustered together on the

PSA plot as a result of their life history being so different to most teleosts. It was for this reason that the PSA developed here was conducted on just elasmobranchs with the attributes selected to better reflect their biological differences and so tease them apart.

That tope ranked as the most vulnerable of the case study species in the gillnet fishery and second in otter trawl fisheries is initially surprising, as neither of these fishing methods would be used to target this species in practice. Although tope represent a small proportion of the bycatch in both fisheries, their large size and extremely low reproductive potential (1.33) rendered them most vulnerable in this assessment. Tope fishing around the UK has been largely recreational, with occasional bycatch being landed; numbers caught were never great enough to sustain a target fishery. Given their low numbers and productivity, conservative precautionary management was put in place in UK waters, in the form of the 'Tope (Prohibition of Fishing) Order 2008', with measures including the prohibition of fishing for tope (other than by rod and line), a 45 kg per day limit on tope that are brought onboard, and the prohibition of persons to land tope in England that are beheaded or captured from rod and line. Angel shark (ranking most vulnerable in the otter trawl- and second in the gillnet assessment) is a very rare species, extirpated from much of its former range (Rogers and Ellis, 2000). This species would only very occasionally be caught accidentally, yet its low reproductive potential (1.29) and large uncertainties surrounding much of its biology lead to a high overall vulnerability. Angel shark is subject to the highest form of protection in UK waters through their listing on the Wildlife and Countryside Act, and also being on the list of Prohibited species, where it is prohibited for EU vessels to fish for, to retain on board, to tranship and to land angel shark in EU waters (since Council Regulation (EC) No 43/2009 and Union Regulation (EU) No 23/2010).

Following tope and angel shark (both under strict management) in the rankings, were four species that are all either currently listed as prohibited species or have a minor bycatch allowance to allow for stock rebuilding (spurdog, the common skate-complex and white skate). Similarly, the remaining species included to ground-truth the commercial skate, at the other end of the spectrum also generated intuitive rankings. Lesser-spotted dogfish ranked the least vulnerable in both fisheries. This species is widespread throughout the British Isles, is one of the most fecund elasmobranchs and has been increasing in fishery dependent surveys since at least the early 1990s. Its sister species, the greater-spotted dogfish, was ranked next least vulnerable. Other species including electric ray *Torpedo nobiliana*, starry smooth-hound *Mustelus asterias*, and marbled electric ray *Torpedo marmorata*, ranked between sixth and sixteenth. Again, these rankings all appear credible given their respective body sizes, largely non-commercial nature in this area, fecundity and distributions. With earlier attempts to 'ground truth' this PSA in mind, it is reassuring that the stocks considered the most depleted and for which restrictive management has been introduced recently, were ranked as most vulnerable.

The relative rankings for the commercial skate species landed within the generic TAC also appear plausible, with the larger bodied and less widespread species (e.g. blonde ray, long-nosed skate, Norwegian skate, shagreen ray *Leucoraja fullonica*, and sandy ray *Leucoraja circularis*), for which no appropriate monitoring is available, being ranked higher (eighth to thirteenth), than others within the assemblage. The most commercially important ray, thornback ray was ranked sixteenth and seventeenth most vulnerable in the otter trawl and gillnet fisheries respectively. This species, although relatively large-bodied, is more productive than its compatriots, is widespread across the area, and unlike many of the other skate and rays has appropriate monitoring through fisheries independent surveys, from which trends in stock status can be estimated. Credibly, the smaller bodied, widely distributed species also with informative stock trends (i.e. spotted ray *Raja montagui*, and cuckoo ray *Leucoraja naevus*) ranked lowest in the skate and ray assemblage.

Of course, as a data-limited method, there are several drawbacks within it, including a limit on the many aspects of a complex system of biology and fisher behaviour that can be considered. Devine *et al*. (2012) exposed several weaknesses in the PSA technique and scoring of attributes, stating that the "*susceptibility criteria need to be re-evaluated"*. ICES (2012b) stated that "*these weaknesses need to be further explored within the context of stocks for which ICES provides advice"*. However, some of the 'weaknesses' identified by Devine *et al*. (2012) were mitigated against in our PSA application, by better tailoring the attributes to the species being assessed. For example, the 'management strategy' attribute (included by Patrick *et al*. 2009) was modified to address three distinct attributes (commercial nature of the stock, management in place and stock monitoring) to better reflect the state of the population rather than just whether management strategies are in place. Fisher behaviour was considered in this assessment under the introduced 'Fishery' attribute, detailing whether stocks were non-commercial, important bycatch or highly commercial and targeted - an essential attribute to be accounted for with respect to fisher discard and retention patterns.

A limitation in the current application is the disregard of selectivity varying by life history stage. There is clearly varying size selection of species in different gears. Currently species are assessed irrespective of actual body size (rather their maximum attainable size) or life history stage, when, for example, a juvenile ray would be more susceptible to capture in otter or beam trawl than large meshed gillnets, whilst larger skates may not be caught in beam trawls (Silva *et al*., 2012). This could be incorporated in future assessments, with species broken down into juveniles and adults as a minimum and assessed separately. This could further assist where necessary in subsequently identifying effective management interventions.

This study chose to assess the otter trawl and gillnet fisheries, as these are the main gears catching skates and rays in this area. Although the susceptibility attributes were given due consideration and modification, they did not discriminate well from one another (Figure 3, Figure 4, Figure 8; Table 13) as they are both similar in terms of their area of operation, depth and target species. Additionally, given that most of these species also occur on broadly similar habitat types and sediments, and have comparable morphology affecting capture, the main differences in susceptibility will be derived from differences in spatial distribution in this particular case study.

Although modifying attributes to fit a specific species assemblage or on a fishery by fishery basis will not allow direct comparison between PSAs, it will make each assessment more robust and appropriate for defining vulnerability of a stock relative to its compatriots. Given that species *x* is assessed relative to species *y*, in each assessment, it would be unwise to compare across different applications anyway, given the different experts involved and potential variations in PSA methodologies (e.g. Field *et al*., 2010).

One of the attributes introduced here was ‘genetic distinctness’, as some authors have suggested that taxa with low rates of speciation may be more prone to extinction (Heard and Mooers, 2000). Whilst expert opinion did not rank this attribute highly in terms of fisheries management, it may be ranked more highly if such PSA approaches are used to address biodiversity considerations, especially since monotypic families may also be deemed of greater importance in the maintenance of phylogenetic diversity (Vézquez and Gittleman, 1998). Conversely, breeding cycle was weighted of high importance to elasmobranchs by the experts, given that the fecundity attribute does not provide any indication of the frequency of breeding, which can range from multiple broods per year to triennial cycles.

3.5.2 Modelling confidence of expert responses

In this study the distributions of the trait scores are assumed to be independent. However, it is known that some life history traits are correlated (for example, species with high growth rates tend to also have a low age at maturity) and the same may well be true of ratings within an individual expert's assessment. The analyses would, therefore, be improved if these correlations could be quantified and incorporated into the analysis. Doing so might well lead to an increase in the 'true' uncertainty of the scores but estimating the covariance structure of the scores would require a much larger sample size. It may therefore be better to view the differences between individual assessments as a measure of variation between the experts we used rather than an estimate of the variation in a larger population of experts or an indicator of some 'true' value of uncertainty.

The scoring of biological attributes can be agreed by a small group of experts with appropriate knowledge of life history and biology. Given the use of published material and research study results, there is no need for a large group of people to all repeat the same exercise, although here the productivity sheets were made available to all experts for review. However, it was felt more important to collate the range of views on susceptibility attributes, where a lack of published data means the scores are much more open to interpretation and scores can be more subjective. The issues surrounding the use of expert opinion in PSAs leading to subjectivity and a lack of reproducibility were highlighted by Hordyk and Carruthers (2018) however by consolidating knowledge from four experts and also formally considering uncertainty this application mitigates such biases where possible.

The range in the distribution of susceptibility scores and associated confidences highlights the importance of collating a range of independently derived expert opinions, to allow these subjectivities to be 'smoothed' out. If there is a range of expertise within chosen experts, some could have their scores down-weighted, and other up-weighted. This procedure was not investigated in this study, as it was initially believed that the confidence score would allow for the spread of knowledge and quantified in this way. However Aspinall (2010) highlights the potential bias that can accompany expert confidence, where those with lowest confidence rated better in their (known-answer) seed questions (to calibrate proficiency), and thus were given more 'weight' overall in the analysis, than those who had greater confidence.

The spread of the geographic location of experts appears to have a bearing on these assessments. Although all experts were selected based on their knowledge of these species and/or fishing area, all experts will have some preconceived ideas based on their 'local' fisheries in which they have the greatest understanding. In this case, one of the experts did not score all species and several requests for expert opinion were rejected due to their lack of confidence in the area. The geographic influence needs to be given due consideration – especially as there is a wide range of species which are only targeted commercially in certain areas, and also as there can be different national and regional fishery regulations in coastal waters.

The most geographically remote expert (number four), had the lowest scoring confidence for every species and in both fisheries assessed. This indicates that possibly they were either unsure of the overall method or had limited understanding of the fisheries operating in that region. Conversely, expert one (more local to the Celtic Sea) had a much greater confidence in the species' susceptibility but less so for the less frequently encountered species.

The similar average probability distributions (Figure 8) indicated that the experts are more confident in their knowledge of a particular species than with the more subtle technical differences in catchability of demersal gears. The incorporation of more varied fisheries (e.g. longline and beam trawl) into the assessment would provide a useful comparison, with a wider spread in susceptibility scores expected. Furthermore, in order to evaluate the potential effectiveness of management methods, all fishing pressures exerted on these species need to be given due consideration.

The overall vulnerability rankings for species based on the susceptibilities perceived by the four independent assessors, showed them to be relatively consistent (Appendix II). There were only minor differences in placing, and the three assessors who scored all 21 species included the 10 highest ranking species (from the final assessment) in their individual top 14 places. The greatest difference in ranks between individual assessors was seven positions, and this was found for Norwegian skate in the gillnet assessment and starry smooth-hound in the otter trawl assessment. In the case of Norwegian skate, two of the three assessors who scored this species gave the same ranking (seventh), with the third assessor placing its vulnerability seven ranks lower (fourteenth). Given that this large-bodied deep-water species was placed ninth and tenth most vulnerable overall in the gillnet and otter trawl assessments respectively, this seven rank discrepancy highlights the value of canvassing a range of expert opinions, whereby either a consensus score can be achieved following discussions, or discrepancies smoothed by averaging over scores.

3.5.3 Application of PSA in management of skate fisheries

These assessments have allowed the highest priority species within the skate complex to be identified, using probability modelling to convey expert opinion. The main challenge from this point is utilising such assessments to inform management advice. While the approach helps highlight where knowledge gathering and management action should be prioritised, PSAs do not have the ability to calculate the maximum sustainable yield (MSY) or an appropriate quota. That said, in the USA, information generated during the PSA process has been shown to be useful in setting Acceptable Biological Catch (ABC), for data-limited species where reliable catch data are available. A tiered approach is used to define precautionary catch limits that account for scientific uncertainty in the estimate of a stock's Over Fishing Limit (OFL), so less productive species are managed with more precaution and a larger buffer between the ABC and OFL (Berkson *et al*., 2011; Carmichael and Fenske, 2011). Further potential utilization of PSAs in assessment, could be in the incorporation of information (such as productivity estimates) in the development of priors, including intrinsic growth rate (McAllister *et al*., 2001; Martell and Froese, 2013), depletion (Cope *et al*., 2015) and fishing mortality rates (Osio *et al*., 2015).

For some potential methods to derive catch limits, which may employ PSA information (e.g. setting an ABC using depletion-based stock reduction analysis), a time-series of catch is required. The skate species examined in this PSA have only a very short time series of reliable catch data, as up until 2008, skates and rays were reported in generic categories, rather than to species level. Since 2008 (for the North Sea), and 2009 (for the Celtic Seas), the European Commission has obliged member states to provide species-specific landings data for the major skate and ray species, in order to improve understanding of skate stocks in the area (CEC, 2008, 2009). Compliance with this legislation has varied from 0–100% by region and member state and, whilst improving, there are some data quality and species identification issues (ICES, 2013b) [10].

With the reform of the Common Fisheries Policy (CFP) already underway in EU waters, which promotes an increase in regionalised management (CEC, 2013), and in order to meet initiatives to eliminate discards and protect sensitive species, such as elasmobranchs, there may conceivably be a move away from such high reliance on quota systems. More regionalised management could employ technical measures and effort restrictions, and PSA

[10] Whilst there have been further improvements in the reporting of skate landings to species since this study was undertaken, there are still some issues regarding the data quality (ICES, 2016).

approaches may help promote discussions with stakeholders on how best to introduce appropriate and pragmatic management measures.

In this assessment, five of the top ranked species already have some form of restrictive management in place (prohibited status or zero TAC), based on perceived stock depletion. Therefore, managers can focus consideration on the next high-ranking species to ensure that monitoring is fit for purpose, and where necessary make proactive precautionary management decisions. In the case of the skate and ray assemblage caught in mixed fisheries and managed under the generic skate TAC at present, future advice may need to be better geared towards managing the most vulnerable member of the complex (e.g. blonde ray). Managers must also remain vigilant to those species in the more intermediate rankings, whilst collecting more data for future assessments.

Future management scenarios could be tested using PSAs to re-score under alternative management options (e.g. maximum landing length, minimum landing size, spatial or temporal restrictions, reduced soak time or tow duration, depth restrictions) and help identify the effects these interactions will have across all species rather than just the main target commercial or important bycatch species (e.g. Watling *et al*., 2011). Indeed, a critique of PSAs by Hordyk and Carruthers (2018) suggests the use of operating models for exploited stocks in the place of PSAs, which can be incorporated into a management strategy evaluation (MSE) framework to assess alternative management options. However, this PSA approach is applicable to both target and non-target species alike in single- and multi-species data-deficient situations (e.g. artisanal fisheries in developing countries, e.g. Judi *et al*., 2019).

It may also be emphasised that, whilst PSA approaches may be useful in the initial evaluation of certain management options, it is important that fishers from relevant sectors of the fleet can be involved in such processes. Engaging stakeholders to identify the merits of those measures they deem most pragmatic would enhance the iterative process of applying PSA approaches within regional management.

3.6 Conclusions

This PSA approach, which incorporates the modelling of uncertainty in expert responses, has identified the relative vulnerability risk for elasmobranch species within two fisheries in the Celtic Sea. Currently this PSA cannot be used to identify appropriate catch levels. However, by expanding management to the most vulnerable commercial species (e.g. blonde ray) within a complex such as this, which is currently managed under a generic quota system, this approach can provide a starting point for investigating alternative management options. The innovative incorporation of expert opinion, probability scoring, and uncertainty modelling adds independent robustness to any rankings and subsequent advice or management priorities and measures resulting from this assessment.

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Chapter 4

Lengths at maturity and conversion factors for Rajidae of the British Isles

4 Lengths at maturity and conversion factors for Rajidae of the British Isles

This Chapter was based on the following publication:

McCully, S. R., Scott, F. and Ellis, J. R. (2012). Lengths at maturity and conversion factors for skates (Rajidae) around the British Isles, with an analysis of data in the literature. *ICES Journal of Marine Science*, **69**(10), 1812–1822.

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The candidate was responsible for data collection and collation, analysis, interpretation, leading the authorship and production of Table 14–Table 17. Dr. F. Scott was responsible for the R-code modelling the maturity ogives and subsequent production of Figure 9–Figure 11. This work was undertaken under the supervision of Dr. J. Ellis who was also involved in data collection, reviewing literature and collated material for Table 19 and Table 20, and commented on and contributed to the interpretation and text. Whilst the underlying data included data collected by the candidate and Dr. J. Ellis during fishery-independent trawl surveys and other field studies, further maturity data were collected by other Cefas sea-going staff on annual trawl surveys.

Minor updates to the introduction and discussion have been made to incorporate relevant recent literature.

4.1 Abstract

Biological data on skates (Rajidae) from around the British Isles were collected between 1992 and 2010. The relationship between total length and weight for nine species (*Amblyraja radiata*, *Dipturus batis*[11], *Leucoraja fullonica*, *L. naevus*, *Raja brachyura*, *R. clavata*, *R. microocellata*, *R. montagui*, and *R. undulata*) are provided by sex and ICES ecoregion (when significantly different). Conversion factors for disc width to total length are provided. The lengths at first maturity and of

[11] The original paper states *Dipturus batis*-complex, as at the time of publishing, the taxonomic separation of common blue skate *D. batis* and flapper skate *D. intermedius* (see Griffiths *et al*., 2010; Iglésias *et al*., 2010) had not been internationally accepted. These two species have now been accepted as two distinct species (Last *et al*., 2016a, b). Re-examination of original data indicates that only one specimen would have likely referred to *D. intermedius* and as a small (80 cm L_T) immature individual would not impact the analyses (given that mature *D. batis* were all >100 cm L_T), maturity ogives or interpretation, thus for the purposes of clarity the text has been amended to refer only to the smaller-bodied *D. batis*.

the largest immature skates are reported by sex, and the lengths at 50% maturity are estimated. Spatial differences in the length at maturity of *R. clavata* (females only) and *L. naevus* (both sexes) were observed. The lengths at maturity are discussed in relation to the results of earlier studies, and methodological differences are considered to have influenced reputed decreases in the length at maturity. A more standardized approach to collecting and reporting maturity information is required if potential spatial differences and temporal changes are to be investigated.

4.2 Introduction

Skates (Rajidae) are vulnerable to overfishing because they are long-lived, slow-growing, late to mature, have protracted breeding cycles, and produce few young, which, coupled with their generally large size, morphology, and aggregating nature renders them susceptible to capture in many fisheries (Ellis *et al*., 2010). Although the issue is now widely recognized by fisheries managers, it should also be noted that concerns over skate stocks in northern Europe were expressed early in the 20th century (Section 1.2). For example, Howell (1921), and Steven (1932) both held concerns over localized and regional declines in skate stocks, and about the accompanying lack of both biological and ecological knowledge of the various species. By the 1970s, Holden (1977) questioned whether elasmobranch fisheries were sustainable, given the species' biology and susceptibility to capture, and suggested that skate stocks had not been replacing themselves for 15–20 years. This insightful work provided the catalyst for increased biological studies on elasmobranchs, with the importance of key life history parameters recognized as essential for fisheries assessment and management, and ultimately the sustainable exploitation of elasmobranchs.

Species that attain and mature at a large body size are typically less resilient to overexploitation (Holden, 1977; Brander, 1981), because such characteristics are often associated with slow rates of population growth. Hence, the depletion of some larger species of skate may allow smaller sympatric species, which may grow faster and mature earlier, to increase in relative terms. Dulvy and Reynolds (2002) reported that extirpated skates tended to have a large body size, as seen in the extirpation of the common skate complex *Dipturus batis* from the Irish Sea (Brander, 1981; *Dipturus batis* is now recognized as two species, *Dipturus batis* and *Dipturus intermedius*; Last *et al*., 2016a, b), and white skate *Rostroraja alba* from the English Channel (Rogers and Ellis, 2000; Ellis *et al*., 2010). The barndoor skate *Dipturus laevis* was also thought to have declined dramatically in the Northwest Atlantic (Casey and Myers, 1998), although more recent investigations into the life history parameters of this species have shown that it may be more resilient to overfishing than previously thought (e.g. Gedamke *et al*., 2009).

Improved biological knowledge, including length–weight and total length–disc width conversion factors, are needed to support the assessment and management of skate fisheries. Such conversion factors are required to estimate the weights of fish measured in market sampling and on board commercial fishing vessels. Additionally, weight-at-size conversion factors can be used in recreational fisheries, if anglers are to return fish alive (Kohler *et al*., 1995). Similarly, total length-disc width conversions are needed when a specimen has a damaged tail or is sampled in a state already processed for market. The ICES Working Group on Elasmobranch Fishes (WGEF) collated a variety of conversion factors for elasmobranchs (ICES, 2007), although data for some factors were limited for several of the skates in UK waters.

Length at maturity is another key biological parameter given that it is fundamental to the application of demographic and other assessment models and can be used in helping to inform on size restrictions (Caddy and Mahon, 1995). Examination of the spatial differences in life history parameters can also be used to better ascertain potential stock boundaries (Pawson and Ellis, 2005), and knowledge of temporal changes in such parameters can help inform on potential fishing impacts.

Overexploitation of fish can lead to density-dependent changes in certain life history characteristics (Fahy, 1989a), and in some elasmobranch populations, density-dependent regulation can be achieved by compensatory increases in fecundity and growth rate, and a reduced length at maturity (Ellis and Keable, 2008). Reduced female size at maturity, potentially in response to fishing pressure and decreases in population size, have been discussed for several elasmobranchs, including spurdog *Squalus acanthias* (Sosebee, 2005; Bubley *et al*., 2013) and yellownose skate *Dipturus chilensis* (Paesch and Oddone, 2008). However, because of the sporadic nature of many biological studies of elasmobranchs, and that sources of biological material and methods are often different between disparate studies, relating observed temporal differences in life history parameters to the effects of overexploitation can be problematic (Ellis and Keable, 2008).

The present study provides information on the length–weight and total length-disc width relationships for the main skate species found over the continental shelf of the British Isles, including starry ray *Amblyraja radiata*, common (blue) skate *Dipturus batis*, shagreen ray *Leucoraja fullonica*, cuckoo ray *Leucoraja naevus*, blonde ray *Raja brachyura*, thornback ray *Raja clavata*, small-eyed ray *Raja microocellata*, spotted ray *Raja montagui*, and undulate ray *Raja undulata*. The observed lengths at first maturity and largest immature fish found are given, and the length at 50% maturity (L_{50}) is estimated.

4.3 Materials and methods

4.3.1 Field studies and biological sampling

Skates were caught during groundfish surveys in the North Sea, English Channel, Irish Sea, Bristol Channel, and Celtic Sea during bottom trawl surveys by RVs “Corystes”, “Cirolana”, and “Cefas Endeavour”. Data collection started on some surveys in 1992, but >80% of the records were collected after 2000. Additional data on the length at maturity of *R. clavata* were collected from commercial fishing vessels during a UK Fishery Science Partnership (FSP) project collecting information on this species in the southern North Sea (Ellis *et al*., 2008). Additional data on total length–disc width and length at maturity were also available for *R. undulata*, *R. brachyura*, and *Dipturus batis* from ongoing field studies on skate discard survival. The surveys used in the study are summarised in Table 14.

Total length (L_T) was measured to the centimetre below from the tip of the snout to the end of the tail (unless damaged), and total weight (W) was recorded to the nearest 1 g (juveniles) or 5 g (larger individuals). At the start of the period, data on disc width (D) were also collected, but in recent years this information has only been collected for larger fish and/or less abundant species.

Table 14: Summary of groundfish surveys (GFS), beam trawl surveys (BTS), Fisheries Science Partnership (FSP), and other programmes used for the collection of biological information. Sampling gears used on RV surveys were Portuguese high headline trawl (PHHT), Grand Ouverture Verticale Trawl (GOV), and 4 m beam trawl (BT).

Survey	Years	Quarter	Sampling gear	ICES Ecoregion	ICES Division	*n*
Data collection framework survey	2005–2010	1	PHHT	Celtic Sea	Irish and Celtic Seas (7.a, f–h, j)	1 578
North Sea GFS	2002–2004	1	GOV	North Sea and eastern Channel	North Sea (4.b, c)	214
Western Channel BTS	2006–2010	1	BT	Celtic Sea	Western English Channel (7.e)	560
West Coast GFS	1995 and 2004	1	PHHT	Celtic Sea	Western English Channel and Celtic Sea (7.e, f – h, j)	161
Gear trials	2008	1 and 3	GOV	North Sea and eastern Channel	North Sea (4.b, c)	396
Thames thornback ray FSP	2007–2008	1–4	Commercial longline, otter trawl, and gillnet	North Sea and eastern Channel	Southern North Sea (4.c)	2 887
Skate and ray discard survival project	2010	2	Gillnet	North Sea and eastern Channel	English Channel (7.d–e)	118
Eastern English Channel BTS	2002–2009	3	BT	North Sea and eastern Channel	Southern North Sea and eastern English Channel (4.c and 7.d)	1 257
North Sea GFS	2004–2009	3	GOV	North Sea and eastern Channel	North Sea (4.a–c)	1 047
Bristol Channel and Irish Sea BTS	1992–2009	3	BT	Celtic Sea	Irish Sea, Bristol Channel and parts of the Celtic Sea (7.a, f, g)	7 497
Irish Sea and Celtic Sea GFS	2003–2009	4	GOV	Celtic Sea	Irish Sea, Bristol Channel and Celtic Sea and western English Channel (7.a, e, f–h)	2 466

4.3.2 Maturity scale

All skate were classified as immature (A), maturing (B), mature (C), or active (D), according to the maturity key given in Table 15. Only fish at stages C and D are considered to be mature (i.e. capable of reproducing). Male maturity was usually assigned based on clasper state. For specimens where the external observation of clasper state was felt to be inconclusive (e.g. for fish that may or may not have reached stage C), those fish were dissected and the internal reproductive organs examined to gauge maturity more accurately.

Female maturity was assigned based on examination of internal reproductive organs. In recent years, however, females of either <40 cm (*R. montagui* and *L. naevus*), <45 cm (*R. clavata*), <55 cm (*L. fullonica*, *R. brachyura*, *R. microocellata* and *R. undulata*) are not usually examined if alive, and are assumed to be immature (based on preliminary observations of the data shown here). Different states of egg-case formation were not recorded, because very few active females were observed during surveys, either because the surveys were conducted outside the main spawning season and/or away from the spawning grounds.

Quantitative data to validate the maturity stage information (e.g. clasper length for males, oviducal gland width for females) were not collected owing to time constraints. Similarly, although estimates of fecundity are needed for many species of skate species, there is currently no resource to allow for the collection, preservation, and subsequent laboratory examination of skate ovaries, and this was not undertaken.

Table 15: Maturity scale used for skates in the present study.

Maturity stage	Males	Females
A (Immature)	Claspers undeveloped, shorter than extreme tips of posterior margin of pelvic fin. Testes small and thread-shaped	Ovaries small, gelatinous, or granulated, but with no differentiated follicles visible. Oviducts small and thread-shaped, width of oviducal gland not much greater than the width of oviduct
B (Maturing)	Claspers longer than posterior margin of pelvic fin, their tips more structured, but claspers soft and flexible and cartilaginous elements not hardened. Testes enlarged, sperm ducts beginning to meander	Ovaries enlarged and with more transparent walls. Follicles differentiated in various small sizes (ca. <5 mm). Oviducts small and thread-shaped, width of oviducal gland greater than width of the oviduct, not hardened
C (Mature)	Claspers longer than posterior margin of pelvic fin, cartilaginous elements hardened and claspers stiff. Testes enlarged, sperm ducts meandering and filled with sperm	Ovaries large with enlarged follicles (ca.>5 mm), with some very large, yolk-filled follicles (ca. 10 mm) also present. Uteri enlarged and wide, oviducal gland fully formed and hard
D (Active)	Clasper reddish and swollen, sperm present in clasper groove, or flowing if pressure exerted on cloaca	Egg capsules beginning to form in oviducal gland, partially visible in uteri, or egg capsules fully formed and hardened and in oviducts/uteri, or egg case being exuded from cloaca

4.3.3 Data analysis

Maturity data and length–weight data were collated by species, sex, and ICES ecoregion. Generalized linear models (GLMs) were used to investigate the length–weight relationship and the proportion of fish mature at length. To maximise wider utility of these data, sex was always disaggregated in these analyses, and potential spatial differences (by ecoregion) were examined for the three most abundant species (*L. naevus*, *R. clavata* and *R. montagui*).

Initially, a sex-disaggregated length–weight relationship ($W = aL_T^b$) was fitted for each species, combining both ecoregions. The function was log-transformed so that a linear regression could be fitted. To investigate whether this relationship varied between ecoregion, a GLM was used to fit the length–weight relationship with ecoregion as an interaction. The errors were assumed to be Gaussian. The fitted parameters (a and b), sample size, length range, and significant differences between parameter values were returned for each ecoregion (Table 16). The sample sizes included in Table 16 cannot be used to examine the sex ratio, because some studies (e.g. tagging programmes) only provided maturity information for male skate.

The linear relationship between total length and disc width was calculated according to the equation $D = aL_T + b$ (Table 17). Data were not separated into ecoregions, because data for most species (except *A. radiata*) were for the Celtic Seas ecoregion.

The relationship between the proportion of fish mature at length was also investigated (Table 18) through a GLM model where the error distribution and link function were binomial (Crawley, 2007). The numbers of mature and immature fish at length were used to model the proportion of mature fish using a logistic model as a function of length, x, as $p = e^{a+bx} / 1+e^{a+bx}$. Therefore, $\ln(p/q) = a + bx$, where p is the proportion of mature fish, and $q = 1 – p$, the proportion of immature fish. This gives a linear predictor, $a + bx$, for the logit transformation of p, $\ln(p/q)$. A linear regression was not used because data analyses were weighted by sample size, there may have been non-constant binomial variance, and linear regression can predict values outside the range 0–1.

Additionally, analyses were examined in relation to overdispersion where, in general, the residual scaled deviance should be roughly equal to the residual degrees of freedom. Data were separated by sex and then into mature and immature skate, with one dataset for combined ecoregions, and a second dataset that kept them separate to identify any potential significant differences in the length at maturity between ecoregions.

Initially, a GLM was used to fit the number mature and immature against length, with ecoregion not considered as a factor. A function was written to fit the GLM on subsets of the data, i.e. by species and sex. The function returned the parameters of the fit and their significance, the Akaike information criterion (AIC), the log-likelihood, the number of observations, and the estimated L_{50}. Subsequently, another GLM function was written that used ecoregion as an interaction with length. This was analysed for three species (*R. clavata*, *R. montagui* and *L. naevus*), because there were sufficient data for both ecoregions. Where the interaction was significant, two *b* parameters were produced (one for each ecoregion), though the intercept parameter (*a*) was not fitted separately for each ecoregion, thus yielding different relationships between the proportion mature at length for each ecoregion. The significance level was set at 0.05. Model fitting was carried out in the statistical environment R v 2-13.2 (R Development Core Team, 2011).

Table 16: Length-weight relationships and length at maturity for skates (Rajidae) around the British Isles by sex and ecoregion, where significantly different (marked in bold).

Species	Ecoregion	Number of fish used in length–weight calculation (length range)		Total weight and total length ($W = aL_T^b$)						Number of fish used for maturity studies (number of mature fish)		First maturity		Largest immature		50% mature (L_{50})	
		Male	Female	Male			Female			Male	Female	Male	Female	Male	Female	Male	Female
				a	*b*	r^2	*a*	*b*	r^2								
A. radiata	North Sea	426 (8–49)	446 (8–49)	0.0084	3.004	0.96	0.0114	2.915	0.95	426 (181)	446 (148)	30	32	44	46	36.2	38.4
D. batis	Combined	30 (20–118)	32 (19–135)	0.0041	3.123	0.95	0.0026	3.222	0.99	30 (2)	32 (2)	115	125	98	97	–	–
L. fullonica	Combined	17 (21–96)	17 (24–70)	0.0014	3.317	0.99	0.0036	3.075	0.98	17 (2)	17 (0)	75	–	82	–	–	–
L. naevus	Combined	943 (11–72)	948 (10–69)	0.0041	3.105	0.99	0.0035	3.147	0.99	944 (128)	948 (75)	48	45	64	65	56.4	59.4
	Celtic Seas	834 (11–72)	819 (10–69)	0.0041	3.105	0.99	0.0036	3.147	0.99	835 (100)	819 (61)	49	51	64	65	**57.3**	**59.8**
	North Sea	109 (17–63)	129 (15–62)	0.0032	3.161	0.99	0.0030	3.183	0.97	109 (28)	129 (14)	48	45	57	58	**50.8**	**53.6**
R. brachyura	Combined	357 (13–100)	386 (12–102)	0.0027	3.256	0.99	0.0026	3.271	0.99	359 (25)	387 (17)	55	60	91	93	78.0	83.4
R. clavata	Combined	3123 (10–94)	3073 (10–98)	0.0046	3.082	0.99	0.0037	3.148	0.99	5917 (1119)	3229 (206)	47	47	88	90	66.6	76.6
	Celtic Seas	2427 (10–89)	2368 (10–98)	**0.0042**	**3.106**	0.99	**0.0036**	**3.162**	0.99	2427 (276)	2368 (107)	56	47	76	90	–	**78.2**
	North Sea	696 (13–94)	705 (13–92)	**0.0061**	**3.003**	0.99	**0.0046**	**3.090**	0.99	3490 (843)	861 (99)	47	57	88	82	–	**73.7**
R. microocellata	Combined	703 (13–80)	733 (12–85)	0.0032	3.195	0.99	0.0028	3.248	0.99	705 (65)	733 (26)	66	73	74	83	68.9	77.9
R. montagui	Combined	1900 (10–67)	1775 (10–76)	0.0042	3.100	0.99	0.0031	3.194	0.99	1911 (310)	1775 (84)	40	49	66	70	50.9	62.5
R. undulata	Combined	58 (22–89)	33 (17–60)	0.0035	3.162	0.99	0.0043	3.112	0.99	85 (28)	34 (1)	80	79	88	83	82.3	NA

Table 17: Relationship between total length (L_T) and disc width (D) for nine species of skate, where $D = aL_T + b$ and sample size (n), length range examined and correlation coefficient.

Species	*n*	Length range (cm)	*a*	*b*	r^2
Raja brachyura	401	12–105	0.7125	–0.3288	0.99
Raja clavata	1962	11–96	0.6572	0.9095	0.98
Raja microocellata	477	12– 83	0.7193	–0.9008	0.99
Raja montagui	1141	10–69	0.6605	0.2841	0.99
Leucoraja naevus	596	10–67	0.5840	–1.0050	0.99
Amblyraja radiata	486	8–49	0.6592	0.0873	0.94
Raja undulata	331	35–100	0.5648	4.7130	0.97
Leucoraja fullonica	25	24–96	0.6239	–2.6440	0.99
Dipturus batis	37	44–130	0.6771	3.2687	0.97

Table 18: GLM results from fitting the proportion of fish mature to length, with ecoregion as an interaction, and significance level set at 0.05.

Species	Sex	*a*	*b* (combined)	*b* (CS)	*b* (NS)	*p*-value	L_{50} (combined)	L_{50} (CS)	L_{50} (NS)	AIC[12]	*n*[13]
R. clavata	M	-23.096	0.349	NA[14]	NA	0.17	66.161	NA	NA	234.390	5 917
	F	-19.161		0.245	0.260	0.00		78.17	73.67	168.095	3 229
R. montagui	M	-16.976	0.334	NA	NA	0.39	50.818	NA	NA	182.142	1 911
	F	-14.202	0.227	NA	NA	0.91	62.490	NA	NA	125.636	1 775
L. naevus	M	-18.668		0.326	0.367	0.00		57.34	50.81	90.823	944
	F	-22.193		0.371	0.414	0.00		59.80	53.62	84.707	948

4.4 Results

4.4.1 Length-weight and total length-disc width relationships

Total weight and total length were strongly correlated for all species (r^2 ≥0.95). The constants required for the conversion of these measurements are listed in Table 16. The results of the GLM, using ecoregion as a factor, indicated that there was a significant difference in weight at a given length for *R. clavata*, with fish from the Celtic Seas ecoregion significantly heavier than in the North Sea ecoregion. No significant spatial differences in the length–weight relationship were observed in *R. montagui* and *L. naevus*.

Total length and disc width were also highly correlated for all species (r^2 ≥0.94), and the constants required for the conversion of these measurements are given in Table 17.

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[12] AIC, Akaike information criterion, which measures the goodness of fit.
[13] *n*, number of observations.
[14] NA, the interaction was not significant and results were combined across ecoregions (CS, Celtic Seas ecoregion; NS, North Sea ecoregion).

4.4.2 Length at maturity

Maturity data were analysed for the seven most commonly caught species of skate (Table 16 and Table 18, Figure 9–Figure 11), and descriptive notes are provided for the less frequent species.

4.4.2.1 *Raja brachyura*

This was one of the larger skate species routinely sampled during surveys and, although fish of up to 102 cm total length were caught, data were limited for large fish. The lengths at first maturity were 60 cm and 55 cm for females and males, and L_{50} was reached at 83.4 cm and 78.0 cm, respectively (Figure 9a, b). The largest immature *R. brachyura* were 91 cm (male) and 93 cm (female; Table 16). There were insufficient data to investigate spatial differences in length at maturity.

4.4.2.2 *Raja clavata*

Across all areas, female *R. clavata* first matured at 47 cm and L_{50} was estimated at 76.6 cm (Table 16, Figure 9c). First maturity in males was also 47 cm, although L_{50} was attained at a smaller length (66.6 cm; Table 16, Figure 9d). The largest immature female and male measured 90 and 88 cm, respectively. The GLM indicated a significant difference in the length at maturity of females between the two ecoregions, and L_{50} for females from the North Sea was 4.5 cm less than in the Celtic Seas (Figure 9c; Table 18).

4.4.2.3 *Raja microocellata*

The smallest mature male and female observed were 66 cm and 73 cm, respectively, with L_{50} at 68.9 cm (males) and 77.9 cm (females; Figure 9e, f). The largest immature fish were 74 cm (male) and 83 cm (female; Table 16). Only a few *R. microocellata* were caught in the North Sea ecoregion, and sample sizes of mature fish (especially females) were small.

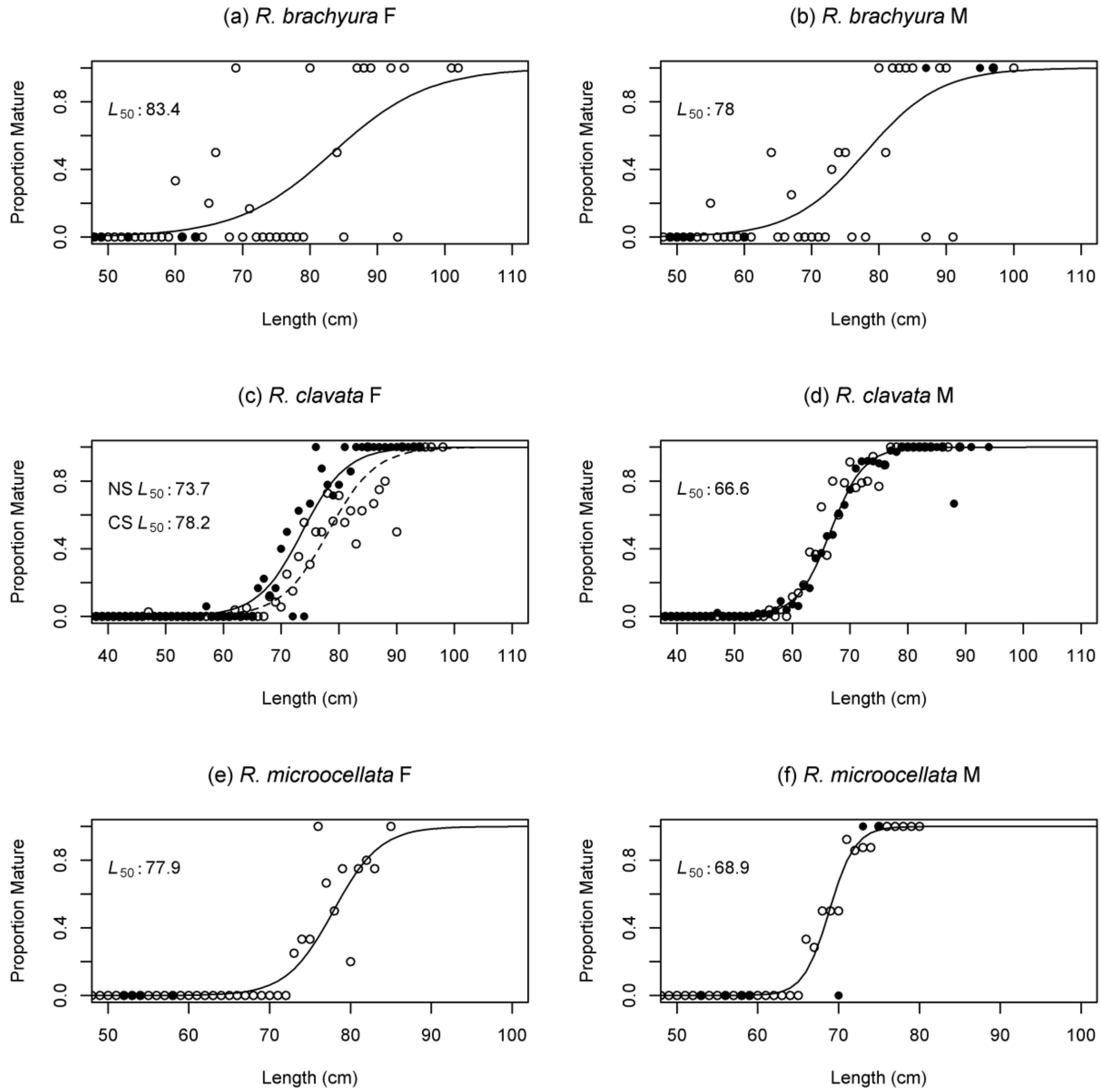

Figure 9: Proportion of mature (a) female and (b) male *R. brachyura*, (c) female and (d) male *R. clavata*, and (e) female and (f) male *R. microocellata*. Data from Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line) in all plots apart from female *R. clavata*, (c), where ecoregion was found to be a significant factor [Celtic Sea (CS, open symbols dashed line) and North Sea (NS, filled symbols and solid line)].

4.4.2.4 *Raja montagui*

The smallest mature female and male observed were 49 cm and 40 cm, respectively, and, whereas L_{50} for females was 62.5 cm, that for males was reached at just 50.9 cm (Figure 10a, b). The largest immature males and females were 66 cm and 70 cm, respectively (Table 16). There were no significant differences in length at maturity between ecoregions. The outlying points for male maturity (Figure 10b) resulted from low sample sizes at certain lengths.

4.4.2.5 *Leucoraja naevus*

Males and females first matured at 48 cm and 45 cm, respectively, and L_{50} was at 56.4 cm and 59.4 cm (Table 16; Figure 10c, d). The largest immature males and females were 64 cm and 65 cm. The GLM highlighted a significant difference in the L_{50} for both males and females between ecoregions, that for female and male *L. naevus* in the North Sea being 6.2–6.5 cm less than in the Celtic Seas (Table 18).

4.4.2.6 *Amblyraja radiata*

This was the smallest species sampled in the study and was only captured in the North Sea. The largest fish were 49 cm long, and length at first maturity was 30 cm and 32 cm for males and females (Table 16). The L_{50} values for females and males were 38.4 cm and 36.2 cm respectively (Figure 10 e, f). The largest immature fish were 46 cm (female) and 44 cm (male).

