Casting A Wide Net:

Ecological insights to strengthen marine spatial planning for coastal shark conservation

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By

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SUMMARY

Industrialised fishing of the oceans has driven extensive declines in predatory fish biomass. Many shark species are now threatened with extinction, with implications for ecosystem functioning and socioeconomic equity. Spatial protection and fisheries management require ecological evidence to enable recovery but knowledge gaps remain, including population status and critical habitats. I use baited remote underwater video (BRUVS) and laser ablation inductively coupled mass spectrometry (LA-ICP-MS) to address knowledge gaps in Tobago and the UK. Trinidad and Tobago is a regional shark trade hub, but a UNESCO Man and the Biosphere Reserve, marine protected area plans, an updated Fisheries Management Bill and Sustainable Shark and Ray Management Plan for Tobago present conservation opportunities. The departure of the UK from the European Union presents opportunities to overhaul marine resource management, including the Welsh Marine Evidence Strategy (2019-2025). Regional goals can align with the international Decade of Ocean Science for Sustainable Development.

BRUVS yielded surprisingly high species richness in Northeast Tobago, unexpected given shark fishing in Trinidad or Tobago. Habitat relief, depth and season drive shark abundance; specific habitat areas may be important for wider Caribbean shark populations and should feature in Biosphere and MPA management. BRUVS yielded novel spatiotemporal habitat insights for the nursehound, *Scyliorhinus stellaris*, in the Cardigan Bay Special Area of Conservation (SAC), UK, including important nearshore reef areas and potential temporal niche partitioning with smallspotted catsharks, *Scyliorhinus canicula*. Further work should assess shark nursery status, and advocate for stronger shark protection within SAC networks.

LA-ICP-MS elemental analysis of *S. canicula* vertebrae yielded population structure and heavy metal contamination insights. Shared young-of-year and sub-adult habitat use precedes adult dispersal, sexual segregation, and potentially multiple birthing grounds that could be important for population recruitment. Heavy metal hotspots and bioaccumulation have implications for regional fisheries and may be a physiological stressor.

SCIENTIFIC ARTICLES PUBLISHED DURING STUDENTSHIP

Goetze et al. (Accepted). Directed conservation of the world's reef sharks. *Nature Ecology and Evolution*

Cook, N.D. et al., 2024. Incidence and species diversity of elasmobranchs around a southern Caribbean island (Tobago): opportunities for conservation in a regional trade hub. *Journal of the Marine Biological Association of the UK* **104** (e8), 1-10

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MacNeil et al., 2020. Global status and conservation potential of reef sharks. *Nature* **583,** 801-806. doi.org/10.1038/s41586-020-2519-y

CONFERENCE PRESENTATIONS DURING STUDENTSHIP

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Oral presentation: Lifetime pollutant exposure patterns in the smallspotted catshark *Scyliorhinus canicula* in the Bristol Channel, UK

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“How inappropriate to call this planet Earth, when it is quite clearly Ocean”

- Arthur C. Clarke

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- Jacques Cousteau

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abbreviations

BRUVS	Baited Remote Underwater Video Stations
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMS	Convention on the Conservation of Migratory Species of Wild Animals
EU	European Union
GMR	Galapagos Marine Reserve
IUCN	International Union for Conservation of Nature
LA-ICP-MS	Laser-ablation inductively-coupled-plasma mass spectrometry
MAB	Man and the Biosphere Reserve
MPA	Marine Protected Area
SAC	Special Area of Conservation
RFMO	Regional Fisheries Management Organisation
UN	United Nations
UNESCO	United Nations Educational, Scientific and Cultural Organization

For Sophia

For bringing perspective

Chapter 1: GENERAL INTRODUCTION

1.1 The Anthropocene Ocean

Four and a half billion years of evolution, extinction and reorganisation have thus far culminated in the Anthropocene. Today, *Homo sapiens* is the singular definitive species that shapes the planet, the first hyperkeystone species (Worm and Paine 2016), and a super predator (Worm 2015). We are yet to discover an ecosystem that bears no consequence of anthropogenic activity: most tropical forests are on a trajectory to an altered state (Malhi et al. 2014); larval fish ingest accumulated prey-size plastics in Hawaiian coastal surface slick nurseries (Gove et al. 2019); disease prevalence is elevated in corals that are in contact with plastic debris (Lamb et al. 2018); international shipping is a primary introduction pathway for marine invasions (Molnar et al. 2008); since the first human settlement of New Zealand as many as 36% of land bird species have become extinct (Johnson et al. 2017); and, it has been projected that by 2100 up to 60% of European forest lands will have reduced economic value and lower carbon sequestration than present day forests (Hanewinkel et al. 2013). Biodiversity decline exceeds rates expected from the fossil record while the future loss of currently critically endangered species would elicit extinction rates seen only five times in 540 million years (Barnosky et al. 2011). This is the sixth mass extinction.

Industrialisation, human population growth and anthropogenic activity are linked with widespread oceanic impacts: coral cover on the Great Barrier Reef declined over 50% between 1985 and 2012 (De'Ath et al. 2012); mangrove forests in Southeast Asia declined an average of 0.18% annually from 2000 to 2012 (Richards and Friess 2016); long-term loss of seagrasses in the United Kingdom may be as high as 92% (Green et al. 2021); and linear negative monthly trends are observed for Arctic sea ice in recent decades, with potential ramifications for patterns of atmospheric circulation and precipitation (Serreze et al. 2007). In particular, industrialised fishing of global oceans has reduced the biomass of large predatory fish to approximately 10% of pre-exploitation levels (Myers and Worm 2003). Important gaps in our knowledge of marine biodiversity remain (Mora et al. 2011), therefore gaining insights into species population status, trends, and the potential ecosystem ramifications of ongoing decline should be a priority (Luypaert et al. 2020).

1.2 Sharks

1.2.1 Status and trends

Sharks are an important component of healthy marine ecosystems, and in some systems they can act as keystone species (Libralato et al. 2006; Bornatowski et al. 2018). Long-term trends, however, indicate uncertain stability for global shark populations (Myers and Worm 2005; Ferretti et al. 2010). Widespread depletion identified at the beginning of the 21st Century (Myers and Worm 2003) has continued (Pacoureau et al. 2021), with ever increasing vulnerability for elasmobranchs generally (Dulvy et al. 2014). Recent estimates suggest that over a third of shark and ray species are threatened with extinction (Dulvy et al. 2021).

Many of the threats facing sharks can be attributed directly to human activities. Overfishing is generally agreed to be the key driver of population decline (Queiroz et al. 2019; MacNeil et al. 2020; Dulvy et al. 2021; Yan et al. 2021), but the intricacy of the impacts of human pressures on sharks is such that even marine protected areas (MPAs) can fail to protect sharks and other predatory fish if they are in close proximity to human population centres (Ward-Paige et al. 2010; Cinner et al. 2018; Juhel et al. 2018). Sharks can ultimately be depleted to functional extinction where protection is either ineffective or absent (MacNeil et al. 2020), with negative implications for community composition and species diversity (Simpfendorfer et al. 2023). Nevertheless, there remain bright spots where shark populations persist (Hearn et al. 2010; Letessier et al. 2019b; Murray et al. 2019) or where shark fisheries are sustainably managed (Simpfendorfer and Dulvy 2017). This, together with the potential for spatial protection to contribute to the persistence or recovery of some shark species (Speed et al. 2018; Simpfendorfer et al. 2023), present the case for being optimistic about the chances of shark conservation success based on sound ecological evidence and appropriate design (Dwyer et al. 2020; Conners et al. 2022), and supported by the required governance resources and capacity (MacNeil et al. 2020; Simpfendorfer et al. 2023).

1.2.2 Ecology and economics

Sharks are typically long-lived, late to mature and slow to reproduce, rendering them inherently vulnerable to rapid depletion with limited capacity to recover from exploitation. Population doubling time may be as high as 14 years for both the scalloped hammerhead, *Sphyrna lewini*, and the blue shark, *Prionace glauca* (Froese and Pauly 2000), which together account for 40.3% of fins sampled in the biggest shark fin market in mainland China, and 43.2% of fins sampled in Hong Kong (Cardeñosa et al. 2020).

Given the considerable diversity of sharks it follows that trophic ecology is varied and complex, including several keystone species (Ferretti et al. 2010; Heithaus et al. 2012) that exert disproportional ecological impacts relative to their biomass (Worm and Paine 2016). Amongst large shark species the great white, *Carcharodon carcharias*, is an apex predator (Hussey et al. 2015), while the trophic position of tiger sharks, *Galeocerdo cuvier*, is less clear and ranges from apex predator to facultative scavenger (Hammerschlag et al. 2016) according to context and habitat factors (Ferreira et al. 2017). Some species are more accurately described as mesopredators (Roff et al. 2016; Bond et al. 2018), occupying a trophic rank below apex predators in a particular food web but with the potential to be an apex predator themselves in another system (Prugh et al. 2009; Ritchie and Johnson 2009). Yet other species may undergo ontogenetic changes in their trophic levels, and even facultative herbivory and seagrass digestion have been observed in bonnethead sharks, *Sphyrna tiburo* (Leigh et al. 2018).

Public desire to interact with wild animals has driven widespread development of ecotourism. However, general trends of biodiversity loss suggest that future ecotourism may be dependent on increasing focus of activities in fewer geographical locations where populations of target species are stable and interactions therefore more likely. Furthermore, ecotourism is frequently based on the occurrence of megafauna (Lindsey et al. 2007; Mazzoldi et al. 2019). Among marine species, sharks are a key component of ecotourism initiatives globally, and shark-related tourism is an important part of the economy in a number of countries (Gallagher and Hammerschlag 2011; Pires et al. 2016; Haas et al. 2017; Zimmerhackel et al. 2019). The potential for establishing well managed tourism as an alternative to shark fishing is considerable. For example, the opportunity to see sharks is an important determinant of tourists' motivation to visit Galapagos and around a third of tourists surveyed were willing to donate to shark conservation efforts (Cárdenas and Lew 2016). Moreover, long-term ecological and social sustainability are likely to be more achievable through non-extractive resource use. This is especially pertinent where enforcement resources are limited and self-enforcement and compliance are key factors in species protection.

1.2.3 Fisheries

1.2.3.1 Market demand and fisheries value

Since the 1950s global trade in shark products has steadily increased, driven mainly by market demand from a growing middle class in China. The most sought after products are shark meat and fins, with additional but less important demand for liver oil (Dent and Clarke 2015). Culturally, offering and consuming shark fin soup is an indicator of social status and sign of affluence, hence its key role in trade.

Contemporary international trade in shark products remains highly valuable. Although a 2003 peak in global catch rates was followed by a decline in the shark fin trade, the annual volume stabilised around 18% below the peak at an estimated 16,000 tonnes with a value of US$300 million in 2008-2011 (Dent and Clarke 2015). Conversely, the global shark meat trade continued to expand to meet growing demand from Australian and European markets, thereby widening trade links that were traditionally almost exclusively with Asia. The value of trade in shark meat now exceeds that of shark fin, at a volume of 120,000 tonnes valued at US$450 million annually (Abel and Grubbs 2020).

1.2.3.2 Shark fisheries impacts

The impacts of industrialised fishing on global shark populations have been pronounced (MacNeil et al. 2020; Simpfendorfer et al. 2023). Seminal work estimated that as many as 25% of shark and ray species were threatened with extinction (Dulvy et al. 2014), with more recent analysis highlighting declines of up to 70% in oceanic shark species (Pacoureau et al. 2021) and elevated extinction risk for a third of shark and ray species (Dulvy et al. 2021). Large coastal shark species are particularly vulnerable to depletion where there is extensive overlap between habitat use and fishing pressure (Queiroz et al. 2019). Overfishing remains the primary cause of marine defaunation (MacNeil et al. 2020; Pacoureau et al. 2021) and annual global fisheries-related shark mortality may conservatively be 100 million individuals (Worm et al. 2013).

1.2.3.3 Fisheries management and trade regulation

Shark fisheries that are actively and sufficiently managed for biological sustainability are uncommon, despite this being an inherently feasible goal (Simpfendorfer and Dulvy 2017). Although Regional Fisheries Management Organisations (RFMOs) seek to strengthen international coordination with this objective, evidence suggests disparity between RFMOs for how effectively this is achieved (Cardeñosa et al. 2021b). Furthermore, some shark species are included in international trade and conservation conventions such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS; Table 1.1). However, despite being CITES-listed, the scalloped hammerhead is exploited nearly throughout its range to supply fins to Hong Kong markets (Fields et al. 2020) while other CITES-listed shark species feature prominently in the global fin trade (Cardeñosa et al. 2018).

Table 1.1 Shark species and Appendix inclusion under the Convention on the International Trade of Endangered Species of Fauna and Flora (CITES), the Convention on the Conservation of Migratory Species of Wild Animals (CMS), and extinction risk according to The International Union for the Conservation of Nature Red List of Threatened Species (NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered; correct on 28th August 2023).

Species	Common name	IUCN Red List	CITES Appendix	CITES Effective	CMS Appendix	CMS Effective
Alopias spp.	Threshers	EN *	II	4/10/2017	II	2014
Carcharhinus falciformis	Silky	VU	II	4/10/2017	II	2014
Carcharhinus longimanus	Oceanic whitetip	CR	II	14/9/2014	I	2020
Carcharhinus obscurus	Dusky	EN	n/a	n/a	II	2017
Carcharodon carcharias	Great white	VU	II	12/1/2005	n/a	n/a
Cetorhinus maximus	Basking	EN	II	13/2/2003	I & II	2005
Galeorhinus galeus	Tope	CR	n/a	n/a	II	2020
Isurus oxyrinchus	Shortfin mako	EN	n/a	n/a	II	2008
Isurus paucus	Longfin mako	EN	n/a	n/a	II	2008
Lamna nasus	Porbeagle	VU **	II	14/9/2014	II	2008
Prionace glauca	Blue	NT ***	n/a	n/a	II	2017
Rhincodon typus	Whale	EN	II	13/2/2003	I & II	2017/1999
Sphyrna lewini	Scalloped hammerhead	CR	II	14/9/2014	II	2014
Sphyrna mokarran	Great hammerhead	CR	II	14/9/2014	II	2014
Sphyrna zygaena	Smooth hammerhead	VU	II	14/9/2014	II	2020
Squalus acanthias	Spiny dogfish	VU	n/a	n/a	II	2008
Squatina squatina	Angelshark	CR	n/a	n/a	I & II	2017

* Extinction risk for pelagic thresher shark *Alopias pelagicus*

** Extinction risk for European population is Critically Endangered

*** Extinction risk for Mediterranean population is Critically Endangered

1.2.3.4 Illegal, Unreported and Unregulated Fishing

The high value of global trade in shark products renders it unsurprising that effective fisheries regulation is confounded by widespread illegal, unreported and unregulated (IUU) fisheries and high seas (mis-)management. There are several drivers behind the proliferation of IUU fishing, which can be broadly classed as economic (e.g. subsidies), institutional (e.g. flags of convenience) and social (e.g. readily available cheap labour; Le Gallic and Cox 2006). The continued challenge of IUU fishing is periodically highlighted by seizures of high volumes of shark products, not only at sea (e.g. Table 1.2) but also at the point of both market export (da Silva Ferrette et al. 2019) and import (Cardeñosa et al. 2021a). Furthermore, the Covid-19 pandemic and associated Anthropause saw a substantial increase in illegal fishing activity in the Chagos MPA, Western Indian Ocean, attributed to reduced enforcement capacity and acute socioeconomic pressures (Collins et al. 2023). This opportunistic overexploitation is unlikely to have been a globally unique response to perceived opportunities.

The Galapagos Islands, Ecuador, are a world famous shark hotspot (Salinas-de-León et al. 2016) with strict protection measures, yet illegal poaching remains a major management challenge. Around 90% of elasmobranch species in the Galapagos Marine Reserve (GMR) are listed as Threatened or Near Threatened by IUCN (Camhi et al. 2009); all shark fishing, landing and trading was banned in the GMR in 2003 (Carr et al. 2013), and shark fin export was banned throughout Ecuador (2004; Schiller et al. 2015). Nevertheless, of the over 40 species of shark found in the waters of Ecuador, around 30 are frequently fished (Carr et al. 2013). Large scale industrial shark finning has continued in the GMR since the 1950s, with an estimated 105,500 tonnes of shark taken by the Ecuadorian fleet alone up until 2010 (Schiller et al. 2015). Given the additional prevalence of foreign shark fishing boats, true total extraction is likely to be considerably greater.

Table 1.2 Illegal shark fishing seizures in the Galapagos Marine Reserve (GMR), 2001-2004. Adapted from Carr et al. (2013)

Date	Vessel (Nationality)	Seizure location in GMR	Fishing gear	Catch information
3/2001	B/P Dilsun (Ecuador)	Isabela Island	Longline	Shark bodies (350) Shark fins (600)
3/2001	B/P Maria Canela II (Costa Rica)	Wolf Island	Longline	Shark bodies (60) Shark fins (1036)
7/2001	B/P Indio (Costa Rica)	Darwin Island	Longline	Shark bodies (1300) Shark fins (619)
3/2003	B/P Marcelo Caiza (unknown)	Isabela Island	Net	Shark fins (4147) Reconstructed to comprise 942 sharks
9/2003	F/M Canaima XI (unknown)	Isabela Island	Unknown	Shark fins (815) Reconstructed to comprise 202 sharks

1.3 Global Biodiversity Objectives

Concurrent with the onset of the sixth mass extinction, or perhaps as a result of it, global wealth has never been greater; but the situation is precarious. Despite its depleted state, the ocean provides food security, primary protein, coastal defence and livelihood opportunities to an estimated annual global value of US $3 trillion (UN DESA 2020). With the global population projected to reach 9.8 billion by 2050 (UN DESA 2019), the urgency of addressing ocean decline is reflected in the United Nations Sustainable Development Goals (SDGs; UN DESA 2020). There is an argument, however, that even more ambitious targets for rebuilding marine life should prioritise increasing the abundance of key habitats and keystone species, and restoring benthic ecosystem complexity (Duarte et al. 2020). Fundamentally, rather than preserving current conditions, global objectives should be to restore marine ecological structure, functioning and resilience to enhance the provision of ecosystem services.

The Convention on Biological Diversity Global Biodiversity Framework has the key goal of protecting at least 30% globally of land areas and of sea areas by 2030. Similarly, United Nations SDG 14, Life Below Water, seeks to conserve and sustainably use the oceans, seas and marine resources for sustainable development. Together with the international Decade of Ocean Science for Sustainable Development (2021-2030; Ryabinin et al. 2019), these international biodiversity and development objectives require bold and ambitious actions to achieve success. The opportunities are timely but success is critical, particularly given projections of widening socioeconomic equity gaps driven by future ocean biomass loss (Boyce et al. 2020).

1.3.1 Shark conservation management

Market gravity as a measure of human impact, specifically as a function of market size and proximity and their interaction (insert refs), can negatively impact predatory fish communities (Ward-Paige et al. 2010; Bakker et al. 2017; Cinner et al. 2018; MacNeil et al. 2020). Moreover, this is generally true for shark populations (Ward-Paige et al. 2010; MacNeil et al. 2020). Although the resulting pathways of trophic-wide impacts are relatively poorly understood, reduced predation and competition pressures on other species may result in community assemblage effects (Simpfendorfer et al. 2023). Moray eels, Muraenidae, are positively correlated with market gravity in the greater Caribbean, which may be linked to fisheries depletion of sharks (Clementi et al. 2021b). In Australia, simulated removal of tiger sharks and changes in grazing behaviour of dugong, *Dugong dugon*, suggest that the continued loss of apex predators could exacerbate the ecological impacts of climate change (Nowicki et al. 2021). Ultimately, given that many shark species have low resilience and are typically slow to recover from exploitation (Ward-Paige et al. 2012), the ecological impacts of population collapse are likely to be both considerable and long-term.

At local and national scales, increased recognition of ongoing shark population collapse and the likely resulting ecological and economic impacts has prompted widespread conservation responses. Typically this is via the establishment of MPAs and shark-specific sanctuaries. Population benefits have been observed in some shark species in some MPAs (McCook et al. 2010; Edgar et al. 2014; Speed et al. 2018), although well enforced measures supported by strong governance are important to prevent ecological extinction in reef sharks (MacNeil et al. 2020). Ultimately, positive effects of MPAs on upper trophic levels are contingent on multiple factors including MPA size (Juhel et al. 2018; Dwyer et al. 2020), location (Cinner et al. 2018), community buy-in (Shiffman and Hammerschlag 2016), enforcement (Kaplan et al. 2015), high levels of protection, wealth and governance capacity (Simpfendorfer et al. 2023).

1.3.2 Knowledge gaps and research pathways

Funding for shark research show bias towards a relatively small number of charismatic species (Shiffman et al. 2020). This risks exacerbating a disconnect between the number of exploited shark populations and the number that are subject to sustainable management programmes

(Jorgensen et al. 2022) which can, in turn, fail to approach shark fisheries management in the context of a socio-ecological system. The proper incorporation of a human component, however, should be a central consideration for the design of conservation interventions to yield mutually beneficial outcomes for both sharks and humans (Booth et al. 2019).