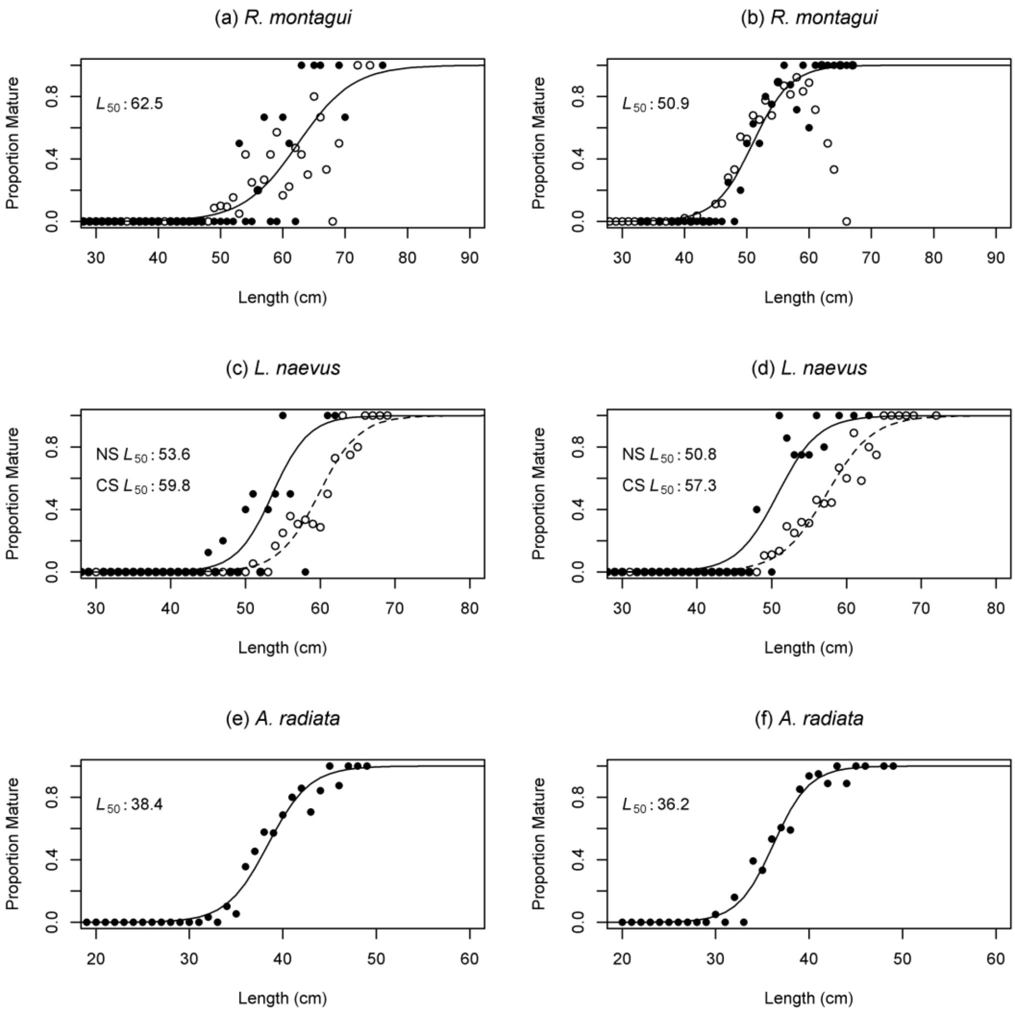

Figure 10: Proportion of mature (a) female and (b) male *R. montagui*, (c) female and (d) male *L. naevus*, and (e) female and (f) male *A. radiata*. Data from Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line) in all plots apart from female and male *L. naevus*, (c and d), where ecoregion was found to be a significant factor [Celtic Sea (CS, open symbols dashed line) and North Sea (NS, filled symbols and solid line)].

4.4.2.7 *Raja undulata*

Data were limited for this species, so the data provided here should be viewed as preliminary. The lengths at first maturity were broadly similar in both sexes (80 cm and 79 cm in males and females, respectively). L_{50} was estimated at 82.3 cm for males (Figure 11b), but no reliable estimate of this parameter was possible for females, given the small overall sample size (*n* = 34) and very low numbers of mature fish (*n* = 1).

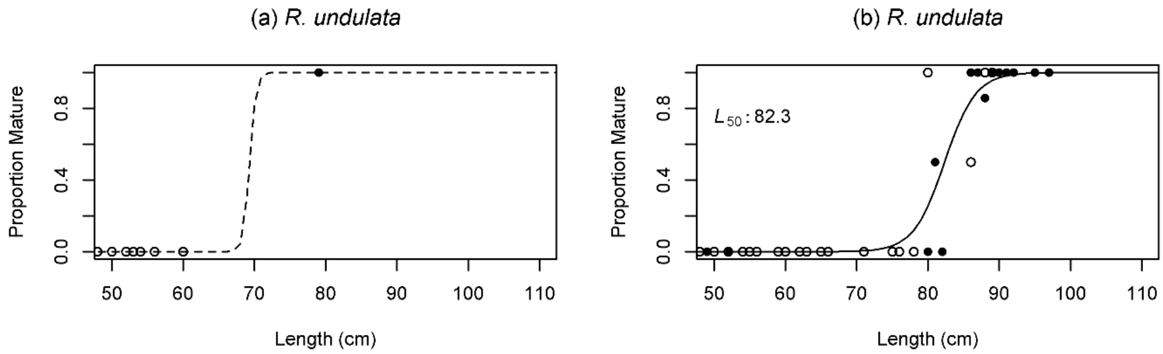

Figure 11: Proportion of mature (a) female and (b) male *R. undulata*. Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line). For female *R. undulata*, (a), the GLM algorithm did not converge due to lack of data and no reliable estimate of L_{50} can be given. The dashed line in (a) is therefore only a guide.

4.4.2.8 *Other species*

Limited data were available for *L. fullonica*[15] and the *Dipturus batis* and, given uncertainty in their general biology, only qualitative information on their maturity status can be provided. There were 34 records of *L. fullonica* in the database (all but three of which were from the Celtic Seas), 17 males (21–96 cm) and 17 females (24–70 cm). All 17 females were immature, but two of the larger males (75 and 96 cm) were mature (stage C); the largest immature male was 82 cm.

There were 62 records of *D. batis* and all but one of these were from the Celtic Sea; samples are most likely to refer to *D. batis* (Griffiths *et al*., 2010). There were 32 females (length range 19–135 cm), of which only two were mature (a fish 125 cm long at maturity stage C, and a 135 cm fish at stage D), and all the others (up to 97 cm) were immature. Of the 30 males (length range 20–118 cm), the two largest (115–118 cm) were mature (stage C), and the others (up to 98 cm) were immature.

[15] Following publication of this study, more detailed studies on the biology of *Leucoraja fullonica* and the related *L. circularis* have been undertaken (see Chapter 6).

4.5 Discussion

4.5.1 Length-weight and total length-disc width conversion factors

The present study provides the most recent length–weight data for the species around the British Isles, with large sample sizes, and these data are also provided by sex and ecoregion (if significant differences were observed). In earlier studies, Holden (1977) provided length–weight relationships for *R. brachyura*, *R. clavata*, *R. montagui*, and *L. naevus*, and Ryland and Ajayi (1984) gave length–weight relationships for *R. clavata*, *R. microocellata* and *R. montagui*. Length–weight relationships for all these species and for *R. undulata* were reported for the Bay of Biscay, English Channel, and Celtic Sea by Dorel (1986), but data were combined for both sexes and, with the exception of *R. undulata*, the sample sizes were smaller than in this study. More recently, Coull *et al*. (1989) provided length–weight information for *R. clavata*, *R. montagui* and *L. naevus* in Scottish waters, but data were limited by sample size and/or size range of fish examined. Other conversion factors (including gutted-weight and wing-weight relationships) were given by Bedford *et al*. (1986) for *R. clavata*, *R. brachyura*, *R. montagui*, *A. radiata* and *L. naevus*.[16]

The length–weight relationships for the three most abundant species (*R. clavata*, *R. montagui* and *L. naevus*) were compared by ecoregion, but significant spatial differences in this relationship were only observed for *R. clavata*. This may be due to the smaller sample size (especially for larger fish) in the North Sea. However, most data for the North Sea ecoregion were collected during July and August, which is after the main spawning season (Holden, 1975), whereas data for the Celtic Seas ecoregion mostly originated from surveys in either March or from September to December, and so temporal factors may also have influenced this result.

There were close relationships between total length and disc width for all species. Although there are no national or EC minimum or maximum size limits for rajids, local bylaws in some English and Welsh inshore waters provide a minimum landing size (MLS) of 40–45 cm disc width for skates, and these are enforced by Inshore Fisheries Conservation Authorities (IFCAs). On average, a disc width of 40–45 cm equated to estimated total lengths of 61.0–68.7 cm, although there were species-specific differences in the total length-disc width relationship. For example, *L. naevus* has a narrower disc than the other species studied, and a disc width of 40–45 cm would correspond to an estimated length of 70.2–78.8 cm, beyond the maximum length of the species. In contrast, *R. brachyura* at 40–45 cm disc width are ~56.6–63.6 cm long. Hence, if generic minimum landing sizes

[16] Since this study was published, Silva *et al.* (2013) have provided length-weight relationships for a wide range of fish species around the British Isles, including elasmobranchs.

were implemented for all species of skate, this would result in increased discarding of some species and may not benefit larger skate species, such as *D. batis*, *R. undulata* or *R. brachyura*, which mature at a much larger size. In fact, the only species that attained L_{50} by 41 cm disc width (lengths estimated from Table 17 and compared with L_{50} as given in Table 16) were *A. radiata*, *L. naevus* and male *R. montagui*.

4.5.2 Length at maturity

The lengths at maturity for selected species of skate around the UK, as reported in previous studies, are summarized in Table 19 and Table 20. The L_{50} values for most of the species examined tended only to show subtle differences from values reported in earlier studies.

Only preliminary maturity estimates are available for *R. brachyura*, as few mature fish were caught. *R. brachyura* and *R. montagui* can be confused, and so it is possible that some of the smaller mature fish may have resulted from occasional misidentifications. The current analysis however gives increased weight to larger sample sizes at each length, and so potential outlying data points will not unduly influence the ogive and estimates of L_{50} if based on low sample sizes. Although the current estimates compared well with previously reported values (Gallagher *et al*., 2005), dedicated studies to better elucidate the length at maturity for this species are required, particularly in the case of large females.

More data were available for *Raja clavata* (Table 19 and references therein).The present study indicated that there were significant spatial differences in the L_{50} value of female *R. clavata*, although this was not apparent in males. The results of the present study for *R. clavata*, which is based on a large sample size and included samples from several areas of abundance (e.g. southern North Sea, Bristol Channel, and Irish Sea), were broadly comparable with several earlier studies (Walker, 1999; Gallagher *et al*., 2005), but are less than reported by Steven (1934), as discussed further below.

There has been no previous estimate of the L_{50} value for *R. microocellata*, although Ryland and Ajayi (1984) reported the length at first maturity which, for both sexes, was lower than recorded here. The L_{50} for male *R. montagui* was lower than reported previously in the North Sea (Walker, 1999) and Irish Sea (Gallagher *et al*., 2005), but for females, the present estimate was higher than reported previously in the Irish Sea (Gallagher *et al*., 2005) and on par with that reported by Walker (1999). The occasional outlying data points for male *R. montagui* from the Celtic Sea were based on very small sample sizes for certain 1 cm length groups. The ogive, however, was more influenced by the larger sample sizes (and 100% maturity) at intervening length groups and from North Sea samples.

The L_{50} values for male and female *L. naevus* were larger in the Celtic Seas than in the North Sea, which may be due to there being different stocks in the two areas, although other investigations to confirm this (e.g. tagging and genetic studies) are required. The L_{50} values in the North Sea were 50.8 cm and 53.6 cm for males and females, respectively, slightly less than reported by Walker (1999). Within the Celtic Seas ecoregion, the L_{50} for males and females were 57.3 and 59.8 cm, respectively, and these values compare well with the estimate of Du Buit (1976) for the species in the Celtic Sea, but are marginally higher than reported by Gallagher *et al*. (2005) for the Irish Sea.
Male and female *A. radiata* appeared to have a marginally smaller L_{50} than reported by Walker (1999), but length at maturity in the North Sea is very different from that reported for the same species in the Northwest Atlantic (Templeman, 1987).

Data for *R. undulata* were limited, because few mature fish have been sampled in existing surveys (Ellis *et al*., 2012), although estimates are available for populations around the Portuguese coast (Moura *et al*., 2007). More recently, Stéphan *et al*. (2014) examined lengths at maturity for *R. undulata* from the Normano-Breton Gulf (i.e. the same stock unit as fish examined in this paper) and estimated L_{50} as 78 and 83 cm L_T for males and females, respectively. The estimate for males was 4 cm smaller than that estimated in this paper, however the sample size (n = 889) and number of mature fish examined by Stéphan *et al*. (2014) was much greater, and their values are, therefore, deemed more appropriate estimates for this species.

It is uncertain whether the differences in length at maturity noted for various species above are attributable to bona fide spatial or temporal differences, or simply reflect subtle differences in sampling (e.g. maturity staging, sample sizes).

It has been suggested that there may have been temporal changes, with a reduced L_{50} in recent times. Steven (1934) suggested that L_{50} was at 66–70 cm and 51–55 cm disc width for females and males, respectively. Converted to length, these maturity estimates are far higher than observed in all subsequent studies (Fitzmaurice, 1974; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Walker, 1999), leading to some authors questioning whether the length at maturity has decreased over time as a result of fishing pressure (Nottage and Perkins, 1983; Whittamore and McCarthy, 2005). However, Fries *et al*. (1895) stated that a male *R. clavata* “rather more than 60 cm long” had fully developed claspers, and a fish of that length would likely be smaller than the estimated length of about 75 cm suggested by Steven (1934), who reported that males matured at 51–55 cm disc width.

The L_{50} for *R. clavata* in the present study was larger than reported by Whittamore and McCarthy (2005), probably the result of methodological differences. In recent years, several studies have combined fish at stage B (maturing[17]) with later maturity stages when estimating the proportion mature (e.g. Whittamore and McCarthy, 2005; Krstulović Šifner *et al*., 2009). Similarly, Demirhan *et al*. (2005) included females with ovaries containing "eggs greater than 0.5 mm" as mature. That these studies reported lower lengths at maturity than earlier works and the present study would appear to be due to the inclusion of fish that were not fully mature in the proportion mature at length. A more robust and standardized approach to reporting the proportion mature is therefore required.

Some earlier studies on skate maturity have failed to identify clearly either the maturity scale used, or to what the length at maturity referred (i.e. first or 50% maturity). The adoption of standardized maturity scales, as proposed by Workshop on Sexual Maturity Staging of Elasmobranchs (WKMSEL; ICES, 2010, 2013) could rectify such disparities in future. For comparative purposes, all reports of skate maturity should consistently state the lengths at first and 50% maturity (L_{50}) and the largest immature fish. Although most recent studies on skate maturity have provided information on total sample size, this often includes a disproportionate number of juveniles, and there is rarely an indication of either the number of mature fish observed or the number of fish examined over the length range spanning first to 100% maturity. If published life history information and maturity data are to be used in stock assessments, it is important that reliable estimates (based on appropriate sample sizes, size ranges and methods) can be identified.

It is often suggested that overexploitation can lead to a reduction in the length at maturity and maximum size. Although it is difficult to ascertain whether the length at maturity for *R. clavata* has decreased, given that the only 'evidence' is inferred from the work of Steven (1934), there is little indication of a reduced maximum length. The maximum size of *R. clavata* reported here (98 cm) is similar to that reported by Nottage and Perkins (1983; 102 cm), Ryland and Ajayi (1984; 99 cm), and Fahy (1989b; 101 cm). Although one early published study reported a maximum length of ca. 120 cm (Holt, 1910; length estimated from disc width), a discard observer trip in 2009 reported one *R.*

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[17] Given that there has been confusion in the wider scientific community between 'maturing' and 'mature', the term 'developing' may be a better term that 'maturing' (i.e. Stage B).

clavata of 130 cm (Lockley, 2009). Hence, there is little indication of a decrease in the maximum length of *R. clavata* over recent time.

4.5.3 Future studies in the UK

Ongoing fishery-independent surveys, including several that are internationally coordinated, catch relatively high numbers of some of the more widespread skate species (as shown in Table 16), although data are limited for species with patchy distributions. Additionally, catch rates for larger fish and species can also be low in such surveys. In recent years, some skate species, including *R. brachyura*, *R. clavata* and *R. undulata*, have been subject of more dedicated field surveys. For example, in 2007 and 2008, a UK FSP project used inshore fishing vessels with commercial gears to tag and release *R. clavata* in the Greater Thames Estuary (Ellis *et al*., 2008). That study provided additional length and maturity information for 2 887 fish. Similarly, recent studies on the survival of discarded skates in southwest England have provided more information on larger *R. brachyura* and *R. undulata*. These results highlight the potential value of dedicated surveys for some of the larger-bodied elasmobranchs that can be locally abundant in certain areas, because sample sizes of mature fish in commercial gears and on commercial fishing grounds can be greater than taken in existing groundfish surveys. Dedicated surveys may also be required if detailed information is to be collected for offshore species (e.g. *L. circularis* and *L. fullonica*; Chapter 6), given the low catch rates of these species in existing groundfish surveys, and limited information on their movements and life history.

Table 19: Summary table for earlier estimates of length at maturity for *Raja clavata*, with values estimated from the disc width (using the relationship in Table 17) denoted by an asterisk.

Area (and ICES Division)	Sex	*n*	Length range examined (cm)	Length (cm) at First maturity	Length (cm) at 50% maturity (L_{50})	Source
Plymouth (7.e)	M	–	17–92 *	74.7 *	76.2–82.3 *	Steven (1934)
	F	–	17–129 *	97.5 *	99–105 *	
Irish waters (7.b)	M	386	39–83	56–64 *		Fitzmaurice (1974)
	F	331	40–88	67.8–75.5 *		
Solway Firth (7.a)	M	271	18.4–101.6	61.8	-	Nottage and Perkins (1983)
	F		32.5–102.1	62.4	-	
Bristol Channel (7.f)	M	1 019	13–99.0	60.5	-	Ryland and Ajayi (1984)
	F	1 124		59.5	-	
English Channel (7.d-e)	M	960	10–101	80	-	Dorel (1986)
	F			95	-	
Bay of Biscay (8)	M	23	11–98	80	-	Dorel (1986)
	F			95	-	
North Sea (4)	M	41	ca. 20–90		67.9	Walker (1999)
	F	52			77.1	
Irish waters (7.a)	M	165	ca. 17–92	61	65.7	Gallagher *et al.* (2005)
	F	90		58	71.8	
North Wales (7.a)	M	54	ca. 27–78	-	58.8	Whittamore and McCarthy (2005)
	F	135	ca. 18–92	-	70.5	
Portugal (9)	M	906	12.5–105.0	59.0	67.6	Serra-Pereira *et al.* (2011)
	F	861	13.8–96.5	69.9	78.4	
Tunisia	M	-	-	[75]		Capapé (1976)
	F	-	-	[85]		
Southern France	M	120	15.4–76.2	62.5		Capapé *et al.* (2007)*
	F	137	15.4–103.6	80.8		
Sicily	M	712	-	57–59		Cannizzaro *et al.* (1995)
	F	763	-	77–79		
Adriatic Sea	M	-	-	[55–60]		Jardas (1973)
	F	-	-	[80–85]		
	M	183	12–95	47	59.3	Krstulović Šifner *et al.* (2009)
	F	181		47.5	61.2	
Black Sea	M	52	34–95	-	64.0	Demirhan *et al.* (2005)
	F			-	66.7	
	M	99	14.3–92.0	68.0	71.8	Saglam and Ak (2011)
	F	131	15.6–93.0	72.0	74.6	

Table 20: Summary table for the length (cm) at maturity for UK skate species from earlier studies.

Species	Area	Sex	*n*	Length range examined	Length (cm) at		Source
					First maturity	50% maturity (L_{50})	
A. radiata	North Sea	M	273	ca. 10–54	-	39.6	Walker (1999)
		F	323		-	39.5	
L. naevus	North Sea	M	51	ca. 30–65	-	55.0	Walker (1999)
		F	62		-	55.0	
	Celtic Sea	Combined	276	13–70	60	-	Dorel (1986)
		F	-	-	-	[59]	Du Buit (1976)
	Irish waters	M	353	ca. 13–70	52	56.9	Gallagher *et al.* (2005)
		F	191		49	56.2	
R. brachyura	English Channel	Combined	100	17–105	100	-	Dorel (1986)
	Irish waters	M	123	ca. 15–103	75	81.9	Gallagher *et al.* (2005)
		F	61		81	83.6	
R. microocellata	Bristol Channel	M	1218	14–90.6	58.0	-	Ryland and Ajayi (1984)
		F	1374		57.5	-	
	English Channel	Combined	97	15–87	70	-	Dorel (1986)
R. montagui	Irish waters	M	274	ca. 17–67	48	53.7	Gallagher *et al.* (2005)
		F	175		52	57.4	
	North Sea	M	87	ca. 25–70	-	56.7	Walker (1999)
		F	80		-	62.2	
	English Channel	Combined	81	ca. 12–70	60 (Male) 65 (Female)	-	Dorel (1986)
	Bristol Channel	M	986	12–72.9	56.2	-	Ryland and Ajayi (1984)
		F	1019		57.3	-	

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Chapter 5

Reproductive biology and life history relationships of data-limited elasmobranchs: starry smooth-hound *Mustelus asterias*

5 Reproductive biology and life history relationships of data-limited elasmobranchs: starry smooth-hound *Mustelus asterias*

This Chapter was based on the following publication:

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The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures 2–11. This work was undertaken under the supervision of Dr. J. Ellis who also produced Figure 1, was involved in data collection, commenting on and contributing to the interpretation and text.

Minor updates to the introduction and discussion have been made to incorporate relevant recent literature.

5.1 Abstract

The reproductive biology and other life history parameters were investigated for *Mustelus asterias* in British waters, caught from both commercial fisheries and research vessel surveys. In total, 504 specimens (238 males, 24–99 cm total length (L_T) and 266 females, 28–124 cm L_T) were examined, with further information collected from 238 uterine pups. The lengths at 50% maturity were estimated as 70.4 and 81.9 cm L_T for males and females, respectively. Ovarian fecundity ranged from one to 28, and uterine fecundity from four to 20. The number, mass and L_T of pups were positively correlated to maternal L_T. Full term pups ranged from 205–329 mm L_T, and the smallest free-living fish caught was 24 cm L_T. Parturition occurred in February in the western English Channel and June–July in the eastern English Channel and southern North Sea, indicating either protracted spawning or asynchronous parturition for the stock as a whole. The reproductive cycle is thought to extend beyond one year. Developmental abnormalities observed included atresia in oocytes, uterine eggs that failed to develop, a partly developed pup and an abnormal male with a single aberrant clasper.

Data relating to conversion factors, oocyte numbers and diameter, and gonado- and hepato-somatic indices are presented, and the seasonality of the reproductive cycle discussed.

5.2 Introduction

Starry smooth-hound *Mustelus asterias* Cloquet, 1819, is a medium bodied triakid shark (attaining ca. 140 cm total length, L_T; Quéro *et al*. 2003), that occurs on the continental shelf of the Northeast Atlantic from the North Sea south to Mauritania), including the Mediterranean (Compagno, 1984) and Black Seas (Eryilmaz *et al*., 2011).

For much of the 20th century, two smooth-hound (*Mustelus*) species were thought to occur in British seas: starry smooth-hound *M. asterias*, and common smooth-hound *M. mustelus* (L., 1758). These two species are morphologically quite similar, and genetic identification is a more reliable method for discriminating between these two species, and recent genetic studies have not found evidence of *M. mustelus* occurring in British waters (Farrell *et al*., 2009). Whilst data are confounded in both fishery-independent trawl surveys and commercial catch data (and so often presented as *Mustelus* spp.), information and data referring to *M. mustelus* from the British Isles likely refers to *M. asterias* (ICES, 2014). The extent to which previously published studies on smooth-hounds may have been compromised by taxonomic problems is unclear.

M. asterias is an aplacentally viviparous species, with *in utero* pups absorbing nutrients from a yolk-sac that is depleted during development (Capapé 1983), possibly with additional nutrition provided through matrotrophy, which could be associated to mucoid histotrophy (Farrell *et al*., 2010a), as seen in *M. antarcticus* (Storrie *et al*., 2009). Various aspects of the reproductive biology of *M. asterias* were reported by Capapé (1983) for specimens from the Mediterranean Sea. *Mustelus* were little studied around the British Isles for many years, with scientific papers providing biological information in this region typically limited to sample sizes of <50 fish (Ford, 1921; Ellis *et al*., 1996; Henderson *et al*., 2003). More recently, Farrell (2009, 2010a, b), examined larger sample sizes of *M. asterias* from the western British Isles. The reproductive biology, including size at maturity, ovarian and uterine fecundities were determined, with a possible two-year reproductive cycle (12-month gestation and possible resting period) being alluded to (Farrell, 2010a). With some important biological parameters remaining uncertain or unknown, additional studies to inform on the reproductive cycle of *M. asterias* are needed, including greater sample sizes (especially for mature females), and from a wider area of the stock range.

The relative abundance of *Mustelus asterias*, seems to have increased in the waters around the British Isles, as evidenced by increasing catch rates in several fishery-independent surveys over the first decade of the 2000s, and increased reported landings by the commercial fleet (ICES, 2014). Whether this represents an increase in overall population size or a northward shift in areas of abundance is currently unclear. Couch (1862) considered *Mustelus* to be common, but not abundant, in the English Channel, where it was caught usually in May and June. That some of the specimens caught at this time in south-west England had retained hooks (of a type presumed to have originated from Iberian fisheries) in their jaws, led Couch (1862) to suggest that this species undertook a seasonal, northwards migration to the British Isles. Similarly, Le Danois (1913) also considered *Mustelus* to migrate into the English Channel from May to October. Whilst seasonally abundant in the English Channel, some of the early ichthyological lists for Essex (Laver, 1898) and Suffolk (Patterson, 1910) did not list *Mustelus*, suggesting this species was not a regular visitor to the southern North Sea at that time.

Traditionally, *M. asterias* was often discarded by the English fleet, but an increased proportion is now retained (Silva and Ellis 2019; ICES, 2014). The increased proportion landed may be attributed to a combination of factors, including larger catches, improved knowledge on processing and greater market demand (which may have increased given restrictive landings of *Squalus acanthias*; ICES, 2014). It should also be noted that the recent increase in overall reported landings will also be associated with improved species reporting. Barbuto *et al*. (2010) reported *S. acanthias* being sold as 'palombo' (*Mustelus* spp.) in Italian markets, but it is unclear as to the extent to which landings of these small sharks may be confounded in European landings statistics (ICES, 2014). The main nations exploiting *M. asterias* are France and England, and the English Channel and southern North Sea are important fishing grounds (ICES, 2014).

Whilst some triakid sharks, including *Mustelus* spp., are often considered relatively productive, relative to other elasmobranch groups (Frisk *et al*., 2001; Conrath and Musick, 2002), the late age at maturity and longevity (6 and 18 years, respectively: Farrell *et al*., 2010b), and reproductive behaviour of this species means that this stock and expanding commercial fishery should be assessed and managed appropriately if overfishing of this species in northern European seas, such as occurred with *S. acanthias*, is to be avoided.

Based on a Productivity Susceptibility Analysis (PSA) of a range of elasmobranchs occurring in British shelf seas (McCully Phillips *et al*., 2015; Chapter 3), *M. asterias* was identified as a species of a high priority for research efforts, as it was ranked as the most vulnerable of the currently unmanaged shark species in the assemblage (preceded by tope *Galeorhinus galeus* (L., 1758), angel shark *Squatina squatina* (L., 1758), and *S. acanthias*, all of which have some form of management). Given this result, the increased commercial importance of this data-limited species, the lack of management on this stock, questions surrounding some biological parameters and good sample availability at the present time, detailed studies on the life history were initiated on the North-eastern area of the stock range.

5.3 Materials and Methods

Samples of *M. asterias* were obtained from two main sources (Table 21). Larger specimens (52–124 cm L_T) comprising mostly of mature fish (66%), were sourced whole from various inshore fishing vessels (mostly using longlines) that would land this species. These vessels operated in the southern North Sea and eastern English Channel (Figure 12). Further samples (24–124 cm L_T), comprising a larger proportion of juvenile specimens (94%), were collected opportunistically from trawl surveys on-board RV Cefas Endeavour in the North Sea, English Channel, Bristol Channel and Irish Sea. Larger fish in good condition were tagged and released during these surveys, and only dead specimens retained for biological study. Samples were collected between November 2011 and March 2015, with 96% of specimens collected after July 2013. All specimens were identified as *M. asterias* based on the relative positions of the pectoral fins and first dorsal fin (Quéro *et al*. 2003). The accuracy of this identification was substantiated for a selection of samples based on genetic studies (Farrell, *unpublished data*).

Specimens were sexed and body length measured on a measuring board. Flexed total length taken in a straight line with the caudal fin depressed (hereafter referred to as L_T), is considered the most reliable metric for the length of sharks (Francis, 2006). Specimens were measured to the cm below, and in utero pups were measured to the mm below. Total mass (M_T) was taken to the g below for free living fish, and 0.1 g below for pups. Information on liver mass (M_L, 0.1g) and reproductive state (see below) were collected and, after viscera were removed, the eviscerated body mass (M_E) was recorded.

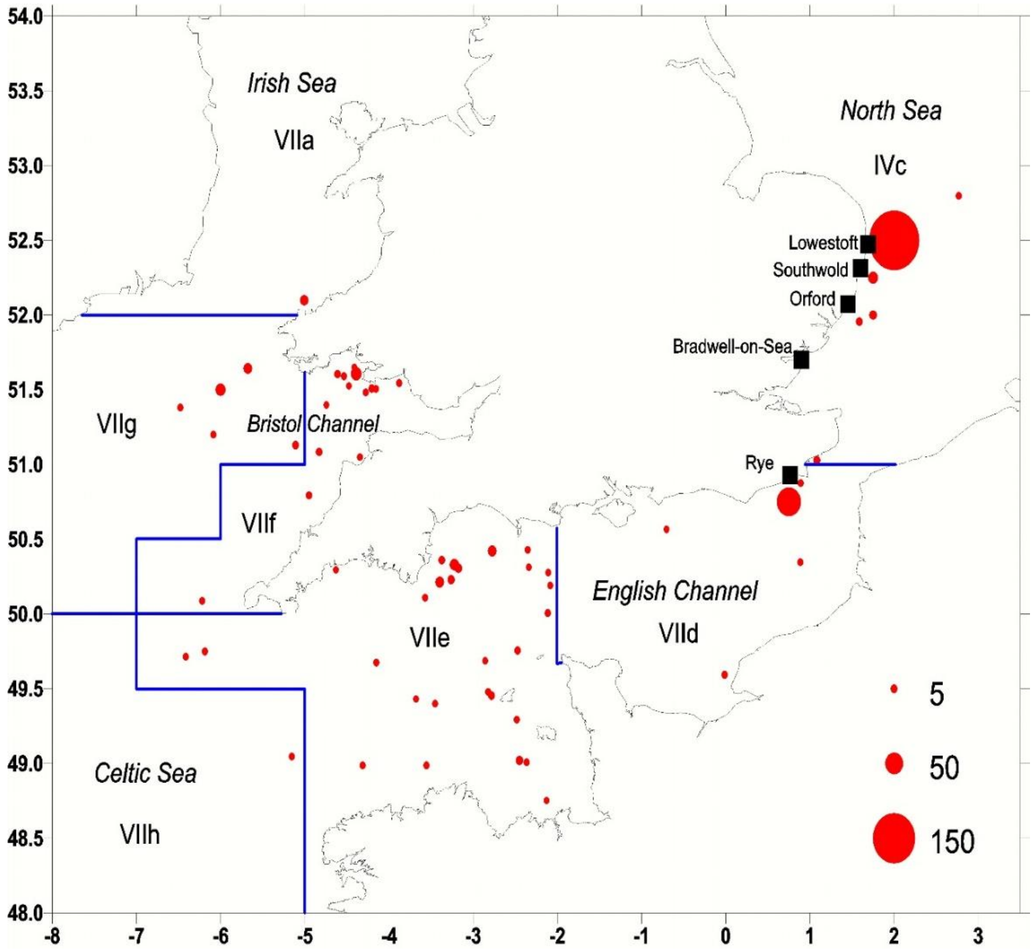


Figure 12: Map of the southern coast of the British Isles with locations of sample collection and ICES divisions.

Table 21: Number of specimens of *Mustelus asterias* sampled by year, month, area, sex and total length range (in parenthesis; cm) by collection source.

Source	Year	Month	Area	Males	Females
Commercial samples	2012	Jul	Bristol Channel/Irish Sea	1 (55)	2 (53-83)
	2013	Jun	southern North Sea	1 (97)	17 (90-124)
		Jul	southern North Sea	6 (88-96)	4 (54-119)
		Aug	southern North Sea	32 (64-99)	8 (52-109)
		Sep	southern North Sea	1 (86)	9 (75-116)
		Oct	southern North Sea		3 (111-116)
		Nov	southern North Sea	7 (79-97)	9 (75-97)
	2014	May	southern North Sea	3 (73-87)	4 (70-81)
		Jun	southern North Sea	9 (71-92)	23 (64-98)
		Jul	southern North Sea	28 (66-97)	19 (60-113)
		Sep	southern North Sea	16 (54-98)	9 (68-86)
		Oct	eastern Channel	27 (63-88)	49 (62-94)
Research vessel samples	2011	Nov	Bristol Channel/Irish Sea	1 (97)	17 (90-124)
	2014	Feb/Mar	western Channel	37 (27-88)	34 (34-101)
		Jul	eastern Channel	9 (24-40)	6 (30-61)
		Aug	southern North Sea		1 (42)
		Sep	Bristol Channel/Irish Sea	27 (28-71)	22 (28-73)
	2015	Feb/Mar	western Channel	33 (32-88)	30 (37-80)

5.3.1 Male reproductive characteristics

Maturity was assigned following gross external examination of the claspers, and internal inspection of the testes and coiling of the sperm ducts (Table 22; adapted from ICES, 2013). Inner and outer clasper lengths were measured with digital calipers (0.1 mm). Inner clasper length was measured as a straight line between the tip of the left clasper and the anterior margin of the cloaca, and outer clasper length extended from the tip of the left clasper to the point along the outer margin where the clasper met the posterior margin of the pelvic fin (e.g. Compagno, 1984). Gonad mass, including the epigonal organ (M_G) was recorded to 0.1 g.

5.3.2 Female reproductive characteristics

Maturity was assigned following internal examination of the ovary and oocytes, and the development of the nidamental glands and uteri (Table 22). The following measurements were recorded: maximum width of the left nidamental gland (0.1 mm, recorded with digital calipers), gonad mass (M_G, including epigonal organ), number of 'mature' (i.e. yolk-filled) oocytes (≥5 mm, which was counted independently by two people and re-examined if necessary to achieve consensus; the number of oocytes showing macroscopic indication of atresia was also noted), diameter of the largest oocyte (0.1 mm), and the numbers of uterine eggs or pups in each uterus. In mid- to late-term gravid females, the pups were removed carefully and, where possible, mass recorded for embryos with and without their yolk sac. The pups were also sexed and measured (mm).

Length at 50% maturity (L_{50}) was calculated using a GLM model where the error distribution and link function were binomial (Crawley, 2007; see McCully *et al*. (2012) and Chapter 4 for further details). The numbers of mature and immature fish at length were used to model the proportion of mature fish using a logistic model as a function of length.

To aid in the interpretation of the reproductive cycle, the hepato-somatic index (I_H) and gonado-somatic index (I_G) were examined in relation to length and maturity stage. These indices were calculated as:

$$I_H = 100\ M_L\ M_T^{-1}$$
$$I_G = 100\ M_G\ M_T^{-1}$$

Table 22: Maturity staging key used for *M. asterias* (adapted from ICES, 2013).

Maturity stage	Males	Females
A	**Immature**: Claspers undeveloped, shorter than extreme tips of posterior margin of pelvic fin. Testes small and thread-shaped, sperm ducts straight	**Immature:** Ovaries small, gelatinous or granulated, but no differentiated oocytes visible. Oviducts small and thread-shaped, width of shell gland not much greater than the width of the oviduct.
B	**Developing**: Claspers longer than posterior margin of pelvic fin, their tips more structured, but the claspers are soft and flexible and the cartilaginous elements are not hardened. Testes enlarged, sperm ducts beginning to meander.	**Developing:** Ovaries enlarged and with more transparent walls. Oocytes differentiated in various small sizes (usually <5 mm) and pale in colour. Oviducts small and thread-shaped, width of the shell gland greater than the width of the oviduct, but not hardened.
C	**Mature**: Claspers longer than posterior margin of pelvic fin, cartilaginous elements hardened and claspers stiff. Testes enlarged, sperm ducts meandering and tightly filled with sperm.	**Mature:** Ovaries large with very large, yolk-filled oocytes, (often 10–30 mm in diameter). Shell gland fully formed and hard. Uteri fully developed but without yolky matter (Stage D) or embryos (Stages E–F) and not dilated (Stage G)
D	**Active**: Clasper reddish and swollen, sperm present in clasper groove, or flows if pressure exerted on cloaca.	**Early gravid:** Uteri filled with yolky matter, which may appear unsegmented, or if segmented, without visible embryos.
E		**Mid-term gravid:** Uteri filled with yolk sacs and small developing embryos that can be counted.
F		**Late gravid:** Uteri filled with well-developed term pups, and the yolk sac has been absorbed (or is very small).
G		**Post partum:** Similar to stage C, but with a greater number of degenerating follicles and uteri dilated.

5.4 Results

In total, 504 *M. asterias* were examined (Figure 13), comprising 266 females (28–124 cm L_T) and 238 males (24–99 cm L_T). Commercially caught and landed *M. asterias* accounted for 57% of the samples and provided larger individuals (52–124 cm L_T). The remaining 43% of fish were caught on fishery-independent trawl surveys and accounted for all of the smaller size-classes (24–124 cm L_T). Overall, 238 in utero pups (from 21 females) were sampled, which comprised of 117 females (64–329 mm L_T), 110 males (76–325 mm L_T) and 11 unsexed individuals (39–70 mm L_T). The smallest free-swimming individual was 24 cm L_T and all the smallest individuals (24–26 cm L_T) were caught in July in the eastern English Channel by 4 m beam trawl. All dead *M. asterias* from this survey were immature (24–61 L_T). Neonates (27–32 cm L_T) were also caught in February–March in the western English Channel and in

September in the Irish Sea. Umbilical scars were evident on all of the smallest individuals, and even on individuals up to and including 43 cm L_T.

The relationship between L_T and M_T was calculated by sex and maturity stage (Table 23; Figure 14). Whilst highly correlated in both sexes, the regression coefficient was slightly greater in males (r^2 = 0.995) than females (r^2 = 0.992). This was due to the greater variance in the M_T of females in relation to maturity stage, with gravid females clustering above (and post-partum females below) the regression line.

The relationship between L_T and M_E (Table 23; Figure 15), which excludes the variability that is associated with the liver, reproductive organs and alimentary tract, M_G and M_L, gave a high correlation coefficient (r^2 = 0.995, for both sexes combined).

Sexual dimorphism in size was pronounced, with the largest male and female measuring 99 cm and 124 cm L_T, respectively. Overall, the heaviest mature male (M_T = 3226 g; M_E = 2792 g) was less than half the mass of the heaviest gravid female (M_T = 8626 g; M_E = 5849 g), even when gutted.

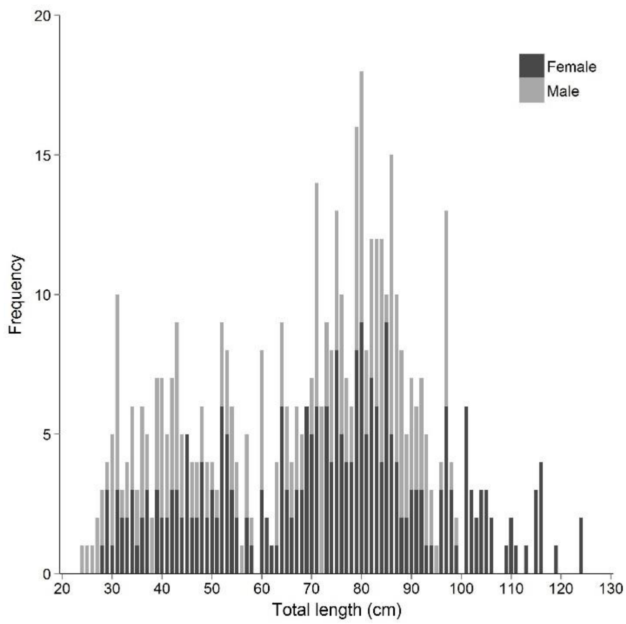


Figure 13: Total length (L_T) frequency of *Mustelus asterias* sampled in this study (n=504) by sex.

Table 23: Equations for relationships in life history traits in *Mustelus asterias.*

Relationship $y=ax^b$ (unless specified)	Sex/Stage	*a*	*b*	r^2	*n*	Fig. Number
L_T to M_T	All Females	0.0014	3.2	0.992	248	Figure 14
	All Males	0.0020	3.1	0.995	237	
	Immature Female (stage A/B)	0.0020	3.1245	0.994	170	
	Immature Male (stage A/B)	0.0014	3.2159	0.991	113	
	Mature Female (inc. early gravid) (stage C/D)	0.0021	3.1396	0.913	54	
	Mature Male (stage C/D)	0.0077	2.8084	0.938	123	
	Mid/late term gravid females (stage E/F)	0.0002	3.7072	0.935	21	
L_T to M_E	Sexes combined	0.0014	3.1580	0.995	484	Figure 15
	Female	0.0016	3.1	0.994	249	
	Male	0.0014	3.2	0.996	235	
L_T to liver mass	Sexes combined	$2e^{-05}$	3.5966	0.907	486	NA
	All Females	$7e^{-06}$	3.805	0.916	249	
	All Males	$4e^{-05}$	3.3285	0.922	237	
L_T to total ovarian fecundity ($y=ax+b$)	Mature females	0.3025	-16.054	0.3771	75	Figure 22a
L_T to total uterine fecundity ($y=ax+b$)	Mid/late term Gravid Females	0.2707	-16.654	0.494	21	Figure 22b
Pup L_T to maternal L_T ($y=ax+b$)	Late term Pups	2.4336	8.2858	0.490	17	Figure 23a
Pup M_T to maternal L_T ($y=ax+b$)	Late term Pups	1.5275	-109.99	0.441	16	Figure 23b

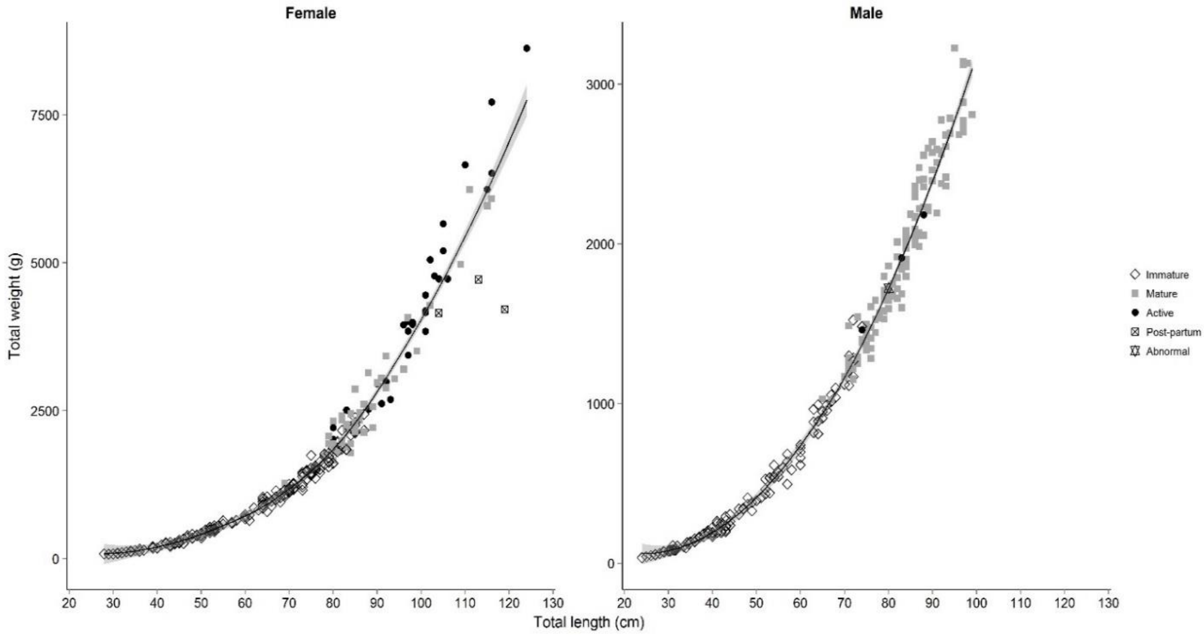


Figure 14: Total length (L_T) and mass (M_T) relationship for female (n=248) and male (n=237) *Mustelus asterias* by maturity stage (with 95% confidence intervals). Maturity stages A and B (Table 22) combined as immature and stages D–F combined as 'active'.