A number of priority research pathways have been identified for sharks globally (Simpfendorfer et al. 2011; Dulvy et al. 2017; Jorgensen et al. 2022). These include population status and long-term monitoring of data poor species; regional and species-level threats assessment, and the identification of ontogenetic critical habitat areas; assessment of suitable candidate species for sustainable fisheries management; and societal engagement, not least in terms of public opinion, community buy-in and support for shark conservation. It is important that efforts are made to align global objectives and enhance the chance of achieving synergistic impacts, either through research design or management tools such as trade regulations or regional fisheries management organisations.

1.4 Thesis outline

1.4.1 Overall aims

This thesis aims to address ecological knowledge gaps for sharks in two study sites that present similar opportunities to strengthen shark protection, and could thus be the catalyst for political buy-in that can be pivotal for shark conservation success (Mizrahi et al. 2019).

1.4.2 Study sites

1.4.2.1 Trinidad and Tobago

Tobago is the smaller of the two main islands that constitute the Republic of Trinidad and Tobago. The north coast is leeward and borders the Caribbean Sea, whereas the south coast is windward and borders the Atlantic Ocean. The southwest of the island is well developed with the largest population centres and is the centre of resort-based tourism, whereas the northeast features smaller coastal towns and villages where government employment schemes, agriculture and artisanal fishing are important livelihoods. The Main Ridge Forest Reserve was established along the central axis of Tobago in 1776, rendering it the oldest legally protected forest reserve implemented specifically for a conservation purpose. Almost 200 years later in 1973, the Buccoo Reef Marine Park was established in the southwest of the island as a restricted area and no-take MPA under the Marine Areas (Preservation and

Enhancement) Act (Figure 1.1). The MPA comprises 7 km^2 of lagoon and barrier reef environments and despite no formal management plan the inferred objective was conservation of critical ecosystems and species (Hoetjes et al. 2002; Lapointe et al. 2010).

The coral reefs of Tobago are among the southernmost in the Caribbean. The southwest region includes the only barrier reef on the island and the coastal zone is dominated by low relief shallow limestone, contrasting with high relief rocky coastlines in the northeast and fringing reefs that slope to a depth of 10 - 40 m (Mallela et al. 2010; Alemu 2016). Additionally, there are a number of small offshore islands surrounded by deep water that are important seabird colonies. Benthic community composition is spatially heterogeneous (Mallela et al. 2010), and particularly degraded sites are linked with human activity and terrestrial runoff (Lapointe et al. 2010). Despite being outside the regional hurricane belt, coral reefs in Tobago have periodically been negatively impacted by reduced recruitment and increased coral disease and bleaching associated with storm events in the wider Caribbean (Mallela et al. 2010). In 2020, Northeast Tobago was granted UNESCO Man and Biosphere status, and there are plans for a new 600 km^2 MPA in the northeast region. These conservation and environmental protection measures have facilitated the proliferation of nature-based tourism as a viable alternative livelihood for many local entrepreneurs.

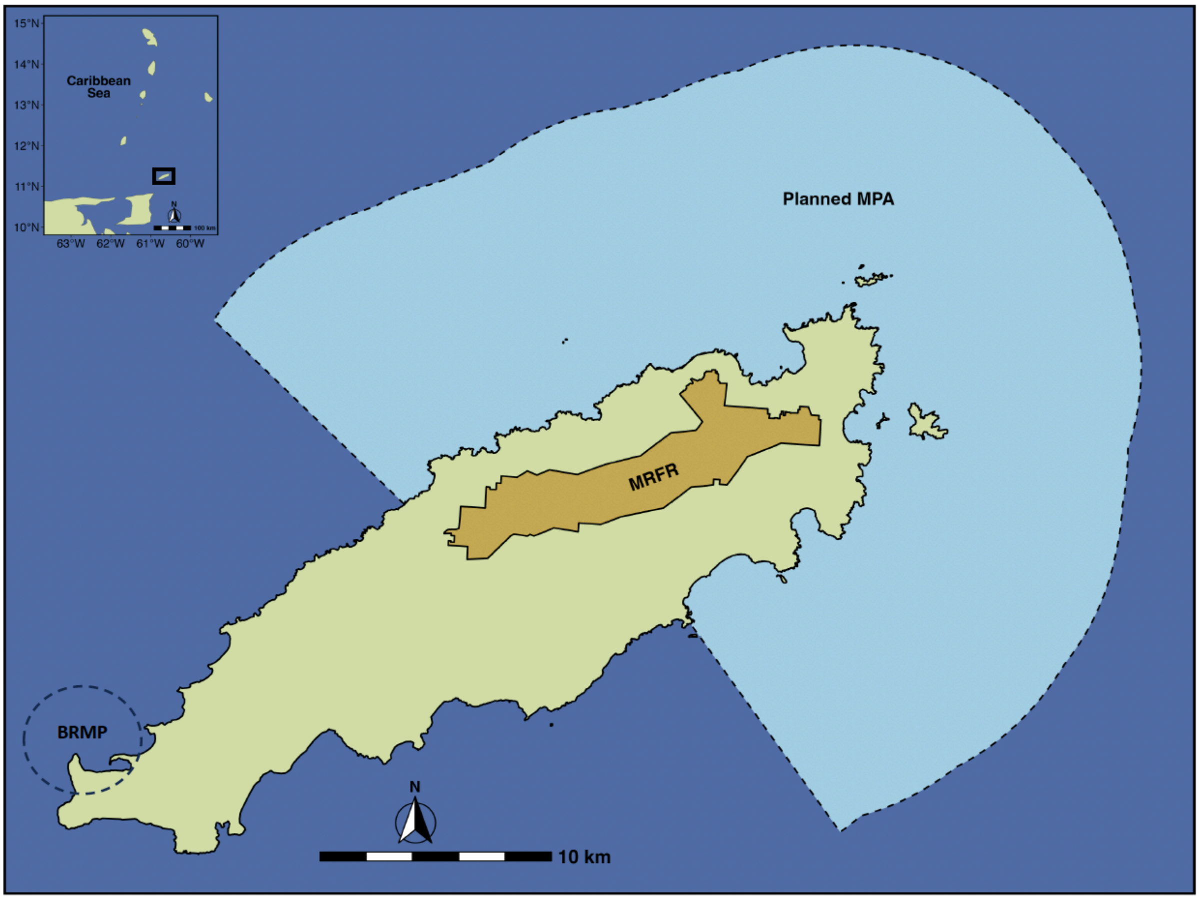


Figure 1.1 Tobago, showing the location of the existing Buccoo Reef Marine Park (BRMP) in the southwest, the Main Ridge Forest Reserve (MRFR) in the interior of the island, and the approximate coastal boundaries of the planned MPA for the northeast.

1.4.2.2 Cardigan Bay Special Area of Conservation

An area approximately 1000 km^2 in Cardigan Bay, west Wales, was proposed as a candidate Special Area for Conservation (SAC) by the European Union in 1996. This was followed by formal designation under the EC Habitats Directive in 2004 (Figure 1.2; Simon et al. 2010). The SAC programme seeks to maintain or restore "habitats and species of European importance to a Favourable Conservation Status" which, for Cardigan Bay, are the following qualifying features:

- sandbanks which are slightly covered by sea water all the time;
- reefs;
- submerged or partially submerged sea caves;
- bottlenose dolphin, *Tursiops truncates*;

- sea lamprey, *Petromyzon marinus*;
- river lamprey, *Lampetra fluviatilis*; and
- grey seal, *Halichoerus grypus*.

The SAC is a mixed use zone and relatively shallow, mostly less than 30 m deep and generally reaching 50 m only in the outer parts of the bay. Due to the general shallowness, wind and wave action dominate the physical processes. The seabed is relatively level with gentle banks and troughs but there are areas of greater topographical interest, particularly closer to shore and in the vicinity of headlands. Recent data show that 30% of visitors to Wales visited a wildlife attraction or nature reserve while 27% specifically undertook wildlife watching, with both figures showing increases on previous estimates (McAllister et al. 2021). Multiple dolphin watching boats depart daily from New Quay during the tourist season, thus demonstrating the importance of the bottlenose dolphins to the regional blue economy. Rapid expansion of the Cardigan Bay scallop fishery in the first decade of the 21st Century culminated in it constituting 30% of the total scallop catch for England and Wales (Bear 2013). Contemporary small-scale fisheries continue to operate from towns including New Quay, landing species including spider crab, *Maja squinado*, and mackerel, *Scomber scombrus* (personal observ.). Given its importance, Cardigan Bay SAC has the potential to be a critical component of national programmes and objectives that include the Welsh Marine Evidence Strategy (2019-2025), the Welsh National Marine Plan, and the Well-being of Future Generations (Wales) Act 2015.

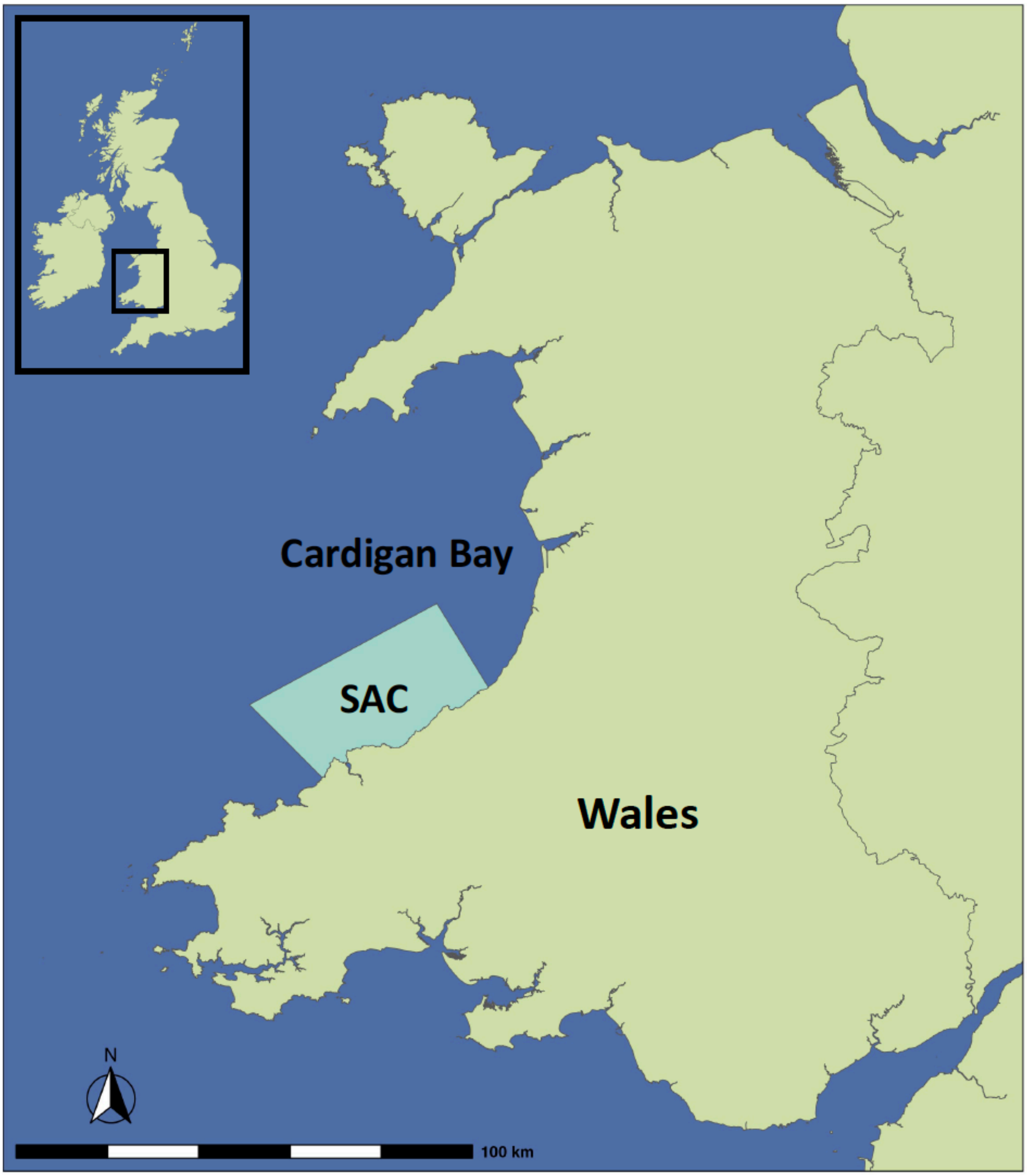


Figure 1.2 Wales, UK, showing the boundaries of the Cardigan Bay Special Area of Conservation (SAC) within the wider Cardigan Bay region.

1.4.3 Specific aims and objectives

Recent work highlights Tobago as having high potential conservation value for sharks (MacNeil et al. 2020); together with recent UNESCO MAB Reserve declaration, current plans for a large MPA, and the development of a shark fisheries management regulations, this is a realistic ambition. Meanwhile the political departure of the UK from the European Union presents an opportunity to fundamentally overhaul regional marine resource management. The outcome should place a greater emphasis on ecological and fisheries regeneration (Kemp et al. 2023a), recognising the social-ecological as well as the socio-economic components of fisheries. This is important in order to avoid continued long-term decline in UK fisheries (Kemp et al. 2023b). These ambitions should be equally realistic, given that the UK arguably has the necessary resources and governance to achieve success. Nevertheless, the review and ongoing development of national biodiversity action plans require the availability of a local ecological evidence base, but there is a relative paucity of such information for sharks. This thesis aims to address some of this paucity. The methods used in this thesis differ in terms of both the spatial and temporal scale of their applicability, yet should contribute to addressing these evidence gaps and assessing the respective study sites regarding their importance for regional shark populations.

1.4.3.1 Chapter 2: Tobago BRUVS study

This study represents the first widespread, standardised sampling of elasmobranchs in Tobago using BRUVS, with the following objectives: 1) establish a baseline of species richness and relative abundance, 2) investigate the influence of season, relief, depth and water temperature on relative abundance, and 3) investigate spatial variation in relative abundance. Given historical and ongoing fisheries pressure and a lack of elasmobranch-specific protection measures in Trinidad and Tobago, the hypothesis is that shark and ray communities would be comparable to elsewhere in the Caribbean and Western Atlantic where management is absent.

1.4.3.2 Chapter 3: Cardigan Bay BRUVS study

This study represents the first standardised BRUVS sampling of the shark community assemblage in Cardigan Bay SAC, Wales, UK, with the following specific objectives to: 1) establish a baseline of species present; 2) investigate spatial and temporal variations in species relative abundance of shark species observed; and, 3) assess the influence of sampling month on regional spatiotemporal habitat use by sharks.

1.4.3.3 Chapter 4: LA-ICP-MS vertebral natural tags analysis for *S. canicula*

This study tests the hypothesis that adult populations of smallspotted catsharks in the UK are regionally spatially distinct, sexually segregated, and connected by birthing grounds that are essential habitats. To test this hypothesis, we assessed smallspotted catshark vertebral elemental composition across south and west Wales, and south Devon for 1) spatial variations; 2) ontogenetic variations; and, 3) the evidence for critical habitats.

1.4.3.4 Chapter 5: LA-ICP-MS vertebral heavy metal analysis for *S. canicula*

This study is based on the hypothesis that spatiotemporal variation in industrial heavy metal trace element composition is linked to pollutants from human activity, and where heavy metal presence is detected this has direct implications for consumption of fisheries target species. To test this hypothesis, we assessed 1) spatial variations in catshark vertebral elemental composition in historically industrialised areas (south and west Wales), and compared it to less historically industrialised areas (south Devon); 2) ontogenetic trends in pollutant attenuation; and, 3) comparability between our findings and international guidelines for food safety.

1.4.4 Methods selection and overview

Two main methods are used in this thesis, complementary in both spatial scale of applicability, and associated research questions regarding aspects of shark ecology. Baited remote underwater video stations (BRUVS; Whitmarsh et al. 2017) were exclusively field-based, while laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) comprised laboratory analysis of field samples. This section provides an overview of each of the methods, linking their application to specific overarching elements of the thesis and justifying their inclusion in my studies.

1.4.4.1 Baited remote underwater videos

Technology advances, not least the advent of compact camera systems, have facilitated the increasingly widespread use of BRUVS in aquatic ecology studies (Figure 1.3). BRUVS are a non-invasive approach to species sampling that work on the basic principle of deploying baited autonomous cameras that are later retrieved and yield permanent video datasets. In addition to being non-invasive, BRUVS offer several advantages over traditional ecological methods; repeatability, autonomous operation, habitat accessibility, permanent datasets, large scale comparability using standardised approaches (MacNeil et al. 2020; Simpfendorfer et al. 2023), and the capacity to sample taxa that are commonly under-represented by other methods, including mobile (Colton and Swearer 2010) or depleted (Jabado et al. 2021; Ferreira et al. 2023) species. Although BRUVS have been used to study both teleost fish (Cappo et al. 2004; Watson et al. 2010; Dorman et al. 2012; Harvey et al. 2012; Stat et al.

2019) and marine mammals (Thompson et al. 2019), they are increasingly frequently used to study aspects of elasmobranch ecology. In this context, several BRUVS studies have provided seminal ecological insights and evidence for shark conservation management scales (Ward-Paige et al. 2010; MacNeil et al. 2020; Simpfendorfer et al. 2023).

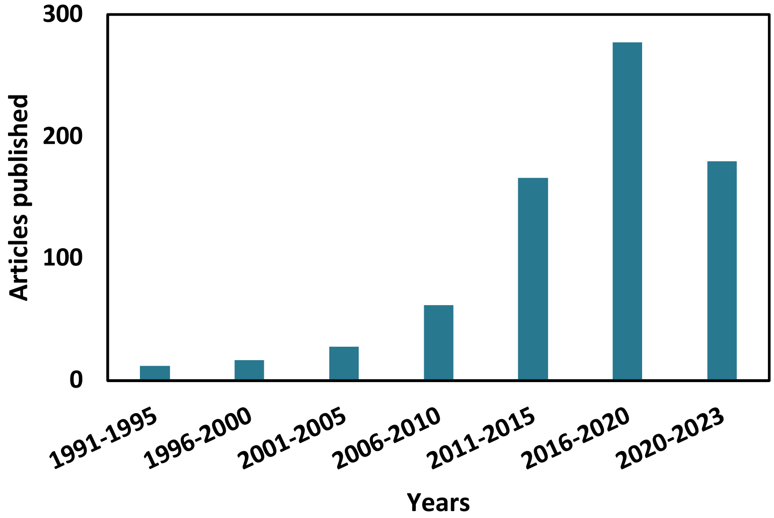


Figure 1.3 Total number of articles published at 5 year intervals since 1990 returned by a simple Web of Science All Fields search for the terms "baited AND video" OR "BRUVS" (as of 23rd August 2023).

Specific BRUVS setups can vary, but the basic components comprise a frame on which a camera is mounted (Willis et al. 2000; Cappo et al. 2001) and a bait canister that typically contains an oily fish bait to maximise bait plume dispersal (Dorman et al. 2012; Whitmarsh et al. 2017), with a tether to a surface buoy to mark location (Murray et al. 2019). Common variations on this basic setup employ two cameras in stereo alignment that can be diver-operated (Goetze et al. 2019) or autonomous (Harvey et al. 2012), and allow size estimates of study subjects.

Figure 1.4 Stereo baited remote underwater video stations (BRUVS), Cardigan Bay. The tether point for the rope can be seen in the bottom right of the image, such that when the BRUVS is deployed the bait arm and camera fields of view are horizontally aligned with the substrate.

BRUVS are commonly used in tropical environments but have been successfully deployed in temperate locations including the UK, albeit with generally higher susceptibility to variations in turbidity and underwater visibility (Unsworth et al. 2014; Jones et al. 2021). Equipment modifications can strengthen the performance of BRUVS by improving the quality of footage obtained in these environments (Jones et al. 2019). The most commonly used measurement parameter in BRUVS studies is MaxN (Whitmarsh et al. 2017), defined as the maximum number of individuals of a species observed simultaneously in a single video frame. Therefore, MaxN eliminates the possibility of double counts and allows for estimates of relative abundance. Although MaxN is inherently a conservative estimate of abundance, and hence arguably advantageous by encouraging conservative approaches to management, it may yield underestimates when true abundance is high. Alternative parameters to MaxN include MaxIND (Sherman et al. 2018) and MeanCount; MaxIND is dependent on a reliable means of identifying individuals, but this can yield novel insights into social network structure (Mourier et al. 2012; Mourier and Planes 2021).