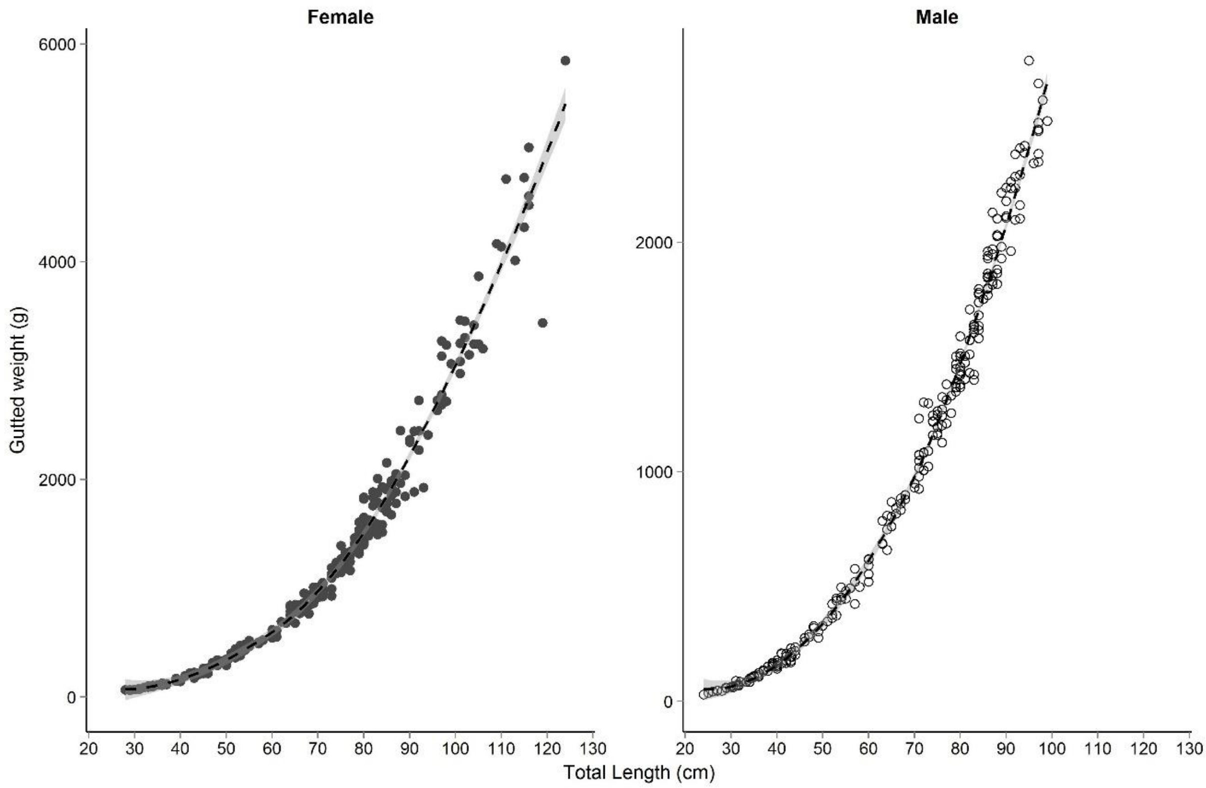


Figure 15: Total length (L_T) and eviscerated mass (M_E) relationship for female (n=248) and male (n=237) *Mustelus asterias* (with 95% confidence intervals).

5.4.1 Reproductive biology of males

The smallest mature male was 65 cm L_T, and the largest immature male was 74 cm L_T. The length at 50% maturity (L_{50}) for males was estimated at 70.39 cm L_T, with 100% maturity (L_{100}) attained at approximately 75 cm L_T (Figure 16).

One abnormal male (80 cm L_T) was caught in October 2014 off Rye (eastern English Channel). This specimen, which was otherwise healthy as evidenced by a large liver (I_H = 7.35%), and heavy gonad mass and I_G (29.9 g; 1.73%), had a single aberrant clasper (Figure 17 (a); Figure 18), although the testes appeared normal (Figure 17 (b)) and there was semen in the sperm ducts.

The relationships between inner- (L_{IC}) and outer-clasper length (L_{OC}) and L_T displayed a sigmoid-like relationship when a local regression ("loess") smoother was added (Figure 18), with clear phases of maturity identified in both measurements. The abnormal male (80 cm L_T) was a clear outlier.

The mean I_H (Table 24) increased as expected as the fish developed from immature (I_H = 4.40%) to developing (6.88%), however once mature the mean I_H decreased slightly in both mature (5.35%) and active (6.36%) males. Testes mass increased with L_T and maturity (Figure 19; Table 25); with a mean and maximum M_G for mature fish of 24.51 g, and 51.6 g respectively. The mean mass of active males was similar 22.60 g (n = 3) and I_G was 1.22% for both these stages (Table 25). The abnormal male had both a larger M_G and I_G value than the average mature fish.

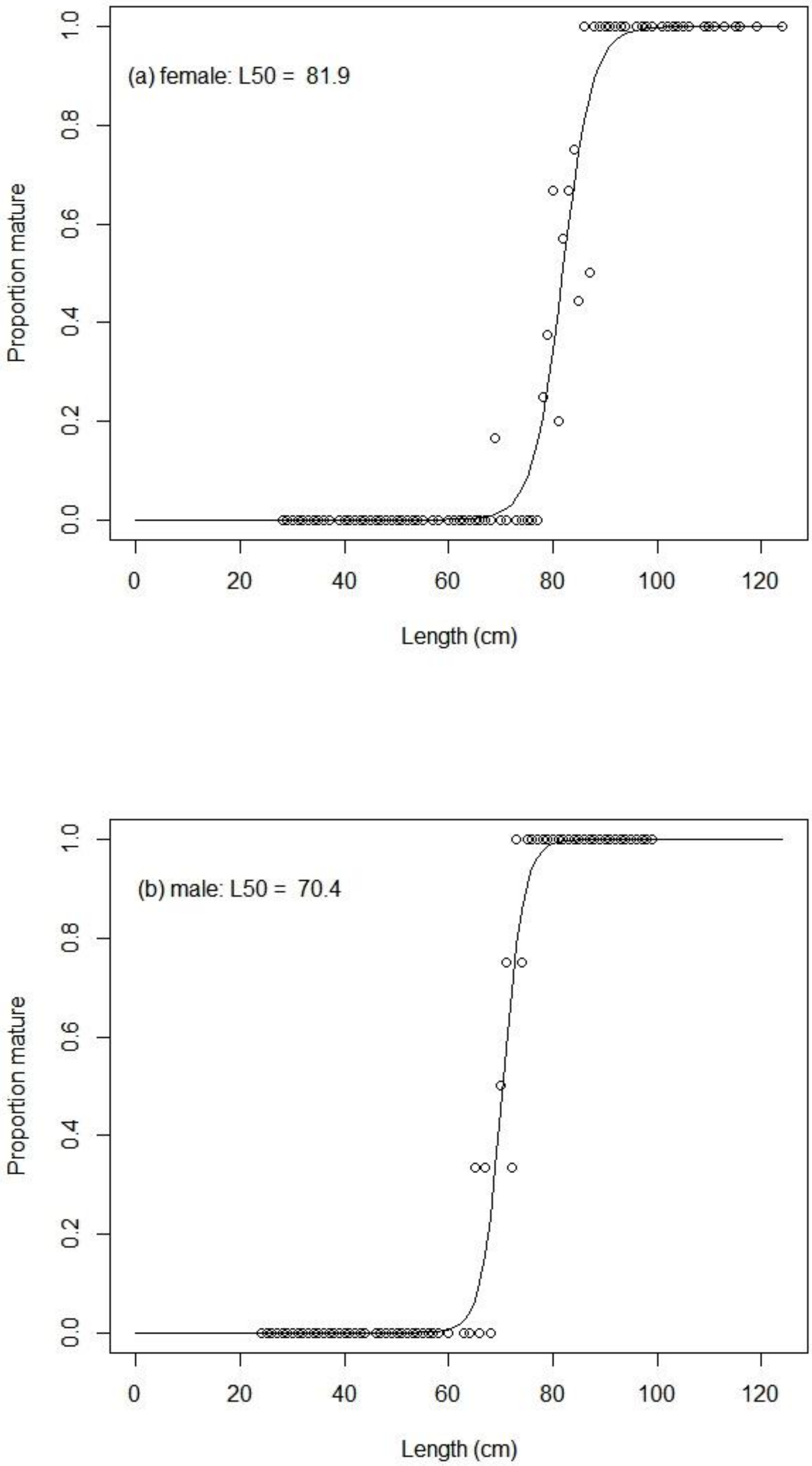


Figure 16: Maturity total length (L_T) ogive for (a) female (n = 248; L_{50} = 81·9 cm) and (b) male (n = 237; L_{50} = 70·4 cm) *Mustelus asterias*.

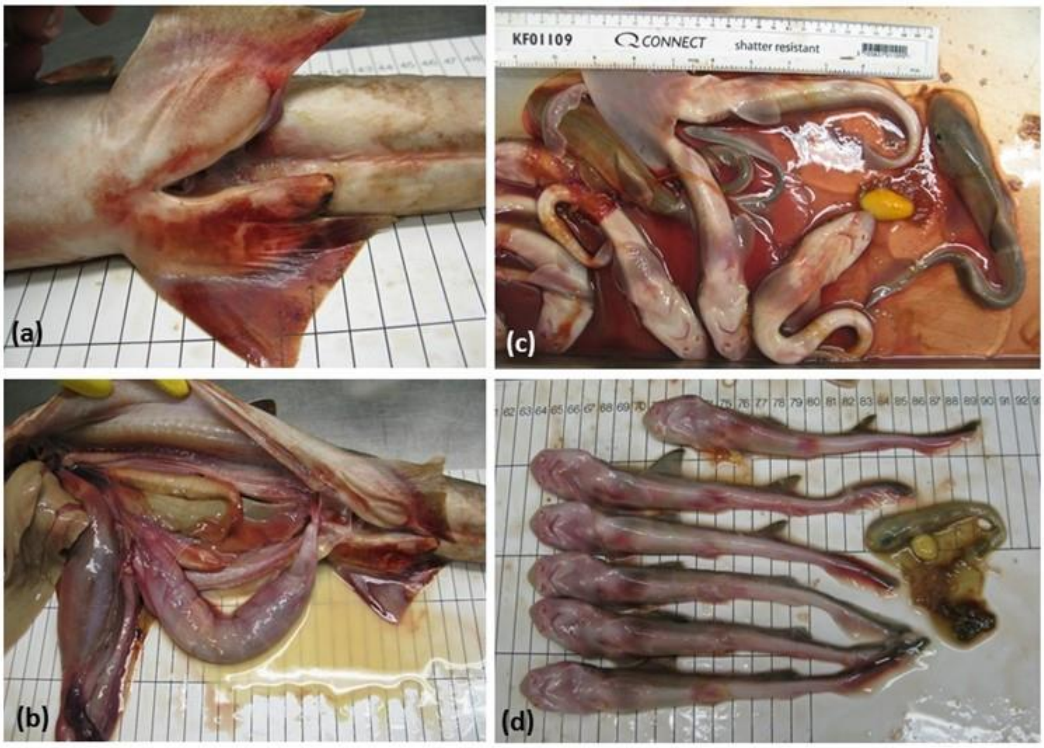
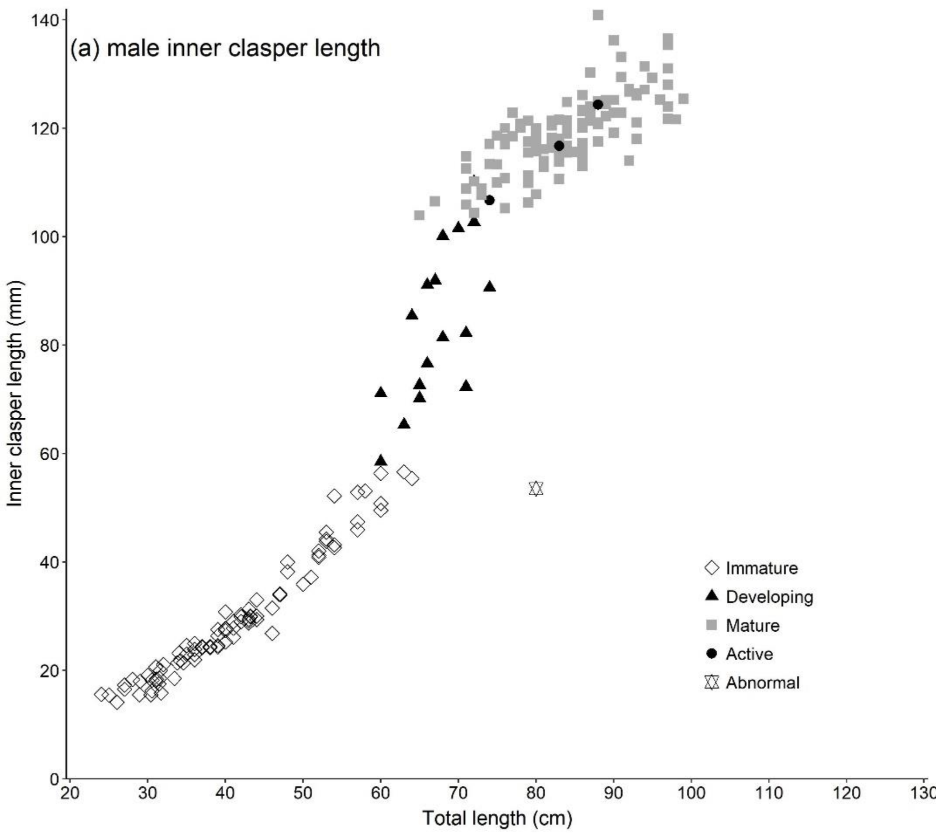


Figure 17: Abnormalities in the development and reproductive systems of *Mustelus asterias* showing (a) an abnormal male with a single deformed clasper, but (b) with well-developed internal testes, (c) an encapsulated yolk sac that has failed to develop and (d) a partially developed embryo in a litter of term pups.



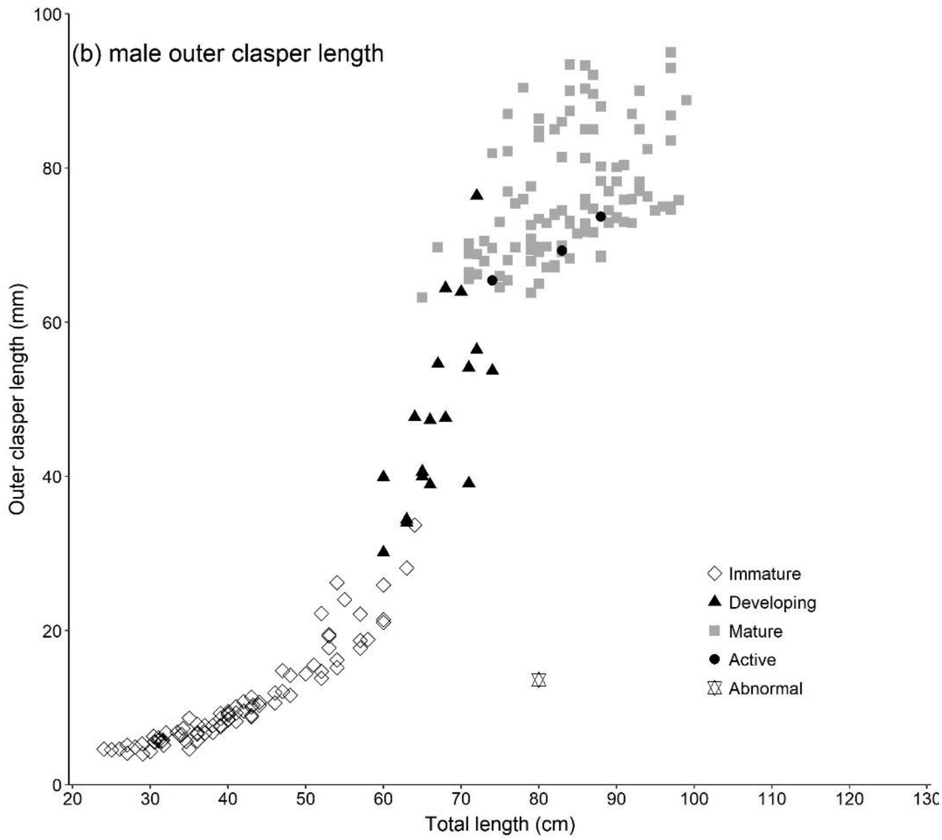


Figure 18: Male total length (L_T) relationship with (a) inner (n = 215) and (b) outer clasper lengths (n = 216) in *Mustelus asterias* by maturity stage (with 95% confidence intervals).

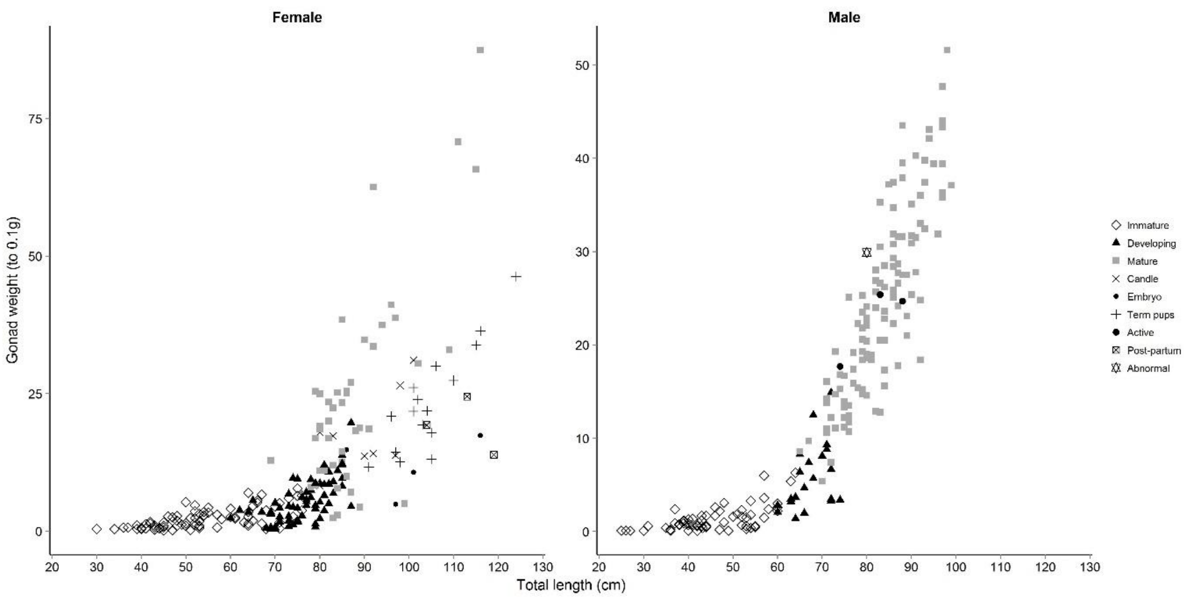


Figure 19: Total length (L_T) relationship with gonad mass (M_G) for (a) female (n = 227) and (b) male (n = 210) *Mustelus asterias* by maturity stage.

5.4.2 Reproductive biology of females

The smallest mature female was 69 cm L_T, the largest immature female was 87 cm L_T, with L_{50} estimated at 81.86 cm L_T and L_{100} at 88 cm L_T (Figure 16). The seasonality of female maturity stages seen in the samples (Figure 20), shows that mature females were present in each month samples were obtained, while late-gravid females were only found in February and June–July, and post-partum females were only observed in July–August.

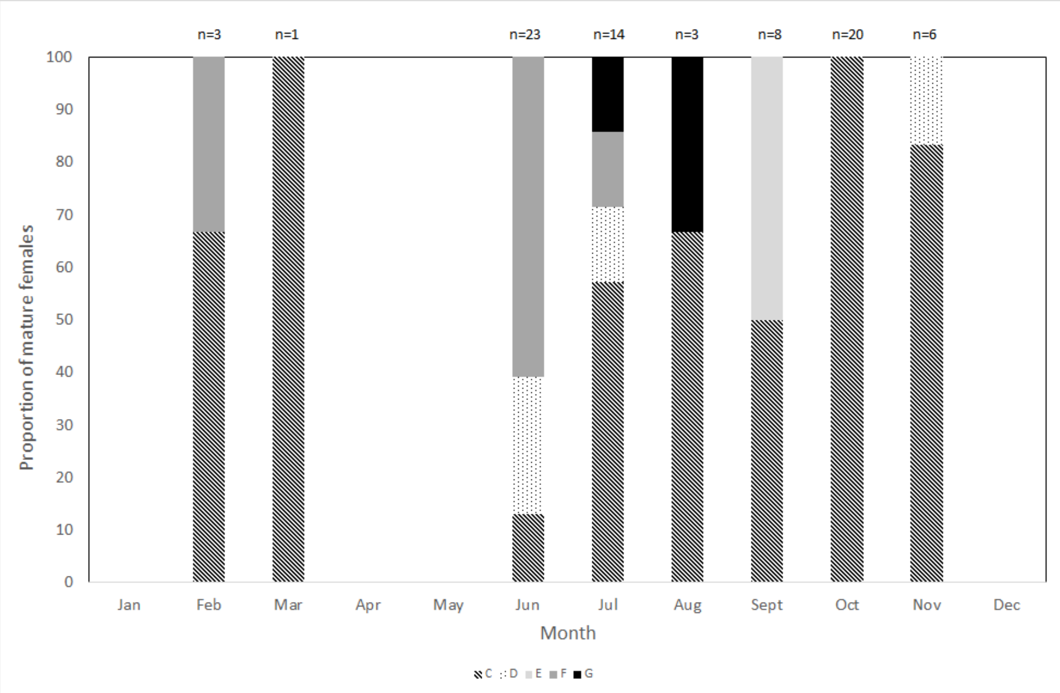


Figure 20: Percentage of females of *Mustelus asterias* by maturity stage and month.

The relationship between L_T and nidamental gland width was not as clearly defined as for other metrics but did follow a broad sigmoid-shaped curve (Figure 21a). Immature and developing fish clustered together (broadly equating to nidamental gland widths of <10 mm and 10–20 mm, respectively). However, mature fish (mature, early-gravid, embryo and full-term maturity stages) had similar-sized nidamental glands (20–35 mm). Several post-partum females had narrower nidamental glands in relation to L_T, suggesting the gland may regress slightly at this stage.

The relationship between maximum oocyte diameter and female L_T was more variable, depending on maturity stage (Figure 21b). Maximum oocyte diameter for developing females (stage B, n = 67) ranged from 1–7.8 mm (with the majority <5 mm, as per the maturity scale, Table 22). Mature females (stage C, n = 45) had a broad range in maximum oocyte diameter (4.1–20.7 mm, with the latter the largest observed mature oocyte). Stage D (early gravid, n = 9) females with encapsulated yolk sacs had maximum oocyte diameters of 4.3–18.3 mm, while mid-term gravid (stage E, n = 4) females had the smallest oocyte diameters of the mature females (4.1–4.3 mm). Those females with full-term pups (stage F, n = 17) were again producing larger yolk-filled oocytes (5.5–10 mm) and the three post-partum females (stage

G) had oocytes of up to 8.3–11.6 diameter. These oocytes were, however, still smaller than observed in mature, non-gravid females.

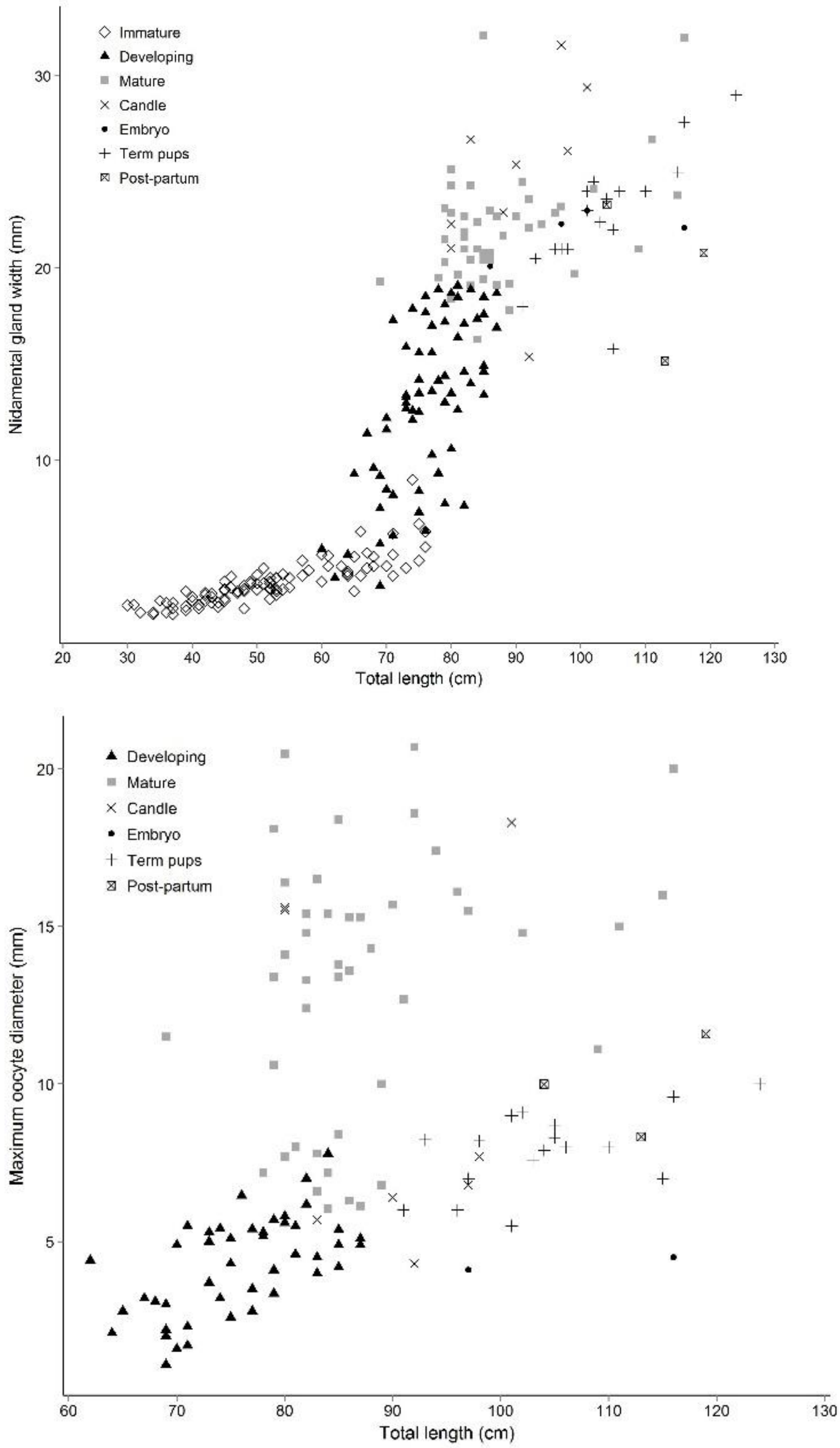


Figure 21: Total length (L_T) relationship with (a) nidamental gland width by maturity stage (n=237) and (b) maximum oocyte diameter by maturity stage (n=119) of *Mustelus asterias*.

The mean M_G in females (Table 25) followed a logical progression with increasing mass from immature to mature, then decreasing when the female entered the early gravid stage. The lowest M_G was observed in mid-term gravid specimens, and ovarian mass began to increase again in females carrying term pups. Mean M_G for post-partum females was slightly less than that of the full-term females, but this was based on a very small sample size (n = 3). Expressed in terms of I_G, the same trend was apparent, with the largest mean I_G in mature females (0.84%) and the lowest in immature and developing females (0.36%). Similar patterns were observed in the I_H of females (Table 24), with the liver reserves increasing through development, peaking at the mature stage (stage C; 9.91%). Subsequently, the liver decreased in relative terms during gestation, with the lowest mean I_H observed in females with full-term pups (stage F; 3.30%), before starting to increase in post-partum females (mean I_H = 4.68).

Ovarian fecundity ranged from 1–28 'mature' yolk-filled oocytes and there was a linear relationship between L_T and ovarian fecundity F_O (Table 23; Figure 22a). In keeping with the results above in relation to M_G and I_G, early-gravid females with encapsulated yolk sacs (stage D) had fewer mature oocytes (mean = 3.4; range = 0–11; n = 9) than fully mature (stage C) females (mean = 11.7; range = 0–28; n = 45) and late-gravid females and post-partum females (stages F–G; mean = 13.3; range = 0–27; n = 20).

In total, 30 gravid females (stages D–F) were sampled, with the smallest early- mid- and late-gravid females at 80, 86 and 91 cm L_T respectively. The mean M_T of early embryos (females at stage E, 97–116 L_T) was 17.6 g (range = 8.1–33.1 g), whilst full-term embryos (females at stage F, 91–124 L_T) were 51.4 g (21.2–91.5 g). Of the 21 mid- to late-gravid females the uterine fecundity ranged from 4–20 (mean = 11.25). Like ovarian fecundity, uterine fecundity increased with maternal L_T (Figure 22b; Table 23). Both the L_T and M_T of pups also increased significantly with maternal L_T (Figure 23;Table 23). The mean L_T of 17 sets of full-term pups was 261 mm and ranged from 211–317 mm for pups relating to mothers at 96 and 124 cm L_T, respectively. The smallest mother (stage F, 91 cm L_T) had the lowest mean pup mass (23.3 g), and the largest mother (124 cm L_T) had the heaviest mean pup mass (82.6 g). Whilst significant linear relationships were observed in all of these cases, the r^2 values only ranged from 0.42–0.49, and further data would be desirable. The sex ratio between litters of in utero pups was not significantly different (paired t-test, d.f = 20, P>0.05), with 110 males and 117 females (1:1.06).

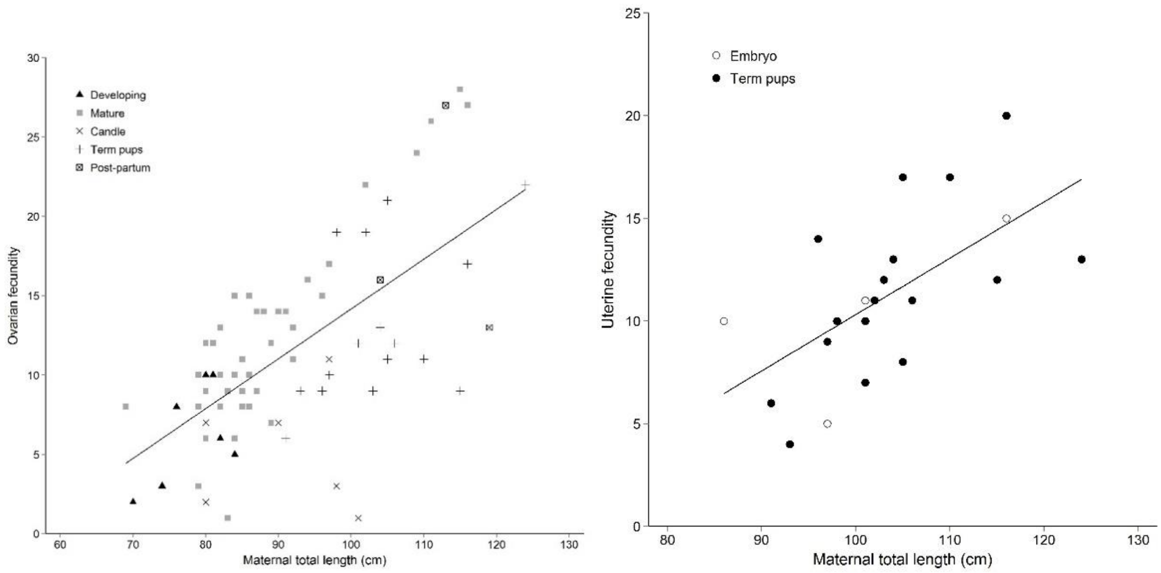


Figure 22: Maternal total length (L_T) relationship with (a) ovarian fecundity (n = 7518) and (b) uterine fecundity by maturity stage (n=21 gravid females) in *Mustelus asterias* (see Table 23)..

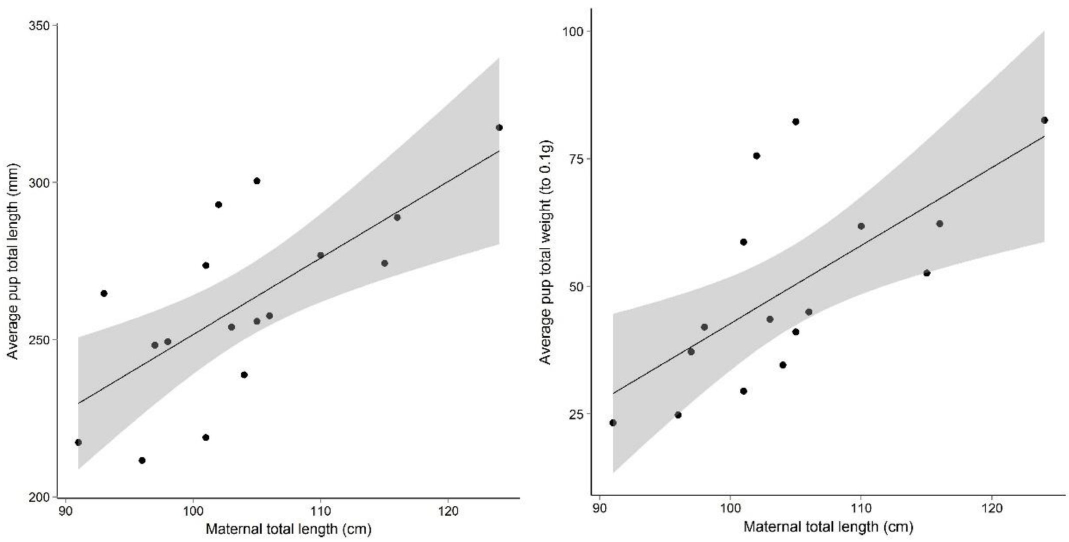


Figure 23: Maternal total length (L_T) relationship with (a) average full-term pup L_T (n=17), and (b) average full-term pup total mass (M_T) (n=16) in *Mustelus asterias* (see Table 23), with 95% confidence intervals.

Atretic oocytes were identified in many females, usually only one or two oocytes undergoing atresia were observed. Some females carrying either term-pups (n = 11) or mid-term pups (n = 2) contained uterine eggs that had failed to develop in one or both uteri (Figure 17 (c)). These undeveloped eggs ranged from 1–5 in number (mean = 1.7; mode = 1), with the remaining pups all developing normally. One litter of 13 pups (Figure 17 (d)) contained 12

[18] no fish at stage E (embryo) was shown, as none had yolk-filled oocytes

full-term pups (mean L_T = 317 mm; mean M_T = 26.4 g) and a single partly developed pup (211 mm L_T; 4.2 g M_T comprising a 3.8 g embryo and 0.4 g yolk sac).

In terms of reproductively active females, more data were available for specimens carrying (near) term pups (n = 17), and all but one of these were caught in June and July in the southern North Sea. Three post-partum females were caught in July and August. Females in the earliest stages of pregnancy (stage D, n = 9) were observed from June to November and the few females with mid-term pups (n = 4) were all captured during September. There were insufficient data to examine monthly size distribution of pups.

Table 24: Hepato-somatic index (I_H) of *Mustelus asterias* sampled by sex and maturity stage.

Sex	**Female I_H**				**Male I_H**			
Maturity Stage	**Min**	**Mean**	**Max**	***n***	**Min**	**Mean**	**Max**	***n***
A	2.63	5.04	9.18	103	2.70	4.40	7.38	91
B	4.86	8.49	14.07	67	4.11	6.88	11.38	22
C	4.80	9.91	15.46	45	2.19	5.35	13.80	120
D	6.19	8.05	10.09	9	4.59	6.36	8.75	3
E	6.42	6.97	7.79	4				
F	2.12	3.30	5.57	17				
G	3.77	4.68	6.37	3				
Abnormal	NA	NA	NA	0	NA	7.35	NA	1

Table 25: Mean gonad mass (M_G) and gonado-somatic index (I_G) of *Mustelus asterias* by sex and maturity.

Sex	**Female**					**Male**				
Maturity Stage	**M_G (g)**	**Min I_G**	**Mean I_G**	**Max I_G**	***n***	**M_G (g)**	**Min I_G**	**Mean I_G**	**Max I_G**	***n***
A	2.29	0.036	0.393	1.238	103	1.23	0.026	0.383	1.447	91
B	5.36	0.035	0.326	0.807	67	5.80	0.173	0.533	1.203	22
C	24.40	0.127	0.841	1.812	45	24.51	0.463	1.217	1.918	120
D	17.85	0.344	0.583	0.812	9	22.60	1.132	1.220	1.328	3
E	11.95	0.143	0.319	0.609	4					
F	23.60	0.231	0.456	0.635	17					
G	19.23	0.330	0.438	0.519	3					
Abnormal	NA	NA	NA	NA	0	29.90	NA	1.730	NA	1

5.5 Discussion

5.5.1 Maximum size and sex ratio

Given the taxonomic problems affecting the genus *Mustelus*, the maximum length (L_{max}) of *Mustelus asterias* is somewhat uncertain. General accounts cite an L_{max} of about 140 cm (Quéro *et al*. 2003), although other authors have given more conservative sizes of 120–122 cm L_{max} in Atlantic waters (Le Danois, 1913; Wheeler, 1969), which is similar to the largest fish observed in the present study (124 cm). The largest specimen sampled by Farrell (2010a, b) was 112 cm, with Capapé (1983) providing fecundity data for females of 123 cm. Larger fish have been reported in other studies for both the Atlantic (Ellis *et al*. 2005: 133 cm) and

Mediterranean (Capapé 1983: 148 cm; Ismen *et al*., 2009: 154 cm), but these values should be used with caution, given potential identification issues.

Sampling of commercially caught *M. asterias* in the southern North Sea was undertaken, with a few specimens appearing in these waters in May, peaking in July, with small quantities captured until November. Both sexes were present in the samples throughout these months, but these data cannot be used to inform on the natural sex ratio, as larger specimens were selected preferentially (90% of the samples >75 cm L_T). All maturity stages were present in these samples, with the exception of active males. Nearly all (94%) of the full-term gravid females, and all three of the post-partum females were from these commercial samples, caught in June–July, and July–August respectively. Coupled with the presence of neonates (<32 cm L_T) in the surrounding waters in July, this indicates that females give birth in the southern North Sea and eastern English Channel, and that potential movements from southern waters are made in mixed sex and life history stage groups.

Within the samples caught in research vessel surveys, immature individuals comprised the bulk (86%) of the samples. One full-term gravid female was examined, and this specimen was caught in February off the French coast in the western English Channel. The sex ratio was not significantly different from the expected 1:1 in any season or area of sample collection. This is in contrast to an earlier study by Ford (1921), who examined three commercial landings of *Mustelus*, all of which favoured males, with two landings significantly different from an expected 1: 1 sex ratio.

5.5.2 Reproductive biology

The estimated L_{50} in this study (70.4 and 81.9 cm L_T for males and females respectively) was smaller than estimated by Farrell *et al*. (2010a), at 78 and 87 cm L_T. Similarly, the smallest sizes at maturity were also smaller: 65 and 69 cm L_T for males and females respectively, as opposed to 72 and 83 cm L_T in the Farrell *et al*. (2010a) study. Even though the confirmed mature female at 69 cm L_T was exceptional, the next smallest mature females were at 78 cm L_T and subsequent length classes (Table 25). The maturity scale used in the present study, where fish were considered mature if they had large (typically 10 – 30 mm in diameter) yolk-filled oocytes (see Table 22 for other criteria), has been in use in UK fisheries independent surveys since 2005, and is very similar to that adopted by ICES (2013). It is largely comparable to that of Farrell *et al*. (2010a), however by designating mature fish as having "*Oocytes obviously enlarged, yellow and can be easily counted and measured*", this is likely to occur when oocytes are <10 mm, and thus maturity could be assigned at a smaller size, than in the present study.

Both Farrell *et al*. (2010a) and the present study have confirmed that there are potentially large differences in various life history parameters of *M. asterias* between Atlantic waters and the Mediterranean, although these studies differ temporally and there can be methodological differences between such disparate studies. Surprisingly, there also appeared to be some subtle differences between the present study and the recent study by Farrell *et al*. (2010a), who collected data from 2006–2009. Although from different regions of the British Isles, the study areas were adjacent and there is thought to be a single stock in the Northeast Atlantic (ICES, 2014), although has not been fully substantiated. The reasons for subtle differences may potentially relate to temporal changes, methodological differences or simply artefacts of the sample sizes available. Studies on other members of the genus *Mustelus* elsewhere in the world have often reported spatial and temporal differences in key demographic parameters (Yamaguchi *et al*., 2000; Park *et al*., 2013), suggesting marked variability in such parameters for this genus.

Only three active (stage D) males were observed – one in March, and two in October, all collected from the English Channel. Further samples of this stage are required to better define the mating season. Both measurements of clasper length gave similar results and can be used as a suitable quantitative metric for maturity studies, with inner clasper length showing less variability.

Farrell (2010a) reported that the fecundity of *M. asterias* around the British Isles ranged from 8–27 (ovarian fecundity) and 6–18 (uterine fecundity), and so the fecundity reported here (1–28 ovarian fecundity, and 4–20 uterine fecundity) shows a slightly larger overall range, with a greater number of full-term pups reported. Whilst the fecundity data in the present study and Farrell *et al*. (2010a) are similar, the latter study was based on smaller sample size of mature females (n = 34; versus 78 in this study). It may be noted that a litter of 25 pups from a *M. asterias* (*ca.* 9500 g mass) caught off Bradwell-on-Sea (Essex; southern North Sea) is housed in the fish collection at the Natural History Museum (BMNH 1979.11.26.224–248). Within the Mediterranean Sea, Capapé (1983) recorded higher ovarian and uterine fecundities of 10–45 and 10–35, respectively, with fecundity-length relationships reported as $F_O = 1.533\ L - 141.001$ (n = 36; r^2 = 0.99) and $F_U = 1.042\ L - 92.339$ (n = 32; r^2 = 0.98) recorded over the 98–123 cm length range. However, the larger fecundity of this study may relate to different stock units of *M. asterias*, or from confounded data from other *Mustelus* spp. Capapé (1983) also commented on earlier fecundity estimates from this species in the Mediterranean, which ranged from 4–15 in one study, and up to 60 pups in another. Such a large disparity in estimates may indicate that these data have been compromised by taxonomic problems.

The L_T of full-term pups in this study agreed with the average lengths reported by Farrell *et al*. (2010a; 21–31 cm L_T), increasing in length from January to July. Similarly, Ford (1921) noted term pups to be 29–33 cm long. The overall sex ratio of uterine pups was equal, which supports the findings of Farrell *et al*. (2010a). This study has confirmed that atresia occurs quite regularly, with some oocytes not being ovulated and fertilised successfully, which explains why estimates of F_O are usually higher than F_U.