BRUVS have wide-ranging ecological applications for elasmobranch ecology, and can be used to establish population baselines (Chapter 2; Garzon et al. 2021), elucidate long-term population trends (Flowers et al. 2022), examine behavioural interactions (Shea et al. 2020; Sherman et al. 2020b), investigate the effects of environmental drivers (Goetze et al. 2018) and anthropogenic pressures on predator community structure (Juhel et al. 2018; Clementi et al. 2021a; Clementi et al. 2021b), and provide insights on regional (Ward-Paige et al. 2010; Letessier et al. 2019a) and global scales (MacNeil et al. 2020; Simpfendorfer et al. 2023). BRUVS are also suitable for use in temperate, high energy marine environments, provided sampling effort is sufficient to be able to measure relevant change (Bicknell et al. 2019). Research priorities for many shark species include establishing population status and identifying movement ecology and critical habitat use (Jorgensen et al. 2022). The use of BRUVS, therefore, has the potential to address a number of such objectives, and is suitable for use in both of the study areas within the scope of this thesis.

1.4.4.2 Laser ablation inductively coupled plasma mass spectrometry

Natural tags are elements that reliably reflect environmental conditions (McMillan et al. 2018). They can be attenuated via several pathways and incorporated into hard skeletal structures of animals, and thus used as an indicator of habitat use (Kerr and Campana 2014). Microchemistry studies in teleost fish have used elemental composition patterns in otoliths to investigate both spatial and temporal aspects of species ecology (Thorrold et al. 1997). In Chinook salmon, *Oncorhynchus tshawytscha*, variations in otolith concentrations of strontium isotopes allow for fine-scale determination of natal origins (Brennan et al. 2015). Similarly, microchemistry analysis of the calcified cartilaginous vertebral column of elasmobranchs can yield comparable ecological insights (Natanson et al. 2002; Smith et al. 2013; Mohan et al. 2018). This has direct application in addressing knowledge gaps that are fundamental to the success of conservation management, including species or community population structure, spatiotemporal movement, and critical habitat use (Jorgensen et al. 2022). Traditional approaches to gather this information for sharks include acoustic telemetry (Chapman et al. 2005) and satellite tagging (Hammerschlag et al. 2011), but this inherently yields information limited to the period of tag deployment. Contrastingly, microchemistry analysis of elemental composition that reflects environmental exposure can provide whole lifetime insights (Smith et al. 2016; McMillan et al. 2018; TinHan et al. 2020), which is particularly important given substantial ontogenetic variations in habitat use shown by many shark species (Kinney and Simpfendorfer 2009). Furthermore, and in addition to natural tags, vertebrae can incorporate heavy metals (Vas 1991; Mohammed and Mohammed 2017; Bevacqua et al. 2021), which in turn enables the potential use of sharks as bioindicators of environmental quality. Accordingly, microchemistry analysis of vertebrae offers several advantages over traditional tagging approaches, both in terms of spatial and temporal insights into habitat use. It is, however, inherently destructive and dependent on specimen mortality, although opportunistic fisheries sampling affords one avenue of achieving results without directed killing.

Briefly, laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) works by ablating material elemental composition analysis through mass spectrometry. First, sections of the vertebral column are removed from specimens, separated into individual vertebrae, the connective tissue is removed and the vertebrae are manually cleaned with a scalpel, then mounted and ground into longitudinal sections suitable for mass spectrometry analysis. Next, a transect line is manually assigned to the corpus calcareum of each sample; this controls the path of the laser, which continuously ablates the material as it passes along the transect according to pre-defined settings (Figure 1.5; also see Chapter 4). The ablated particles are then passed to the plasma torch for digestion and ionisation, and then introduced to a mass spectrometer for elemental and isotopic analysis. Therefore, with continuous ablation along a growth axis transect, LA-ICP-MS can yield lifetime patterns of elemental composition that reflect environmental exposure. See Chapter 4 for full details of preparation, equipment settings, and data output processing.

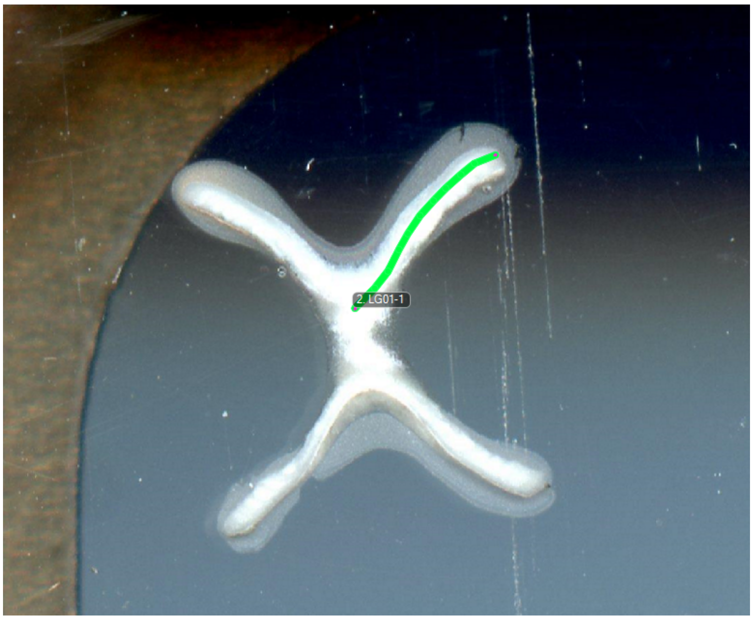


Figure 1.5 Longitudinal vertebral section from a smallspotted catshark, *Scyliorhinus canicula*, with a manually assigned growth axis transect for laser ablation.

The advancement of LA-ICP-MS analysis of natural tags can be used to address key research questions regarding shark ecology. Opportunistic sampling of fisheries bycatch has enabled important nursery areas to be identified for shortfin mako sharks (*Isurus oxyrinchus*; see LaFreniere et al. 2023) and bull sharks (*Carcharhinus leucas*; see TinHan et al. 2020), and pupping areas for school sharks (*Galeorhinus galeus*; see McMillan et al. 2018). Similarly, population connectivity has been elucidated by the identification of essential habitats and migration corridors for both smalltail (*Carcharhinus porosus*; see Feitosa et al. 2020) and scalloped hammerhead sharks (*Sphyrna lewini*; see Coiraton et al. 2020).

In addition to the application of natural tags to address population ecology knowledge gaps, LA-ICP-MS can also be used to investigate heavy metal contamination (Vas 1991; Mohammed and Mohammed 2017). This has implications for environmental monitoring, physiological impacts, and human health consumption risks. Although the relationship between soft tissue and vertebral contamination levels requires investigation and clarification for different species, the latter, critically, allows for full lifetime analysis and therefore adds an important temporal component to contamination insights.

1.4.5 Species

Species have been selected for this PhD to represent a range of ecological characteristics, fisheries importance, conservation status and potential non-extractive tourism value. Thus, it will be possible to demonstrate the intended wide applicability of the study methods and approaches used. The scalloped hammerhead is a widely distributed and highly migratory species that features heavily in commercial shark fisheries, while being simultaneously important for non-extractive nature-based tourism in certain locations. Conversely, the nursehound and smallspotted catsharks are less widely distributed, are more typically targeted by artisanal, recreational or small-scale commercial fisheries, and do not explicitly support any nature-based tourism activities.

Table 1.3 Study species for this PhD, with global IUCN Red List status and population trend.

Scientific name	Common name	IUCN status	Global trend	Study site
Sphyrna lewini	Scalloped hammerhead	Critically Endangered	Decreasing	Tobago
Scyliorhinus canicula	Smallspotted catshark	Least Concern	Stable	Cardigan Bay
Scyliorhinus stellaris	Nursehound	Vulnerable	Decreasing	Cardigan Bay

1.4.5.1 Scalloped hammerhead shark, *Sphyrna lewini*

Figure 1.6 Artisanal fisheries landings including scalloped hammerhead sharks, *Sphyrna lewini*, in northeast Trinidad, Trinidad and Tobago.

The scalloped hammerhead shark is a large coastal species that inhabits tropical and sub-tropical waters throughout the world. Ontogenetic shifts in distribution occur, with juveniles typically demersal and resident in high density nearshore coastal nurseries and adults generally pelagic and solitary. Despite highly migratory behaviour, oceanic barriers may limit connectivity and drive ocean-level genetic differentiation (Duncan et al. 2006). Consequently, regional ecology is distinctive and characterised by high genetic connectivity such as between coastal sites in Central Mexico and Ecuador, with connected populations between the key eastern tropical Pacific MPAs of Galapagos, Cocos and Malpelo.

Adults are apex predators (trophic level > 4; Bond et al. 2018) (Borrell et al. 2011; Bornatowski et al. 2014) and highly selective of habitat types such as seamounts, where sex ratios are skewed towards females (Klimley 1987; Hearn et al. 2010). In some locations, adults form aggregations, whether for mating or for feeding. The northern Galapagos islands of Darwin and Wolf, for example, are a hotspot supporting significantly elevated local concentrations of shark biomass (Hearn et al. 2010), with two annual peaks in *S. lewini* abundance between January and February and August to October (Bessudo et al. 2011). The Darwin and Wolf Marine Sanctuary was established as a 40,000 km^2 no-take reserve in March 2016, within which *S. lewini* accounts for 48% of overall reef fish biomass (Salinas-de-León et al. 2016). Similarly, scalloped hammerhead sharks remain in the region around the Mid-Atlantic Ridge in the equatorial Atlantic Ocean for extended periods and thus demonstrate medium-term site fidelity, despite regular and extensive vertical movements likely associated with foraging (Bezerra et al. 2019).

Sphyrna lewini is one of several shark species that utilise nursery grounds (Heupel and Hueter 2002; Reyier et al. 2008; Heupel and Simpfendorfer 2011), defined as areas where sharks are more commonly encountered in the area than other areas, have a tendency to remain or return for extended periods, and use the area repeatedly across years (Heupel et al. 2007). The primary ecological benefits of nursery grounds are likely to be a combination of enhanced prey availability in nutrient rich habitats, and reduced predation. Kāne’ohe Bay (Ō̲’ahu, Hawai’i) is a nursery ground that has been extensively studied (Holland et al. 1993; Bush and Holland 2002; Lowe 2002; Bush 2003), where an estimated 180 to 660 adult female scalloped hammerhead sharks use the area for parturition annually (Duncan and Holland 2006). Here, pronounced weight loss in neonate sharks has been recorded for a number of months and attributed to malnutrition and starvation. This is unusual, and suggests that the local primary ecological benefit may be as a refuge from predation rather than higher postnatal prey availability. Equally it is possible that due to a lag effect shark philopatry may persist despite declining water quality and prey availability to suboptimal levels when compared with historical data (Duncan and Holland 2006). Nevertheless, refuge from predation has also been proposed as an important ecological benefit for juvenile blacktip sharks, *Carcharhinus* *limbatus*, in a Florida coastal nursery (Heupel and Hueter 2002), and may also be linked to the use of the estuarine Tolomato River in Florida by young-of-year *S. lewini*, where population dynamics satisfy the criteria for shark nursery habitats (Wargat et al. 2024).