It was noted that not all early gravid encapsulated yolk sacs will develop successfully into an embryo, supporting an earlier observation of Le Danois (1913), and so fecundity estimates on earlier stages of the gestation period may also be slight overestimates. Furthermore, early gravid females with encapsulated yolk sacs had maximum oocyte diameters of 4.3–18.3 mm, possibly indicating that were still ovulating or they were going to resorb oocytes not ovulated.

The increased M_T of full-term embryos in comparison to early stage embryos was indicative of nutrition in addition to yolk-sac reserve. The markedly lower M_T of one post-partum female (119 cm L_T) indicated that the condition of some females can be reduced during the reproductive cycle, while gravid females had a greater M_E, in addition to increased energy reserves in the liver. These observations provide further supporting evidence of maternal investment during pregnancy, feasibly through mucoid histotrophy, as previously suggested by Farrell *et al*., (2010a).

5.5.3 Reproductive cycle

In full-term gravid and post-partum females, the largest oocytes observed were 11.6 mm; hence while there is likely to have been some ovarian development from earlier gravid stages (maximum oocyte diameter for mid-gravid females (stage E) was <5 mm, and not all fish at this stage had maturing oocytes), these oocytes are still smaller than expected for ovulation (ca. 18–21 mm). The nidamental gland of post-partum females appeared to be narrower than in mature fish, and this would also suggest that ovulation is unlikely to occur straight after parturition. Therefore, ovarian and uterine cycles are not synchronised, suggesting that the reproductive cycle likely lasts longer than one year. Whilst Farrell *et al*. (2010a) postulated that the reproductive cycle may be ca. two years, Capapé (1983) reported that gestation alone lasted 12 months and the full reproductive cycle could last up to 15 months. The limited samples of reproductively active females between November and April restricts full appraisal of the ovarian and uterine development cycle, and more samples from these times of the year, which may be more effectively sampled from the western English Channel and Bay of Biscay, would be needed to provide such data.

It is noted that females with term pups were found both in February and June–July. Whilst the specimen caught in February was a single fish, annual beam trawl surveys of the western English Channel often catch neonates (27–32 cm L_T) in February–March, indicating that parturition has occurred in this area at this time. However, a similarly sized cohort is also evident in an eastern English Channel beam trawl survey conducted each July (Ellis *et al*., 2005) and a summertime parturition was evident in the data collected from the southern North Sea. Farrell *et al*. (2010a) also identified parturition in the summer months in the western area of the British Isles. This would indicate that either parturition for the stock as a whole is protracted or may occur in at least two broad 'seasons'. In the case of the latter scenario, it is unclear as to whether individual fish would consistently spawn in early spring (or summer), although it is conceivable that individual fish could alternate such spawning times if the reproductive period was ca. 15 months, as suggested by Capapé (1983).

5.5.4 Management implications

Given the increasing commercial interest in *M. asterias*, it would be prudent to investigate assessment methods that have been developed successfully and applied to other *Mustelus* spp., such as *Mustelus antarcticus* Günther, 1870 in Australia (e.g. Xiao and Walker, 2000; Pribac *et al*., 2005). The life history parameters (e.g. L_{50}, fecundity estimates) generated within this and previous studies are essential for incorporation into demographic assessment models. Uncertainty in the duration and periodicity of the full reproductive cycle, however, remains an important parameter to substantiate. Given the increased data collection that has been undertaken for *M. asterias* in recent years (e.g. life history parameters and survey trends), this improved knowledge should help inform and test biologically-meaningful management measures, and hopefully ensure that future exploitation is undertaken at a sustainable level.

5.6 References

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Chapter 6

Reproductive biology and life history relationships of data-limited elasmobranchs: sandy ray *Leucoraja circularis* and shagreen ray *Leucoraja fullonica*

6 Reproductive biology and life history relationships of data-limited elasmobranchs: sandy ray *Leucoraja circularis* and shagreen ray *Leucoraja fullonica*

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McCully Phillips, S. R. and Ellis, J. R. (2018). *Leucoraja fullonica* and *Leucoraja circularis* in the Northeast Atlantic. Working Document to the ICES Working Group on Elasmobranch Fishes, Lisbon, 19–29 June 2018.

The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures. This work was undertaken under the supervision of Dr. J. Ellis who was also involved in data collection and commenting on the text. Sample collection was courtesy of scientists onboard fishery-independent surveys. Samples of *L. circularis* were kindly collected by Dr. Paco Baldo (Instituto Español de Oceanografía, IEO, Cadiz) and team from the IEO Spanish Porcupine Bank Survey, and specimens of both species were retained from scientists onboard the French Southern Atlantic Bottom Trawl Survey (EVHOE (EValuation Halieutique Ouest de l'Europe); conducted by L'Institut Français de Recherche pour l'Exploitation de la Mer, IFREMER, France). Dissections were assisted by lead scientists (among others) at both institutes, namely Dr. Cristina Rodríguez-Cabello (IEO, Santander, Spain) and Dr. Pascal Lorance (IFREMER, Nantes, France).

Updates to the document have been made by increasing the sample sizes, reanalysing the biological data, processing the dietary data and updating text in relation to new literature.

6.1 Abstract

Sandy ray *Leucoraja circularis* and shagreen ray *L. fullonica* are large-bodied skate species occurring on the edge of the continental shelf and upper slope in the Northeast Atlantic and Mediterranean. They are not sampled effectively in many fishery-independent trawl surveys, which generally sample shelf seas. Consequently, they are data-limited stocks with no formal assessments, have no defined reference points, and are of uncertain stock status.

Fishery-independent survey data from northern European seas (2000–2017) showed that catch rates of sandy ray were low, with the 669 individuals recorded primarily during the

Spanish survey of the Porcupine Bank (64%) and from the French EVHOE survey (34%). CPUE in these surveys was greatest at depths of 300–600 m, being on average 1–1.4 individual per hour (ind.h^{-1}). The proportion of hauls across surveys with a positive catch was greatest (0.9%) at 301–400 m depth. Catch rates were of a similar low level for shagreen ray, with 362 individuals present in the data, primarily from the EVHOE survey (67%). CPUE of this survey was greatest (0.77 ind.h^{-1}) at depths of 301–400m, however, the proportion of hauls across surveys with a positive catch was greatest (1.1%) at the 101–200m depth band. The spatial and depth distribution of both species overlaps with commercially important fisheries for hake *Merluccius merluccius* and anglerfish *Lophius* spp., putting these Threatened skate species at risk of bycatch.

Biological data were collected from 116 specimens of *L. circularis* (47 male: 23–93 cm L_T and 69 female: 21–116 cm L_T) and 54 specimens of *L. fullonica* (25 male: 19–86 cm L_T and 29 female: 28–100 cm L_T). Conversion factors relating total length to weight, gutted weight, wing-width and liver weight are presented, along with data on hepato- and gonado-somatic indices. Information on diet composition is also given, with evidence of predation on other elasmobranchs found in both species. Quantitative data were collected on maturity classification and the length at 50% maturity for *L. circularis* was estimated at 81 cm L_T and 100 cm L_T for males and females, respectively. This large size at maturity makes them more biologically vulnerable than other skate species managed under the generic TAC. This inherent biological vulnerability, low representation of mature individuals in fisheries-independent trawl surveys and spatial overlap with important commercial fisheries suggests that both Threatened skate species would benefit from being removed from the generic TAC in favour of alternative species-specific management measures (e.g. trip limits).

6.2 Introduction

Sandy ray *L. circularis* and shagreen ray *Leucoraja fullonica* (Figure 24) are large-bodied skate species occurring on the edge of the continental shelf and upper slope and on offshore banks in the Northeast Atlantic and Mediterranean Sea (Stehmann and Bürkel 1984; ICES, 2012).

Very few data are available for these lesser-known skate species, with some earlier data compromised by taxonomic ambiguities. For example, the description of *Raia circularis* given by Day (1880–1884) clearly refers to cuckoo ray *L. naevus*. In contrast, Couch (1862) did provide an accurate description of *L. circularis* (as *Raja circularis*), and noted that it was "*a common species, at least in the west of England*". Yarrell's (1841) *A history of British fishes* gave no accurate descriptions of either species, with information for shagreen ray *Raia chagrinea* confounded with long-nosed skate. Day (1880–1884) reported that *L. fullonica* occurred in deeper water, with occasional records from the Moray Firth, Firth of Forth, off Yorkshire (Scarborough and Whitby) and Portrush (Ireland). The more offshore nature of these two species, combined with taxonomic and nomenclatural confusion, means that historic ichthyological information is also limited and uncertain.

Figure 24: Shagreen ray *Leucoraja fullonica* (left) and sandy ray *Leucoraja circularis* (right) with their regional IUCN Red List assessment status.

6.2.1 Occurrence, assessment and advice

Given the fragmented distribution records of these data-limited species, they are currently treated as occurring over a management unit that covers ICES Subareas 6–7 (waters west of the British Isles), but these stocks likely extend into the north-western parts of Division 4.a (northern North Sea) and Subarea 8 (Bay of Biscay). ICES advice has been very limited, given the absence of appropriate data from fishery-independent surveys. Consequently, both stocks are assessed as data-limited using trends in available landings data, and it is further noted that there is a degree of uncertainty in these data (ICES, 2016).

The latest ICES advice indicated that, "*when the precautionary approach is applied, landings should be no more than 34 tonnes in each of the years 2019 and 2020*" for *L. circularis* (ICES, 2018a), and "*no more than 168 tonnes in each of the years 2019 and 2020*" for *L. fullonica* (ICES, 2018b). These skates are managed as part of the generic skate and ray Total Allowable Catch (TAC). ICES Working Group for Elasmobranch Fishes (WGEF) estimates of landings (2009–2015) have ranged from 46–77 t for *L. circularis* and 196–301 t for *L. fullonica*, however there have been known issues with misidentification of both species, so the accuracy of these data are uncertain (ICES, 2016).

In the Northeast Atlantic, *L. circularis* is classified as 'Endangered' by the IUCN (McCully *et al*., 2015), given that it is suspected to have declined in the Northeast Atlantic and Mediterranean Sea by more than 50% in the last three generations. *L. fullonica* is suspected to have experienced continued population declines of 30–50% over three generations and is therefore classified as 'Vulnerable' by the IUCN (McCully and Walls, 2015).

6.2.2 Biology

There are very limited published investigations on the life history of either of these large-bodied skates, with several studies based on small sample sizes (Mnasri *et al*., 2009; Zupa *et al*., 2010), or individual specimens (Consalvo *et al*., 2009; Alkusairy and Saad, 2018; Saad and Alkusairy, 2019).

Leucoraja circularis is a very data-limited skate species. The maximum recorded size is ca. 120 cm total length, L_T (Stehmann, 1990), but most individuals caught are between 70–80 cm L_T (Serena, 2005, Ebert and Stehmann, 2013). Very little is known regarding its biology and reproductive cycle, other than that it is oviparous, and produces egg-cases that measure 88–90 by 50–60 mm (Stehmann and Bürkel 1984; Mnsari *et al*. 2009). Age at maturity, longevity, size at birth, reproductive age, gestation time, reproductive periodicity, fecundity, rate of population increase and natural mortality are all unknown (McCully *et al*., 2015). It is an offshore species, occurring on the outer continental shelf and upper slope, and offshore banks, down to depths of up to 800 m.

Slightly more data are available for the congener *L. fullonica*, which reaches a maximum size of between 100–120 cm L_T (Bauchot, 1987; Muus and Nielsen, 1999). To date, information in the literature has been largely restricted to notes on occurrence in trawl surveys and distributional range (Ellis *et al*., 2015). Very little is known regarding its biology and reproductive cycle, other than that it is oviparous, and produces egg-cases that measure about 80 mm by 50 mm (Stehmann and Bürkel 1984). McCully *et al*. (2012; Chapter 4) reported on a limited number of specimens from trawl surveys of the Celtic Sea (1992–2011), with total length (L_T) ranging from 21–96 cm and 24–70 cm in males and females, respectively. All female specimens were immature, while only two of the males (75 and 96 cm L_T) were mature; the largest immature male caught was 82 cm L_T.

This Chapter examines the catch rates of both species in fishery-independent trawl surveys to provide a better understanding of the species range and demographics within the Northeast Atlantic. Some of the key life-history parameters, which have been largely unknown to date, are described, including the provision of estimates of the length at maturity, which are essential to inform assessment and potential management options. These data will populate some key life-history data gaps for species identified as high priority (Chapter 2) and susceptible to fisheries across the main part of their distribution (Chapter 3), while being evaluated as to whether the data provided within this Chapter support such assertions and vindicate the approaches taken in Chapters 2 and 3 as appropriate.

6.3 Materials and methods

6.3.1 Occurrence and bathymetric distribution

Catch data of both species from fishery-independent surveys covering much of the Northeast Atlantic range were extracted from the Database of Trawl Surveys (DATRAS) hosted by ICES (https://ices.dk/data/data-portals/Pages/DATRAS.aspx). The full catch data (termed 'exchange data') from seven surveys were extracted from 2000–2017 (Table 26).

A total of 15,842 unique survey hauls were considered, including those with zero catch of either species. Data from all stations were mapped to show species occurrence in relation to the survey area using R software version 3.4.3 (R Core Team, 2017) and the ggplot2 (Wickham, 2016) and mapdata packages (Brownrigg, 2018). Bathymetry data were sourced from the General Bathymetric Chart of the Ocean (GEBCO, 2016) online repository. Catches were plotted as actual numbers caught, rather than Catch Per Unit Effort (CPUE), given the low catch rates encountered.

Table 26: Summary of ICES DATRAS data used in analyses.

Survey name	Year From	Year To	Missing years in time-series[19]
Q1 North Sea International Bottom Trawl Survey (Q1 NS-IBTS)	2000	2017	
Q3 North Sea International Bottom Trawl Survey (Q3 NS-IBTS)	2000	2017	
Irish Groundfish Survey (IGFS)	2003	2017	
Spanish Porcupine Bank Survey	2001	2017	
Scottish Rockall Bank	2001	2016	2004, 2010, 2017
Scottish West Coast Survey	2000	2017	
French Southern Atlantic Bottom Trawl Survey (EVHOE)	2000	2016	2017

[19] Either due to survey design or other factors such as ship breakdown.

6.3.2 Biology

Cadavers were retained from fishery-independent surveys for subsequent biological study. The EVHOE survey of the Celtic Sea obtained samples of both species between 2014–2019. Additional specimens of *L. circularis* were retained from the Spanish Porcupine bank survey and further specimens of *L. fullonica* were retained from UK (Cefas) fishery-independent surveys and Cefas' observer programme. All specimens were initially frozen prior to detailed examination in the laboratory (see Table 27 for measurements collected). Some specimens that were subjected to more prolonged freezing were dehydrated and therefore excluded from length-weight analyses. Initial biological sampling of cadavers involved the same two scientists, to ensure consistency in data collection, with at least one of these scientists involved in all subsequent sampling events. This was undertaken to minimise sampler bias. Maturity for males was assigned based on gross external examination and measurement of the claspers and internal inspection of the testes. For females, maturity was assigned following internal examination of the ovaries, examination and measurements of oocytes and the nidamental gland. Specimens were classified as immature (A), developing (B), mature (C), or active (D), according to the maturity key given in Table 28.

Table 27: Parameters collected from the *L. circularis* and *L. fullonica* cadavers.

Parameters collected from all specimens	Sex-specific parameters collected
Sex	Males: Outer clasper length[20] (mm)
Total length (L_T cm)	Males: Inner clasper length[21] (mm)
Disc width (mm)	
Total weight (g)	Females: Nidamental gland width (mm)
Liver weight (0.1 g)	Females: Number of mature follicles
Gonad weight (0.1 g) (including epigonal organ)	Females: Maximum follicle diameter (mm)
Weight of stomach contents (0.1 g)	
Gutted weight (g)	
Maturity stage	
Stomach 'fullness' score (0–10)	
Identification of stomach contents	

Biological data were also analysed using R software version 3.4.3 (R Core Team, 2017), with Figures generated using the ggplot2 (Wickham, 2016) package. Trend lines were fitted to the

[20] The outer distance along the clasper from the connection to the pelvic fin to the tip of the clasper.
[21] The inner distance along the clasper from the posterior margin of the cloaca to the tip of the clasper.

data (excluding total length to wing width) using a smoothed conditional mean fitting local regression to the data (loess fit). The relationship between total length and wing width was represented as a straight line.

Table 28: Maturity scale used in the present study.

Maturity stage	Males	Females
A (Immature)	Claspers undeveloped, shorter than extreme tips of posterior margin of pelvic fin Testes small and thread-shaped	Ovaries small, gelatinous, or granulated, but with no differentiated oocytes visible Oviducts small and thread-shaped, width of shell gland not much greater than the width of oviduct
B (Developing)	Claspers longer than posterior margin of pelvic fin, their tips more structured, but claspers soft and flexible and cartilaginous elements not hardened Testes enlarged, sperm ducts beginning to meander	Ovaries enlarged and with more transparent walls. Oocytes differentiated in various small sizes (<5 mm). Oviducts small and thread-shaped, width of shell gland greater than width of the oviduct, but not hardened
C (Mature)	Claspers longer than posterior margin of pelvic fin, cartilaginous elements hardened, and claspers stiff Testes enlarged, sperm ducts meandering and tightly filled with sperm	Ovaries large with enlarged oocytes (>5 mm), with some very large, yolk-filled oocytes (ca. 10 mm) also present Uteri enlarged and wide, shell gland fully formed and hard
D (Active)	**Clasper reddish and swollen, sperm present in clasper groove, or flowing if pressure exerted on cloaca**	Egg capsules beginning to form in shell gland, partially visible in uteri, or egg capsules fully formed and hardened and in oviducts/uteri, or egg case being exuded from cloaca

6.3.3 Diet analysis

The stomachs of 111 specimens of *L. circularis* (21–116 cm L_T) and 41 specimens of *L. fullonica* (29–100 cm L_T) were dissected from the body cavity and the contents examined. The fullness of the cardiac stomach was estimated on a scale of 0–10, 0 being empty and 10 being full. The contents of the cardiac stomach were then placed into a sorting tray and weighed to the nearest 0.1 g. Contents were identified to the lowest possible taxon, either macroscopically or with a stereomicroscope and individual prey taxa counted. Prey taxa were also scored using a points system, where scores (which totalled 10 for each specimen containing food) were allocated to each prey taxa proportionally. The stomach fullness was multiplied by the points to give a semi-quantitative index of relative prey volume (Hyslop, 1980). The proportion of fish with empty stomachs (i.e. fullness score = 0) was used to calculate the index of vacuity and along with specimens with everted stomachs (therefore preventing the mass of stomach contents and fullness to be recorded) were excluded from further analysis.

In order to quantify the diet, the following indices were calculated for each prey taxon in the diet of both species:

- Frequency of occurrence (%O) - the percentage of all the stomachs that contained food in which each prey taxon was observed.
- Percentage by number (%N) - the total number of each prey taxon as a percentage of the total number of enumerated prey items. Digested remains which could not be enumerated were given a nominal abundance of one.
- Percentage by points (%P) - the sum of relative prey volumes (i.e. fullness × points) for each prey taxon as a percentage of the total scores for all prey taxa.
- Index of relative importance (IRI), calculated as:
  IRI = (%N + %P) x %O (Pinkas *et al*., 1971)
- Percentage of relative importance (%IRI) expressed as IRI divided by the sum of all IRI, multiplied by 100 (%IRI = (IRI/∑IRI) x 100) (Cortés, 1997)

Inanimate objects found in stomachs, such as hook and monofilament line were recorded, but with no points or counts assigned and were only recorded as the frequency of occurrence (%O) and excluded from calculations of %IRI.

6.4 Results

6.4.1 Geographical and bathymetric distributions

6.4.1.1 *Leucoraja circularis*

Records of *L. circularis* were closely associated to the outermost part of the continental shelf and slope waters along the Celtic Sea, and around the Porcupine Bank (Figure 25). Occasional records were made from the Rockall bank and northern North Sea. The nominal record made from the shallower water of the central North Sea are outside of their geographical range and are likely misidentifications (Bird *et al*., 2020).

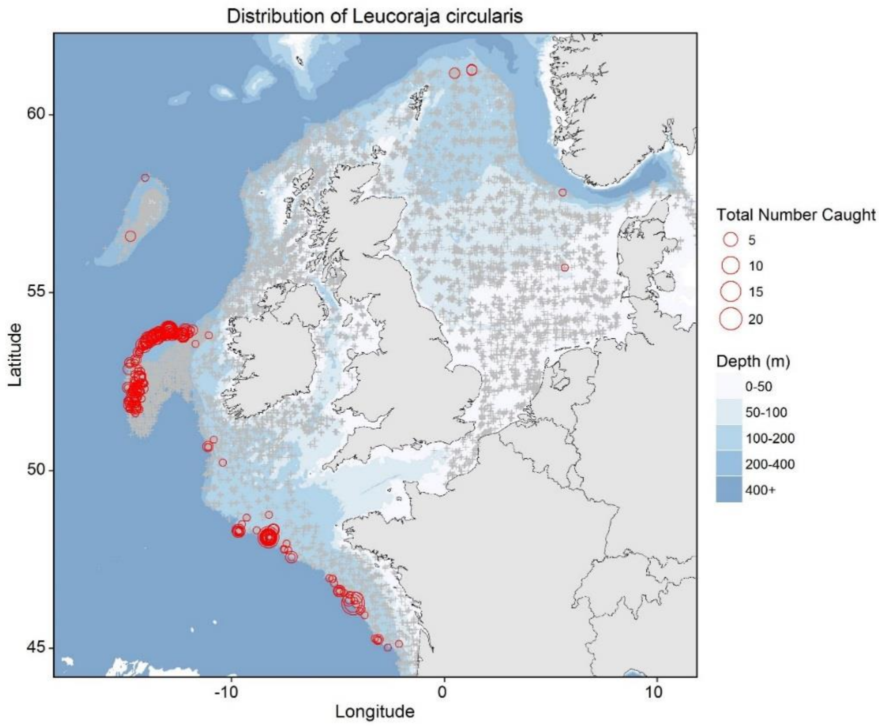

Figure 25: Occurrence of *L. circularis* in the Northeast Atlantic from fishery-independent surveys (grey cross indicates a station with zero catch). See Table 26 for the list of surveys considered.

The number of catch records was low, with a total of 669 individuals, primarily from the Spanish Porcupine Bank survey (64%) and the French EVHOE survey (34%; Table 29). CPUE in the EVHOE survey was greatest at depths of 301–400 m at 1.4 ind.h^{-1} but remained relatively high at 401–500m at 1.3 ind.h^{-1} (Table 30).

Table 29: Numbers of *L. circularis* and *L. fullonica* present in fishery-independent survey data.

Survey	*L. circularis*		*L. fullonica*	
	Total number	%	Total number	%
French Southern Atlantic Bottom Trawl Survey (EVHOE)	226	33.78	243	67.11
Irish Groundfish Survey (IGFS)	3	0.45	22	6.08
North Sea International Bottom Trawl Survey (NS-IBTS)	8	1.20	46	12.72
Scottish Rockall Bank	3	0.45	46	12.70
Spanish Porcupine Bank Survey	429	64.13	0	0
Scottish West Coast Survey	0	0	5	1.38
Total	**669**		**362**	

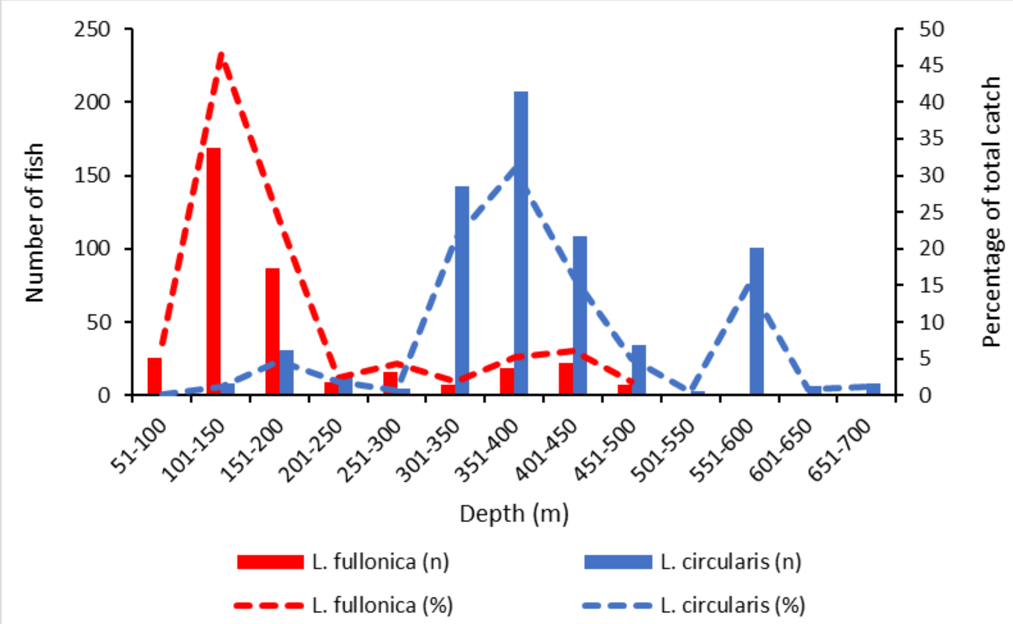

Figure 26: Numbers and percentage of *L. circularis* (blue) and *L. fullonica* (red) caught at each depth band.

Table 30: Nominal CPUE of *L. circularis* in EVHOE survey by year and depth band.

Year	Depth band (m)					
	101-200	201-300	301-400	401-500	501-600	Total
2000	0.02	0.00	0.00	0.00		0.02
2001	0.02	0.00	1.83	0.00	0.00	0.16
2002	0.08	0.00	2.34	1.38	0.00	0.50
2003	0.04	0.34	1.18	1.13	1.00	0.17
2004	0.12	0.00	0.00	1.48	0.00	0.30
2005	0.00	0.67	1.68	1.00	0.00	0.28
2006	0.08	0.80	0.00	1.62	0.00	0.34
2007	0.00	0.00	0.00	2.00	0.00	0.43
2008	0.00	0.00	0.00	1.67	0.00	0.14
2009	0.00	0.00	0.00	0.00	0.00	0.00
2010	0.00	0.00	0.00	0.33	0.00	0.02
2011	0.02	0.00	0.00	0.40	0.00	0.03
2012	0.03	0.00	1.24	0.50	0.00	0.08
2013	0.07	0.97	0.00	1.28	0.67	0.18
2014	0.02	0.28	0.00	1.08	0.00	0.09
2015	0.08	0.56	0.00	0.29	0.00	0.10
2016	0.04	0.29	0.00	1.33	0.00	0.09
Total	0.04	0.26	1.39	1.28	0.11	0.18

In the Porcupine Bank survey, the CPUE was highest at greater depths of 501–600 m at 1.04 ind.h^{-1}, however, an additional peak was also seen at 301–400 m of 1.01 ind.h^{-1} (Table 31).

The proportion of hauls across all surveys with a positive catch was greatest (0.9%) in the 301–400 m depth band. Positive catches from all surveys indicated that 31% of specimens were from the 351–400 m depth band (dominated by EVHOE records), with another peak (15%) found at the 551–600m depth band (dominated by Porcupine Bank records; Figure 26).

Table 31: Nominal CPUE of *L. circularis* in Porcupine Bank survey by year and depth band.

Year	Depth band (m)					
	201-300	301-400	401-500	501-600	601-700	Total
2001	0.00	0.36	0.13	0.00	0.00	0.15
2002	0.11	0.50	0.00	0.57	0.00	0.25
2003	0.00	0.82	0.14	1.28	0.00	0.61
2004	0.00	0.54	0.00	0.00	0.00	0.21
2005	0.00	1.14	0.56	0.00	0.00	0.58
2006	0.16	0.33	0.20	0.84	0.00	0.31
2007	0.00	1.16	0.00	1.86	0.00	0.78
2008	0.00	0.40	0.22	2.40	0.00	0.58
2009	0.00	0.73	0.21	1.04	0.00	0.44
2010	0.00	0.90	0.00	1.50	0.00	0.50
2011	0.00	1.23	0.00	0.55	0.39	0.63
2012	0.17	1.32	0.21	1.25	0.00	0.83
2013	0.00	1.25	0.00	1.07	0.86	0.78
2014	0.00	1.19	0.43	1.90	0.28	0.95
2015	0.00	1.27	0.91	0.93	1.44	0.96
2016	0.00	1.41	0.80	0.25	0.75	0.77
2017	0.00	1.70	0.60	0.00	0.00	0.87
Total	0.03	1.01	0.29	1.04	0.22	0.62

6.4.1.2 *Leucoraja fullonica*

Records of *L. fullonica* were primarily located along the continental shelf of the Celtic Sea, from the areas west of Brittany to the south coast of Ireland and also around the Rockall Bank (Figure 27), with some catches seen in the northern North Sea around the Shetland Isles, and occasional records from the Scottish west coast. There was little overlap in the distribution of *L. fullonica* with *L. circularis*. Of the six surveys examined (Table 26) across the up to 18-year time-series, only the EVHOE survey had hauls where both species were represented. Of the 136 hauls with *L. fullonica* present, just 13% of these also had catches of *L. circularis* which were primarily in waters >300 m depth.

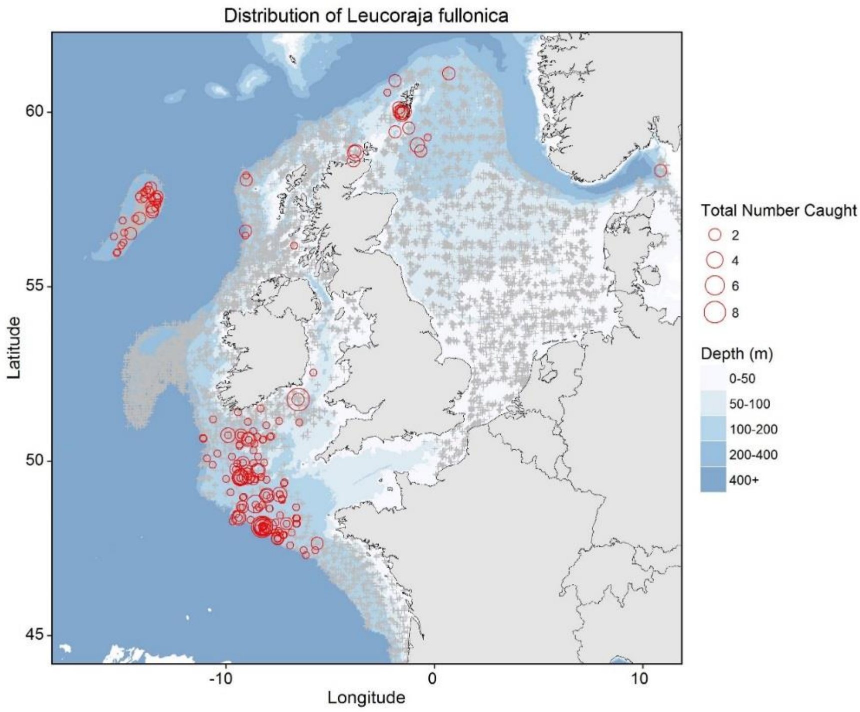

Figure 27: Occurrence of *L. fullonica* in the Northeast Atlantic from fishery-independent surveys (grey cross indicates a station with zero catch). See Table 26 for the list of surveys considered.

Catch records were limited, with records of 362 individuals present in the data, primarily from the EVHOE (67%), Rockall (12%) and North Sea IBTS (12%) surveys (Table 29). CPUE of the EVHOE survey was greatest (0.77 $ind.h^{-1}$) at depths of 301–400 m (Table 32), although, the proportion of hauls across surveys with a positive catch was greatest (1.1%) at the 101–200 m depth band. Positive catches from all surveys, indicated that 47% of individuals were made between 101–150 m (dominated by EVHOE records; Figure 26).

6.4.2 Sex ratio in fishery-independent surveys

The sex ratio of both species found within catches was significantly different (chi-squared test, $P<0.05$), with 256 males to 368 female *L. circularis* (1:1.44) and 134 males to 182 female *L. fullonica* (1:1.36). This was clearer at the larger length classes (Figure 28). The fishery-independent surveys caught fish across much of the perceived length range: *L. circularis*: 13–115 cm L_T and *L. fullonica*: 16–105 cm L_T (Figure 28).

Table 32: Nominal CPUE of *L. fullonica* in EVHOE survey by year and depth band.

Year	Depth band (m)					
	1–100	101–200	201–300	301–400	401–500	Total
2000	0.00	0.09	0.00	0.00	0.00	0.07
2001	0.08	0.26	0.29	1.85	0.32	0.36
2002	0.00	0.27	0.00	0.69	1.26	0.24
2003	0.00	0.27	0.76	1.48	0.77	0.32
2004	0.00	0.22	0.00	0.00	1.33	0.24
2005	0.00	0.15	0.40	0.50	0.00	0.13
2006	0.00	0.22	0.00	0.00	1.33	0.23
2007	0.00	0.38	0.00	0.00	0.40	0.29
2008	0.00	0.17	0.00	0.00	0.67	0.14
2009	0.00	0.19	0.00	0.00	0.00	0.13
2010	0.00	0.29	0.00	0.80	0.00	0.22
2011	0.58	0.08	0.57	0.00	0.33	0.23
2012	0.00	0.13	0.00	0.00	0.50	0.09
2013	0.00	0.18	0.89	0.00	0.52	0.19
2014	0.00	0.04	0.00	0.00	0.65	0.05
2015	0.00	0.24	0.32	0.00	0.29	0.19
2016	0.00	0.10	0.67	1.33	0.00	0.13
Total	0.05	0.19	0.26	0.77	0.61	0.19

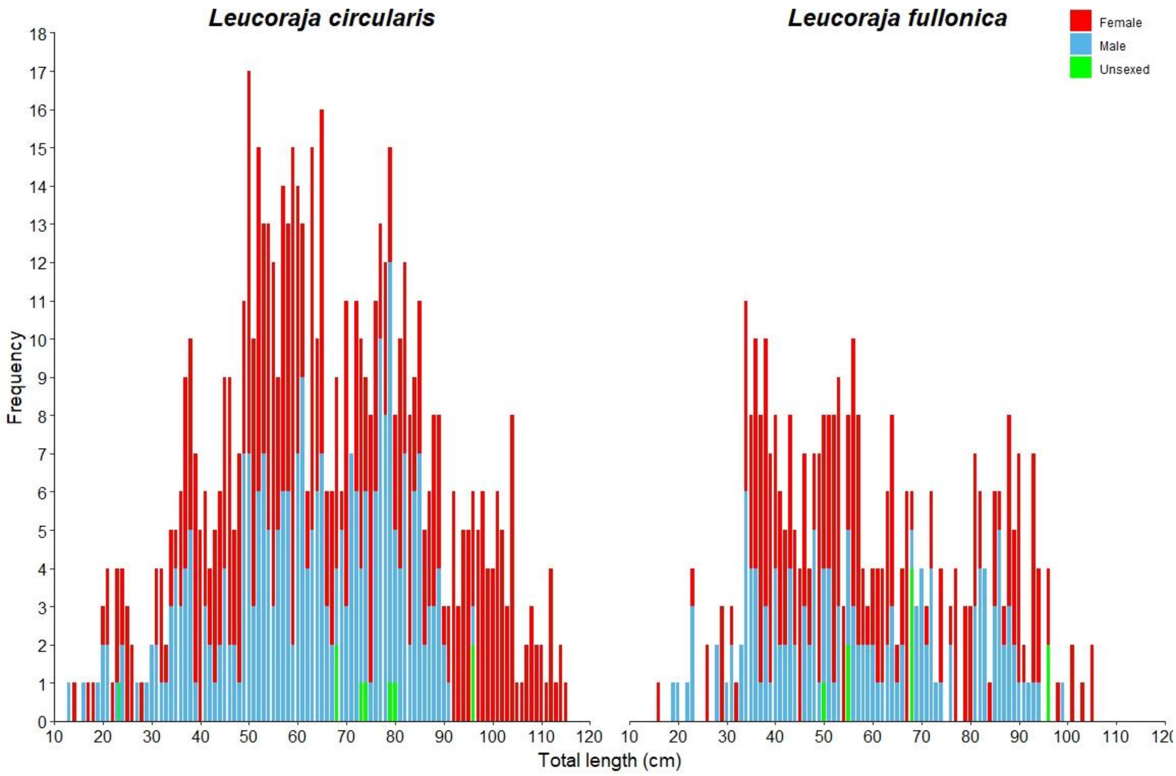

Figure 28: Length range by sex for *L. circularis* and *L. fullonica* caught in fishery-independent trawl surveys (2000–2017).

6.4.3 Biological investigations

Biological data were collected from 116 specimens of *L. circularis* (47 male: 23–93 cm L_T and 69 female: 21–116 cm L_T) and 54 specimens of *L. fullonica* (25 male: 19–86 cm L_T and 29 female: 28–100 cm L_T; Figure 29).

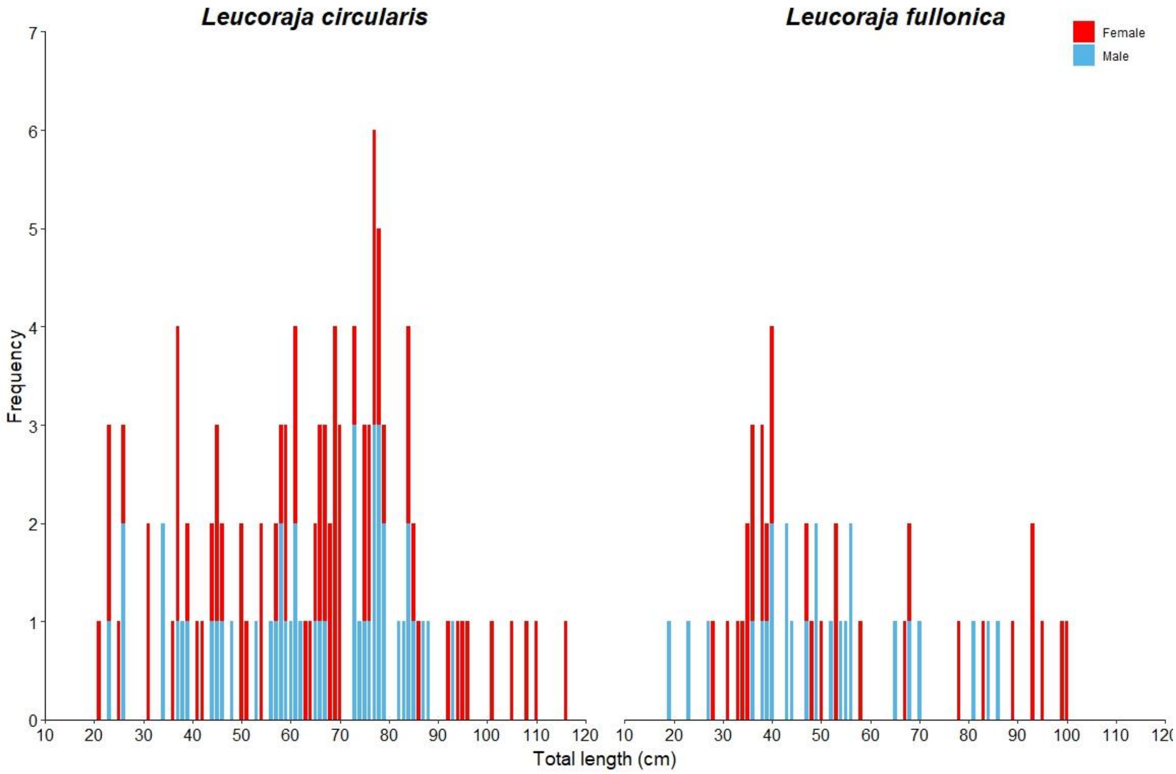

Figure 29: Length frequency of *L. circularis* and *L. fullonica* specimens retained for biological examination (2014–2019).

6.4.3.1 Conversion factors

The relationship between total length and weight in the specimens (by sex) sampled was very similar between the two species, especially in the smaller specimens (Figure 30). *L. circularis*, the larger of the two species, were significantly heavier at a given total length than *L. fullonica* (paired two sample t-test; $p < 0.001$; Table 33). The relationship between eviscerated (gutted) weight to length was also determined (Figure 31) to augment data collected during market sampling programmes. Again, the relationship was very similar between the species, with large overlap within the 95% confidence limits throughout most of the size range. These relationships were not examined by sex, given the small sample size. The linear relationship between total length and wing width (Figure 32) was very similar between the species (Table 33).

Table 33: Conversion factors for life-history parameters.

Relationship $y=ax^b$ (unless specified)	*L. circularis*				*L. fullonica*				Figure
	a	***b***	r^2	***n***	***a***	***b***	r^2	***n***	
Length weight	0.0016	3.2858	0.995	111	0.0010	3.3664	0.993	52	Figure 30
Length gutted weight	0.0016	3.2602	0.993	112	0.0017	3.2080	0.992	46	Figure 31
Length wing width ($y = aL_T+b$)	0.6454	-2.9240	0.994	116	0.6582	-3.7822	0.995	52	Figure 32
Length liver weight	$9.5101e^{-06}$	3.7975	0.973	114	$4.8358e^{-06}$	3.9711	0.982	46	Figure 33

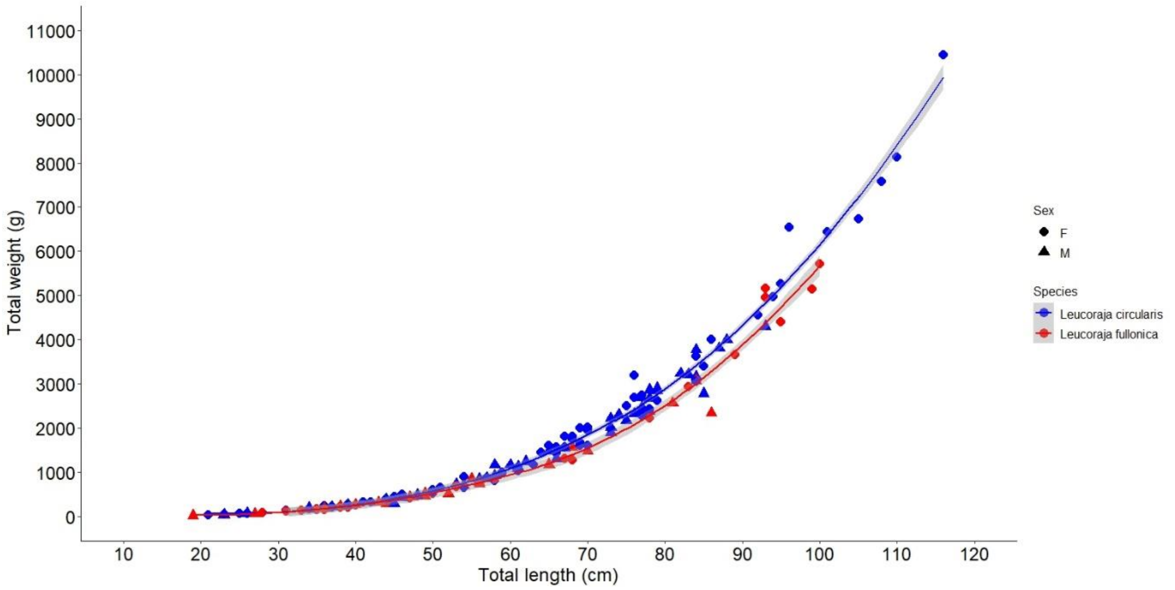

Figure 30: Relationship between total weight and total length (95% confidence interval shaded) for *L. circularis* and *L. fullonica*.

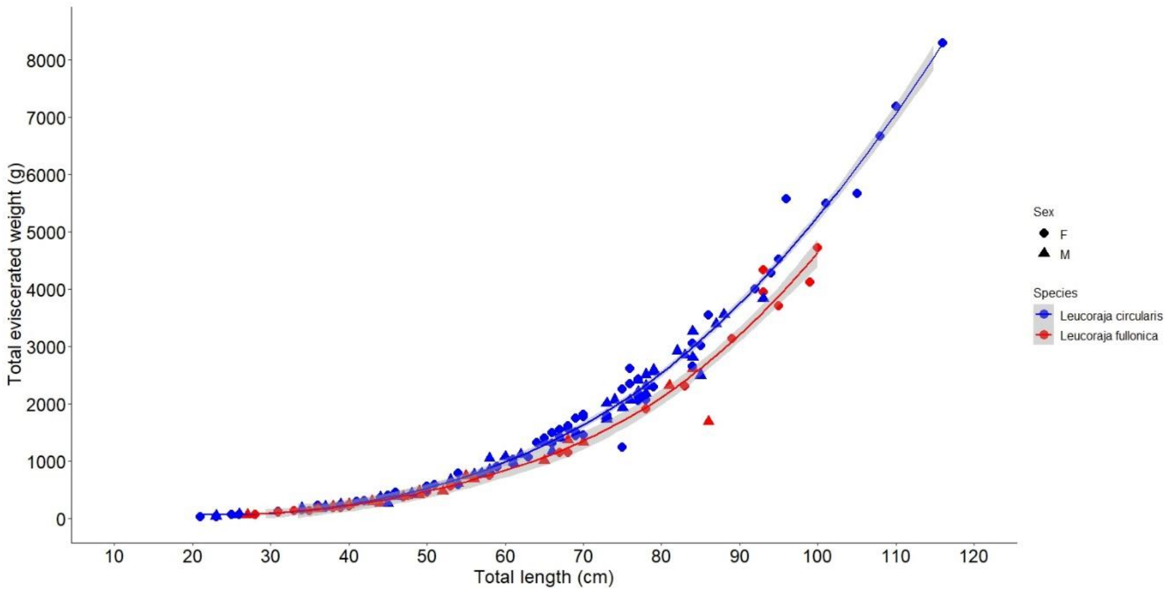

Figure 31: Total length to gutted weight relationship (95% confidence interval shaded) for *L. circularis* and *L. fullonica*.

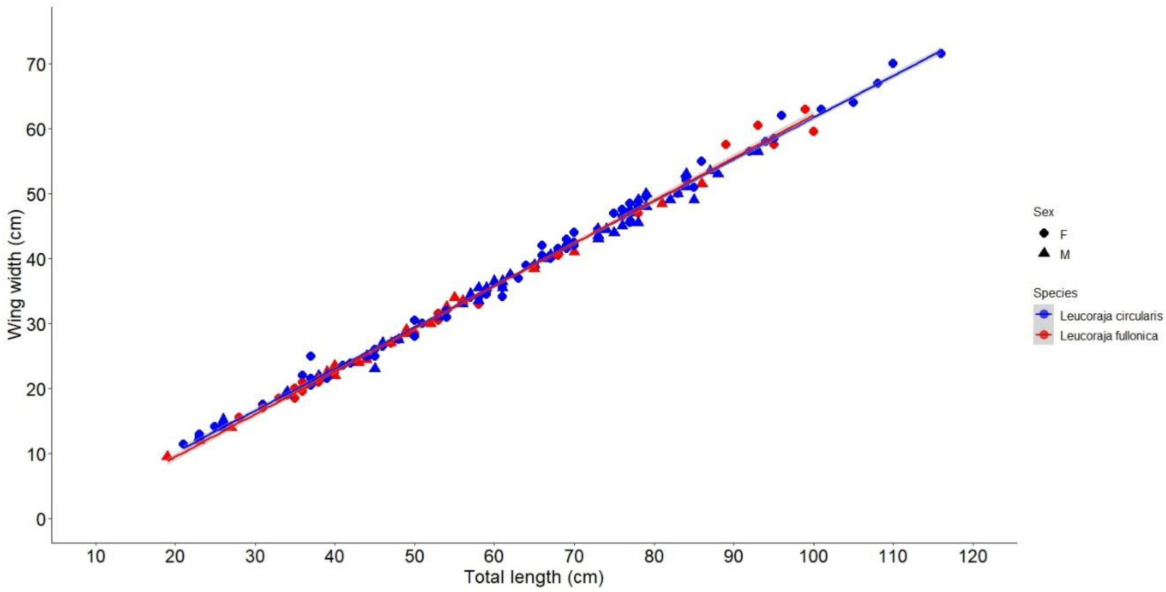

Figure 32: Wing width to total length relationship (95% confidence interval shaded) for *L. circularis* and *L. fullonica*.

6.4.3.2 Hepato-somatic index (I_H)

Livers were removed and weighed for each specimen, to examine the relationship between liver weight and total length (Figure 33). This can give insight into the reproductive cycle of elasmobranch fish and will vary according to factors including sex, maturity stage and season (Oddone and Velasco, 2006). The relationship in both specimens shows a relatively strong exponential trend (r^2 of 0.97 and 0.98 for *L. circularis* and *L. fullonica* respectively). However, this relationship is more variable for large (ca. >80 cm L_T) female *L. circularis* (n = 13), and more data for the different maturity stages are required. There was much closer relationship for the largest (>80 cm L_T) female *L. fullonica* (n = 7).

The liver weight can also be expressed as a percentage of body weight (the hepato-somatic index, I_H; Table 34), which is a frequently used indicator of the energy reserve in an animal (thus the lowest values are usually seen in females nearing the end of the reproductive cycle (McCully Phillips and Ellis, 2015)). The average I_H across all samples was 5.14 (5.07 for *L. circularis* and 5.46 for *L. fullonica*), with the smallest (2.27) exhibited by the smallest sandy ray (L_T = 21cm). The largest index (10.28) was from a mature male *L. fullonica* (L_T = 86cm), with the largest female *L. fullonica* (L_T = 100) having a lower I_H (6.62), possible linked to the presence of large mature follicles (22 mm) which would reduce the available energy reserve. Two further mature female *L. fullonica*, with smaller maximum follicle sizes (11 and 17.5 mm) had higher I_H of 9.47 and 9.73 respectively. The largest mature *L. circularis* specimens (females 105–116 cm L_T n=4) had I_H ranging from 3.50–7.60. In general, the I_H increased with maturity stage (Table 34), except for male *L. circularis* with the developing stage (B) having a great average I_H than the mature (stage C) specimens. There were a lack of specimens of both species at stage D (active) and also developing (stage B) *L. fullonica*.

Table 34: Hepato-somatic index (I_H) of *L. circularis* and *L. fullonica* sampled by sex and maturity stage.

Maturity Stage	**Mean I_H (*L. circularis*)**		**Mean I_H (*L. fullonica*)**	
	Female (n)	Male (n)	Female (n)	Male (n)
A	4.83 (53)	4.38 (23)	4.58 (17)	4.89 (19)
B	5.83 (9)	6.08 (12)	6.99 (4)	-
C	6.01 (5)	5.51 (11)	8.10 (5)	7.64 (3)
D	-	-		

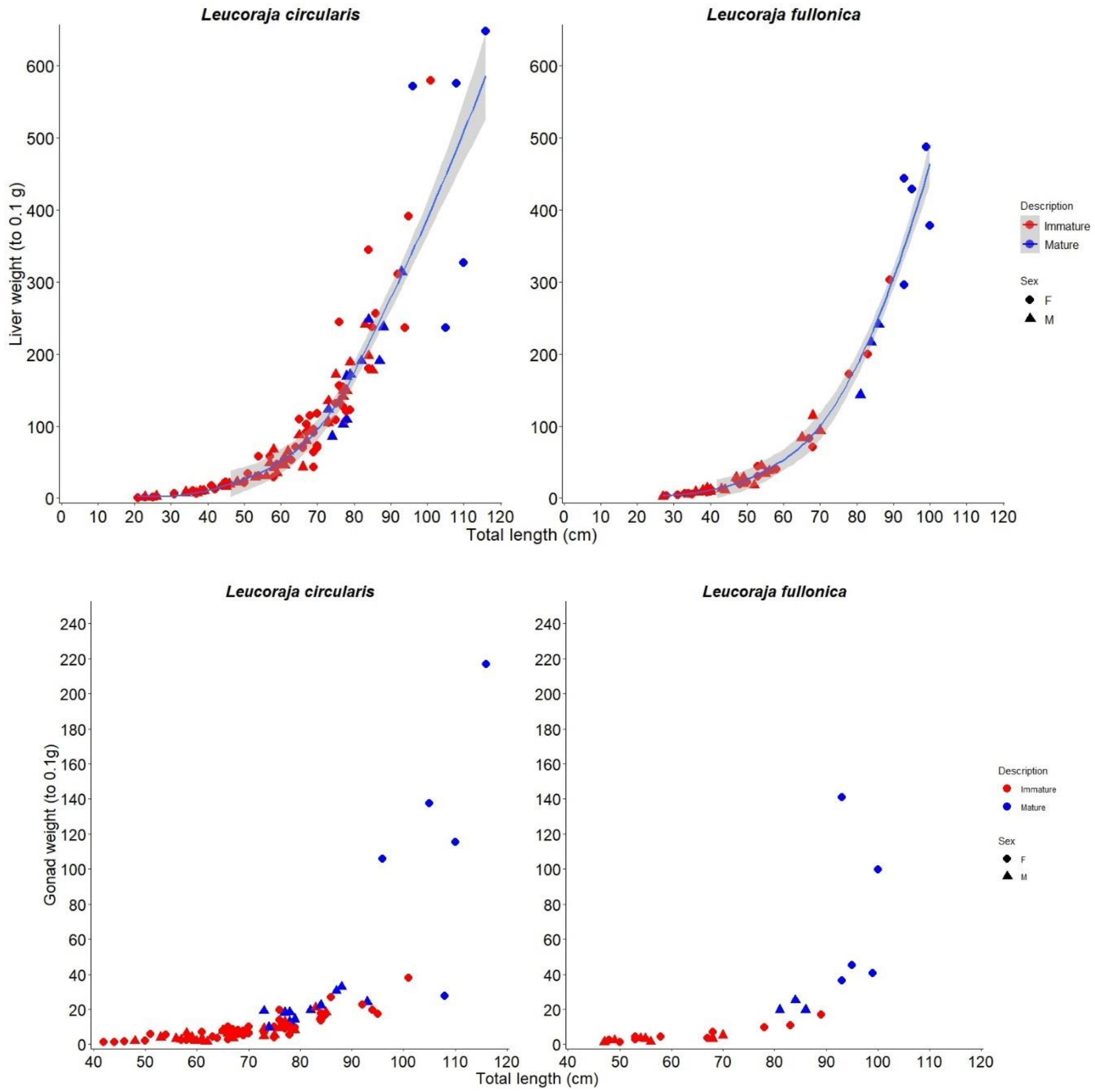

Figure 33: Relationship between total length and liver weight (95% confidence interval shaded) for *L. circularis* and *L. fullonica* (top) and relationship between total length and gonad weight for *L. circularis* and *L. fullonica* (bottom; data <1g not shown, i.e. no fish <40 cm L_T plotted).

6.4.3.3 Gonado-somatic index (I_G)

The association between gonad weight and total body length (Table 33; Figure 33) is expressed as the gonado-somatic index (I_G), and the average I_G by sex and maturity stage is given in Table 35. As expected, this increased over development to the 'mature' stage. *L. circularis* have heavier mean gonad weights at every sex and maturity combination expect for mature males, where *L. fullonica* have larger average gonad weights.

Table 35: Mean gonad weight and gonado-somatic index (I_G) by sex and maturity.

Maturity stage	*L. circularis*		*L. fullonica*	
	Female Gonad weight (I_G; n)	Male Gonad weight (I_G; n)	Female Gonad weight (I_G; n)	Male Gonad weight (I_G; n)
A	5.20 (0.36; n = 53)	2.34 (0.27; n = 22)	1.81 (0.28; n = 17)	1.48 (0.23; n = 19)
B	16.47 (0.46; n = 9)	10.87 (0.45; n = 12)	9.55 (0.52; n = 4)	-
C	120.7 (1.50; n = 5)	20.16 (0.64; n = 11)	72.50 (1.40; n = 5)	21.50 (0.81; n = 3)

6.4.3.4 Maturity

The estimated length at 50% maturity (L_{50}) for L. circularis was 100cm L_T for females and 81 cm L_T for males (Figure 34). The model would not fit for *L. fullonica*, given the limited data and therefore no ogives are given. Table 36 indicates the sizes of the smallest mature and largest immature fish, with data for *L. fullonica* indicating that an L_{50} would likely be slightly smaller than that of *L. circularis*.

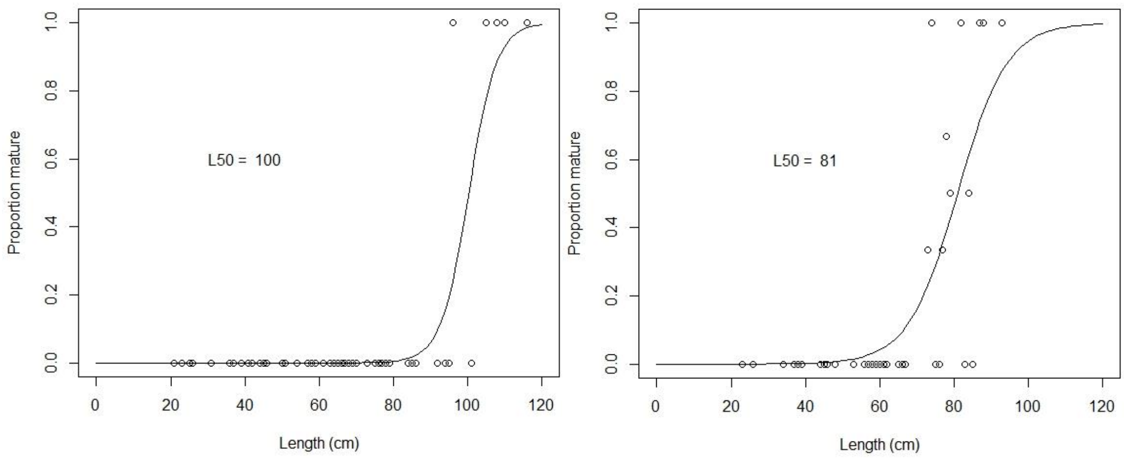

Figure 34: Maturity ogives for female (left) and male (right) *L. circularis*.

Table 36: Maturity estimates (number of samples given in brackets).

	L. circularis		*L. fullonica*	
	Female	*Male*	*Female*	*Male*
Estimated L_{50}	100 cm	81 cm	na	na
Smallest mature	96 cm (n = 5)	73.5 cm (n = 11)	93.5 cm (n = 5)	81 cm (n = 3)
Largest immature	101 cm (n = 64)	85 cm (n = 36)	89 cm (n = 24)	70 cm (n = 22)

Quantitative data were collected for nidamental gland width, which is closely associated with maturity. Figure 35 shows this relationship for immature and mature females of both species.

In *L. circularis* the distinction between immature and mature specimens is clearly defined with immature nidamental glands attaining ~20 mm width and mature specimens exceeding ~ 40 mm in width. The distinction is not as clear in *L. fullonica* but looks likely to occur around 25 mm width.

Similar to the nidamental gland width in females, clasper length of males can also provide a quantitative measure of maturity to augment the qualitative assignment of maturity scales. The outer and inner clasper lengths to total length relationship for the males, by maturity stage, is shown in Figure 36. In *L. circularis,* the outer clasper length (L_{OC}) measurement provided a clear distinction between immature and mature specimens with the outer claspers of all mature fish exceeding ~90 mm. The inner clasper length (L_{IC}) measurement was not as well defined with overlap of developing and mature specimens in the 150–180 mm L_{IC} range. Beyond 180 mm L_{IC}, all fish were mature. A lack of developing and mature specimens of *L. fullonica* prohibit robust interpretation of clasper data with the switch between immature and mature fish occurring between 70–180 mm L_{IC} and 30–110 mm L_{OC}.

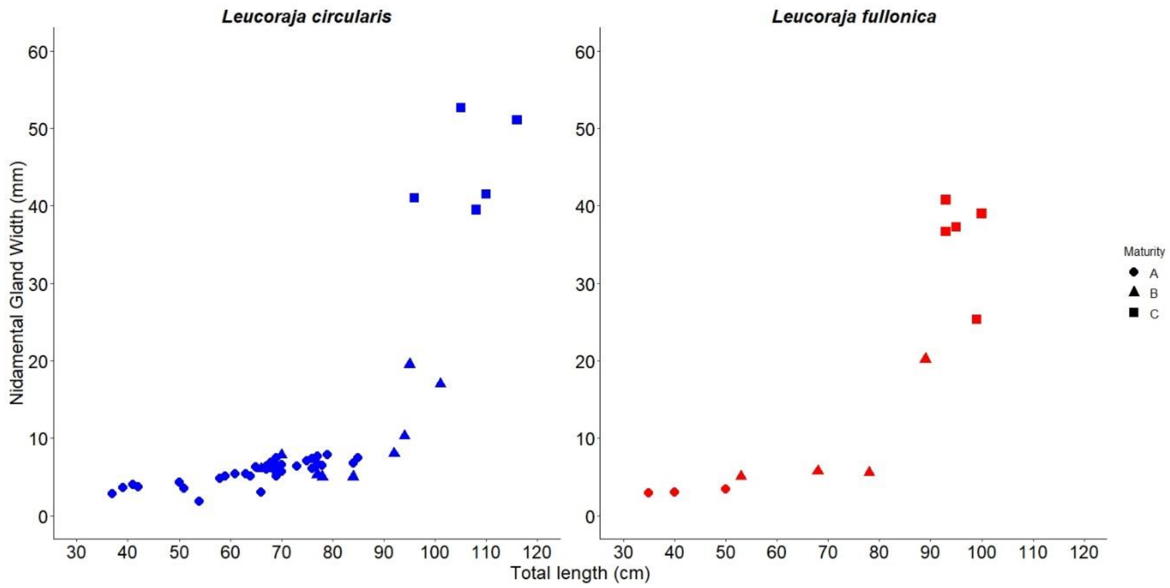

Figure 35: Relationship between nidamental gland width and total length in *L. circularis and L. fullonica*.

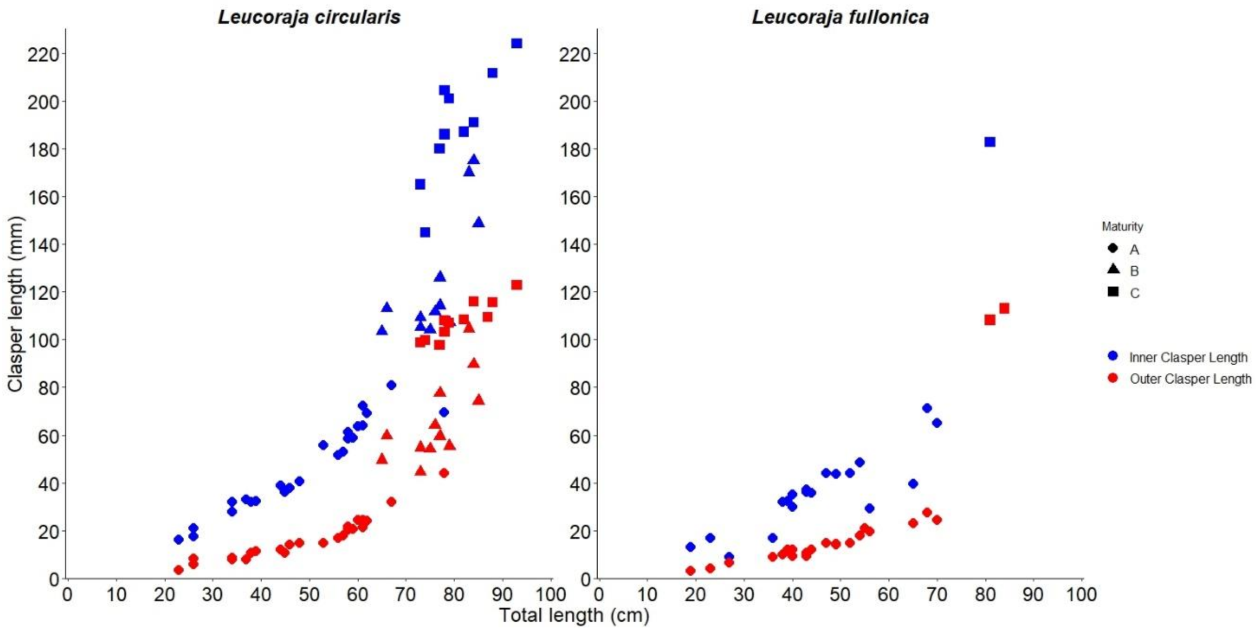

Figure 36: Relationship between inner and outer clasper length and total length in *L. circularis* and *L. fullonica*.

6.4.4 Diet composition and stomach fullness

The weights of the stomach contents for *L. circularis* ranged from 0–680 g, averaging 26.1 g (n = 111; Table 37). The heaviest weight was recorded in the largest fish within the samples (116 cm L_T) with fish recording stomach content weights of <1 g ranging from 21–76 cm L_T. The index of vacuity was low at 2.7% (n = 3) and one fish had an everted stomach.

The identification of most prey items to species level was not possible[22], with the top five prey items belonging to generic categories and digested remains. The most important prey types accounting for 95% of the diet in terms of %IRI, were crustacean remains (59% O; 75% IRI), digested remains (37% O; 10% IRI), fish remains (23% O; 7% IRI), unidentified shrimp (15% O; 4% IRI), unidentified brachyuran crabs (14% O; 2% IRI) and unidentified amphipods (13.5% O; 2% IRI). Fish comprised approximately 7% IRI in the diet of *L. circularis*, with at least five different species identified, including the commercially important boarfish *Capros aper* (Figure 37) and gadoid species. A further 2% IRI of the diet was described by a variety of higher taxonomic classes including: polychaetes, amphipods, euphausiids, isopods, molluscs and echinoderms. Four individuals were found to have digested remains of other elasmobranchs; although not identified to species level given the advanced digestion, it is suspected that two individuals were predating on lesser-spotted dogfish *Scyliorhinus*

[22] Specimens were frozen at sea, transported to institutes and defrosted prior to examination, thus resulting in the stomach contents having a more digested state.

canicula. One individual had a hook and monofilament line in its stomach; apart from some minor bruising to the inner stomach lining, it did not appear to have damaged or perforated the stomach wall (Figure 37).

The weights of the stomach contents for *L. fullonica* ranged from 0–389 g, averaging 34.4 g (n = 41). The heaviest stomach contents weight of 389 g was recorded in a 99 cm L_T female, with fish recording stomach content weights of <1 g ranging from 29–39 cm L_T. The index of vacuity was 7.3% (n = 3). Like *L. circularis*, crustacean remains were the most important (41% O; 68% IRI) prey type identified. However, *L. fullonica* was more piscivorous, with fish remains, lesser-spotted dogfish, cuckoo ray *Leucoraja naevus*, boarfish and horse mackerel *Trachurus trachurus* making up 18.5% IRI. Two specimens had cuckoo rays in their stomachs, with one 86 cm L_T specimen containing a 37 cm L_T cuckoo ray[23] (Figure 38). Four specimens contained lesser-spotted dogfish, one of which had consumed 13 juveniles up to 22 cm L_T. The overall diversity of species found in the diet was less than *L. circularis*, with an absence of isopods in the diet.

Figure 37: Stomach contents of *L. circularis* showing 20 *Capros aper* found in the stomach of a 99cm L_T female (left) and the 15mm hook and monofilament line found in the stomach of a 75cm L_T male (right).

Figure 38: Stomach contents of *L. fullonica* showing a freshly consumed 37 cm L_T cuckoo ray.

[23] Whilst it is possible that this specimen had been consumed in the net (given the low rate of digestion), it was fully contained in the cardiac stomach. However, another specimen was found with the more digested remains of a cuckoo ray in the stomach.

Table 37: Diet composition of *L. circularis* and *L. fullonica*, showing % occurrence, % numbers, % points, IRI and %IRI.

Higher taxa	Prey taxa	*Leucoraja circularis* (n = 111)								*Leucoraja fullonica* (n = 41)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
Polychaeta	Polychaeta (indet.)	3	4	15	2.70	0.46	0.47	2.50	0.04	1		5	2.44	0.00	0.36	0.88	0.02
Amphipoda	Amphipoda	15	49	79	13.51	5.65	2.45	109.44	1.57	2	2	5	4.88	1.00	0.36	6.63	0.16
Euphausiacea	Euphausiacea	4	30	31	3.60	3.46	0.96	15.92	0.23	2	15	40	4.88	7.50	2.88	50.62	1.19
Isopoda	*Cirolana* spp.	1	1	2	0.90	0.12	0.06	0.16	<0.01								
	Eurydice spp.	1	1	2	0.90	0.12	0.06	0.16	<0.01								
	Cirolanidae (indet.)	5	12	24	4.50	1.38	0.75	9.58	0.14								
	Isopoda (indet.)	2	2	4	1.80	0.23	0.12	0.64	0.01								
Decapoda	*Solenocera membranacea*	3	4	24	2.70	0.46	0.75	3.26	0.05	1	1	20	2.44	0.50	1.44	4.73	0.11
	Processa spp.									2	4	32	4.88	2.00	2.30	20.99	0.49
	Crangon allmanni									1	2	12	2.44	1.00	0.86	4.54	0.11
	Pontophilus spinosus									1	1	2	2.44	0.50	0.14	1.57	0.04
	Crangonidae (indet.)	3	6	72	2.70	0.69	2.24	7.91	0.11	1	6	40	2.44	3.00	2.88	14.34	0.34
	Natantia (indet.)	1	1	2	0.90	0.12	0.06	0.16	<0.01	2	4	15	4.88	2.00	1.08	15.02	0.35
	Shrimp (indet.)	17	85	241	15.32	9.79	7.48	264.60	3.80	3	6	45	7.32	3.00	3.24	45.64	1.07
	Anomura (indet.)	1	1	6	0.90	0.12	0.19	0.27	<0.01								
	Corystes sp.	1	1	6	0.90	0.12	0.19	0.27	<0.01								
	Macropipus tuberculatus									1	1	3	2.44	0.50	0.22	1.75	0.04
	Portunidae (indet.)	2	2	10	1.80	0.23	0.31	0.97	0.01								
	Brachyura (indet.)	15	62	67	13.51	7.14	2.08	124.64	1.79	1	1	6	2.44	0.50	0.43	2.27	0.05
	Crustacea (indet.)	65	523	949	58.56	60.25	29.47	5254.20	75.48	17	107	230	41.46	53.50	16.55	2904.38	68.01
Mollusca	*Sepia elegans*									1	1	18	2.44	0.50	1.29	4.38	0.10

Higher taxa	Prey taxa	*Leucoraja circularis* (n = 111)								*Leucoraja fullonica* (n = 41)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Illex spp.	1	1	80	0.90	0.12	2.48	2.34	0.03								
	Squid (indet.)	1	1	30	0.90	0.12	0.93	0.94	0.01								
	Cephalopoda (indet.)	2	2	6	1.80	0.23	0.19	0.75	0.01								
Echinodermata	Echinoidea	1	1	2	0.90	0.12	0.06	0.16	<0.01								
Elasmobranchii	*Scyliorhinus canicula*									4	15	230	9.76	7.50	16.55	234.60	5.49
	Leucoraja naevus									2	2	170	4.88	1.00	12.23	64.54	1.51
	Elasmobranchii (indet.)	4	4	115	3.60	0.46	3.57	14.53	0.21								
Actinopterygii	*Argentina silus*	1	1	90	0.90	0.12	2.80	2.62	0.04								
	Argentina spp.	1	4	48	0.90	0.46	1.49	1.76	0.03								
	Myctophidae (indet.)	1	1	6	0.90	0.12	0.19	0.27	<0.01								
	Gaidropsarus macrophthalmus	1	1	6	0.90	0.12	0.19	0.27	<0.01								
	Gadidae (indet.)	3	3	23	2.70	0.35	0.71	2.86	0.04								
	Helicolenus dactylopterus	1	1	90	0.90	0.12	2.80	2.62	0.04								
	Trachurus trachurus									1	2	63	2.44	1.00	4.53	13.49	0.32
	Capros aper	1	2	70	0.90	0.23	2.17	2.17	0.03	2	21	103	4.88	10.50	7.41	87.37	2.05
	Teleostei (indet.)	4	4	84	3.60	0.46	2.61	11.06	0.16								
Pisces	Fish remains	25	26	565	22.52	3.00	17.55	462.66	6.65	10	7	173	24.39	3.50	12.45	388.93	9.11
Miscellaneous	Unidentified	1	1	6	0.90	0.12	0.19	0.27	<0.01								
	Digested remains	41	30	465	36.94	3.46	14.44	661.07	9.50	12	2	178	29.27	1.00	12.81	404.07	9.46
	Hook and monofilament line	1	1	0	0.90												
	Empty stomach	3								3							
	Everted stomach	1															

6.5 Discussion

This study provides the first biological investigations of these two data-limited skate species in the Northeast Atlantic. Outside of this stock area, there is a single study of *L. circularis* originating from 11 specimens (collected between 1971–2007) from the central Mediterranean Sea, with two mature specimens recorded at ca. 72 cm L_T for the male and 101 cm L_T for the female (Mnasri *et al*., 2009). Similarly, there is a single study of *L. fullonica* originating from the Mediterranean Sea (Zupa *et al*., 2010) detailing ten specimens ranging from 23–76 cm L_T (maturity scale used undefined), whilst Rae and Shelton (1982) provided information on the feeding habits of *L. fullonica* (n = 83) in Scottish waters.

The diets of the more common inshore skates around the British Isles have been relatively well studied (e.g. Ajayi, 1982; Ellis *et al*., 1996), however, the diets of offshore skate species are generally much less known (Gordon and Duncan, 1989). The preliminary feeding habits described in this study indicate that both species predate on other elasmobranchs, with both lesser-spotted dogfish and cuckoo ray present in the diet. Rae and Shelton (1982) also noted one instance of lesser-spotted dogfish in the diet of *L. fullonica* in Scottish waters, along with an eggcase from a black-mouth dogfish *Galeus melastomus*, however the diet was primarily based on teleosts including sand eel, herring and gadoids. Other prey taxa noted were cephalopods and crustaceans (euphausiids and pandalids). Data from the recent study were from further south, and the diet was primarily comprised of decapod crustaceans (70% IRI) although most prey occurrences were too digested to identify to species level[24]. However, piscivory was well represented, accounting for 18.5% IRI, with boarfish *Capros aper*, horse mackerel *Trachurus trachurus* and several unidentified fish remains being present alongside the elasmobranch remains. Cephalopods (*Sepia elegans*) and polychaetes were also present in smaller numbers. No published studies have described the feeding habits of *L. circularis*, with this study detailing a degree of piscivory (boarfish, lesser-spotted dogfish, bluemouth redfish *Helicolenus dactylopterus* and Argentinidae; accounting for 7% IRI) and teuthophagy (*Illex* spp.) but the diet was primarily dominated by decapod crustaceans (81% IRI). Given that both species described were found to predate upon two taxa of elasmobranchs, scyliorhinid catsharks and smaller skates, the former sometimes in large numbers (n = ≥13), it is likely that they could be important predators of elasmobranchs in the deeper waters of this ecoregion and could conceivably prey upon juvenile conspecifics. The presence of

[24] Digested stomach contents were not subject to molecular examination as this was beyond the scope and budget of this work. However, the relative contribution of such techniques and associated biases are discussed in Section 7.5.1.

elasmobranchs and fish in the diet would indicate that these species are at a high trophic level. This would indicate that they may biomagnify contaminants, since high concentrations of mercury have been observed in larger specimens (Nicolaus *et al*., 2017).

The low occurrence of these species in fishery-independent surveys (Figure 27 and Figure 25) has hampered the collection of biological data to date. Therefore, by adopting the multi-institute approach detailed in this Chapter, this has facilitated the collection of valuable life-history data for two very data-limited species. Furthermore, this approach is also cost-effective with no additional charter costs or staff time associated with sample collection and does not increase fishing mortality (making best use of bycatch). Such approaches provide a good framework for data collection programmes for data-limited species in the future. Despite their low occurrence in individual fisheries-independent surveys, the data presented here indicate that much of the perceived length range: *L. circularis*: 13–115 cm L_T and *L. fullonica*: 16–105 cm L_T (Figure 28) are represented in these data.

The collection of life-history data on board fishery-independent surveys has been an invaluable source of data supporting both trend-based assessments applied by ICES for some of the more widespread species, and also through the collection of length and maturity data (Chapter 4). However, the maturity data collected on such surveys are conducted macroscopically with no additional quantified data with which to substantiate the visual assignment of maturity stage. Dedicated studies such as this, and as also demonstrated in Chapter 5, employed a detailed internal inspection alongside measurements of the nidamental gland, clasper lengths and oocyte numbers and diameters, undertaken by just two different samplers, are important in ensuring that the maturity staging of elasmobranchs is a more robust and more importantly, repeatable, method of determining maturity stage, which is required if accurate spatial and/or temporal changes in life-history parameters are to be assessed.

The size at which fish mature is arguably the most important biological factor to determine with respect to fisheries management. The L_{50} for *L. fullonica* could not be modelled, due to the limited sample size, especially in relation to mature females. However, the sizes of the smallest mature and largest immature fish support an approximate estimation of about 75 cm L_T for males and 90 cm L_T for females. This study provides the first estimation of L_{50} for *L. circularis* and at 81 cm L_T for males and 100 cm L_T for females, this large size at maturity vindicates the identification of this species as one of high priority in earlier work. When these estimated lengths at maturity are applied to the catches from fishery-independent surveys, this indicates that 11% of female and 24% of male *L. fullonica* and <12% of female and 16% of male *L. circularis* were mature. This is a very small proportion of the 'population'; however, whether this is a reflection of over-exploitation, a result of a weak life-history strategy or potentially an artefact of sampling methodology (whereby some larger skates may have lower catchability in bottom trawls (Ellis *et al*., 2015)) is unclear.

These two species were both highlighted as potentially vulnerable species in the prioritisation (Chapter 2) with *L. circularis* and *L. fullonica* ranking fourth and eighth respectively; and likewise in the PSA (McCully Phillips *et al*., 2015; Chapter 3) with *L. fullonica* and *L. circularis* ranking twelfth and thirteenth most susceptible overall in Celtic Sea fisheries. The results of this study confirm that the life-history attributes (in terms of total length and large length at maturity) would confer biological vulnerability. In fact, their large size at maturity indicates that they are potentially more vulnerable than first suggested (McCully Phillips *et al*., 2016) and their biology may place them in between the larger-bodied of the *Raja* species managed under the skates and ray TAC (i.e. blonde ray with a L_{50} estimated at 78 and 83 cm for males and females respectively; McCully *et al*., 2012 – Chapter 4), and that of the currently prohibited species, common blue skate (*Dipturus batis*; with L_{50} estimated at 115 and 123 cm L_T for males and females respectively; Iglésias *et al*., 2010).

Excluding skates in the genus *Dipturus,* this estimated length at maturity exceeds that of any other skate species currently managed under the generic TAC. This size at maturity, and that the maximum length is ca. 120 cm, indicate that *L. circularis* may be one of the more vulnerable skate species being exploited in northern European seas, given that earlier studies have indicated that maximum size is a good proxy from which to infer biological vulnerability (Jennings *et al*., 1998, 1999; Dulvy *et al*., 2000; Dulvy and Reynolds, 2002). Therefore, in this case, *L. circularis* as the species maturing at the largest size managed under the complex, should be the focus of increased attentions to ensure that the status of this stock should be subject to improved evaluation to ensure sustainability. It is conceivable that these life-history parameters demonstrate a biological vulnerability beyond that exhibited by any conspecifics managed within the skate TAC, would support more conservative management than currently in force, such as the removal of the species from the generic TAC and introduction of alternative species-specific management measures (e.g. trip limits).

Leucoraja circularis has the lowest total non-zero TAC advised by ICES for any skate species in the Celtic Seas ecoregion (34 t advised for 2019 and 2020; ICES, 2018b). The advice for *L. fullonica* was higher at 168 t (ICES, 2018a). However, although species (stock) specific advice is provided by ICES, these values are not implemented in management, as the current TAC approach is a single TAC for the skate and ray complex (with some species-specific quotas for stocks of concern with localised areas of abundance, such as undulate ray *Raja undulata* in the English Channel and small-eyed ray *Raja microocellata* in the Bristol Channel). This current framework does not necessarily protect the more vulnerable members of the complex and, given the lengths at maturity alluded to in this Chapter, these two species would indeed be the among the most biologically sensitive species within the complex.

This study could be used to support various bespoke management options for these two vulnerable species if declining trends in catch rates and/or landings are sustained. One such approach could be the introduction of a maximum landing length for 'skates' – this would protect the larger-bodied species and females in particular protecting the most fecund part of the population, while not having a large impact on the commercially important stocks (e.g. thornback ray *Raja clavata*, cuckoo ray *Leucoraja naevus*, spotted ray *Raja montagui*). This would, however, depend on the degree of discard survival, which is much less known for deeper water skates than shallow-water skates (Ellis *et al.*, 2017). An alternative strategy could be to move towards genus-specific TACs. With both large-bodied *Leucoraja* species identified here as biologically sensitive, they could have a TAC independent of the main skates and ray TAC (much like that afforded to undulate ray in the English Channel). Given that bottom fishing activities are prohibited in vulnerable marine ecosystems, bottom trawls are restricted to waters of 800 m or less (EU, 2016) and bottom-set gillnets cannot operate below 600 m (CEC, 2013), future studies could usefully ascertain whether such spatial measures are reducing the areal overlap, and thus the susceptibility of these species, with commercial fisheries. However, the favoured depth distributions identified in fishery-independent survey data indicate that these measures are unlikely to afford much protection for these species, with *L. fullonica* not exceeding 500 m depth and *L. circularis* catches negligible below 600 m. The spatial distribution of both species is noticeably distinct from one another, with *L. circularis* inhabiting deeper water with a stronger association to the shelf slope and to offshore banks while *L. fullonica* favour restricted shallower depths which will cover a greater areal extent across continental shelf waters (Figure 26). However, the distribution of both species does indicate a strong overlap with commercially important bottom trawl fisheries for hake *Merluccius merluccius* which are caught in deeper waters along the shelf edge and anglerfish *Lophius* spp. which are caught more widely across shelf waters (ICES, 2018c).

Any potential management measures need to be underpinned with robust data and thus, in the light of the biological sensitivities being exposed, more attention needs to be given to better analyses of historical data (which may not be available electronically), such as examining fishery-independent survey data for long-term trends in abundance and changes in overall length distributions. The lack of previous published material makes inferences on changes in catches or life-history parameters over time difficult to assess. As highlighted in Section 6.2, earlier data and ichthoylogical descriptions were compromised by taxonomic ambiguities. However, the widely cited maximum length of ca. 120 cm L_T for *L. circularis* (Stehmann, 1990; Stehmann and Bürkel 1984) seems plausible and implies limited evidence of an observed decrease in maximum length with specimens of up to 116 cm L_T represented in fisheries-independent surveys since 2000. The reported maximum length for *L. fullonica* is more uncertain ranging from 100 cm L_T (Stehmann and Bürkel 1984) to 120 cm L_T (Muus and Nielsen, 1999) so with specimens caught up to 105 cm L_T this would point towards a slightly smaller maximum size compared to *L. circularis* but changes in maximum length over time cannot be evaluated. The absence of age data for both species preclude the robust estimation (i.e. based on observed age-at-length data rather than derived from the empirical relationship with maximum length) of $L\infty$ (the theoretical length that a fish would reach if they grew indefinitely (Beverton and Holt, 1957)) with which comparisons to observed contemporary maximum lengths can be made. Any historical data collation and analysis should be complemented with contemporary efforts such as expanding the multi-institute efforts in collecting cadavers, encouraging live-returns and tagging studies where possible. Spatial mapping of their distribution with fisheries effort data would also give a better understanding of the spatial and temporal fishing pressures with which they are overlapping, whilst informing whether spatial management would be a suitable option for these species.

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Chapter 7

Diet composition of starry smooth-hound *Mustelus asterias*

7 Diet composition of starry smooth-hound *Mustelus asterias*

This Chapter was based on the following publication:

McCully Phillips S. R., Grant, A. and Ellis, J. R. (2020). Diet composition of starry smooth-hound *Mustelus asterias* and methodological considerations for assessing the trophic level of predatory fish. *Journal of Fish Biology*, 1–11.

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The candidate was responsible for experimental design, dissections, data collection, analysis, interpretation, leading the authorship and production of all Tables and Figures. This work was undertaken under the supervision of Prof. A. Grant and Dr. J. Ellis who provided critical feedback and helped shape the research, analysis and manuscript. Dr. Ellis was also involved in data collection and lead the review of literature and production of Supplementary Tables 1 and 2.

Minor updates to the introduction and discussion have been made to incorporate relevant recent literature.

7.1 Abstract

The stomach contents of 640 starry smooth-hound *Mustelus asterias* from the Northeast Atlantic were examined. The diet was dominated by crustaceans (98.8% percentage of index of relative importance, %IRI), with the two main prey species being hermit crab *Pagurus bernhardus* (34% IRI) and flying crab *Liocarcinus holsatus* (15% IRI). Ontogenetic dietary preferences showed that smaller individuals [20–69 cm total length (L_T) n = 283] had a significantly lower diversity of prey than larger individuals (70–124 cm L_T, n = 348); however, 18 prey species were found exclusively in smaller individuals and eight prey taxa were found exclusively in larger individuals. Larger commercially important brachyurans such as edible crab *Cancer pagurus* and velvet swimming crab *Necora puber* were more prevalent in the diet of larger individuals. Specimens from the North Sea ecoregion had a lower diversity of prey types for a given sample size than fish from the Celtic Seas ecoregion. Whilst cumulative prey curves did not reach an asymptote, this was primarily due to the high taxonomic resolution utilized and 95% of the diet was described by just seven crustacean taxa. The trophic level (TL) was calculated as 4.34 when species-level prey categories were used. This fine-scale taxonomic resolution resulted in a TL estimate close to a whole level above that

estimated using wider taxonomic groupings. This large bias has important methodological implications for TL studies based on categorized prey data, particularly those of predatory fish.

7.2 Introduction

Elasmobranchs constitute a diverse subclass displaying a broad range of feeding habits, from obligate planktivores to carnivorous apex predators consuming conspecifics and marine mammals (Wetherbee and Cortés, 2004). An understanding of the diet and trophic levels (TL) of sharks is key in comprehending their role in the ecosystem and in understanding potential consequences to energy flux and community structure through direct (e.g. harvesting of predators) or indirect (e.g. degradation of benthic habitats through fishing) influences, which could lead to trophic cascades (reviewed in Pinnegar *et al*., 2000). Sharks are generally considered to be top predators with a broad-scale study of 149 species reporting a mean TL of 4.0 (range of 3.1–4.7), on par with that of marine mammals and greater than seabirds (Cortés, 1999). Cortés (1999) calculated fractional TL's of shark species by characterising their diets into eleven functional prey categories and using published TL's of these prey categories. This methodology is utilised in many studies of stomach content analysis (e.g. Ebert and Bizzarro, 2007; Hussey *et al*., 2011) and is often employed due to the problems of identifying prey items to taxa level once partially digested. Other studies have used stable isotope analyses to calculate TL (Pinnegar *et al*., 2002; Estrada *et al*., 2003) rather than examining diet, or have used a comparison of the two, thus providing descriptions of feeding habits over both the short- and longer-term (Hussey *et al*., 2011). There is little evidence to date to show significant differences in estimated TL between the methods when applied to sharks.