A high proportion of global trade in shark products is comprised of a small number of species. In China, a global import hotspot, the most commonly traded species are blue, silky and scalloped hammerhead sharks (Cardeñosa et al. 2020), although it is unclear whether these findings include trade preceding 2014. Fins from *S. lewini* fetch a high value (Abercrombie et al. 2005) and drive consistent market demand and targeted fishing, with additional incidental catch and bycatch associated with aggregative behaviour and high post-capture mortality (Coelho et al. 2012; Gallagher et al. 2014). This is further compounded by a highly mobile nature and ontogenetic shift in habitat use that results in extensive overlap with high seas fishing pressure (Queiroz et al. 2019). Despite lower vulnerability to Atlantic Ocean pelagic longline fisheries than species such as silky sharks, *Carcharhinus falciformis*, and shortfin mako sharks, *Isurus oxyrinchus* (Cortés et al. 2010), fidelity to oceanic migration pathways may exacerbate scalloped hammerhead shark risk throughout their distribution.

Sampling undertaken in the Hong Kong fin market between 1999 and 2002 suggested that fins from up to 2.7 million scalloped hammerhead sharks were traded annually, although this figure likely also includes the smooth hammerhead *S. zygaena* (Clarke et al. 2006). More recent sampling in 2014 and 2015 revealed that *S. lewini* remains the third most commonly traded amongst individually identified species (Fields et al. 2018), highlighting long-term fisheries importance.

Sharks generally are now largely absent from populated areas of the Caribbean (Ward-Paige et al. 2010; MacNeil et al. 2020), although *S. lewini* has been recorded on baited remote underwater videos in Tobago (Chapter 2). Here, small-scale artisanal fisheries catch large numbers of scalloped hammerhead sharks (personal observ.), however there is a paucity of official landings data. Nevertheless, widely reported population collapse demonstrates the pervasive impacts of fishing on scalloped hammerhead sharks (Baum et al. 2003; White et al. 2008; Hayes et al. 2009; Baum and Blanchard 2010; Barreto et al. 2016).

Sphyrna lewini is listed as Critically Endangered by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species of Fauna and Flora. In 2014 it was added to Appendix II of the Convention on International Trade of Endangered Species of

Fauna and Flora (CITES) and in 2015 to the Conventional on Migratory Species, thereby strengthening trade regulation. Despite this, *S. lewini* remains among the most commonly recorded species in the Hong Kong fin trade (Cardeñosa et al. 2018), while continued overfishing, susceptibility to bycatch mortality, and decreasing population trends place it among the seven priority groups for conservation (Dulvy et al. 2017).

Scalloped hammerheads are among the most frequently advertised species for shark tourism, particularly in Central and South America and Southern and Eastern Africa (Gallagher and Hammerschlag 2011). Their lifetime non-extractive tourism value is considerable; one individual *S. lewini* in the Isla del Coco National Park, Costa Rica, is worth an estimated US$1.6 million, far exceeding the single use market value of US$195 (Friedlander et al. 2012). This is in line with dichotomous estimates of extractive and non-extractive value of other species (Vianna et al. 2012; Vianna et al. 2018) and demonstrates potential economic gains from enhanced shark protection.

MPAs have the potential to protect certain life stages of *S. lewini* given its use of coastal nursery grounds, ongoing site or natal fidelity in adults, and aggregation behaviour associated with topographical features. However, as a highly migratory species they regularly travel beyond the relatively small areas that can be effectively managed for conservation. As a consequence, there is considerable overlap between their distribution and areas of high fishing pressure (Queiroz et al. 2019).

Illegal fishing and fishing the line, where fishing boats patrol protection boundaries, can severely undermine management measures such as MPAs. This highlights the importance of enforcement, while tourism activities in areas where sharks are a valuable ecotourism resource can potentially serve as a deterrent to illegal activity. To maximise success there is a need for improved population parameters and local data, especially abundance estimates, reproductive cycles, fecundity, habitat use and movement ecology, all of which vary regionally for *S. lewini* (Gallagher and Klimley 2018). As a principle, precautionary management is important, especially where fisheries continue to operate or where potential conservation gains are highest (MacNeil et al. 2020).

S. lewini is among the most comprehensively studied of the large hammerheads, yet population status remains a critical knowledge gap (Gallagher and Klimley 2018) as most estimates are derived from fisheries data rather than *in situ* assessments and rates of regional fisheries decline vary widely (Baum et al. 2003). Although upper estimates of decline have been contested there is general consensus that global population trends are decreasing, and even some evidence of local or regional extirpation (Perez-Jimenez 2014).

1.4.5.2 Smallspotted catshark, *Scyliorhinus canicula*

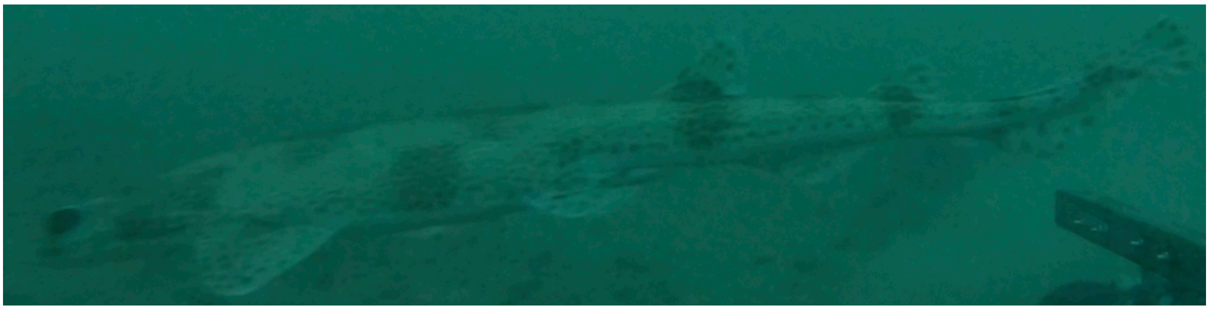


Figure 1.7 Smallspotted catshark, *Scyliorhinus canicula*, observed on a baited remote underwater video station in Cardigan Bay, west Wales.

The smallspotted catshark is a small demersal shark, widely distributed throughout the Northeast Atlantic and the Mediterranean (Finucci et al. 2021). Genetic population connectivity varies throughout its range (Gubili et al. 2014; Kousteni et al. 2015), while even within the UK there is evidence to suggest that regional populations may be spatially discrete (Leah et al. 1991). This highlights a consideration for species management, insomuch that distinct populations should be considered as discrete stocks, each subject to a specific suite of local ecological processes. One such ecological process is removal and discarding of landed specimens by recreational anglers in the UK, up to several metres above the high tide limit and occasionally with cut line and a hook *in situ* (personal observ.). This may be linked to common consideration of *S. canicula* as a pest, given it is a non-target species that scavenges bait (personal comms.).

Figure 1.8 Two of nine dead smallspotted catsharks *Scyliorhinus canicula* discovered on a small grassy hill several metres above the high tide limit in Barry on 6th May 2023.

Adults are mesopredators (trophic level 3.8; Froese and Pauly 2000) and therefore have the potential to be apex predators under certain ecological conditions (Prugh et al. 2009; Ritchie and Johnson 2009), such as the depletion of upper trophic level species. Prey items include small bony fish and a range of invertebrates including molluscs and cephalopods (Yemisken et al. 2019), illustrating a centrally important position within marine food webs (Wieczorek et al. 2018).

Smallspotted catsharks are oviparous. Females deposit egg cases containing embryos and juveniles hatch after approximately 8 months, at approximately 10 cm total length in the Bristol Channel (Ellis and Shackley 1997). Areas where egg cases are deposited may therefore constitute critical habitats that support essential life stages for oviparous elasmobranchs. The criteria for such egg case nurseries include being a geographic location where eggs are deposited at high densities, a benthic habitat where eggs are contacting benthic or stationary materials, a site used as an egg case nursery over multiple years, and distinct from habitats that juveniles identify with post-hatching (Hoff 2010; Hoff 2016). Furthermore, juvenile nurseries should support young-of-year juveniles consistently and in high abundance, be distinct from the egg case nursery, and have attributes as to contribute significantly to population recruitment success (Hoff 2016). Importantly, these may be distinct, yet again, from general shark nursery habitat areas as generally applied to viviparous shark species (Heupel et al. 2007; Heupel et al. 2018). This demonstrates the ontogenetic ecological complexity of many shark species, and the need for management that addresses separately these nuances (Kinney and Simpfendorfer 2009). Opportunistic sampling (Cau et al. 2013; Cau et al. 2017) and acoustic telemetry (Wearmouth et al. 2013) have yielded some insights into the location of egg case nurseries, but generally relative little is known about these, or juvenile habitat areas, beyond the results of trawl surveys and fisheries-dependent sampling (Martin et al. 2010; Moore et al. 2023). Nevertheless, it is thought that adults form sexually discrete segregations (Rodríguez-Cabello et al. 2007; Papadopoulo et al. 2023), likely driven by a combination of male dispersal with ontogenetic development (Gubili et al. 2014), and female avoidance behaviours (Kimber et al. 2009; Micarelli et al. 2020).

S. canicula is not currently a fisheries target in the UK but is common bycatch, although post-release survival is presumed to be high (Revill et al. 2005). Nevertheless, it is an important component of regional fisheries elsewhere in its distribution (Capapé et al. 2008; Marques et al. 2021). Furthermore, catch declines suggest inherent vulnerability to overexploitation and population depletion (Ligas et al. 2013), albeit less so than for larger shark species. There are certain levels of health risk associated with human consumption, however, with heavy metal contamination detected in the soft tissues of fisheries-landed specimens (Marques et al. 2021; Filice et al. 2023).

Given relatively limited species range, however, spatial protection such as MPAs can confer conservation gains on smallspotted catsharks (Rodríguez-Cabello et al. 2008), and do not need to be as large as for other more wide-ranging species. As such, the identification of consistent use of migratory corridors linked to discrete habitat areas (Papadopoulo et al. 2023) has the potential to further increase such gains, should protective management measures be put in place. Hence, *S. canicula* has potential as a model species for sustainable fisheries management. Its lower trophic level compared to other species widely consumed suggests an inherently lower risk of exposure to heavy metal biomagnification and bioaccumulation, although this will depend on the environmental conditions in the regions in which a fishery is operating.

1.4.5.3 Nursehound, *Scyliorhinus stellaris*

Figure 1.9 Nursehound, *Scyliorhinus stellaris*, observed on a baited remote underwater video station in Cardigan Bay, west Wales.