The genus *Mustelus* is extremely diverse with 27 valid species worldwide (Ebert *et al*., 2013) and new species are still being described periodically (e.g. Cubelio *et al*., 2011). The dietary preferences of species in this genus have been well described (Appendix III and IV), with dietary studies covering 18 of these species. The genus is generally reported to feed on crustaceans (primarily crabs) with some species also consuming fish. Their carcinophagus nature is also indicated by their dentition (rows of small teeth, generally molariform with some species having teeth with short erect cusps; Compagno, 1984) which is well adapted to this mode of feeding (Smale and Compagno, 1997).

One member of this genus, starry smooth-hound *Mustelus asterias* Cloquet 1819, occurs on the continental shelf of the Northeast Atlantic. Previous studies have documented reproductive, age, and growth parameters (Farrell *et al*., 2010a, b; McCully Phillips and Ellis, 2015), however a full contemporary study on the diet of this species is lacking. Earlier dietary studies of this stock (Ford, 1921; Ellis *et al*., 1996) were based on limited sample sizes from restricted geographic locations. Recent increases in both relative abundance and commercial exploitation of this stock around the British Isles (see McCully Phillips and Ellis, 2015), where this shark is one of the larger fish species in some habitats, provides the motivation for improving our understanding of this species' role within the ecosystem. This paper describes the breadth of the diet of *M. asterias* in relation to geographic and ontogenetic differences, estimates the TL of the stock, and discusses its ecological role.

7.3 Materials and methods

7.3.1 Dietary data

The stomach contents of 640 specimens of *M*. *asterias* (20–124 cm total length, L_T) were examined between July 2012 and August 2017. Capture locations (see McCully Phillips and Ellis, 2015) comprised the southern North Sea (ICES Division 4.c; n = 334), Celtic Sea (ICES Divisions 7.a.f–h; n = 128), eastern English Channel (ICES Division 7.d; n = 92) and western English Channel (ICES Division 7.e; n = 86).

Most samples (58%) were sourced from commercial fishing operations, including inshore longline vessels which provided larger specimens that were either examined fresh or frozen after capture for subsequent examination. The remaining specimens (42%) were collected opportunistically from trawl surveys on-board R.V. *Cefas Endeavour*, with dead specimens examined on board or frozen and examined in the laboratory.

After collection of biological parameters (including total length L_T, mass M_T, sex and maturity), the stomachs were dissected from the body cavity. The fullness of the cardiac stomach was estimated on a scale of 0–10, 0 being empty and 10 being 100% full. The contents of the cardiac stomach were then placed into a sorting tray and weighed to the nearest 0.1 g. Contents were identified to the lowest possible taxon, either macroscopically or with a stereomicroscope, using the relevant regional taxonomic keys (Hayward and Ryland, 1990) and individual prey taxa counted. Prey taxa were also scored using a points system, where scores (which totalled 10 for each specimen containing food) were allocated to each prey taxa proportionally. The stomach fullness was multiplied by the points to give a semi-quantitative index of relative prey volume (Hyslop, 1980).

The proportion of fish with empty stomachs (i.e. fullness score = 0) was used to calculate the index of vacuity. These specimens and specimens with either everted stomachs or where the cardiac stomach had burst (therefore preventing the mass of stomach contents and fullness to be recorded) were excluded from further analysis.

7.3.2 Data analysis

In order to quantify the diet, the following indices were calculated for each prey taxon in the diet for all *M. asterias* and for each of the predator size categories:

- Frequency of occurrence (%O) - the percentage of all the stomachs that contained food in which each prey taxon was observed.
- Percentage by number (%N) - the total number of each prey taxon as a percentage of the total number of enumerated prey items. Digested remains which could not be enumerated were given a nominal abundance of one.
- Percentage by points (%P) - the sum of relative prey volumes (i.e. fullness × points) for each prey taxon as a percentage of the total scores for all prey taxa.
- Index of relative importance (IRI), calculated as:
  IRI = (%N + %P) x %O (Pinkas *et al*., 1971)
- Percentage of relative importance (%IRI) expressed as IRI divided by the sum of all IRI, multiplied by 100 (%IRI = (IRI/∑IRI) x 100) (Cortés, 1997)

Inanimate objects found in stomachs, such as broken shell, gravel, stone and monofilament line were recorded, but with no points or counts assigned and were only recorded as the frequency of occurrence (%O) and excluded from calculations of %IRI.

Once the diet had been quantified, additional analyses were undertaken to investigate diet preferences by size and area. The specimens were allocated to one of two size categories (<70 cm, n = 283; ≥70 cm, n = 348), which provided broadly comparable sample sizes and also occurred at the approximate length at first maturity (McCully Phillips and Ellis, 2015). Spatial differences in the diet were examined for the North Sea ecoregion (data from ICES Divisions 4.c and 7.d) and Celtic Seas ecoregion (data from ICES Divisions 7.a and 7.e–g). Diet composition in relation to both size and ecoregion was examined using a one-way analysis of similarities (ANOSIM) using the vegan package (Oksanen *et al*., 2018) in R (R Core Team, 2017). Data were square-root transformed and a Bray-Curtis dissimilarity index was used. SIMPER analyses were conducted in Primer v.5 (Clarke and Gorley, 2001), to investigate which prey items were key to discriminate between groups. A regression was used to examine the relationship between stomach content mass as a percentage of body mass.

Cumulative Prey Curves (CPCs) were carried out in R (R Core Team, 2017) using the vegan package (Oksanen *et al*., 2018) to determine whether the sample size adequately described the diet composition. Cumulative prey curves were produced for all specimens, and by geographic area (southern North Sea and eastern English Channel, and Celtic Sea and western English Channel) to determine if the diet was better described in one area compared to another.

The complete identification of dietary prey was used to estimate the TL and Levins' measure of niche breadth to assist in describing the ecological role of *M. asterias* around the UK. TL was calculated using TL values from all prey species identified (Appendix V), or where data were unavailable using the following equation as a proxy:

$$TL_i = 1 + \sum_j (TL_j . DC_{ij})$$

where TL_i is the fractional TL of the prey *j*, and DC_{ij} represents the fraction of *j* in the diet of *i*. TL was also calculated using the same equation, but applied using the methodology of Cortés (1999), where all prey species were categorised as either 'decapod crustaceans' (TL = 2.52), 'invertebrates' (TL = 2.5), 'molluscs' (TL = 2.1) or 'cephalopods' (TL = 3.2).

Levins' measure of niche breadth (*B*) was calculated using the following formula:

$$B = 1/\sum p^2$$

where *p* is the proportion of each prey group in the diet. The higher taxa listed in Table 38 were used as the sub-categories for calculating niche breadth. The miscellaneous and digested remains categories were removed for this purpose, and the resultant proportions of diet re-calculated accordingly.

7.4 Results

In total, 640 specimens of *M*. *asterias* (20–124 cm L_T; Figure 39) were examined and only four specimens (48–82 cm L_T) had empty stomachs, leading to a low index of vacuity (0.6%). Two specimens had everted stomachs and the stomachs of a further three specimens were damaged upon extraction, thus these specimens were unable to provide data on either the mass of stomach contents or fullness. Thus, dietary data were available for 631 specimens, and these data were used for subsequent analyses.

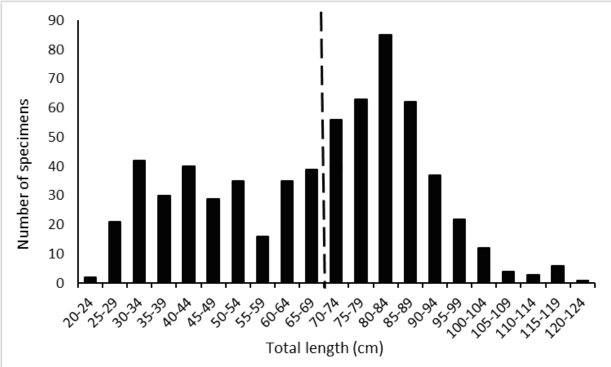

Figure 39: Length-frequency distribution of *M. asterias* analysed (the small and large size classes are indicated by the dashed line).

7.4.1 Diet summary

Crustaceans comprised the main part of the diet observed, accounting for 98.8% IRI. This subphylum included a diverse range of prey taxa (49 taxa overall) with 31 identified to species-level. The order Decapoda was the main crustacean group predated upon (with 44 taxa identified) and the infraorder Brachyura the most species-rich prey taxa, with 17 identified to species-level or unique genus. Excluding unidentified, digested crustacean remains, the most important prey taxa were *Pagurus bernhardus* L. 1758 (34% IRI, 45% O; Table 38) and *Liocarcinus holsatus* (Fabricius, 1798; 15% IRI, 25% O).

Fourteen categories of minor prey taxa (within the phyla Cnidaria, Mollusca, Echinodermata and class Polychaeta) were recorded. Hydroids were the best represented of these minor taxa (2% O, 0.04% IRI), with polychaetes found in 1% of stomachs (0.01% IRI). Echinoderms and molluscs (excluding squid bait) were both minor taxa (<0.01% IRI).

Other miscellaneous items identified within the stomach contents included broken shell, gravel, monofilament line and bait (chopped squid). There were nine records of gravel or stones in stomachs from all length classes and one incidence of monofilament line. The squid found in 33 stomachs was ingested from the bait used in the longline fishery in which they were caught, with all bar one record being from large (‘mature’) fish.

7.4.2 Ontogenetic differences in the diet

ANOSIM showed a significant difference between the two size-classes (R = 0.139 p = 0.001). SIMPER analysis showed that the small size-class had (in order of magnitude) greater average abundances of unidentified crustacea, *L. holsatus*, *Corystes cassivelaunus* (Pennant 1777), *Atelecyclus rotundatus* (Olivi 1792) and unidentified digested remains, while *P. bernhardus*, *Necora puber* (L. 1767) and *Cancer pagurus* L. 1758 were more abundant in the diet of larger fish.

Small individuals (20–69 cm L_T; n = 283) had a higher diversity of prey type than larger individuals, with 59 of the 68 prey categories found in their diet. However, 18 prey species were exclusive to smaller individuals; in most cases the prey type was only seen in one or two specimens, but *Upogebia* sp. Leach 1814, *Pisidia longicornis* (L. 1767), and *Processa* sp. Leach 1815, were recorded in 15 (0.5% IRI), five and three fish respectively. The most important prey types identified to species-level, for this size-class were *L. holsatus* (24% O; 13% IRI), *P. bernhardus* (23% O; 8% IRI) and *C. cassivelanus* (16% O; 5% IRI). Amphipods (4% IRI) were also well represented, both in terms of numbers (15% N) and frequency of occurrence (11%).

Larger individuals (70–124 cm L_T; n = 348) had 48 of the 68 prey categories. Eight of the identified prey taxa were found exclusively in larger individuals. The proportion of *L. holsatus* in the diet of larger individuals (25% O; 13% IRI) was almost identical to smaller fish. The proportion of *P. bernhardus* in the diet of large fish was, however, higher (64% O), with this important prey taxa accounting for 58% IRI. The third most important taxa of larger fish was *N. puber* (17% O; 5% IRI), a species of much less importance for smaller individuals (0.03% IRI). Sections of squid, bait from the longline fishery, had an IRI of 1%.

7.4.3 Spatial differences in the diet

Spatial differences in dietary preferences were examined by comparing fish from the two ecoregions (North Seas and Celtic Seas; Appendix VI). Whilst a greater range of prey taxa were recorded for the North Seas ecoregion (n = 54) than in the Celtic Seas ecoregion (n = 48), the sample size from the North Seas ecoregion (n = 421) was double that from the Celtic Seas ecoregion (n = 210). Indeed, there was a higher diversity of prey taxa in the Celtic Seas ecoregion than North Sea ecoregion for a given sample size. The CPCs both exhibited a similar shape without reaching an asymptote (Appendix VII). ANOSIM found a significant difference in diet between the two ecoregions (R = 0.186, p = 0.001). Specimens from the North Sea had greater abundances of *P. bernhardus*, *L. holsatus*, unidentified digested remains and *N. puber,* while specimens from the Celtic Seas had greater abundances of unidentified crustacea, *C. cassivelaunus*, *A. rotundatus* and Xanthidae MacLeay 1838.

7.4.4 Predation on commercial species

Within the crustacean prey items, two commercially-important crab species were found: *N. puber* (velvet swimming crab) and *C. pagurus* (edible crab); overall these species were found in 10% and 7% of all stomachs respectively and accounted for 1.8% and 0.8% IRI. Thus, *N. puber* and *C. pagurus* were the fourth and seventh most important prey species identified. *N. puber* and *C. pagurus* were predominantly found in the diets of the larger size-class (17% and 11% IRI) and were recorded mostly in specimens from the North Sea ecoregion (Appendix VI). Commercially-harvested shrimps (*Crangon* spp. Fabricius 1798) were a limited component of the diet (IRI's of <1%), and no piscivory was observed.

7.4.5 Cumulative prey curves

The CPC did not reach an asymptote (Figure 40) with 68 prey categories identified in 631 fish. However, when the species were ranked by importance (%IRI), it was apparent that 95% of the diet was composed of just seven prey categories and 99% by 15 categories (Figure 41). Similarly, when prey data were summed by numbers (% N) and the points (% P; Figure 41), 95% of the diet was represented by 25 and 22 prey taxa, respectively. The fullness/points method was considered an appropriate proxy for 'mass' (Figure 42).

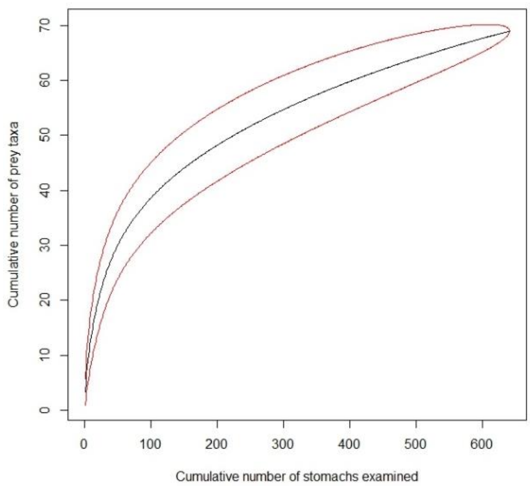

Figure 40: Cumulative prey curve for all samples of *M. asterias* (n = 631) by prey category.

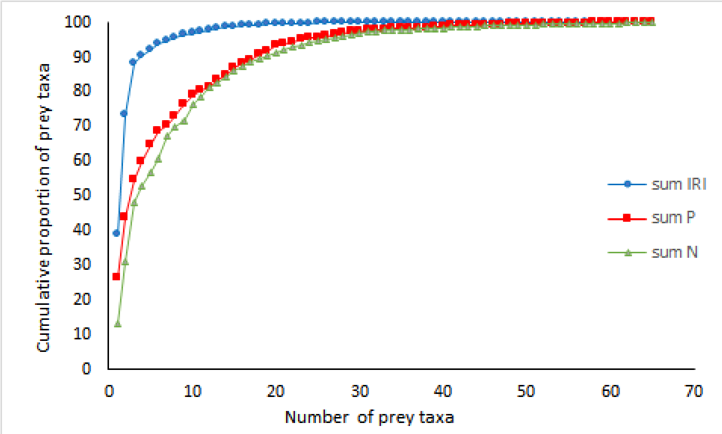

Figure 41: Ranked cumulative proportion of prey categories in the diet of *M. asterias* by % IRI (blue circles and line), numerical abundance of prey taxa (% N: green triangles and line), and points (% P: red squares and line).

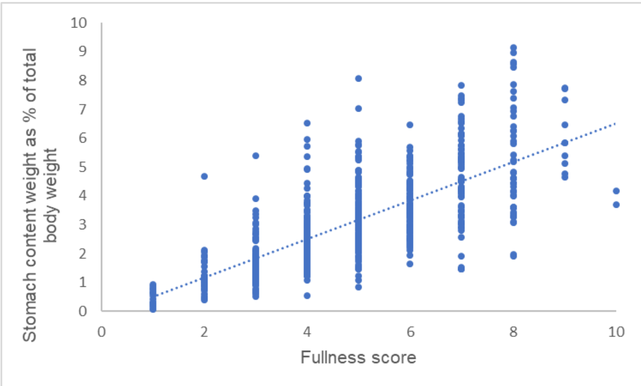

Figure 42: Stomach content weight as proportion of total body weight in relation to stomach fullness (y = 0.6677x - 0.1546; R^2 = 0.52).

7.4.6 Niche breadth and trophic level

The niche breadth of the *M. asterias* diet based on data aggregated by each of the nine sub-categories, was 2.04, indicating a selective diet comprised primarily of anomuran and brachyuran decapods. The estimated TL from the Cortés (1999) methodology, using the relative proportions of just four prey categories, was 3.52. In contrast, the TL estimate based on data from all 65 prey taxa was 4.34.

Table 38: Diet composition of *M. asterias* around the British Isles, showing % occurrence, % numbers, % points, IRI and %IRI for juvenile (<70 cm), subadult and adult (≥70 cm) and all specimens.

Higher taxa	Prey taxa	Small Size Class (20 - 69 cm: n = 283)								Large Size Class (70 - 124 cm: n = 348)								All fish (20 - 124 cm: n = 631)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
Cnidaria	*Tubularia* sp.									1	1	4	0.29	0.08	0.03	0.03	0.00	1	1	4	0.16	0.04	0.01	0.01	0.00
	Hydrallmania falcata									1	1	5	0.29	0.08	0.03	0.03	0.00	1	1	5	0.16	0.04	0.02	0.01	0.00
	Hydroida (indet.)	7	9	41	2.47	0.88	0.26	2.82	0.06	6	6	24	1.72	0.46	0.16	1.07	0.02	13	15	65	2.06	0.65	0.21	1.76	0.04
Total Cnidaria									0.06								0.02								0.04
Polychaeta	*Arenicola* sp.	1	1	15	0.35	0.10	0.10	0.07	0.00									1	1	15	0.16	0.04	0.05	0.01	0.00
	Polychaeta (indet.)	6	6	45	2.12	0.58	0.29	1.85	0.04	1	1	7	0.29	0.08	0.05	0.04	0.00	7	7	52	1.11	0.30	0.17	0.52	0.01
Total Polychaeta									0.04								0.00								0.01
Stomatopoda	*Rissoides desmaresti*									2	2	41	0.57	0.15	0.27	0.24	0.00	2	2	41	0.32	0.09	0.13	0.07	0.00
Isopoda	*Idotea linearis*	3	3	89	1.06	0.29	0.57	0.92	0.02	4	10	57	1.15	0.77	0.37	1.31	0.02	7	13	146	1.11	0.56	0.47	1.15	0.02
Amphipoda	*Gammarellus homari*	1	1	8	0.35	0.10	0.05	0.05	0.00									1	1	8	0.16	0.04	0.03	0.01	0.00
	Amphipoda	32	151	418	11.31	14.69	2.69	196.51	3.91	1	1	3	0.29	0.08	0.02	0.03	0.00	33	152	421	5.23	6.55	1.36	41.37	0.88
Decapoda-Caridea	*Palaemon* sp.									2	2	24	0.57	0.15	0.16	0.18	0.00	2	2	24	0.32	0.09	0.08	0.05	0.00
	Alpheus glaber	1	3	80	0.35	0.29	0.51	0.29	0.01									1	3	80	0.16	0.13	0.26	0.06	0.00
	Processa sp.	3	3	29	1.06	0.29	0.19	0.51	0.01									3	3	29	0.48	0.13	0.09	0.11	0.00
	Pandalina brevirostris	2	3	18	0.71	0.29	0.12	0.29	0.01									2	3	18	0.32	0.13	0.06	0.06	0.00
	Pandalus montagui	1	1	12	0.35	0.10	0.08	0.06	0.00	1	1	6	0.29	0.08	0.04	0.03	0.00	2	2	18	0.32	0.09	0.06	0.05	0.00
	Pandalidae (indet.)	2	2	11	0.71	0.19	0.07	0.19	0.00	1	1	4	0.29	0.08	0.03	0.03	0.00	3	3	15	0.48	0.13	0.05	0.08	0.00
	Crangon allmanni	18	31	246	6.36	3.02	1.58	29.25	0.58	17	23	107	4.89	1.78	0.70	12.09	0.21	35	54	353	5.55	2.33	1.14	19.24	0.41

Higher taxa	Prey taxa	Small Size Class (20 - 69 cm: n = 283)								Large Size Class (70 - 124 cm: n = 348)								All fish (20 - 124 cm: n = 631)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Crangon crangon	7	12	103	2.47	1.17	0.66	4.53	0.09	27	43	310	7.76	3.33	2.02	41.44	0.73	34	55	413	5.39	2.37	1.34	19.97	0.43
	Crangon sp.	6	7	74	2.12	0.68	0.48	2.45	0.05	12	14	75	3.45	1.08	0.49	5.42	0.09	18	21	149	2.85	0.90	0.48	3.96	0.08
	Natantia (indet.)	2	2	18	0.71	0.19	0.12	0.22	0.00	1	1	8	0.29	0.08	0.05	0.04	0.00	3	3	26	0.48	0.13	0.08	0.10	0.00
Decapoda-Anomura	*Callianassa tyrrhena*	1	1	20	0.35	0.10	0.13	0.08	0.00									1	1	20	0.16	0.04	0.06	0.02	0.00
	Upogebia stellata	1	1	10	0.35	0.10	0.06	0.06	0.00									1	1	10	0.16	0.04	0.03	0.01	0.00
	Upogebia sp.	15	19	493	5.30	1.85	3.17	26.61	0.53									15	19	493	2.38	0.82	1.59	5.74	0.12
	Thalassinoidea (indet.)	4	5	85	1.41	0.49	0.55	1.46	0.03	13	15	112	3.74	1.16	0.73	7.05	0.12	17	20	197	2.69	0.86	0.64	4.04	0.09
	Anapagurus laevis	2	2	39	0.71	0.19	0.25	0.31	0.01									2	2	39	0.32	0.09	0.13	0.07	0.00
	Pagurus bernhardus	66	83	1317	23.32	8.07	8.47	385.94	7.68	223	332	4039	64.08	25.68	26.26	3328.22	58.38	289	415	5356	45.80	17.88	17.32	1612.28	34.36
	Pagurus prideaux	3	3	39	1.06	0.29	0.25	0.58	0.01	3	7	78	0.86	0.54	0.51	0.90	0.02	6	10	117	0.95	0.43	0.38	0.77	0.02
	Paguridae (indet.)	10	10	149	3.53	0.97	0.96	6.83	0.14	3	3	35	0.86	0.23	0.23	0.40	0.01	13	13	184	2.06	0.56	0.60	2.38	0.05
	Galathea sp.	5	5	63	1.77	0.49	0.41	1.58	0.03									5	5	63	0.79	0.22	0.20	0.33	0.01
	Munida rugosa									1	1	16	0.29	0.08	0.10	0.05	0.00	1	1	16	0.16	0.04	0.05	0.02	0.00
	Pisidia longicornis	5	5	32	1.77	0.49	0.21	1.22	0.02									5	5	32	0.79	0.22	0.10	0.25	0.01
Decapoda-Brachyura	*Hyas coarctatus*	1	1	14	0.35	0.10	0.09	0.07	0.00	1	1	15	0.29	0.08	0.10	0.05	0.00	2	2	29	0.32	0.09	0.09	0.06	0.00
	Macropodia rostrata	1	1	10	0.35	0.10	0.06	0.06	0.00	2	2	15	0.57	0.15	0.10	0.14	0.00	3	3	25	0.48	0.13	0.08	0.10	0.00
	Macropodia tenuirostris	1	1	24	0.35	0.10	0.15	0.09	0.00									1	1	24	0.16	0.04	0.08	0.02	0.00
	Macropodia sp.	1	2	21	0.35	0.19	0.14	0.12	0.00	5	8	47	1.44	0.62	0.31	1.33	0.02	6	10	68	0.95	0.43	0.22	0.62	0.01
	Majidae (indet.)	13	13	162	4.59	1.26	1.04	10.60	0.21	10	15	91	2.87	1.16	0.59	5.03	0.09	23	28	253	3.65	1.21	0.82	7.38	0.16

Higher taxa	Prey taxa	Small Size Class (20 - 69 cm: n = 283)								Large Size Class (70 - 124 cm: n = 348)								All fish (20 - 124 cm: n = 631)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Corystes cassivelaunus	45	67	1283	15.90	6.52	8.26	234.92	4.68	21	48	389	6.03	3.71	2.53	37.66	0.66	66	115	1672	10.46	4.95	5.41	108.39	2.31
	Atelecyclus rotundatus	34	47	786	12.01	4.57	5.06	115.69	2.30	28	41	508	8.05	3.17	3.30	52.09	0.91	62	88	1294	9.83	3.79	4.18	78.37	1.67
	Bathynectes longipes	1	1	10	0.35	0.10	0.06	0.06	0.00									1	1	10	0.16	0.04	0.03	0.01	0.00
	Cancer pagurus	4	4	69	1.41	0.39	0.44	1.18	0.02	39	60	776	11.21	4.64	5.05	108.55	1.90	43	64	845	6.81	2.76	2.73	37.41	0.80
	Carcinus maenus	4	12	104	1.41	1.17	0.67	2.60	0.05	17	32	512	4.89	2.47	3.33	28.35	0.50	21	44	616	3.33	1.90	1.99	12.94	0.28
	Liocarcinus arcuatus	1	1	10	0.35	0.10	0.06	0.06	0.00									1	1	10	0.16	0.04	0.03	0.01	0.00
	Liocarcinus depurator	6	10	178	2.12	0.97	1.15	4.49	0.09	12	23	278	3.45	1.78	1.81	12.37	0.22	18	33	456	2.85	1.42	1.47	8.26	0.18
	Liocarcinus holsatus	69	165	1742	24.38	16.05	11.21	664.65	13.23	86	237	1628	24.71	18.33	10.59	714.56	12.53	155	402	3370	24.56	17.32	10.90	693.18	14.77
	Liocarcinus pusillus	12	14	180	4.24	1.36	1.16	10.69	0.21	1	1	4	0.29	0.08	0.03	0.03	0.00	13	15	184	2.06	0.65	0.60	2.56	0.05
	Liocarcinus sp.	12	15	220	4.24	1.46	1.42	12.19	0.24	15	20	260	4.31	1.55	1.69	13.95	0.24	27	35	480	4.28	1.51	1.55	13.10	0.28
	Necora puber	5	5	66	1.77	0.49	0.42	1.61	0.03	58	85	1398	16.67	6.57	9.09	261.06	4.58	63	90	1464	9.98	3.88	4.73	85.99	1.83
	Portunidae (indet.)	7	8	217	2.47	0.78	1.40	5.38	0.11	10	13	155	2.87	1.01	1.01	5.79	0.10	17	21	372	2.69	0.90	1.20	5.68	0.12
	Monodaeus couchi									1	2	21	0.29	0.15	0.14	0.08	0.00	1	2	21	0.16	0.09	0.07	0.02	0.00
	Pilumnus hirtellus	2	2	28	0.71	0.19	0.18	0.26	0.01	3	6	53	0.86	0.46	0.34	0.70	0.01	5	8	81	0.79	0.34	0.26	0.48	0.01
	Xantho sp.	1	1	10	0.35	0.10	0.06	0.06	0.00									1	1	10	0.16	0.04	0.03	0.01	0.00
	Xanthidae (indet.)	13	71	471	4.59	6.91	3.03	45.65	0.91	12	36	222	3.45	2.78	1.44	14.58	0.26	25	107	693	3.96	4.61	2.24	27.14	0.58
	Goneplax rhomboides	1	2	12	0.35	0.19	0.08	0.10	0.00	5	5	95	1.44	0.39	0.62	1.44	0.03	6	7	107	0.95	0.30	0.35	0.62	0.01
	Brachyura (indet.)	7	7	247	2.47	0.68	1.59	5.62	0.11	6	10	179	1.72	0.77	1.16	3.34	0.06	13	17	426	2.06	0.73	1.38	4.35	0.09
Other crustacean	Crustacea (indet.)	175	177	5323	61.84	17.22	34.25	3182.86	63.36	120	124	2815	34.48	9.59	18.30	961.83	16.87	295	301	8138	46.75	12.97	26.32	1836.76	39.14

Higher taxa	Prey taxa	Small Size Class (20 - 69 cm: n = 283)								Large Size Class (70 - 124 cm: n = 348)								All fish (20 - 124 cm: n = 631)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
Total Crustacean									98.71								98.59								98.79
Mollusca	*Nucula* sp. (shell)									1	1	7	0.29	0.08	0.05	0.04	0.00	1	1	7	0.16	0.04	0.02	0.01	0.00
	Mytilus edulis	1	1	12	0.35	0.10	0.08	0.06	0.00	1	1	1	0.29	0.08	0.01	0.02	0.00	2	2	13	0.32	0.09	0.04	0.04	0.00
	Corbula gibba	1	1	6	0.35	0.10	0.04	0.05	0.00									1	1	6	0.16	0.04	0.02	0.01	0.00
	Bivalvia (indet.)	2	3	37	0.71	0.29	0.24	0.37	0.01									2	3	37	0.32	0.13	0.12	0.08	0.00
	Sepiolidae	1	1	8	0.35	0.10	0.05	0.05	0.00									1	1	8	0.16	0.04	0.03	0.01	0.00
	Cephalopoda (beak)									1	1	12	0.29	0.08	0.08	0.04	0.00	1	1	12	0.16	0.04	0.04	0.01	0.00
Total Mollusca									0.01								0.00								0.00
Echinodermata	*Ophiura albida*	1	1	14	0.35	0.10	0.09	0.07	0.00	1	1	5	0.29	0.08	0.03	0.03	0.00	2	2	19	0.32	0.09	0.06	0.05	0.00
	Ophiura sp.	1	1	3	0.35	0.10	0.02	0.04	0.00									1	1	3	0.16	0.04	0.01	0.01	0.00
	Echinoid									1	1	4	0.29	0.08	0.03	0.03	0.00	1	1	4	0.16	0.04	0.01	0.01	0.00
Total Echinodermata									0.00								0.00								0.00
Miscellaneous	Broken shell	1		0	0.35					1		0	0.29					2		0	0.32				
	Gravel/stone	7		0	2.47					2		0	0.57					9		0	1.43				
	Monofilament line	1		0	0.35													1		0	0.16				
	Squid (bait)	1	1	35	0.35	0.10	0.23	0.11	0.00	32	36	558	9.20	2.78	3.63	58.96	1.03	33	37	593	5.23	1.59	1.92	18.37	0.39
	Digested remains	23	23	784	8.13	2.24	5.05	59.19	1.18	18	18	377	5.17	1.39	2.45	19.88	0.35	41	41	1161	6.50	1.77	3.75	35.88	0.76
Total Miscellaneous									1.18								1.38								1.16

7.5 Discussion

7.5.1 Feeding ecology of smooth-hounds

The genus *Mustelus* is species-rich genus with a circumglobal distribution. Members of the genus are morphologically similar (Compagno, 1984) and most of these species are important predators of crustaceans (Appendix IV). However, whilst most species are carcinophagous, studies on *Mustelus henlei* (Gill 1863) reported that squid and teleosts were the primary prey (Gomez *et al*., 2003; Espinoza *et al*., 2012; Amariles *et al*., 2017). Whilst most *Mustelus* spp. (including *M. asterias*) have molariform dentition, *M. henlei* have cusped teeth (Compagno, 1984). So, the degree to which the teeth of *Mustelus* spp. have cusps, cusplets or true molariform dentition may be an indicator of their feeding habits.

The diet of *M*. *asterias*, which has a molariform dentition, was found to be almost exclusively comprised of crustaceans in the present study, which supports the findings of earlier studies (Ford, 1921; Ellis *et al*., 1996). However, Ford (1921) recorded fish in 4.2% of stomachs (n = 48) and Ellis *et al*. (1996) reported fish to account for 1.9% of the overall diet (n = 46), whilst no fish were recorded in the stomach contents in the present study, despite the much larger sample size (n = 631). The sampling sites for these earlier studies (Plymouth and the Irish Sea) were also sampled in the present study, with the current study also including a broader length range (20–124 cm) than examined by Ellis *et al*. (1996; 43–100 cm; size data not provided by Ford (1921)). Consequently, neither a size-related bias or regional differences would account for the absence of fish in the present study, which may be related to prey availability.

There has been a well-documented increase in regulatory discarding of marine fish over recent decades, with an estimated 1 million tonnes of marine organisms annually being discarded back into the North Sea alone (Tasker *et al*., 2000). The additional availability of carrion on which scavengers can prey may have been beneficial to many such species, including the crustaceans *L*. *holsatus* and *P*. *bernhardus* (Groenewold and Fonds, 2000), the two most important prey species for *M. asterias* identified in this study. It is possible that fishing practices have provided important food resources for fish species that either scavenge directly or feed on invertebrate scavengers (Olaso *et al.*, 1998). These data were collected prior to the full implementation of the demersal landings obligation, however, it is likely that once this management measure is in full force, it could negatively impact the availability and abundance of some prey taxa that are currently important in the diet.

Predation on non-crustacean taxa was limited and, in some instances, may simply have resulted from accidental ingestion. For example, various hydroids were observed, often co-occurring with certain crustaceans such as spider crab (Majidae, Samouelle 1819), *Xantho* spp. Leach 1814 and *Liocarcinus pusillus* (Leach 1816), which often associate with hydroids (e.g. Zintzen *et al.*, 2008). The possibility that some cryptic prey were missed or under-represented in this study is possible, however this risk is also present when using DNA metabarcoding due to primer bias (Alberdi, 2018). There were limited records of polychaetes in the diet and this coupled with the dentition supporting a carcinophagus diet, we believe that softer bodied prey were not under-represented in this study.

Molecular approaches are very beneficial in determining the presence of prey species that are digested rapidly, however, the exoskeletons of crustaceans are more resilient to digestion and thus can be used for identification beyond digestion times of soft tissues. There is also the possibility of these methods over-estimating prey taxa through secondary consumption, which along with cannibalism, is nearly impossible to detect (Nielsen *et al*., 2018), yet can be a significant potential source of error (Sheppard *et al*., 2005). Furthermore, dietary metabarcoding data often contain biases such that there exists high uncertainty around quantitative estimates and in many instances biomass of prey cannot be inferred (Deagle *et al*., 2019; Lamb *et al*., 2019), whereas the relative fullness and frequency of occurrence methods are favoured and recommended for the standardisation of feeding studies for their ability to discern relative prey diversity and abundance (Amundsen and Sánchez-Hernández, 2019).

The index of vacuity was found to be very low in the present study (0.6%), which contrasts with values up to 59% reported for other *Mustelus* spp. (Appendix IV). The abundance and diversity of crustaceans in the diet, combined with their lower energetic contents and slower digestion rates compared to fish prey (Blaber and Bulman, 1987; Heupel and Bennett, 1998), may result in the more common occurrence of such prey, thereby resulting in low indices of vacuity for crustacean feeders.

7.5.2 Ontogenetic and regional differences in the diet of *M. asterias*

There were significant (p = 0.001) differences between the diets of juvenile and sub-adult/adult *M. asterias*, which may relate to differences in gape, jaw structure and dentition (e.g. Wilga *et al*., 2016). Larger individuals were found with larger crustaceans more commonly in their stomachs, including *P. bernhardus* and *N. puber,* whilst smaller *M. asterias* had smaller swimming crabs (e.g. *L. pusillus*) and other small crustaceans such as *P.*

longicornis and amphipods more commonly in their diet. This ontogenetic dietary difference could be an important parameter to recognise in size-structured ecosystem models. Many multispecies models developed for northern European seas (e.g. Araujo *et al*., 2005; Mackinson and Daskalov, 2007) have combined 'sharks' under a single category. As ecosystem models develop, more discrete ecosystem components will be included requiring relevant species- and size-specific dietary data, especially as such models generally have explicit categories for commercially important shellfish such as edible crab (which was found to be an important prey species).

Mustelus asterias from both ecoregions were primarily carcinophagous but significant differences in the diet were observed, which may be described by some minor differences in characteristic prey types. The diet of *M. asterias* from the Celtic Seas ecoregion was dominated by brachyuran crabs while those in the North Sea showed a prevalence of anomuran crabs (*P. bernhardus*). This is likely a consequence of prey availability rather than dietary preferences, given the higher diversity of benthic invertebrates, including crustaceans, in the south-west compared to the southern North Sea (Rees *et al*., 1999; Ellis *et al.*, 2007).

7.5.3 Predation on commercial crustaceans

The frequency in the diet of *M. asterias* of commercially fished crustaceans (*N. puber* and *C. pagurus*) is particularly notable. Whilst the overall role of these species was only 1.83% and 0.80% IRI respectively, the corresponding values for the larger size category were 4.58% and 1.90% IRI. Furthermore, individual samples processed over the course of the study demonstrated that *M. asterias* could consume many individuals of these species ($n \leq 6$), highlighting that *M. asterias* may be a locally important predator. Consequently, further studies on the occurrence and feeding habits of *M. asterias* on important habitats of these crab species could usefully be undertaken.

There was no observed predation on *Nephrops norvegicus* (L. 1758) during this study, however, few if any *M. asterias* specimens were captured close to the muddy *Nephrops* grounds, and most specimens were from areas of sand and gravel sediments. Whilst most of the crustaceans consumed were mobile epifaunal species, various burrowing species (e.g. *Rissoides desmaresti* (Risso 1816), *Alpheus glaber* (Olivi 1792), Thalassinoidea Latreille 1831 and *Goneplax rhomboides* (L. 1758)) were found occasionally, indicating that burrowing crustaceans can be an important part of the diet. Given the increasing catch rates of *M. asterias* around the British Isles, further studies to determine whether they are important predators on *Nephrops* grounds could usefully be undertaken, given that other demersal sharks can also be predators of *N. norvegicus* (Symonds and Elson, 1983).

7.5.4 Cumulative prey curves

The use of CPCs in dietary studies is an important method for ensuring that sample sizes are adequate for describing the diet of a species. However, in many instances the combining of prey taxa into more generic taxonomic groups may result into an artificial finding of the asymptote being reached (Silva-Garay *et al*., 2018). In this study, a large range of crustaceans were identified to species-level, and the CPC (including all 68 prey categories) did not reach an asymptote, despite the large sample size. It is evident that this is due to the finer-scale taxonomic resolution used, which is required to provide a more detailed and robust description of the breadth of diet. We propose that cumulative % IRI is a more informative metric to determine whether sample sizes are appropriate for quantifying the diet. In the present study 95% of the diet of *M. asterias* was ascribed to just seven prey taxa and 99% by 15 prey categories. This dietary preference was also reflected by the low niche breadth (2.04) which indicated a selective diet despite the large number of prey categories (n = 68) observed. Given the diversity of many crustacean taxa and that the exoskeletons are slow to digest (therefore allowing their identification) dietary studies of carcinophagus fish may report a large number of species which can result in cumulative prey curves not reaching an asymptote. Furthermore, the broad spatial and temporal extent of sample collection may have also allowed for a broader range of prey taxa to be observed.

7.5.5 Trophic level

The TL calculated for *M. asterias* (4.34) was greater than that calculated in previous studies by Cortés (1999; 3.7), Cotter *et al*. (2008; 3.9), and Pinnegar *et al*. (2002; 4.0). These differences seem to be a result of the higher taxonomic resolution of stomach contents used in the present study, with items identified and assigned a TL by species rather than by higher taxonomic group (e.g. crustaceans and fish). Cortés (1999) summarised data from two studies with a total of 72 specimens, breaking down the diet into crustaceans, fish, cephalopods and invertebrates. Applying this methodology to our data resulted in an estimated TL of 3.52, nearly a complete level lower than the species-based estimate of this study. The greatest contributor to this difference was that the average crustacean TL used by Cortés (1999; 2.52) was lower than most of those given in the literature for the various crustacean taxa (mean = 3.03, Appendix V). The TL of *Mustelus* species examined in Cortés (1999) ranged from 3.5–4.2, with *Mustelus californicus* Gill 1864 and *Mustelus palumbes* Smith 1957, both TL 3.5, best representing the predominantly carcinophagic diet of *M. asterias*. Hussey *et al*. (2011) also reported that published TLs derived from stomach content analysis are likely to be underestimated when using functional prey categories for large predators. In their case the broad prey category of 'cephalopods' underestimated the TL calculated for *Sphyrna lewini* (Griffith and Smith 1834).

Where identification of prey items beyond broad categories is not possible, it may be preferable to estimate TL using stable isotopes. Pinnegar *et al*. (2002) and Cotter *et al*. (2008) calculated TL from nitrogen stable isotope analyses and provided estimates more akin, albeit still lower than the present study. As Domi *et al*. (2005) alluded to, the use of stable isotopes is beneficial in describing feeding habits over the longer-term (when muscle tissue is used), as calculations are based on assimilated rather than just ingested food. However, Estrada *et al*. (2003) found no statistical difference between TL derived from stable isotope analysis and those calculated using diet data (from Cortés, 1999) for five shark species.

It is therefore recommended that, where possible, studies estimating TL using data from stomach content analyses apply the highest taxonomic resolution available, in order to reduce the likelihood of TL being underestimated. Augmenting traditional diet analyses (which provides a more detailed understanding of prey composition) with stable isotope analyses of a range of tissues would provide another metric to allow direct comparison of the diet across the short- and long-term, which could be of considerable importance in wide-ranging species, such as *M. asterias*.

7.6 References

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Chapter 8

Discussion

8 Discussion

Since the late 1990s, there has been much progress in the conservation and sustainable exploitation of elasmobranchs in northern European seas (see Chapter 1). A central tenet to this are Plans of Action (POAs). National Plans of Action (NPOAs), such as the UK Shark, Skate and Ray Conservation Plan (Defra, 2011), have been developed under the auspices of the International Plan of Action for Conservation and Management of Sharks (IPOA-Sharks; FAO, 1999). This International Plan has the overarching objective "*to ensure the conservation and management of sharks and their long-term sustainable use*" (FAO, 1999) with ten goals detailed to support this objective. These goals cover a range of themes including improved species-specific catch and landings data, monitoring, reducing bycatch and minimising waste. States are encouraged to adopt and implement National Plans which consider such goals through the development of overarching objectives and actions through which States will address shark conservation and management issues pertinent to their relevant fisheries and elasmobranch species.

8.1 Informing Plans of Action (POAs)

The main driver of this study has been to support the implementation of the UK-POA (the national shark, skate and ray conservation plan; Defra, 2011), which aims to ensure sustainable exploitation of exploited elasmobranchs while protecting those species of conservation concern. Such NPOAs need to be underpinned by nationally focussed fisheries research, in terms of data collection and biological understanding. However, given that many species of elasmobranch are migratory and have stock distributions that often extend over multiple jurisdictions, the international expertise of relevant regional fisheries bodies, such as ICES, are generally required to allow for more robust stock assessments.

Both the UK-POA (Defra, 2011) and the EU-POA (COM, 2009) set objectives and actions which are not clearly demarcated, or evidence based. A significant shortfall of the UK-POA is that it neither considers the range of species occurring in national waters nor prioritises actions and has no target dates set against actions (see Chapter 2.4). This equivocal approach could lead to research being focused on a single 'preferred' species or set of species. For example, the UK-POA defined explicit actions for only porbeagle shark *Lamna nasus* and spurdog *Squalus acanthias*. This approach could be to the detriment of a range of other vulnerable species (e.g. shagreen ray *Leucoraja fullonica* and sandy ray *L. circularis*; Chapter 6), if the focus of research efforts is not based on an initial prioritisation that considers the vulnerability of all species.

Chapter 2 lays down a foundation on which a comprehensive POA could be based. It begins with an unbiased evidence base of which elasmobranch species are present in national waters. An initial qualitative assessment has been developed that is appropriate for all species, even when data-limited, and can help prioritise the species on which national plans could usefully focus attention. Once species have been prioritised, a more quantitative approach can then be adopted to examine vulnerabilities at a finer scale, while identifying key data gaps hampering assessment. Chapter 3 gives an example of one such approach (Productivity Susceptibility Analysis, PSA) applied to a species 'complex' allowing managers to focus attention and undertake proactive research. The remaining Chapters provide worked examples of such research on data-limited and/or vulnerable species, evidencing data collection programmes and requirements in support of improved assessment and management objectives.

Additionally, the UK-POA makes less explicit provision for some elasmobranch species and does not fully acknowledge the data-limitations for most elasmobranch species. For example, the UK-POA states that "*additional scientific information should be collected on the life history, rate of reproduction and habitat types*" for <u>depleted</u> and <u>vulnerable</u> species. Whilst such data are clearly needed for some data-limited species that are Threatened, such data are also needed for commercial species, irrespective of whether or not they are depleted at the current time, in order to inform assessments and management advice. If this is not explicitly acknowledged, then the current approach in the UK-POA could result in it becoming more 'reactive' (i.e. initiating actions and objectives only after a species has become depleted) than 'proactive'. A proactive approach would collect fundamental data (e.g. life-history parameters, catch rates) for species identified as potentially vulnerable and/or exploited prior to it showing evidence of depletion.

For example, starry smooth-hound *Mustelus asterias* was identified by the analysis in Chapters 2 and 3 as a stock of potential concern, in terms of fisheries sustainability, given the combination of its life-history characteristics and the absence of any management measures. Relevant data on the reproductive biology and diet were collected and presented in Chapters 5 and 7, along with allied projects not presented in this thesis (McCully Phillips *et al*. (2019) examines movements, behaviour and discard survival). Despite smaller shark species such as starry smooth-hound being generally more productive (see Chapter 5) than many larger-bodied commercially exploited sharks (e.g. carcharhinid species, Castro *et al*., 1999), there has been growing concern regarding overexploitation of smooth-hounds elsewhere in the world (Francis, 1989; Walker, 1992; Colloca *et al*., 2017). This concern extends to the use of smaller shark species in the international fin trade (Cardeñosa *et al*., 2020), indicating that even the more productive elasmobranch taxa could be susceptible to over-exploitation.

This work has shown that continued monitoring and data collection from exploited species and stocks which may not be flagged as the most biologically vulnerable is key within British waters, especially given that the greatest commercial exploitation is directed towards skates and rays (MMO, 2018; Section 1.1.2). From within this assemblage, thornback ray *Raja clavata* is the most widespread and commercially important species in terms of biomass. As a result, this species has been the focus of several industry-led initiatives (Ellis *et al*., 2008; McCully *et al*., 2013) and numerous scientific papers encompassing biology and ecology (summarised in Heessen *et al*., 2015). In contrast many other skate species, principally those of less commercial importance and/or those that have distributions that are not sampled effectively, have been largely overlooked. An improved understanding of other skate species is required – particularly those of larger-body size which could be more vulnerable (Dulvy *et al*., 2000; Dulvy and Reynolds, 2002). The work undertaken in Chapters 2–3 highlights that species including (but not limited to) blonde *Raja brachyura*, undulate *Raja undulata*, shagreen *Leucoraja fullonica* and sandy ray *L. circularis* should be prioritised.

In fact, the European Red List of Marine Species (Nieto *et al*., 2015) demonstrates the importance that Rajiformes should play in conservation planning, with 30% of them being endemic (i.e., they are found nowhere else in the world) to Europe. This contrasts with 7.4% of Europe's Carcharhiniformes and 3.6% of Squaliformes, as larger charismatic species which typically receive more attention in conservation focussed research. Of the 17 Endangered (EN) elasmobranchs, only three species are considered endemic to Europe – yet only one of these (sandy ray) occurs in UK waters. Similarly, of the 10 Vulnerable (VU) elasmobranchs only two species are endemic to Europe and again, only one of these (shagreen ray) occurs in UK seas. Thus clearly "*highlighting the responsibility that European countries* [the UK] *have to protect the global populations of these species*" (Nieto *et al*., 2015). Although both sandy and shagreen ray occur in the Mediterranean, catches are sporadic and their status is cause for concern with both assessed as Critically Endangered (McCully *et al*., 2016; McCully 2016) in this region. Therefore, with the eastern Atlantic being the main part of their distribution, urgent research and management action in the UK is of even greater importance to conserve this endemic species.

On a broader note, whilst both the FAO and the EU-POA defined ‘shark’ as all species of sharks, skates, rays and chimaeras (i.e. Chondrichthyes), the UK-POA addresses only elasmobranchs, thus excluding chimaeras (Holocephali), despite them being vulnerable species (Simpfendorfer and Kyne, 2009) and occurring in the deeper-waters west of the UK (Ebert and Stehmann, 2013). It is also noted that chimaeras are not explicitly addressed by ICES Expert Groups with neither the Working Group for Elasmobranch Fishes nor the Working Group on the Biology and Assessment of Deep-sea Fisheries assessing holocephalans.

We know from past experiences (detailed in Section 1.2) that species can be lost or severely depleted prior to the introduction of management (e.g. spurdog (Pawson *et al*., 2009) and white skate *Rostoraja alba* (Dulvy *et al*., 2000) in British waters and barndoor skate *Dipturus laevis* from the Grand Banks in the northwest Atlantic (Casey and Myers, 1998)). We need to learn from this and develop a more proactive evidence-based approach for examining all species present in national waters. This is required as a first step to guide subsequent management actions and prioritise future research direction. As commercial fisheries and fish marketability can change over time, such prioritisations should be updated on a regular basis.

Indeed FAO (1999) stated that “*States which implement the Shark-plan should regularly, <u>at least every four years</u>, assess its implementation for the purpose of identifying cost-effective strategies for increasing its effectiveness*”. In reality this has not been fulfilled and aside from a ‘light-touch’ review of the EU-POA (STECF, 2019). The EU-POA (COM, 2009) has made limited progress in some areas, with STECF (2019) attributing this to be a consequence of a lack of SMART (specific, measurable, achievable, realistic and time-bound) objectives. This review does however highlight that of the 16 EU Member States with waters of ecological importance to elasmobranchs, the UK was the only one with a NPOA (Defra, 2011) in accordance with IPOA guidelines, although the Netherlands does have a ‘living’ strategy linking high-level objectives to Policy Aims (LNV, 2019). Since the inception of the UK-POA, there has been only one progress review undertaken (Defra, 2013), and no independent peer-review. This brief review was retrospective and detailed only what has been done against the original plan, with no consideration of future direction, targets or revised objectives. By contrast, the Australian NPOA (DAFF, 2004) was reviewed and revised in 2012 (DAFF, 2012). This review determined new time-limited actions in order of priority (see Section 2.4). In a similar way, a revision of the UK-POA could usefully be undertaken setting priority direction for the next decade. The work undertaken in Chapters 2–3 could be used as an evidence base to prioritise species and actions within such a Plan.

The UK-POA recognises the importance of a robust biological understanding for elasmobranchs in fulfilment of the objective: "*For depleted, vulnerable species additional scientific information should be collected on the life history, rate of reproduction and habitat types*", in which Cefas as a national fisheries laboratory, was tasked as a partner. The data collected in Chapters 4–6 are in full support and alignment with this objective. A further objective in which Cefas was named as a partner states that "*Scientific advice should be followed in European TAC and Quota negotiations and the domestic management of elasmobranchs*". The work undertaken in Chapters 2–6 has been presented to the ICES WGEF Expert Group and taken into consideration within the scientific advice drafted, with references made to the Productivity Susceptibility Analysis (PSA; Chapter 3) in skate advice in 2014 (ICES, 2014).

The utility of PSA's as management tools has been limited in Europe to date. They have informed advice and where management should be prioritised, but not currently been used to set catch limits. In its simplest form, PSA's could be used within the ICES community, and specifically to aid elasmobranch assessment, to help set Acceptable Biological Catch (ABC) for even the most data-limited stocks (e.g. sandy and shagreen ray, as Category 5 stocks). Carruthers *et al*. (2014) reviewed 25 methods for setting ABC and the most rudimentary catch based (static) method as used by the Mid-Atlantic Fisheries Management Council for Atlantic mackerel (MAFMC, 2010), requires only the median catch from the last 3-years. Given the limited species-specific time-series of landings for skate stocks in the ICES area (since 2008/2009) and even shorter availability of total catch data, this basic static method would be appropriate for application on Category 5 stocks such as sandy and shagreen ray. This method assumes ABC equals the Overfishing Limit (OFL). However, Restrepo *et al*. (1998) suggested the use of average catches with a downward adjustment based on uncertainty about stock status, and here PSA can be used to inform the level of the buffer needed between the ABC and OFL (Berkson *et al*., 2011; Carmichael and Fenske, 2011) whereby the less productive species are managed with more precaution and a larger buffer than more productive species. The utility of PSA's to provide input into Management Strategy Evaluation (MSE) has also been questioned. Cortés *et al*. (2015) stated that "the effort needed to conduct an MSE is incomparably greater than required for a PSA" which is in contrast to PSAs with their ability to triage a large amount of species with comparably little resource. However, those authors also pointed out that an MSE which estimates a Harvest Control Rule

(HCR) for a comparable species could be applied to a species which scores similarly to the study species. In the case of the skate species managed by ICES where HCR are lacking, this approach is not currently supported.

8.2 Life-history parameters

As noted above, data collection is a key component of POAs for sharks, both in terms of fisheries data (e.g. landings, discards, size composition) and biological knowledge (e.g. stock structure, life-history parameters). Existing monitoring programmes, such as fishery-independent surveys, were not initially designed to collect data for elasmobranchs (Rago, 2005) but can provide an invaluable platform for cost-effective data collection. As evidenced in Chapter 4, data from across wide geographic areas and years can be collated to provide important life-history information, such as length at maturity, length-weight and length-width conversion factors. For example, robust weight-at-length data (e.g. McCully *et al*., 2012, 2015; Silva *et al*., 2013) are required for the derivation of biomass trends from numbers at length data (utilised in ICES elasmobranch advice since 2017; ICES, 2017). Similarly, length-width data can inform fisheries management, given that disc width is more commonly used for skates in commercial fisheries (e.g. by the fishing industry), including in relation to Inshore Fisheries and Conservation Authorities (IFCA) bylaws relating to Minimum Landing Sizes (MLS).

Fishery-independent data (i.e. data collected on surveys in the absence of fishing-industry involvement – usually relating to trawl data collected onboard research vessels) across a wide spatial and temporal scale, has the ability to provide information for less frequently encountered species (see Chapter 6) and to detect subtle changes in parameters over time and between areas. For example, geographic variations in parameters such as length at maturity were identified for cuckoo ray *Leucoraja naevus* (Chapter 4), supporting the view that the North Sea should be considered as a separate stock unit. Given the issues of delineation of stock identity for skates (ICES, 2018) the collection of such data is key. However, it is important to consider potential methodological differences when using data from disparate sources to examine spatio-temporal changes, as such variations may influence estimated parameters such as length at maturity. For example, Chapter 4 rebutted the purported declines in length at maturity for thornback ray which are likely to be an artefact of methodological inconsistencies and a lack of standardised data collection (the importance of which are detailed below). Information on geographical variation in life-history parameters could also be an important consideration if regional management (a central tenet of the reformed CFP; CEC, 2013) is to be implemented. For instance, regional minimum or maximum landing sizes could be implemented at a size to reflect maturation of key commercial elasmobranch species in that area.

Heavily exploited elasmobranch stocks may be expected to display a compensatory density-dependent change in some life history parameters, as speculated by Holden (1973). This study discussed three compensatory mechanisms for density dependence: increase in growth rate (resulting in earlier maturation and or greater fecundity), changes in natural mortality and increases in fecundity. However, there is relatively little evidence of such and in particular this has not conclusively been demonstrated for any skate stock. As Chapter 4 determines, often variability in parameters such as length at first, or 50%, maturity, which can lead to purported declines attributed to density-dependence, are more likely an artefact of methodological inconsistencies between studies. This sentiment was echoed by Fahy (1989a) who considered purported changes in fecundity of different spurdog stocks and stated the "*various ways in which fecundity may be expressed: by the number of ovarian ova, candled ova/embryos, or free embryos*", with only studies with comparative counts of all three parameters evidencing a decline as development progresses (Fahy, 1989a). Much of the published work considering compensatory changes in life-history (and mainly reproductive) parameters due to density-dependence has focussed on spurdog as the study species (e.g. Gauld, 1979; Fahy, 1989a; Silva, 1993; Sosebee, 2005). Silva (1993) reported density-dependent changes in juvenile growth rates and number of embryos with maternal size in spurdog. Similarly, Sosebee (2005) suggested that the observed reduction in the length at 50% maturity could relate to the declining abundance of reproductive females in the population following exploitation. However, there was no evidence of density-dependent effects on either fecundity or size at first maturity, which may either be limited by body size, or slower to respond and thus remained undetected during the study period (Sosebee, 2005). The lack of conclusive studies evidencing density-dependent effects could be a consequence of methodological differences, such as sampling locations, seasons and maturity scales used. These factors can be largely addressed by further studies using fisheries-independent surveys which are standardised and often with long time-series, such as those used in Chapter 4.

The utility of fishery-independent surveys as a platform to collect additional data is a good use of existing resources, while also limiting additional fishing mortality when only dead or moribund specimens are retained. However, not all elasmobranch species are sampled effectively in existing fishery-independent trawl surveys (Rago, 2005), which may relate to the spatial distribution of surveys and/or issues of gear selectivity (i.e. the gear used in surveys were designed to target commercial teleost species, not elasmobranchs). With this in mind, close cooperation with the fishing industry, therefore, should be considered as an approach to augment samples obtained from fishery-independent surveys, through the purchasing of whole (i.e. un-gutted) fish (as used in Chapter 5). This benefits the commercial fisher by paying market value for un-gutted (i.e. heavier) fish and can also provide data from the commercially valuable (i.e. larger) specimens, which are often missing from some fishery-independent trawl (e.g. beam trawl) surveys, which often are more selective for smaller individuals (Silva *et al*., 2019). Using specimens from both fishery-independent surveys and the commercial fishing sector, Chapters 5 and 6 show that a large amount of missing biological data can be collected and processed relatively quickly and cost-effectively. These data can be used to populate assessment models (from semi- to fully-quantitative as evidenced with spurdog, De Oliveira *et al*., 2013) and be used to support pragmatic and bespoke management measures, such as maximum landing lengths (MLL) and minimum landing sizes (MLS) as biologically meaningful measures (Pawson and Ellis, 2005). Indeed a MLL is identified in Chapter 5 as a suitable management measure for starry smooth-hound given that this study has shown that larger females have more and larger pups (which are potentially more likely to survive).

To date, biological sampling of lesser-known elasmobranch species has been hampered by low rates of encounter in fisheries-independent surveys. If only a few individuals are captured on a survey, it is not usual practise to fully dissect them for biological sampling due to the low sample size and perceived limited scientific benefits. However, programmes such as that demonstrated in Chapter 6 that bring dead or moribund bycatch of these species from several different national surveys ashore for processing allows for relevant data to be collected in a standardised way across a number of years, until the sample sizes are robust enough to estimate life-history parameters. In-situ sampling of these cadavers onboard fishery-independent surveys traditionally only collect data on length, weight, sex and maturity, so this model of data collection allows for standardised assignment of maturity stage, including quantified parameters, as well as the collection of other data (e.g. dietary data). Furthermore, this approach makes better use of fishery-independent surveys while also increasing collaboration between national laboratories by pooling specimens (Chapter 6) resulting in better use of natural and financial resources.

Chapter 7 further supports the notion of making best use of data and using cadavers collected to support the life-history work (Chapter 5). This succeeded in providing not only a full dietary profile of starry smooth-hound, but also identified methodological improvements that can vastly alter the 'real' trophic level of a species. This implies that, to date, many dietary studies of predatory fish may have underestimated the trophic level of their study species. This can have ramifications in food web and ecosystem modelling and may alter forecast predictions especially where management measures are introduced and evaluated. For example the landings obligation is likely to reduce fish discards, and thus the carrion on which brachyuran crabs scavenge, thus their numbers may reduce, either potentially displacing starry smooth-hounds or pushing them to forage on alternative species, such as commercially important crabs – potentially impacting economically valuable shellfish fisheries.

In terms of data collection, it is also noted here that conservative and restrictive management measures (e.g. prohibited listings) can have the indirect consequence of hampering data collection in some instances, as commercial fishing vessels are prohibited from 'retaining' and 'landing' even dead specimens for scientific study. Hence, if a species is identified as potentially vulnerable (Chapters 2, 3 and 6) and relevant data are limited, then proactive research to collect such information should be prioritised (where possible making best use of dead bycatch to avoid unnecessary increases in mortality). These data can be used to support future assessment and inform on appropriate management by providing a more robust evidence base for species listings and working towards limiting unfounded 'reflex' listings. For example, between 2009 and 2014, the European Union established regulations prohibiting the retention of undulate ray across its Atlantic range (CEC, 2009; 2010). This regulation was not supported by ICES advice (ICES, 2010) which stated that despite recommending the precautionary approach "*There is no basis in the current or previous ICES advice for the listing of undulate ray as a prohibited species*". The prohibition was lifted in 2015 with a small bycatch quota put in place, however no target fisheries on this species are allowed (CEC, 2015a). The prohibited listing of undulate ray hampered the collection of those data necessary to understand the status of the species, which was then found to be an important part of the coastal skate assemblage in several areas (Ellis *et al*., 2012). Those species, even with strong management in place (e.g. prohibited species list, or restrictive TAC) should, however, not be devoid of data collection beyond that of routine fishery-independent surveys, as this can lead to further data-limitations as the acquisition of specimens is hampered, but should continue to be monitored through making best use of dead bycatch where permitted.

8.3 Fisheries management

Thus far, control measures on commercially exploited elasmobranchs around Europe have primarily consisted of quota restrictions (Ellis *et al.*, 2008). Alternative management measures have been little explored and rarely implemented, although biologically meaningful management measures are often promoted (e.g. Pawson and Ellis, 2005).

Some example of alternative management measures that could be adopted to ensure sustainability of fish stocks include minimum or maximum landing sizes, spatial or temporal restrictions, trip limits and gear modifications. Where such measures have been implemented for elasmobranchs, it is often '*too little too late*' and thus have only been in place for a limited amount of time before more draconian measures are needed such as prohibitions. This approach is reactive and does not allow for alternative management measures to be fully appraised in terms of effectiveness before being superseded. For example, in 2006 the ICES advice was that the Northeast Atlantic spurdog stock was "*depleted and in danger of collapse*" (ICES, 2006) yet it was not until 2009 that a MLL of 100 cm total length (L_T) was introduced. However, this management measure was only in place in isolation for one year as by 2010 a zero TAC was established to try to rebuild the stock (ICES, 2019b). If alternative management measures were introduced at an earlier stage prior to stock depletion this would allow for a full evaluation of efficiency and potentially alleviate the number of species listed as prohibited from fishing opportunities.

In reality, measures such as a zero-TAC or prohibited listings are not a panacea for affording a species protection. These measures are effective in stopping target fisheries, but as most elasmobranchs are caught in mixed fisheries, a change in fisher behaviour would be required to afford complete protection. Without such behavioural changes, zero-TAC and prohibited species are simply discarded with largely unknown survivorship and thus unquantifiable catch rates from which managers can assess the effectiveness of such management measures.

Discard survival of elasmobranchs in UK waters and fisheries has been relatively little studied (Revill *et al.*, 2005; Catchpole *et al.*, 2007; Enever *et al.*, 2009) despite their propensity to capture in mixed fisheries as bycatch. Consequently, even low-value species for which there is currently no market demand (e.g. *Scyliorhinus* spp.) may still be susceptible to exploitation if their critical parts of their stock range overlap with fisheries, and their survival rate after discard is low (e.g. *Alopias* spp.; Ellis *et al.*, 2017). The discard survivorship of elasmobranchs is highly variable within and between different species and fisheries, with factors including gear type, soak time, catch mass and composition, handling practices and degree of exposure to air, influencing survival to a large extent (Ellis *et al*., 2017). Furthermore, the utilisation of low-value species extends beyond the food chain, with some species retained as pot bait (for whelk and crab pots). In these circumstances, the fish may not be landed into ports and, therefore, the recording of the actual catches are uncertain, further hampering robust assessments of actual catch and therefore sustainability.

In light of the questionable effectiveness of punitive measures such as a zero-TAC and prohibited species listings, which should be seen as a last resort, it would be pragmatic to consider such biologically meaningful management options at an early stage, especially for species which are commercially exploited yet have no formal management in place (e.g. starry smooth-hound). The work undertaken in Chapter 5 could be used to support the implementation of a MLL – thus affording the stock some practicable management to support sustainability. Chapter 5 found that the largest male and female specimens were 99 cm and 124 cm L_T with 50% maturity (L_{50}) at 70.4 cm and 81.9 cm L_T respectively, with females observed at an actively reproducing stage at a length of ≥80 cm. These estimates were smaller than those estimated by Farrell *et al*. (2010a) who sampled specimens from adjacent areas of the same Northeast Atlantic stock. The stock management unit of this species has not been fully substantiated and recent work by Brevé *et al*. (2016, 2020) and Griffiths *et al*. (2020) examining tagging data have suggested potential subpopulations and metapopulation-like stock structuring respectively. The latter study postulated at least two sub-populations. One residing in the coastal waters of the southern North Sea and English Channel in spring and summer, moving to deeper waters of the western Channel, Celtic Sea and northern Bay of Biscay in autumn and winter, with the second sub-population residing in the Bristol Channel, Celtic Sea and Irish Sea (Griffiths *et al*., 2020). If these findings are correct, this may indeed go some way in explaining the different maturity estimates of Farrell *et al*., (2010a) who sampled from the second proposed sub-population, and those of Chapter 5, primarily sampled from the first sub-population. The extent to which mixing of any sub-populations may occur is unclear and in order to support appropriate management of this species further work is needed, such as further tagging studies in this overlapping region of the Celtic and Irish Sea, combined with genetic techniques. In the absence of elucidated appropriate management units at the current time for starry smooth-hound, it would be prudent to proceed with a biologically meaningful management measure whilst this species continues to be commercially exploited. When considering both maturity estimates of Chapter 5 and Farrell *et al*., (2010a) a MLL of 100 cm would likely be easily implementable and a suitable biologically meaningful management measure for this stock, which would protect the very largest mature females as the most productive (i.e. valuable) part of the demographic.

The only example of a MLL or MLS currently in operation for elasmobranch species around the UK is that enshrined in local bylaws. The Southern IFCA and the Cumbria Sea Fisheries Committee District (under the North Western IFCA jurisdiction) have implemented a MLS of 40 cm and 45 cm wing-width respectively for skates and rays. Whilst a laudable measure, it should be noted that this may afford limited protection to most skates, as when converted to total length (using conversion factors from Chapter 4), these values are below the length at maturity for most inshore skates and therefore, are only a measure that protects juveniles. The measure would benefit mature fish of the smaller-bodied species, such as starry, cuckoo and spotted ray, but both starry and cuckoo ray are largely offshore species, and this bylaw would not cover their main distributional ranges.

The variability in biological parameters such as length at maturity exhibited across the skate taxa, reflecting the range of sensitivities, supports a move away from managing these species as a complex with a generic TAC. Consideration should be given to managing skates through a more local and/or genus-based approach. Chapter 6 identifies two *Leucoraja* species as very vulnerable, and much like *Dipturus* species, the biology of these species would indicate that prolonged unregulated commercial exploitation on these stocks may not be sustainable. The offshore nature of these two species may afford them slightly more protection than other, more coastal rajid species, in terms of potentially reduced overlap with fisheries. However, there would likely be overlap between these species and important fisheries for hake *Merluccius merluccius*, megrim *Lepidorhombus whiffiagonis* and anglerfish *Lophius* spp.. Consequently, these species would benefit from closer monitoring through more targeted sampling associated with vessels operating in these grounds. A low-level TAC (operating more like a bycatch allowance) for shagreen and sandy ray in the Celtic Seas ecoregion would be beneficial to these stocks and support their conservation. The continued collection of biological material from cadavers of both species would be advocated to facilitate the development of more robust maturity ogives (such as demonstrated in Chapter 4) and to give estimates of fecundity. Furthermore, the fragmented distribution of both species raises questions regarding the appropriate stock units over which management should operate. Currently ICES considers the stock unit for both species to be the Celtic Seas ecoregion (as they occur on the outer shelf of ICES Subareas 6 and 7) although the distribution of both species extends into both ICES Division 4.a and Subarea 8, however the actual stock units are currently unknown. Surveys do not provide the continual coverage to show clear splits in distribution and studies to confirm stock units through tagging, genetics or parasite analyses are yet to be undertaken on these species.

8.4 Future studies

The present work has contributed to knowledge of some key life-history parameters for three priority vulnerable demersal species. This work has also identified other areas for future research, as summarised below.

8.4.1 Reproduction

In terms of priority demersal species, blonde ray *Raja brachyura* is a large-bodied vulnerable skate species (Chapter 3) of commercial importance, yet with limited life-history data. To date published studies have been based on small sample sizes (Catalano *et al*., 2007) and/or from the Mediterranean Sea (Porcu *et al*., 2010, 2015). More robust length at maturity data (Chapter 4 had limited numbers of mature specimens) and fecundity estimates would facilitate a better understanding of biological vulnerability and help inform on sustainable exploitation. Fecundity is, however, a life-history parameter which remains largely unknown for most skate species beyond thornback ray (Holden, 1975; Ellis and Shackley, 1995). As oviparous elasmobranchs, skates are often serial spawners and as such estimates of fecundity in the field are difficult to obtain. Robust estimates are usually only obtainable from egg-laying rates of captive specimens (Koop, 2005) which carry both the potential for captive stress biases and a large financial cost.

8.4.2 Habitat use

The identification of ecologically important grounds and habitats for most vulnerable elasmobranchs beyond some key species, is an area of research which is little known around the British Isles. Electronic tagging of porbeagle (Pade *et al*., 2009; Biais *et al*., 2017) and basking sharks (Sims *et al*., 2003, 2005a) has been used to detail the horizonal and vertical movements and habitat use of these wide-ranging sharks. However, given the difficult access to specimens and large costs associated with studies using data storage tags, these are based on small sample sizes (between four and nine animals). Therefore, inference to stock or population level movements is limited when the whole demographic (i.e. representative numbers across sex and life-history stages) is not characterised. Studies of elasmobranch behaviour and habitat use within restricted areas such as sea loughs off the coast of Ireland and Scotland have been documented for lesser-spotted dogfish *Scyliorhinus cancicula* (Sims *et al*., 2001), greater-spotted dogfish *S. stellaris* (Sims *et al*., 2005b), spurdog (Thorburn *et al*., 2015) and flapper skate *Dipturus intermedius* (Wearmouth and Sims, 2009[25]; Neat *et al*., 2015), with most species exhibiting some form of residency, refugia behaviour or restricted movements. However, the geographically-constrained study areas mean that their findings may not necessarily be representative of more widely distributed offshore habitats utilised by these species and their wider populations.

Knowledge of the habitat utilisation of many commercially important elasmobranch species – particularly the smaller-bodied skates that are included within the generic skates and rays TAC is largely deficient. Given the large number of skate stocks around the British Isles (22 currently assessed stocks by ICES WGEF), habitat utilisation has only been detailed for thornback ray in the southern North Sea (Hunter *et al*., 2005, 2006), with more limited data for other rajid species (Humphries *et al*., 2016). Electronic tagging can also be used to support the delineation of mating/pupping/spawning and nursery grounds (Heupel *et al*., 2007), yet to date very little is known about the spawning grounds for oviparous species such as rajids. Where possible, this information can help to support biologically meaningful spatial management (evaluated by Stevens, 2002). Interestingly, *de facto* refugia for elasmobranch species have been identified in both the shelf (Shephard *et al*., 2012) and deep-water (Henry *et al*., 2016) seas, with research postulating that relatively stable fishing effort (i.e. the fishing intensity in an area has been relatively even in pressure across a time-frame) has created such accidental refugia which are being exploited by elasmobranchs. This theory, if correct, will leave elasmobranchs vulnerable to changes in fisheries management such as spatial closures and the demersal landings obligation which are likely to displace the effort of fishers.

8.4.3 Discards and discard survival

As part of the reformed Common Fisheries Policy (CFP; CEC, 2013) a 'landing obligation' has been introduced (CEC, 2015b) to eliminate the discarding of unwanted fish at sea. This obligation is therefore likely to reduce the volume of demersal elasmobranchs being discarded, unless a derogation is passed. Derogations may be granted for some fish species on the grounds of demonstratable 'high' survivorship once discarded. Some elasmobranch species have been shown to have a high survival (e.g. lesser-spotted dogfish, Revill *et al*., 2005), therefore by including such species in the landing obligation this could result in higher

[25] This paper is based on common skate (*Dipturus batis*), however this was published prior to the taxonomic separation of *D. batis* and *D. intermedius*. Closer examination of this paper, the size and location of the study specimens and the subsequent publication by Neat *et al*. (2015) in the same area, it is almost certain that the study specimens were in fact flapper skate *D. intermedius*.

fishing mortality – especially on the smaller individuals (i.e. fish of a typically non-commercially valuable size, that would normally be discarded). In response to the landing obligation, ICES has been moving towards the provision of 'catch' advice (i.e. official landings plus dead discards = total removals) in its assessment and advice process (rather than just using official landing data; ICES, 2019a). Therefore, a good understanding of the level of discarding and the associated survival of species (to quantify dead discards) is important to ensure robust estimates of removals are available in the assessment process. Estimates of the volume of fish discarded often come from national observer programmes. However, the coverage of fisheries observers is often not adequate (covering <1 % of trips in England and Wales; Catchpole *et al*., 2011) at a spatial, temporal or fleet level (i.e. some métiers like inshore longliners which can be an important fleet targeting skate, are not sampled due to their small size) to be able to provide robust estimates of discards. This approach can also be inadequate to represent and provide data for some patchily distributed species (e.g. undulate ray). Dedicated projects investigating the discard levels and subsequent survival of a species are expensive yet can give species-specific ranges for survival in different métiers (e.g. McCully Phillips *et al*., 2019).

8.4.4 Age and growth

Unlike commercially important teleosts, there is no requirement under the European Data Collection Framework (DCF) to age elasmobranchs, in support of age-based stock assessments. As a consequence, this area of research has continued to lag behind that of ageing teleost fish – especially in Europe. Although vertebrae (e.g. Stevens, 1975), spines (e.g. Holden and Meadows, 1962) and thorns (e.g. Moura *et al*., 2007; Serra-Pereira *et al*., 2008) have been used to count rings, the validation of these bands as annuli (i.e. one translucent and opaque band pair represents one year of age) has proved difficult for many species. Methods of verification can include incremental analysis of vertebrae centra or spines (e.g. Carlson *et al*., 1999), bomb radiocarbon dating (e.g. Campana *et al*., 2006), tag and recapture studies (Simpfendorfer *et al*., 2000), (oxy)tetracycline marking (e.g. Kinney *et al*., 2016) and so are labour and/or data intensive to achieve. A review by Cailliet (1990) found that of the 39 elasmobranch species for which studies attempted to verify the temporal periodicity of band deposition, there were only sufficient data to achieve this for six species. These biological parameters are however essential in the estimation of growth, mortality and productivity rates (Campana, 2014) – all key variables in demographic and assessment modelling.

Research on elasmobranch age and growth from around the British Isles was principally conducted in the latter part of last century (Steven, 1936; Holden and Meadows, 1962; Holden, 1972; Holden and Vince, 1973; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Fahy, 1989b). However, since this time this area of research has largely been overlooked with age and growth estimates only generated on assumptions of annual band pair deposition for a handful of species (Gallagher *et al*., 2005; Whittamore and McCarthy, 2005; Farrell *et al*., 2010b). Where the enumeration of band pairs has previously been verified as representative of age for a species, this approach is appropriate, however this cannot be assumed to hold true for all species. For example, Natanson and Cailliet (1990) found that bands from tetracycline-injected Pacific angel shark *Squatina californica* were not deposited annually and were actually related to somatic growth. Given that changes in life-history parameters such as growth rates and age at maturity can occur following sustained exploitation (Walker, 1999), contemporary validated estimates of age and growth from commercially exploited elasmobranchs should be a priority in supporting sustainable exploitation.

8.4.5 National archive

Currently no national archive repository of elasmobranch specimens or biological material exists to support worldwide initiatives in elasmobranch research. Although natural history museums (e.g. Natural History Museum, London) are invaluable in the provision of specimens (including ‘type’ specimens) to support taxonomic research, usually only a limited number of specimens of larger species are able to be housed. Similarly, gene banks only house small amounts of genetic material, to support genetic studies. As yet no coordinated UK initiative representing marine fish exists, although fisheries laboratories will often archive the otoliths collected from teleosts fishes (given that these are small structures that can be kept as dried specimens). Indeed, the national DCF fishery-independent surveys collect otolith samples from thousands of marine fish annually (evidenced by the collection of up to 50 000 otoliths annually to age commercially important teleost as part of the DCF; Easey and Millner, 2008). In Australia the National Fish Collection is curated by the Commonwealth Scientific and Industrial Research Organisation (CSIRO, a federal government agency) in support of sustainable fisheries and management – with deep-sea fishes, sharks and rays comprising an important part of this collection due to their inherent vulnerabilities. Given the depleted nature of many elasmobranch species and stocks globally, coupled with recent increases in restrictive management, such materials should be made available to all researchers to limit the collection of further specimens (potentially increasing mortality rates) and to support collaborative efforts in supporting sustainability and conservation efforts through POAs.

8.5 Final thoughts

This thesis has focussed on the demersal component of the elasmobranch NPOA, as this is where the largest scale declines and extirpations have been documented to date in British waters (Section 1.2), such as white skate and the common skate complex. However, going forward other vulnerable species or complexes, such as chimaeras, pelagic and deep-water sharks could usefully be the focus of similar attention and prioritisations. The framework introduced here could facilitate the same proactive collection of evidence on which research and actions can be based, both in other vulnerable marine ecosystems and developing countries alike.

Overall, the approaches taken in Chapters 2 and 3 identified some key potentially vulnerable elasmobranch species with the data collected for Chapters 5 and 6 confirming the vulnerable statuses through financial and natural resource efficient methods, thus vindicating this as an appropriate method and framework for National Plans of Action (NPOA) to follow – especially in developing countries where data are most limited.

The identification of potentially vulnerable elasmobranchs and sustainability of commercially exploited species is ultimately what this body of work and NPOAs are working towards. Improved assessments support sustainability and the data collected here have been presented to the IUCN Shark Specialist Group in their Red List Assessments, ICES WKLIFE and WGEF and used to support data-limited assessments (such as PSA's and length-based assessments) and the work of this expert group throughout the advisory process.

8.6 References

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9 Appendices

9.1 Appendix I: Table of the current legislative and administrative basis for management and conservation of individual elasmobranchs in the UK waters

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	Scientific name	Common name	IUCN global status[26]	CITES	CMS[27]	IUCN regional status	OSPAR[28]	ICES advice, assessment and category[29]	EU TAC[30]	UK Wildlife and Countryside Act	UK list of Priority Habitats and Species	Species of Principal Importance (England NERC/S41)	Environment (Wales) Act (Species of Principal Importance)	Conservation Regulations (Northern Ireland 1995)	Northern Ireland Priority Species List	Scottish Biodiversity List	Sharks, Skates and Rays (Scotland) Order 2012.
Hexanchidae	*Hexanchus griseus*	Bluntnose six-gill shark	NT			LC			✓[$]								✓

[26] IUCN Red list assessment category: NE = not evaluated, DD = data deficient, LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered and CR = critically endangered. Threatened categories (VU, EN and CR) are shaded.

[27] Parentheses indicate the Appendix on which the species is listed, with listings on both Appendices permitted where circumstances so warrant. * indicates presence on the Sharks MoU (Annex I)

[28] OSPAR Regions where the species is under threat and/or in decline given in parenthesis. Where none shown, the species is considered to be under threat and/or in decline across all Regions where it occurs.

[29] Advice given denoted by AD, assessment by SA and the assessment category is given in parentheses. Advice is only indicated where it is species or sometime genus (e.g. Mustelus spp.) specific. Advice is provided for 'other skates and rays' but this is not indicated. Some species have multiple stock units around UK waters, where this occurs, the highest assessment category is given.

[30] Prohibited species present on Annex I of Regulation (EU) 2019/1241 (EU, 2019b) are indicated by ✓(P). Where this is not enforced in all waters, the ICES Divisions to which it applies are indicated after this (e.g. as for Norwegian skate ✓(P: 6a,b, 7a-c,e-h,k)). Species added through annual (or biennial) fishing regulations are indicated by ✓ followed by the Divisions in which this regulation applies (e.g. starry ray ✓(2a, 3a, 7d)).

** As part of ICCAT regulations, it is prohibited to retain on board, tranship or land any part or whole carcass

*** As part of ICCAT regulations, it is prohibited to undertake a directed fishery for species of thresher sharks of the Alopias genus.

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	**Scientific name**	**Common name**	**IUCN global status[26]**	**CITES**	**CMS[27]**	**IUCN regional status**	**OSPAR[28]**	**ICES advice, assessment and category[29]**	**EU TAC[30]**	**UK Wildlife and Countryside Act**	**UK list of Priority Habitats and Species**	**Species of Principal Importance (England NERC/S41)**	**Environment (Wales) Act (Species of Principal Importance)**	**Conservation Regulations (Northern Ireland 1995)**	**Northern Ireland Priority Species List**	**Scottish Biodiversity List**	**Sharks, Skates and Rays (Scotland) Order 2012.**
	Heptranchias perlo	Sharpnose seven-gill shark	NT			DD											
Chlamydoselachiidae	*Chlamydoselachus anguineus*	Frilled shark	LC			LC			✓$								
Lamnidae	*Isurus oxyrinchus*	Shortfin mako	EN	✓(II)	✓(II)*	DD		SA#			✓	✓					
	Lamna nasus	Porbeagle shark	VU	✓(II)	✓(II)*	CR	✓	AD/SA#	✓(all)		✓	✓	✓		✓	✓	✓
Cetorhinidae	*Cetorhinus maximus*	Basking shark	EN	✓(II)	✓(I,II)*	EN	✓	AD	✓(P)	✓	✓	✓	✓		✓	✓	
Alopiidae	*Alopias superciliosus*	Big-eye thresher shark	VU	✓(II)	✓(II)*	EN		AD	✓**,***								
	Alopias vulpinus	Thresher shark	VU	✓(II)	✓(II)*	EN			✓***								
Scyliorhinidae	*Apristurus aphyodes*	White ghost catshark	LC			LC			✓$								✓
	Apristurus laurussonii	Iceland catshark	LC			LC			✓$								✓
	Apristurus manis	Ghost catshark	LC			LC			✓$								✓

$ Article 7 of EU (2018) states that it is prohibited for EU vessels to fish for: deep-sea sharks in ICES subareas 5 to 9, in Union and international waters of ICES subarea 10, in international waters of ICES subarea 12 and in Union waters of CECAF 34.1.1, 34.1.2 and 34.2 and to retain on board, tranship, relocate or land deep-sea sharks caught in those areas, with the exception of cases where TACs apply for bycatches in fisheries for black scabbardfish that use longlines as set out in the Annex

stock assessment undertaken by ICCAT

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	Scientific name	Common name	IUCN global status[26]	CITES	CMS[27]	IUCN regional status	OSPAR[28]	ICES advice, assessment and category[29]	EU TAC[30]	UK Wildlife and Countryside Act	UK list of Priority Habitats and Species	Species of Principal Importance (England NERC/S41)	Environment (Wales) Act (Species of Principal Importance)	Conservation Regulations (Northern Ireland 1995)	Northern Ireland Priority Species List	Scottish Biodiversity List	Sharks, Skates and Rays (Scotland) Order 2012.
	Apristurus melanoasper	Black roughscale catshark	LC			LC			✓$								✓
	Apristurus microps	Smalleye catshark	LC			LC			✓$								✓
	Galeus melastomus	Black-mouth dogfish	LC			LC		AD/SA(3)									✓
	Galeus murinus	Mouse catshark	LC			LC			✓$								
	Scyliorhinus canicula	Lesser-spotted dogfish	LC			LC		AD/SA(3)									
	Scyliorhinus stellaris	Greater-spotted dogfish	NT			NT		AD/SA(3)									
Pseudotriakidae	*Pseudotriakis microdon*	False catshark	LC			DD											
Triakidae	*Mustelus asterias*	Starry smooth-hound	NT			NT		AD/SA(3)									
	Mustelus mustelus	Smooth-hound	VU			VU											
	Galeorhinus galeus	Tope shark	CR		✓(II)	VU		AD	✓(1, 2a, 4-8, 12, 14)		✓	✓	✓		✓	✓	✓
Carcharhinidae	*Prionace glauca*	Blue shark	NT		✓(II)	NT					✓	✓	✓			✓	
Sphyrnidae	*Sphyrna zygaena*	Smooth hammerhead	VU	✓(II)	✓(II)*	DD			✓**								
Dalatiidae	*Dalatias licha*	Kitefin shark	VU			EN		AD	✓(1, 2a, 4,14) $		✓	✓				✓	✓

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	Scientific name	Common name	IUCN global status[26]	CITES	CMS[27]	IUCN regional status	OSPAR[28]	ICES advice, assessment and category[29]	EU TAC[30]	UK Wildlife and Countryside Act	UK list of Priority Habitats and Species	Species of Principal Importance (England NERC/S41)	Environment (Wales) Act (Species of Principal Importance)	Conservation Regulations (Northern Ireland 1995)	Northern Ireland Priority Species List	Scottish Biodiversity List	Sharks, Skates and Rays (Scotland) Order 2012.
Etmopteridae	*Centroscyllium fabricii*	Black dogfish	LC			LC			✓[$]								✓
	Etmopterus princeps	Great lantern shark	LC			LC			✓(1, 2a, 4, 14)[$]								✓
	Etmopterus spinax	Velvet belly	LC			NT			✓[$]								✓
Somniosidae	*Centroscymnus coelolepis*	Portuguese dogfish	NT			EN	✓	AD	✓(1, 2a, 4, 14)[$]		✓	✓				✓	✓
	Centroselachus crepidater	Longnose velvet dogfish	NT			LC			✓[$]								✓
	Scymnodon ringens	Knifetooth dogfish	VU			LC			✓[$]								✓
	Somniosus microcephalus	Greenland shark	VU			NT			✓[$]								✓
Oxynotidae	*Oxynotus centrina*	Angular roughshark	VU			VU											
	Oxynotus paradoxus	Sailfin roughshark	DD			DD			✓[$]								✓
Centrophoridae	*Centrophorus squamosus*	Leafscale gulper shark	EN			EN	✓	AD	✓(1, 2a, 4, 14)[$]		✓	✓				✓	✓
	Deania calcea	Birdbeak dogfish	NT			EN			✓(1, 2a, 4, 14)[$]								✓
	Deania hystricosa	Rough longnose dogfish	DD			DD											
	Centrophorus uyato	Little gulper shark	EN			VU											

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	Scientific name	Common name	IUCN global status[26]	CITES	CMS[27]	IUCN regional status	OSPAR[28]	ICES advice, assessment and category[29]	EU TAC[30]	UK Wildlife and Countryside Act	UK list of Priority Habitats and Species	Species of Principal Importance (England NERC/S41)	Environment (Wales) Act (Species of Principal Importance)	Conservation Regulations (Northern Ireland 1995)	Northern Ireland Priority Species List	Scottish Biodiversity List	Sharks, Skates and Rays (Scotland) Order 2012.
Squalidae	*Squalus acanthias*	Spurdog	VU		✓(II)*	EN	✓	AD/SA(1)	✓(2-10)[31] TAC[32]		✓	✓	✓		✓	✓	✓
Echinorhinidae	*Echinorhinus brucus*	Bramble shark	EN			EN											
Squatinidae	*Squatina squatina*	Angel shark	CR		✓(I,II)*	CR	✓	AD	✓(P)	✓	✓		✓		✓	✓	✓
Torpedinidae	*Tetronarce nobiliana*	Common electric ray	DD			LC											
	Torpedo marmorata	Marbled electric ray	DD			LC											
Arhynchobatidae	*Bathyraja pallida*	Pale ray	LC			LC											
	Bathyraja richardsoni	Richardson's ray	LC			LC											
	Bathyraja spinicauda	Spinytail ray	NT			LC											
	Bathyraja sp.		NE			NE											
Rajidae	*Amblyraja hyperborea*	Arctic skate	LC			LC											
	Amblyraja jenseni	Jensen's skate	LC			LC											

[31] With the exception of avoidance programmes as set out in Annex IA of Article 16 of EU (2020)

[32] Precautionary TAC only for vessels participating in the avoidance programme.