The nursehound is relatively under-studied compared both to other shark species of higher conservation interest, and the smallspotted catshark (Table S3.1). It has a trophic level of 4 (Froese and Pauly 2000) and therefore likely exerts important predatory pressure in Northeast Atlantic and Mediterranean marine communities (Santoro et al. 2023). It is, however, listed as Vulnerable by the IUCN Red List (Table 1.3), and may be at risk of local extinction in parts of its distribution (Ragonese et al. 2013).

Long-term trawl monitoring can provide broad insights into the distribution, relative abundance and population structure of demersal sharks, including *S. stellaris* (Martin et al. 2010). This shows nursehounds to be among the most abundant shark species in the eastern English Channel, and to be spatially segregated by sex. In addition, acoustic telemetry work has suggested that nursehounds undertake diurnal refuging behaviours and show moderate philopatry to preferential habitat areas (Sims et al. 2005). Furthermore, there are pronounced seasonal trends in nursehound bycatch occurrence in crab and lobster pot fisheries in the Bristol Channel, Celtic Sea, and Irish Sea, some of which does get retained (Moore et al. 2023), and nursehound is commonly available in fishmongers and takeaway food establishments in the UK (Hobbs et al. 2019). Despite this fisheries importance, the lack of research attention has resulted in extensive species knowledge gaps. These include population size, distribution and trends, life history, and usage patterns. Addressing these knowledge gaps would enable the design and incorporation of species actions into regional management plans; any conservation benefit currently conferred on nursehounds is an indirect result of general fisheries management regulations, such as regional gear restrictions.

Chapter 2: ELASMOBRANCH DIVERSITY AROUND THE SOUTHERN CARIBBEAN ISLAND OF TOBAGO: OPPORTUNITIES FOR CONSERVATION IN A REGIONAL TRADE HUB

2.1 Abstract

Sharks are scarce in much of the Caribbean due to widespread depletion. Trinidad and Tobago, in the southern Caribbean, is a shark meat consumer and international exporter of dried shark fins. Despite limited fisheries management there is a small Marine Protected Area (MPA; 7 km^2) in urbanised southwest Tobago, but its effect on sharks and rays (elasmobranchs) is unknown. The rural northeast is a recently designated UNESCO Man and the Biosphere Reserve with a significant marine component and plans for a large MPA, but no baseline data for elasmobranchs exist. Given the local importance of elasmobranchs and a newly drafted Sustainable Shark and Ray Management Plan, we used baited remote underwater video stations within a 40 m depth contour at 270 randomly generated points around Tobago to: (i) establish a baseline of species richness and relative abundance, (ii) investigate the influence of season, habitat relief, depth and water temperature on relative abundance, and (iii) investigate spatial variation in relative abundance. Caribbean reef sharks, nurse sharks, and southern stingrays were observed at all sites, the latter two more frequently in the urbanised southwest. Shark diversity was unexpectedly high in the northeast, driven by rarer species (sharpnose, smoothhound, tiger, scalloped hammerhead, great hammerhead) only observed there. Habitat relief, depth and season likely influence relative abundance of elasmobranchs around Tobago, but research is needed to elucidate species-level effects. Shark species richness in northeast Tobago is high for the Caribbean, warranting research attention, while the larger MPA presents an opportunity to strengthen elasmobranch management.

2.2 Introduction

An estimated 32.6% of shark and ray species are threatened with extinction, and more rays are threatened than sharks (Dulvy et al. 2021). This is largely attributed to overfishing (Worm et al. 2013; Dulvy et al. 2021) and habitat degradation (Jennings et al. 2008). There are no known examples of shark fisheries actively managed for sustainability beyond those in the

United States, Canada, Australia and New Zealand, and sharks are consequently becoming rare in the coastal waters of many developing nations (Myers and Worm 2003; Ward-Paige et al. 2010; Dulvy et al. 2014; Simpfendorfer and Dulvy 2017; MacNeil et al. 2020). In the Caribbean, sharks are seldom sighted except in areas with strong fisheries management or large Marine Protected Area (MPA) networks (Ward-Paige et al. 2010; MacNeil et al. 2020).

The shark fishery in Trinidad and Tobago, an island nation in the southern Caribbean, reported mean annual shark landings of 569 tonnes between 1974 and 1996 (Shing 1999), and although rays are usually released alive or dead by fishers in Tobago they are sometimes retained as food and to sell (Cáceres 2019). When unreported landings are also included, annual total elasmobranch landings in Tobago alone could be as high as 2,286 tonnes (Cáceres 2019). Notwithstanding a paucity of local elasmobranch abundance trends, decreasing global shark catch rates since 2003 probably reflect population decline rather than improved fisheries management (Davidson et al. 2016). Nevertheless, Trinidad and Tobago remains one of the largest Western Atlantic exporters of shark fins to the Hong Kong market (Eriksson and Clarke 2015). Additional small-scale fishing pressure supplies domestic demand for shark meat, which is typically used in the iconic local dish, 'bake and shark' (Cáceres 2019). Furthermore, fisheries management has historically been hindered by limited government resources and outdated legislation (See 1916 Fisheries Act, Trinidad and Tobago), suggesting that shark populations around these islands could be depleted. However, an updated draft Fisheries Management Bill and draft Sustainable Shark and Ray Management Plan for Tobago are opportunities to strengthen shark fisheries management.

MPAs, within which certain extractive or depositional activities are regulated or prohibited, are used as a tool to protect marine ecosystems. Sharks and rays (elasmobranchs) may benefit from MPAs with management regulations that limit gear types that frequently catch them (e.g. longlines, gillnets) or eliminate fishing pressure (no-take zones), but such no-take zones must also be relatively large (> 20 km in length; Dwyer et al. 2020). Conversely, reef shark declines can still occur within no-take marine reserves that were not designed to protect sharks and where fishing around MPA boundaries is common (Flowers et al. 2022). Buccoo Reef Marine Park, the only MPA in Tobago, was established in 1973 in the southwest of the island, near the largest urban centres. Despite its small size (7 km^2) it is an important component of the island tourism economy (Hassanali 2013), yet has undergone long-term habitat degradation attributable to declining water quality (Lapointe et al. 2010). The influence of the MPA on local elasmobranch populations is unknown given a lack of baseline data preceding its establishment, but its small size, proximity to an urban centre, and the fact it was not designed to protect elasmobranchs, suggest it is likely to have little to no positive effect. Nevertheless, current conservation planning in Tobago presents an opportunity to improve elasmobranch protection and sustainable fisheries management. The Northeast Tobago UNESCO Man and the Biosphere Reserve (MAB; 2020) incorporates the less populated northeast coasts and 683 km^2 of associated marine area, with further plans for MPA zonation and implementation of shark fisheries management measures. Although information on elasmobranch status in the area is largely limited to recreational diver sightings (Fanovich et al. 2017), declaration of the MAB has strengthened political support for improved environmental management. This presents an opportunity to strengthen regional elasmobranch management, but its success likely depends on addressing current knowledge gaps. Baited remote underwater video stations (BRUVS) have been widely used to assess and monitor elasmobranchs (Bond et al. 2012; Goetze et al. 2018; Murray et al. 2019; Cáceres et al. 2022; Flowers et al. 2022), and can potentially yield relevant insights to design specific protection measures. In this context, we undertook the first widespread, standardised sampling of elasmobranchs in Tobago using BRUVS, with the following objectives: (i) establish a baseline of species richness and relative abundance, (ii) investigate the influence of season, relief, depth and water temperature on relative abundance, and (iii) investigate spatial variation in relative abundance. Given historical and ongoing fisheries pressure and a lack of elasmobranch-specific protection measures in Trinidad and Tobago, we hypothesised that shark and ray communities would be comparable to elsewhere in the Caribbean and Western Atlantic where management is absent.

2.3 Methods

Tobago is the smaller of the two main islands that constitute the Republic of Trinidad and Tobago. The west coast is leeward and borders the Caribbean Sea whereas the east coast is windward and borders the Atlantic Ocean. The southwest of the island is relatively developed, supporting resort-based tourism and the largest population centres. It is also the location of the only barrier reef in Tobago, where the Buccoo Reef Marine Park was established in 1973. Despite no formal management plan upon implementation, it was established as a restricted area and no-take MPA under the Marine Areas (Preservation and Enhancement) Act (1970), and its inferred objective was conservation of critical ecosystems and species (Hoetjes et al. 2002; Lapointe et al. 2010). The MPA comprises 7 km^2 of lagoon and barrier reef environments, with adjacent fringing reefs that extend south beyond the boundaries towards Trinidad (Figure 2.1). In contrast, the northeast of the island features smaller coastal towns and villages where government employment schemes, agriculture, tourism, and artisanal fishing are important livelihoods. The coastal zone is typified by steep coastlines bordering fringing reefs that slope to a depth of 10 - 40 m with a number of small offshore islands surrounded by deep water. The area is within a planned 683 km^2 MPA under the UNESCO MAB (Figure 2.1).

Two study sites in the southwest and three study sites in the northeast of Tobago were designated within the estimated 40 m depth contour (Figure 2.1) to both standardise with the wider Global FinPrint programme and enable safe BRUVS retrieval in the event of equipment snagging in complex habitat. GPS coordinates for sampling points (hereafter, stations) were generated via a random number generator using ArcGIS software (Bond et al. 2012) for each study site as follows: the southwest region, which included the established MPA (Buccoo, N = 30) and adjacent open waters (Canoe, N = 40), and the northeast region, which included three sites in the planned MPA (Atlantic, Charlotteville, Sisters, N = 50 per site). Sampling was completed between January 2016 and November 2017. Further stations were then generated for an additional site on the north coast of the planned MPA (Caribbean, N = 50); this site both incorporated previously sampled sites on the north coast and extended to the planned MPA boundary, thereby matching the south coast sampling area to standardise sampling intensity between coasts (Table 2.1). Sampling within the additional site was completed in March 2018.

The BRUVS were comprised of a stainless steel quadpod frame with a GoPro Hero 2 or Hero 3 camera mounted on a central base (Brooks et al. 2011; MacNeil et al. 2020). A bait arm extended 1 m in front of the camera supporting a wire mesh cage in the middle of the field of view. The mesh cage was baited with 1 kg of chopped oily fish (Atlantic bonito *Sarda sarda* or blackfin tuna *Thunnus atlanticus*). Each frame was weighted with dive weights and a rope was attached to a surface buoy to mark location (Murray et al. 2019). A Garmin echoMAP 50s GPS and sounder was used to navigate to each station and measure depth. When the depth was greater than 40 m or currents prevented either safe or successful BRUVS deployment, a replacement station was selected at the nearest location where depth did not exceed 40 m and water conditions were conducive to deployment. BRUVS were deployed between 08:00 and 16:30 to ensure sufficient light for video recording and were left to record for a minimum of 90 minutes before retrieval to standardise with the wider Global FinPrint programme. Up to 14 stations were sampled per day, and BRUVS that were deployed simultaneously were separated by a minimum of 1 km to ensure independent sampling (Harvey et al. 2019).