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	Scientific name	Common name	IUCN global status[26]	CITES	CMS[27]	IUCN regional status	OSPAR[28]	ICES advice, assessment and category[29]	EU TAC[30]	UK Wildlife and Countryside Act	UK list of Priority Habitats and Species	Species of Principal Importance (England NERC/S41)	Environment (Wales) Act (Species of Principal Importance)	Conservation Regulations (Northern Ireland 1995)	Northern Ireland Priority Species List	Scottish Biodiversity List	Sharks, Skates and Rays (Scotland) Order 2012.
	Amblyraja radiata	Starry ray	VU			LC		AD/SA(3)	✓(2a, 3a, 4, 7d)								
	Dipturus batis	Common blue skate	CR			CR	✓	AD	✓(2a, 3-4, 6-10)		✓	✓	✓		✓	✓	✓
	Dipturus intermedius	Flapper skate															
	Dipturus nidarosiensis	Norwegian skate	NT			NT			✓(P: 6a,b, 7a-c,e-h,k)								
	Dipturus oxyrinchus	Long-nose skate	NT			NT			Generic TAC								
	Leucoraja circularis	Sandy ray	EN			EN		AD	Generic TAC		✓					✓	
	Leucoraja fullonica	Shagreen ray	VU			VU		AD	Generic TAC								
	Leucoraja naevus	Cuckoo ray	LC			LC		AD/SA(3)	Generic TAC								
	Malacoraja kreffti	Krefft's ray	LC			LC											
	Malacoraja spinacidermis	Soft skate (or prickled skate)	LC			LC											
	Neoraja caerulea	Blue pygmy skate	LC			LC											
	Raja brachyura	Blonde ray	NT			NT		AD	Generic TAC				✓				
	Raja clavata	Thornback ray	NT			NT	✓(II)	AD/SA(3)	✓(3a)				✓			✓	

Coverage of legislation / policy driver			Global			Europe	Northeast Atlantic			UK		England	Wales	Northern Ireland		Scotland	
Family	**Scientific name**	**Common name**	**IUCN global status[26]**	**CITES**	**CMS[27]**	**IUCN regional status**	**OSPAR[28]**	**ICES advice, assessment and category[29]**	**EU TAC[30]**	**UK Wildlife and Countryside Act**	**UK list of Priority Habitats and Species**	**Species of Principal Importance (England NERC/S41)**	**Environment (Wales) Act (Species of Principal Importance)**	**Conservation Regulations (Northern Ireland 1995)**	**Northern Ireland Priority Species List**	**Scottish Biodiversity List**	**Sharks, Skates and Rays (Scotland) Order 2012.**
	Raja microocellata	Small-eyed ray	NT			NT		AD/SA(3)	TAC[33]								
	Raja montagui	Spotted ray	LC			LC	✓	AD/SA(3)	Generic TAC								
	Raja undulata	Undulate ray	EN			NT		AD/SA(3)	✓(6 and 10) TAC[34]		✓	✓	✓		✓		✓
	Rajella bathyphila	Deepwater ray	LC			LC											
	Rajella bigelowi	Bigelow's ray	LC			LC											
	Rajella kukujevi	Mid-Atlantic skate	LC			LC											
	Rajella fyllae	Round skate	LC			NE											
	Rostroraja alba	White skate	EN			CR	✓	AD	✓(P: 6-10)	✓	✓	✓	✓				✓
Dasyatidae	*Dasyatis pastinaca*	Common stingray	DD			VU											
	Pteroplatytrygon violacea	Pelagic stingray	LC			LC											
Myliobatidae	*Myliobatis aquila*	Common eagle ray	CR			VU											

[33] Precautionary single species TAC for ICES Divisions 7.f, g.
[34] Precautionary single species TAC for ICES Divisions 7.d, e.

9.2 Appendix II: Vulnerability ranking by expert for each species in otter trawl and gillnet fisheries.

Species	FAO Code	Otter Trawl Vulnerability Scores					Greatest difference in individual ranks	Gillnet Vulnerability Scores					Greatest difference in individual ranks
		Expert 1	Expert 2	Expert 3	Expert 4	Overall Rank		Expert 1	Expert 2	Expert 3	Expert 4	Overall Rank	
Angel shark (*Squatina squatina*)	AGN	3	2	2	2	1	1	1	2	3	NA	2	2
Tope (*Galeorhinus galeus*)	GAG	2	4	1	1	2	3	3	4	1	1	1	3
Spurdog (*Squalus acanthias*)	DGS	1	1	3	3	3	2	2	1	2	2	3	1
White skate (*Rostroraja alba*)	RJA	4	3	6	NA	4	3	4	3	6	NA	4	3
Flapper skate (*Dipturus intermedius*)	RJB1	7	5	4	NA	5	3	5	5	4	NA	5	1
Electric ray (*Torpedo nobiliana*)	TTO	10	6	5	NA	6	5	8	6	8	NA	7	2
Common blue skate (*Dipturus batis*)	RJB2	5	11	7	4	7	6	6	8	7	3	6	2
Blonde ray (*Raja brachyura*)	RJH	13	7	8	5	8	6	9	9	5	5	8	4
Long-nosed skate (*Dipturus oxyrinchus*)	RJO	6	9	12	NA	9	6	10	10	13	NA	10	3
Norwegian skate (*Dipturus nidarosiensis*)	JAD	8	8	14	NA	10	6	7	7	14	NA	9	7
Starry smooth-hound (*Mustelus asterias*)	SDS	9	16	10	6	11	7	13	11	9	4	11	4
Shagreen ray (*Leucoraja fullonica*)	RJF	11	13	9	8	12	4	11	14	10	6	12	4
Sandy ray (*Leucoraja circularis*)	RJI	11	10	16	NA	13	6	14	12	12	NA	13	2
Small-eyed ray (*Raja microocellata*)	RJE	15	12	15	9	14	3	12	13	17	7	15	5
Marbled electric ray (*Torpedo marmorata*)	TTR	17	15	11	NA	15	6	16	16	15	NA	16	1
Thornback ray (*Raja clavata*)	RJC	14	17	13	7	16	4	17	17	18	8	17	1
Undulate ray (*Raja undulata*)	RJU	16	14	18	10	17	4	15	15	11	9	14	4
Spotted ray (*Raja montagui*)	RJM	18	18	17	12	18	1	18	18	19	10	18	1
Cuckoo ray (*Leucoraja naevus*)	RJN	19	18	19	11	19	1	19	19	16	10	19	3
Greater spotted dogfish (*Scyliorhinus stellaris*)	SYT	20	20	20	NA	20	0	20	19	20	NA	20	1
Lesser spotted dogfish (*Scyliorhinus canicula*)	SYC	21	21	21	13	21	0	21	21	21	12	21	0

9.3 Appendix III: Taxonomic list of *Mustelus* spp. and summary of published studies on their diets

Scientific name	English name	Dietary studies
***Mustelus albipinnis* Castro-Aguirre, Antuna-Mendiola, González-Acosta and de la Cruz-Agüero, 2005**	Whitemargin smooth-hound	No published studies
***Mustelus antarcticus* Günther, 1870**	Gummy shark	Coleman and Mobley (1984) Bulman *et al*. (2001) Simpfendorfer *et al*. 2001
***Mustelus asterias* Cloquet, 1819**	Starry smooth-hound	Ford (1921) Ellis *et al*. (1996)
***Mustelus californicus* Gill, 1864**	Gray smooth-hound	Talent (1982)
***Mustelus canis* (Mitchill, 1815)**	Dusky smooth-hound	Rountree and Able (1996) Gelsleichter *et al*. (1999) Vianna *et al*. (2000) Taylor *et al*. (2014) Montemarano *et al*. (2016) Malek *et al*. (2016)
***Mustelus dorsalis* Gill, 1864**	Sharptooth smooth-hound	Rojas (2006)
***Mustelus fasciatus* (Garman, 1913)**	Striped smooth-hound	Soto (2001)
***Mustelus griseus* Pietschmann, 1908**	Spotless smooth-hound	Kamura and Hashimoto (2004)
***Mustelus henlei* (Gill, 1863)**	Brown smooth-hound	Russo (1975) Talent (1982) Haesker and Cech (1993) Gomez *et al*. (2003) Espinoza *et al*. (2012) Rodríguez-Romero *et al*. (2013) Amariles *et al*. (2017)
***Mustelus higmani* Springer and Lowe, 1963**	Smalleye smooth-hound	Springer and Lowe (1963) Tagliafico *et al*. (2015)
***Mustelus lenticulatus* Phillipps, 1932**	Spotted estuary smooth-hound	King and Clark (1984)
***Mustelus lunulatus* Jordan and Gilbert, 1882**	Sicklefin smooth-hound	Gomez *et al*. (2003) Navia *et al*. (2006) Navia *et al*. (2007) Moreno-Sanchez *et al*. (2012) Amariles *et al*. (2017)
***Mustelus manazo* Bleeker, 1855**	Starspotted smooth-hound	Taniuchi *et al*. (1983) Yamaguchi and Taniuchi (2000) Kamura and Hashimoto (2004)
***Mustelus mangalorensis* Cubelio, Remya and Kurup, 2011**		No published studies

Scientific name	English name	Dietary studies
***Mustelus mento* Cope, 1877**	Speckled smooth-hound	No published studies
***Mustelus minicanis* Heemstra, 1997**		No published studies
***Mustelus mosis* Hemprich and Ehrenberg, 1899**	Arabian smooth-hound	Goldschmidt *et al*. (1995) Moore *et al*. (2016)
***Mustelus mustelus* (Linnaeus, 1758)**	Smooth-hound	Azouz and Capapé (1971; in part) Morte *et al*. (1997) Smale and Compagno (1997) Jardas *et al*. (2007b) Filiz (2009) Saidi *et al*. (2009b) Gračan *et al*. (2014)
***Mustelus norrisi* Springer, 1939**	Narrowfin smooth-hound	No published studies
***Mustelus palumbes* Smith, 1957**	Whitespotted smooth-hound	Smale and Compagno (1997)
***Mustelus punctulatus* Risso, 1827**	Blackspotted smooth-hound	Azouz and Capapé (1971; in part) Jardas *et al*. (2007a) Saïdi *et al*. (2009a) Lipej *et al*. (2011)
***Mustelus ravidus* White and Last, 2006**	Australian grey smooth-hound	No published studies
***Mustelus schmitti* Springer, 1939**	Narrownose smooth-hound	Capitoli *et al*. (1995) Belleggia *et al*. (2012) Chiaramonte and Pettovello (2000) Molina and Cazorla (2011)
***Mustelus sinusmexicanus* Heemstra, 1997**	Gulf smooth-hound	No published studies
***Mustelus stevensi* White and Last, 2008**	White-spotted gummy shark	No published studies
***Mustelus walkeri* White and Last, 2008**	Eastern spotted gummy shark	No published studies
***Mustelus whitneyi* Chirichigno F., 1973**	Humpback smooth-hound	Sanchez de Benites *et al*. (1983)
***Mustelus widodoi* White and Last, 2006**	White-fin smooth-hound	No published studies

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9.4 Appendix IV: Summary of the feeding habits of Mustelus spp., indicating the geographic locations, sample sizes (NT = total sample size; NF = number of fish with stomach contents), index of vacuity (IV), length range examined, method of diet description (D = qualitative description; O = frequency of occurrence; N = proportion by numerical abundance; P = proportion by points or fullness/points; M = proportion by biomass; IRI = index of relative importance or %IRI) and main prey taxa observed in published studies.

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
M. antarcticus	SE Australia	–	113	–	–	IRI	Crustacea and Cephalopoda	Coleman and Mobley (1984)
	SE Australia	17	7	58.8%	–	M	Crustacea (Decapoda) and Cephalopoda	Bulman *et al*. (2001)
	W Australia	1731	923	46.7%	810–1630	O	Teleostei = 50%; Crustacea = 37.3%; Cephalopoda = 27.8%	Simpfendorfer *et al*. (2001)
M. asterias	British Isles (Plymouth)	–	48	–	–	O	Crustacea (100% of stomachs), Polychaeta (12.5%) and fish (4.2%). The most frequent prey taxa were *Pagurus bernhardus, P. prideaux* (Paguridae), Portunidae, *Atelecyclus rotundatus* (Atelecyclidae), *Galathea* spp. (Galatheidae), *Inachus* spp., *Macropodia* spp. and *Hyas coarctatus* (Majidae) and *Upogebia* spp. (Thalassinoidea).	Ford (1921)
	British Isles	46	0	0%	430–1000	P	Crustacea (97.4%), Teleostei (1.9%) and Holothuroidea (0.7%). The main prey taxa were Portunidae Paguridae and Xanthidae. *Cancer pagurus* comprised 0.7% of the diet. Fish prey included *Agonus cataphractus.*	Ellis *et al*. (1996)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
M. canis	East coast USA	85	85	0%	318-516 mm	O, M, N	Crustaceans and polychaetes dominated in the diet. The most frequent prey taxa were shrimps *Crangon septemspinosa* and *Palaemonetes vulgaris*, polychaetes and the crabs *Callinectes sapidus*, *Libinia* spp., and *Ovalipes ocellatus*.	Rountree and Able (1996)
	Chesapeake Bight	64	64	0%	-	%IRI	Diet dominated by crustaceans (86.1% IRI) and molluscs (9.0% IRI). Main prey species was *Cancer irroratus.*	Gelsleichter *et al*. (1999)
	Brazil	115	56	51.3%	332-1054	O	Crustaceans were observed in 87.5% of those stomachs containing food. The main crustacean prey were stomatopods and brachyuran crabs.	Vianna *et al*. (2000)
	Rhode Island Sound and Narragansett Bay	34	NA	NA	NA	O, M	Diet comprised primarily of crustaceans (64.8% M) and fish (32.3% M). Main prey taxon was *Cancer* spp.	Taylor *et al*. (2014)
	Rhode Island Sound	24	NA	NA	410-800	M	Diet comprised primarily of crustaceans (80% M) and fish (15% M). Main prey taxon was *Cancer* spp. M. canis shown to have a narrow niche breadth compared to other fish in the community studied.	Malek *et al*. (2016)
	Long Island	73	71	2.7%	NA	%IRI	Diet comprised primarily of crustaceans (78.3% IRI) and fish (20.2% M). Main prey taxon was *Cancer irroratus*.	Montemarano *et al*. (2016)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
M. dorsalis	Costa Rica	311	192	38.2%	500-660	O, N. M	Diet comprised of crustaceans (*Squilla hancocki, Squilla parva*, *Farfantepenaeus* sp.) and fish (Clupeiformes, *Caranx* sp., *Lutjanus* sp.)	Rojas (2006)
M. fasciatus	Southern Brazil	17	14	17.6%		O	Crustaceans the most frequent prey group, with *Hepatus pudibundus, Persephona mediterranea, Callinectes sapidus, Farfantepenaeus paulensis* frequent prey taxa.	Soto (2001)
M. griseus	Seto Inland Sea	193	187	3.1%	390-1000	O, N, M	Predated primarily on decapod crustaceans, including *Portunus hastatoides* (Portunidae), *Leptochela gracilis* (Pasiphaeidae), *Diogenes edwardsii* (Diogenidae), *Cancer gibbosulus* (Cancridae) and *Anchisquilla fasciata* (Stomatopoda)	Kamura and Hashimoto (2004)
M. henlei	San Francisco Bay and Tomales Bay (California)	77	68	11.7%	53–94 cm	O		Russo (1975)
	Tomales Bay (California)	54	51	5.6%	67–92 cm	O	The brachyurans *Hemigrapsus* and *Cancer* were in 72% and 35% of all stomachs examined, *Crangon* = 33%, polychaetes = 26% and fish = 27%. Site-specific differences in prey, with Cancer in 75% and 12% of the stomachs at the two study sites.	Haesker and Cech (1993)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
	Colombia (Pacific)	109	51	53.2%	540-860	O, N, M	Main prey species were squid (Loliginidae), *Euphlylax dovii* and *Portunus iridiscens* (Portunidae) and *Squilla panamensis* (Stomatopoda).	Gomez *et al*. (2003)
	Costa Rica	340	282	17.1%	162-665	%IRI	Main prey taxa of smaller specimens were decapod crustaceans (40.4% IRI), fish (25.0% IRI), cephalopods (20.9% IRI) and stomatopods (11.3% IRI). Main prey taxa of larger specimens were fish (51.6% IRI), cephalopods (33.8% IRI) and decapod crustaceans (11.5% IRI).	Espinoza *et al*. (2012)
	Baja California Sur	166	114	31.3%	360-1060	%IRI	The diet was dominated by crustaceans, including galatheids, brachyurans and stomatopods. Main prey species was *Pleuroncodes planipes.*	Rodríguez-Romero *et al*. (2013)
	Colombia (Pacific)	123	117	4.9%	400-775	%IRI	The diet was dominated by teleosts (89.7% IRI), with Crustaceans (brachyurans, shrimps and stomatopods) of lesser importance (8.9% IRI)	Amariles *et al*. (2017)
M. higmani	Surinam	74	(54)	(27.0%)	NA	O	Of those specimens containing identifiable food, the most frequently occurring prey groups were stomatopods (55.6%), brachyuran crabs (31.5%) and hermit crabs (20.4%).	Springer and Lowe (1963)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
	Venezuela	266	NA	13%		%IRI	Decapod crustaceans (especially Paguroidea, Calappoidea and Portunoidea) was the main prey group, followed by fish, stomatopods and cephalopods	Tagliafico *et al*. (2015)
M. lenticulatus	New Zealand	428	NA	NA	Ca. 650-1150	IRI	The main prey taxa were pagurids, brachyuran crabs (*Nectocarcinus antarcticus, Ovalipes catharus, Cancer novaezelandiae*), *Urechis novaezelandiae* (Echiura) and *Struthiolaria papulose* (Gastropoda)	King and Clark (1984)
M. lunulatus	Colombia (Pacific)	292	139	52.4%	430-1370	O, N, M	Main prey species were *Portunus iridiscens* (Portunidae), *Squilla panamensis* (Stomatopoda) and *Hypoconcha panamensis* (Dromiidae).	Gomez *et al*. (2003)
	Colombia (Pacific)	50	47	6.0%	500-1250	O, N, M	Diet dominated by stomatopods (*Squilla panamensis* and *S. parva*), with brachyuran crabs and various natantid and penaeid shrimps also consumed.	Navia *et al*. (2006)
	Colombia (Pacific)	42	39	7.1%	550-1250	%IRI		Navia *et al*. (2007)
	Baja California Sur	40	40	0%	680-1170	%IRI	Diet comprised primarily of crustaceans (57.4%) and fish (37%). Most frequent prey taxa were *Munida tenella, Hemisquilla ensigera californiensis, Decapturus* spp. and *Cancer amphioetus*	Moreno-Sanchez *et al*. (2012)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
	Colombia (Pacific)	116	101	12.9%	450-1120	%IRI	The diet was dominated by crustaceans (93.3% IRI) with fish (6.4% IRI), molluscs and polychaetes of lesser importance. Stomatopods (52.3% IRI) of particular importance.	Amariles *et al*. (2017)
M. manazo	Choshi (Japan)	412	405	1.7%	NA		Crustacea in 84.5% of non-empty stomachs (Brachyura (inc. *Cancer* sp.) = 50.5%; Shrimps = 23.9%; Anomura = 21.7% and Stomatopoda = 5.4%) and fish in 22.9%. Main fish prey were clupeids.	Taniuchi *et al*. (1983)
	Japan and Taiwan	936		0.0-6.1%		O, N. M	Diet described by sampling location. Overall, a range of crustaceans (including stomatopods, brachyuran crabs, hermit crabs and crangonid, penaeid, and alpheid shrimps), fish and polychaetes were important in the diet.	Yamaguchi and Taniuchi (2000)
	Seto Inland Sea	166	164	1.2%	430-1200	O, N, M	Predated primarily on decapod Crustaceans, including *Cancer gibbosulus* (Cancridae), *Portunus hastatoides* and *Liocarcinus corrugatus* (Portunidae). Polychaetes also observed frequently in the stomachs.	Kamura and Hashimoto (2004)
M. mosis	Red Sea	8	4	50%	NA	O	Prey included *Penaeus* spp., other crustaceans, cephalopods and fish.	Goldschmidt *et al*. (1995)
	Arabian Sea and Gulf of Oman	9	9	0%	NA	O, N	Most frequent prey were crustaceans, including brachyurans (e.g. Parthenope, Lupocyclus), penaeid and caridean shrimps and stomatopods	Moore *et al*. (2016)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
M. mustelus	Western Mediterranean	261	253	3.1%	360-750	O, N	*Liocarcinus* spp. and other brachyuran crabs predominated in the diet, with *Squilla mantis,* and various shrimps and fish of secondary importance	Morte *et al*. (1997)
	Southern Africa	402	367	8.7%	(390-1650)	O, N, M	Smaller individuals predated primarily on polychaetes and crustaceans (including shrimps and brachyuran crabs such as *Goneplax angulatus*). Fish, cephalopods and larger crustaceans important in the diets of larger individuals.	Smale and Compagno (1997)
	Adriatic Sea	139	115	17.3%	670-1370	%IRI	The main prey groups were decapod crustaceans (63.1% IRI) and teleosts (31.2% IRI). The most frequently occurring prey species were *Atelecyclus rotundatus* and *Munida rugosa*	Jardas *et al*. (2007b)
	Aegean Sea	72	43	40.3%	383-975	%IRI	Data presented to higher taxonomic groups only. Main prey groups were crustaceans and teleosts,	Filiz (2009)
	Tunisia	540	477	11.7%	340-1585	%IRI	Crustaceans (51.4% IRI) and fish (44.5% IRI) were the main prey groups. The most frequent prey species were *Squilla mantis, Pontocaris lacazei* and *Ethusa mascarone*	Saidi *et al*. (2009b)
	Adriatic Sea	15	14	6.7%	505-1525	%IRI	The dominant prey group were crustaceans (84% IRI), with the most frequently occurring prey species including *Liocarcinus corrugattus* and *L. depurator* (Portunidae) and *Pilumnus* sp. (Xanthidae)	Gračan *et al*. (2014)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
M. palumbes	Southern Africa	265	263	0.8%	(275-1126)	O, N, M	Smaller individuals predated primarily on small crustaceans (including *Pterygosquilla armata,* shrimps and early stages of brachyuran crabs). Crustaceans also main prey group for larger individuals, with fish and cephalopods also consumed.	Smale and Compagno (1997)
M. punctulatus	Adriatic Sea	145	125	13.8%	695-1113	%IRI	The main prey groups were decapod crustaceans (65.0% IRI) and teleosts (30.0% IRI). The most frequently occurring prey species was *Liocarcinus depurator* (Portunidae)	Jardas *et al*. (2007a)
	Tunisia	133	114	14.3%	305-1210	%IRI	Fish (34.0% IRI), crustaceans (30.0% IRI) and molluscs (28.2% IRI) were all important prey groups.	Saïdi *et al*. (2009a)
	Adriatic Sea	151	130	13.9%	500-1350	%IRI	The main prey groups were crustaceans (55.6% IRI), cephalopods (19.5% IRI, bivalves (12% IRI) and teleosts (9.2% IRI). The most frequently occurring prey species were *Solecurtus strigillatus* (Bivalvia), *Ethusa mascarpone* (Brachyura) and *Squilla mantis* (Stomatopoda).	Lipej *et al*. (2011)
	Adriatic Sea	185	179	3.2%	446-1362	%IRI	Diet comprised primarily of malacostracans (74.7% IRI), including *Liocarcinus depurator, L. corrugatus, Squilla mantis and Rissoides desmaresti*, and teleosts (23.3% IRI), with cephalopods and polychaetes infrequent.	Gračan *et al*. (2017)
M. schmitti	Brazil	158	158	0%	-	IRI	Diet dominated by crustaceans, especially hermit crabs (*Loxopagurus, Paguristes*) and brachyuran crabs (*Libinia, Portunus*)	Capitoli *et al*. (1995)

Scientific name	Geographical area	N_T	N_F	I_V	Length range (mm)	Diet analysis	Dominant prey taxa	Source
	Argentina	525	512	2.5%	260-885	%IRI	Diet primarily comprising crustaceans (45.1% IRI), polychaetes (30.0% IRI) and fish (17.9% IRI). Most frequently occurring prey taxa were anchovy (Engraulis), hermit crabs (*Loxopagurus, Pagurus*), spider crabs (*Leucippa*), atelecyclid crabs (*Peltarion*) and glycerid worms.	Belleggia *et al*. (2012)
	Argentina	87	77	11.5%	252-913	N	The crab *Cyrtograpsus* was the main prey species, with young of the year specimens also predating on euphausiids, and larger specimens also feeding on fish	Chiaramonte and Pettovello (2000)
	Argentina	472	425	10.0%	250-810	%IRI	The diet was dominated by crustaceans (89.4% IRI) and polychaetes (10.2% IRI). The most frequently occurring prey taxa were the brachyuran crabs *Neohelice granulata, Corystoides abbreviatus* and *Cyrtograpsus angulatus*.	Molina and Cazorla (2011)
M. whitneyi	Peru	784	NA	NA	320-1020	O	Teleosts (including *Engraulis ringens*), crustaceans and polychaetes.	Sanchez de Benites *et al*. (1983)
***Mustelus* spp.**	Mediterranean Sea	–	–	–	–	O	Crustacea (60%; *Alpheus, Squilla, Dromia, Dorippe, Lambrus* and *Maia*), Teleostei (35%; *Pagellus, Spicara, Gobius, Citharus* and *Solea*) and Cephalopoda (20%; *Loligo, Sepiola* and *Sepia*)	Azouz and Capapé (1971)

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9.5 Appendix V: Trophic level of prey taxa (taken from Cotter *et al.*, 2008 unless otherwise noted).

Higher taxa	Prey taxa	Trophic level
Cnidaria	*Tubularia* sp.	1.6 (Fredriksen, 2003)
	Hydrallmania falcata	1.6 (Fredriksen, 2003)
	Hydroida (indet.)	1.6 (Fredriksen, 2003)
Polychaeta	*Arenicola* sp.	2.63 (average of polychaetes in Nilsen *et al.*, 2008)
	Polychaeta (indet.)	2.63 (average of polychaetes in Nilsen *et al.*, 2008)
Stomatopoda	*Rissoides desmaresti*	2.24 (general benthos in Cotter *et al.*, 2008)
Isopoda	*Idotea linearis*	2.24 as above
Amphipoda	*Gammarellus homari*	1.5 (Fredriksen, 2003)
	Amphipoda	1.5 (Fredriksen, 2003)
Decapoda-Natantia	*Palaemon* sp.	3.29 (as per *Palaemon serratus*)
	Alpheus glaber	3.40 (average of unique spp. values within Decapoda-Natantia)
	Processa sp.	3.00
	Pandalina brevirostris	3.2 (as *Pandalus montagui*)
	Pandalus montagui	3.2
	Pandalidae (indet.)	3.2 (as *Pandalus montagui*)
	Crangon allmanni	3.4
	Crangon crangon	4.09
	Crangon sp.	3.75 (average of *C. allmanni* and *C. crangon*)
	Natantia (indet.)	3.40 (average of unique spp. values within Decapoda-Natantia)
Decapoda-Anomura	*Callianassa tyrrhena*	2.77 (as anomurid decapods)
	Upogebia stellata	2.77 (as anomurid decapods)
	Upogebia sp.	2.77 (as anomurid decapods)
	Thalassinoidea (indet.)	2.77 (as anomurid decapods)
	Anapagurus laevis	2.77 (as anomurid decapods)
	Pagurus bernhardus	3.68
	Pagurus prideaux	3.1
	Paguridae (indet.)	2.77 (as anomurid decapods)
	Galathea sp.	2.77 (as anomurid decapods)
	Munida rugosa	3.00
	Pisidia longicornis	2.77 (as anomurid decapods)
Decapoda-Brachyura	*Hyas coarctatus*	2.99 (as brachyuran crab)
	Macropodia rostrata	2.0 (as majidae)
	Macropodia tenuirostris	2.0 (as majidae)
	Macropodia sp.	2.0 (as majidae)
	Majidae (indet.)	2.0 (as majidae)

	Corystes cassivelaunus	3.7
	Atelecyclus rotundatus	3.1
	Bathynectes longipes	3.68 (*Macropipus* spp. swimming crab)
	Cancer pagurus	3.9
	Carcinus maenus	3.56
	Liocarcinus arcuatus	3.52 (as *L. holsatus*)
	Liocarcinus depurator	3.68 (*Macropipus* spp. swimming crab)
	Liocarcinus holsatus	3.52
	Liocarcinus pusillus	3.52 (as *L. holsatus*)
	Liocarcinus sp.	3.52 (as *L. holsatus*)
	Necora puber	3.68 (*Macropipus* spp. swimming crab)
	Portunidae (indet.)	3.68 (*Macropipus* spp. swimming crab)
	Monodaeus couchi	2.99 (as brachyuran crab)
	Pilumnus hirtellus	2.99 (as brachyuran crab)
	Xantho sp.	2.99 (as brachyuran crab)
	Xanthidae (indet.)	2.99 (as brachyuran crab)
	Goneplax rhomboides	2.99 (as brachyuran crab)
	Brachyura (indet.)	2.99
Other crustacean	*Crustacea* (indet.)	2.99 (as brachyuran crab)
Mollusca	*Nucula* sp. (shell)	2.25 (as bivalve molluscs)
	Mytilus edulis	2.25 (as bivalve mollusc)
	Corbula gibba	2.25 (as bivalve mollusc)
	Bivalvia (indet.)	2.25 (as bivalve mollusc)
	Sepiolidae	3.55 (as Cephalopods mixed)
	Cephalopoda (beak)	3.55 (as Cephalopods mixed)
Echinodermata	*Ophiura albida*	3.2
	Ophiura sp.	3.2 (as *O. albida*)
	Echinoid	2.83 (assumed *P. milliaris*)

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9.6 Appendix VI: Diet composition of *M. asterias* around the British Isles, showing % occurrence, % numbers, % points, IRI and %IRI for fish from the North Sea ecoregion and Celtic Seas ecoregion.

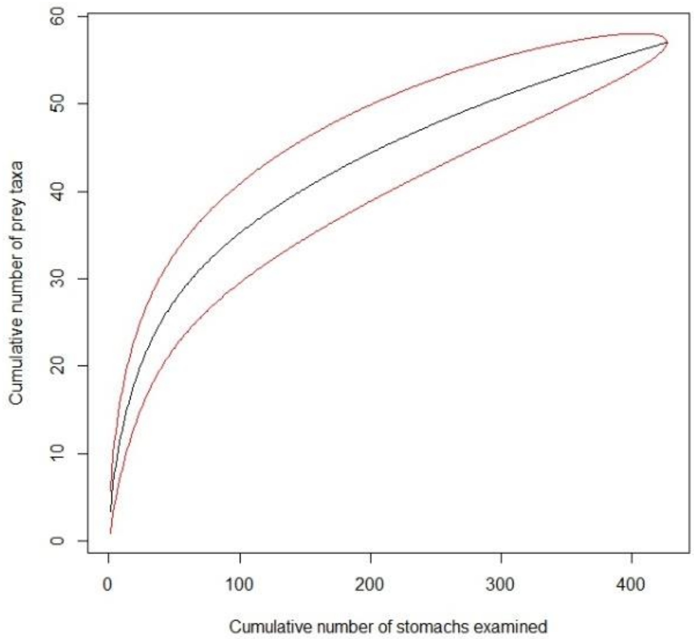
	Prey taxa	Fish in North Sea Ecoregion (n = 421)								Fish in Celtic Seas ecoregion (n = 210)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
Cnidaria	*Tubularia* sp.	1	1	4	0.24	0.07	0.02	0.02	0.00								
	Hydrallmania falcata	1	1	5	0.24	0.07	0.03	0.02	0.00								
	Hydroida (indet.)	6	6	24	1.43	0.40	0.13	0.75	0.01	7	9	41	3.33	1.10	0.35	4.84	0.09
Total Cnidaria									0.01								0.09
Polychaeta	*Arenicola* sp.	1	1	15	0.24	0.07	0.08	0.03	0.00								
	Polychaeta (indet.)	5	5	41	1.19	0.33	0.22	0.65	0.01	2	2	11	0.95	0.25	0.09	0.32	0.01
Total Polychaeta									0.01								0.01
Stomatopoda	*Rissoides desmaresti*	2	2	41	0.48	0.13	0.22	0.17	0.00								
Isopoda	*Idotea linearis*	7	13	146	1.66	0.86	0.77	2.71	0.05								
Amphipoda	*Gammarellus homari*	1	1	8	0.24	0.07	0.04	0.03	0.00								
	Amphipoda	10	36	103	2.38	2.39	0.54	6.95	0.12	23	116	318	10.95	14.23	2.69	185.35	3.54
Decapoda-Caridea	*Palaemon* sp.	2	2	24	0.48	0.13	0.13	0.12	0.00								
	Alpheus glaber									1	3	80	0.48	0.37	0.68	0.50	0.01
	Processa sp.	1	1	8	0.24	0.07	0.04	0.03	0.00	2	2	21	0.95	0.25	0.18	0.40	0.01
	Pandalina brevirostris									2	3	18	0.95	0.37	0.15	0.50	0.01
	Pandalus montagui	2	2	18	0.48	0.13	0.09	0.11	0.00								
	Pandalidae (indet.)	3	3	15	0.71	0.20	0.08	0.20	0.00								
	Crangon allmanni	26	39	195	6.18	2.59	1.02	22.29	0.39	9	15	158	4.29	1.84	1.34	13.62	0.26

	Prey taxa	Fish in North Sea Ecoregion (n = 421)								Fish in Celtic Seas ecoregion (n = 210)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Crangon crangon	32	53	389	7.60	3.51	2.04	42.22	0.73	2	2	24	0.95	0.25	0.20	0.43	0.01
	Crangon sp.	17	20	130	4.04	1.33	0.68	8.11	0.14	2	2	19	0.95	0.25	0.16	0.39	0.01
	Natantia (indet.)	2	2	16	0.48	0.13	0.08	0.10	0.00	1	1	10	0.48	0.12	0.08	0.10	0.00
Decapoda-Anomura	*Callianassa tyrrhena*									1	1	20	0.48	0.12	0.17	0.14	0.00
	Upogebia stellata									1	1	10	0.48	0.12	0.08	0.10	0.00
	Upogebia sp.	4	5	148	0.95	0.33	0.78	1.05	0.02	11	14	345	5.24	1.72	2.92	24.29	0.46
	Thalassinoidea (indet.)	15	17	161	3.56	1.13	0.84	7.03	0.12	2	3	36	0.95	0.37	0.30	0.64	0.01
	Anapagurus laevis									2	2	39	0.95	0.25	0.33	0.55	0.01
	Pagurus bernhardus	264	387	4910	62.71	25.66	25.75	3224.26	55.82	25	28	446	11.90	3.44	3.77	85.82	1.64
	Pagurus prideaux	1	1	10	0.24	0.07	0.05	0.03	0.00	5	9	107	2.38	1.10	0.91	4.78	0.09
	Paguridae (indet.)	2	2	17	0.48	0.13	0.09	0.11	0.00	11	11	167	5.24	1.35	1.41	14.47	0.28
	Galathea sp.									5	5	63	2.38	0.61	0.53	2.73	0.05
	Munida rugosa									1	1	16	0.48	0.12	0.14	0.12	0.00
	Pisidia longicornis	1	1	5	0.24	0.07	0.03	0.02	0.00	4	4	27	1.90	0.49	0.23	1.37	0.03
Decapoda-Brachyura	*Hyas coarctatus*									2	2	29	0.95	0.25	0.25	0.47	0.01
	Macropodia rostrata	2	2	15	0.48	0.13	0.08	0.10	0.00	1	1	10	0.48	0.12	0.08	0.10	0.00
	Macropodia tenuirostris									1	1	24	0.48	0.12	0.20	0.16	0.00
	Macropodia sp.	6	10	68	1.43	0.66	0.36	1.45	0.03								
	Majidae (indet.)	15	19	158	3.56	1.26	0.83	7.44	0.13	8	9	95	3.81	1.10	0.80	7.27	0.14
	Corystes cassivelaunus	18	25	214	4.28	1.66	1.12	11.89	0.21	48	90	1458	22.86	11.04	12.34	534.35	10.20
	Atelecyclus rotundatus	24	31	332	5.70	2.06	1.74	21.65	0.37	38	57	962	18.10	6.99	8.14	273.83	5.23

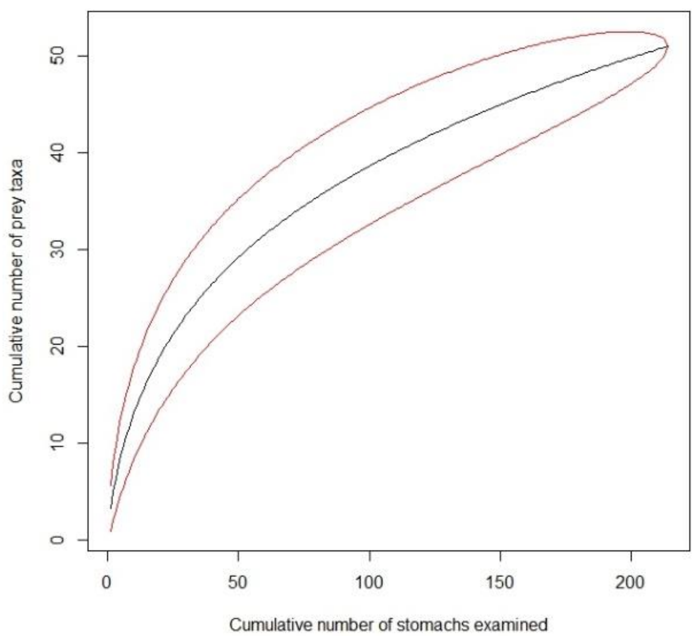
	Prey taxa	Fish in North Sea Ecoregion (n = 421)								Fish in Celtic Seas ecoregion (n = 210)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Bathynectes longipes									1	1	10	0.48	0.12	0.08	0.10	0.00
	Cancer pagurus	42	61	829	9.98	4.05	4.35	83.73	1.45	1	3	16	0.48	0.37	0.14	0.24	0.00
	Carcinus maenus	21	44	616	4.99	2.92	3.23	30.67	0.53								
	Liocarcinus arcuatus	1	1	10	0.24	0.07	0.05	0.03	0.00								
	Liocarcinus depurator	13	25	292	3.09	1.66	1.53	9.85	0.17	5	8	164	2.38	0.98	1.39	5.64	0.11
	Liocarcinus holsatus	107	289	2224	25.42	19.16	11.67	783.56	13.56	48	113	1146	22.86	13.87	9.70	538.52	10.28
	Liocarcinus pusillus	1	1	8	0.24	0.07	0.04	0.03	0.00	12	14	176	5.71	1.72	1.49	18.32	0.35
	Liocarcinus sp.	17	22	280	4.04	1.46	1.47	11.82	0.20	10	13	200	4.76	1.60	1.69	15.65	0.30
	Necora puber	61	88	1429	14.49	5.84	7.50	193.16	3.34	2	2	35	0.95	0.25	0.30	0.52	0.01
	Portunidae (indet.)	13	16	217	3.09	1.06	1.14	6.79	0.12	4	5	155	1.90	0.61	1.31	3.67	0.07
	Monodaeus couchi				0.00	0.00	0.00	0.00	0.00	1	2	21	0.48	0.25	0.18	0.20	0.00
	Pilumnus hirtellus	2	2	22	0.48	0.13	0.12	0.12	0.00	3	6	59	1.43	0.74	0.50	1.76	0.03
	Xantho sp.									1	1	10	0.48	0.12	0.08	0.10	0.00
	Xanthidae (indet.)	9	19	158	2.14	1.26	0.83	4.47	0.08	16	88	535	7.62	10.80	4.53	116.75	2.23
	Goneplax rhomboides	5	5	95	1.19	0.33	0.50	0.99	0.02	1	2	12	0.48	0.25	0.10	0.17	0.00
	Brachyura (indet.)	7	9	207	1.66	0.60	1.09	2.80	0.05	6	8	219	2.86	0.98	1.85	8.10	0.15
Other crustacean	Crustacea (indet.)	158	163	4048	37.53	10.81	21.23	1202.51	20.82	137	138	4055	65.24	16.93	34.31	3342.72	63.81
Total Crustacean									98.48								99.36
Mollusca	*Nucula* sp. (shell)	1	1	7	0.24	0.07	0.04	0.02	0.00								
	Mytilus edulis	1	1	1	0.24	0.07	0.01	0.02	0.00	1	1	12	0.48	0.12	0.10	0.11	0.00
	Corbula gibba									1	1	6	0.48	0.12	0.05	0.08	0.00

	Prey taxa	Fish in North Sea Ecoregion (n = 421)								Fish in Celtic Seas ecoregion (n = 210)							
		Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI	Count of stomachs with prey type present	Sum of numbers of each prey type	Sum of Fullness x Points	%O	%N	%P	IRI	%IRI
	Bivalvia (indet.)									2	3	37	0.95	0.37	0.31	0.65	0.01
	Sepiolidae	1	1	8	0.24	0.07	0.04	0.03	0.00								
	Cephalopoda (beak)	1	1	12	0.24	0.07	0.06	0.03	0.00								
Total Mollusca									0.00								0.02
Echinodermata	*Ophiura albida*	2	2	19	0.48	0.13	0.10	0.11	0.00								
	Ophiura sp.	1	1	3	0.24	0.07	0.02	0.02	0.00								
	Echinoid	1	1	4	0.24	0.07	0.02	0.02	0.00								
Total Echinodermata									0.00								0.00
Miscellaneous	Broken shell	1		0	0.24	0.00	0.00	0.00	0.00	1		0	0.48	0.00	0.00	0.00	0.00
	Gravel/stone	2		0	0.48	0.00	0.00	0.00	0.00	7		0	3.33	0.00	0.00	0.00	0.00
	Monofilament line	1		0	0.24	0.00	0.00	0.00	0.00								
	Squid (bait)	33	37	593	7.84	2.45	3.11	43.61	0.75								
	Digested remains	30	30	763	7.13	1.99	4.00	42.69	0.74	12	12	398	5.71	1.47	3.37	27.65	0.53
Total Miscellaneous									1.49								0.53

9.7 Appendix VII: Cumulative prey curve for a) North Sea ecoregion samples (n = 421) and b) Celtic Seas ecoregion samples (n = 210)



a) North Sea ecoregion



b) Celtic Seas ecoregion