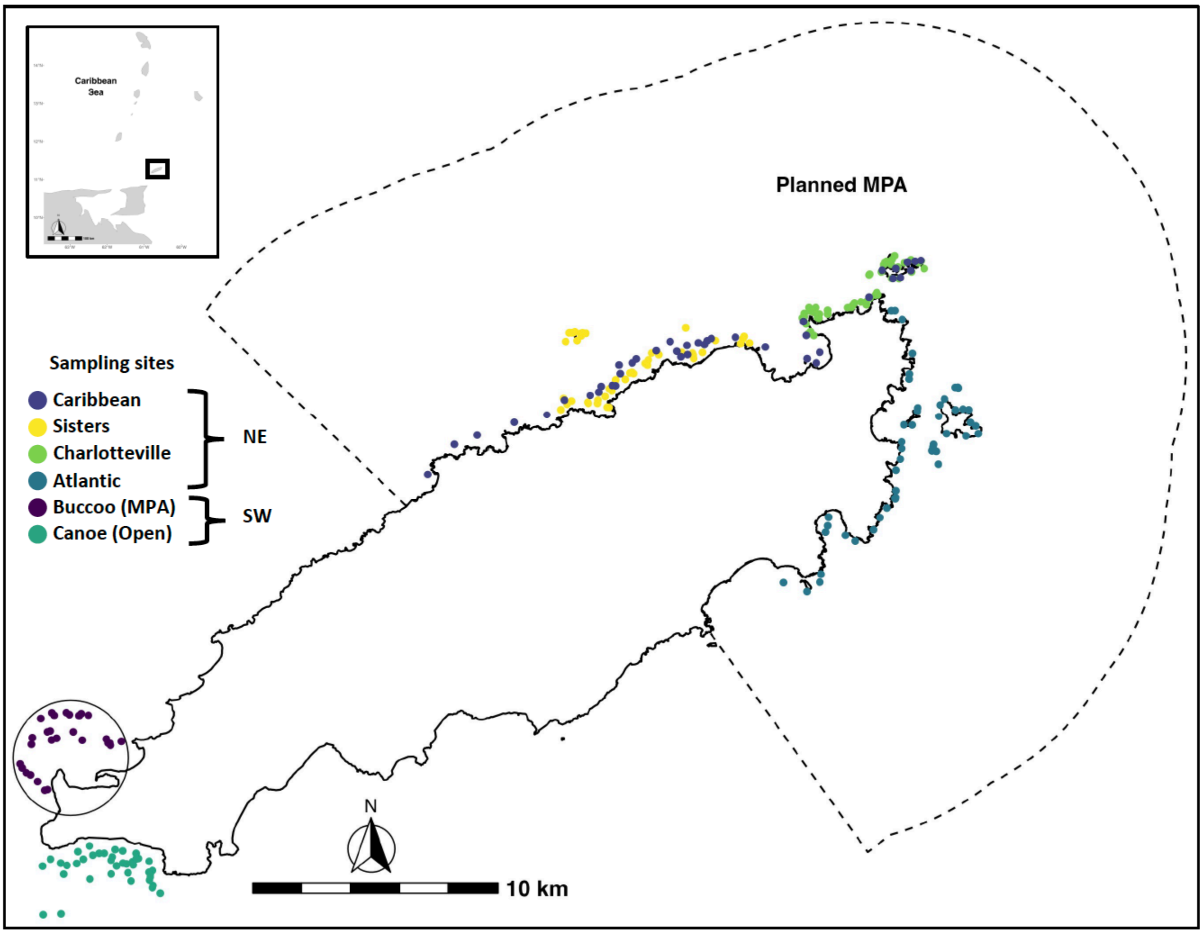


Figure 2.1 Tobago, showing approximate boundaries of Buccoo Reef Marine Park (solid line, SW) and planned Northeast Tobago Marine Protected Area (dashed lines), and locations of all baited remote underwater video stations per study sampling site (Northeast region: Caribbean, Sisters, Charlotteville, Atlantic; Southwest region: Buccoo, Canoe).

Some video files were excluded due to insufficient horizontal visibility (< 2 m) to identify passing elasmobranchs, the BRUVS frame toppling, or incomplete field of view. Consequently, the final number of stations that yielded data in the southwest was 67 (of 70 attempted; MPA

[Buccoo] = 29, Open [Canoe] = 38) and in the northeast was 164 (of 200 attempted; Atlantic = 50, Charlotteville = 24, Sisters = 49, Caribbean = 41).

BRUVS were watched in the Global FinPrint Annotator (Vulcan, Inc.) in real time by at least two independent observers. Species verifications were made by experienced Global FinPrint team members. Data recording began as soon as the BRUVS frame settled on the substrate, and sampling effort was standardised by watching all video files to 90 minutes. For each BRUVS set, all observed shark and ray species were recorded. Additionally, the maximum number of individuals per species in the field of view of the camera at any given point in time was also recorded (MaxN). This approach eliminates the possibility of double counting individuals because any individual repeatedly returning within the field of view of the camera yields only a MaxN value of one (Willis et al. 2000; Cappo et al. 2007).

Sharks that could not be identified to species level due to image quality were excluded from analysis; these included two unknown species in the genus *Carcharhinus*, one unknown species in the genus *Sphyrna*, 12 requiem sharks (unknown species in the Carcharhinidae family) and one unknown shark (unknown species in superorder Selachimorpha). Due to small sample size, tiger, *Galeocerdo cuvier*, great hammerhead, *Sphyrna mokarran*, and scalloped hammerhead sharks, *Sphyrna lewini*, were grouped as large sharks (maturing at sizes > 1.5 m total length). Although such highly mobile species might be less likely to be captured or spend extensive time within relatively small areas such as our study sites, their observation would nevertheless indicate habitat use and allow for the extrapolation of relative abundance estimates. Smoothhound, *Mustelus* spp., and sharpnose sharks, *Rhizoprionodon* spp., were classified to genus due to inability to visually identify overlapping species in the region (e.g. Brazilian sharpnose R. lalandii and Caribbean sharpnose R. porosus; Mendonça et al. 2011), and were grouped as small sharks (maturing at sizes < 1.5 m total length). Nurse sharks, *Ginglymostoma cirratum*, are unusual among coastal Caribbean shark species in that they are rarely targeted by fishers, due to poor quality fins and low meat yield (Demian Chapman personal comm.). Consequently, nurse sharks are more common than other sharks in many jurisdictions in the Caribbean and including them in spatial comparisons can obscure important information about other species (Ward-Paige et al. 2010). We therefore followed Ward-Paige et al. (2010) and analysed our data with and without nurse sharks. All ray species were first analysed as a group to maximise sample size. Species data for the southern stingray, *Hypanus americanus*, were then analysed separately, since it is frequently seen by divers in Tobago (personal observ.) and is important to tourism industries elsewhere in the Caribbean (Vaudo et al. 2017).

We standardised sampling among study sites using the following steps; first, we calculated sampling intensity for each reef then identified a reduced number of stations to standardise intensity and ensure an equal proportion of available habitat was sampled when estimating relative abundance (Table 2.1); next, we randomly selected the reduced number of stations as a subset of the complete dataset for each reef, calculating relative abundance as mean MaxN ± standard error (SE) to standardise sampling effort (Goetze et al. 2018); lastly, we repeated this for 2000 bootstrapped randomised subsets (Bond et al. 2012) and extracted the median mean MaxN ± SE to report as the mean number of observations per BRUVS deployed in each site. Similarly, we tested for differences in mean MaxN both among all sites and between the Northeast and Southwest regions of the island using a Kruskal-Wallis test repeated for 2000 bootstrapped randomised data subsets, and report the median p value extracted from each set of tests. A Shannon-Wiener Diversity Index was calculated as a measure of species diversity using individual species counts for both the southwest and northeast regions as follows:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where *s* equals species richness and p_i equals the proportion of the total sample represented by species *i*. Diversity indices for the southwest and northeast region were then compared using Hutcheson's t-test (Hutcheson 1970). Data were analysed using R software with the 'MASS' package (Venables and Ripley 2002; R Core Team 2022).

We used generalised linear models (GLMs) to investigate the influence of environmental variables (year, season, relief, depth, water temperature, and the interaction between depth and water temperature) on the relative abundance of species and species groups (response variables; Clementi et al. 2021a; Flowers et al. 2022). Season was classified as either dry (December to May) or wet (June to November), and habitat relief was estimated using BenthoBox (www.benthobox.com, Australian Institute of Marine Science). Briefly, habitat relief is calculated in a 5 by 4 grid overlayed on a screenshot from each video and is a measure of complexity. Every rectangle in the grid is given a score following Polunin and Roberts (1993) between 0 (no relief) and 5 (high relief) and the mean is calculated from all rectangles that do not contain open water (MacNeil et al. 2020; Sherman et al. 2020a). We examined error structure using the R package 'DHARMa' (Hartig 2020) to check residual diagnostics for all response variables, selecting a Poisson structure for both aggregated large sharks and Caribbean reef sharks, *Carcharhinus perezi,* and a negative binomial (NB) error structure for all other species and aggregated species (Table S2.1). We then used the 'dredge' function in the R package 'MuMIn' (Barton 2020) to identify all possible variable combinations, followed by an information theoretic approach (Akaike's information criteria, AIC; Akaike 1998) to identify the best predictive model (ΔAIC = 0; Table 2) and retain the top models (ΔAIC < 2; Table S2.2) for model averaging.

2.3.1 Research permits and approvals

All work was conducted under Research Permit 001/2016 issued to Environmental Research Institute Charlotteville by the Department of Natural Resources and the Environment, Tobago House of Assembly.

2.4 Results

2.4.1 Species richness and observation frequency

Sharks and rays were recorded on 56 (24%) and 48 (21%) of 231 BRUVS deployed, respectively. The two most frequently sighted species were southern stingrays and nurse sharks, recorded on 45 (19%) and 19 (8%) BRUVS, respectively. We recorded a total of seven shark species and two ray species overall; all 9 species were recorded in northeast Tobago, whereas only nurse sharks, Caribbean reef sharks and southern stingrays were recorded in the southwest (Table 2.1). Consequently, species diversity was higher in the northeast region (H=1.77) than the southwest (H=0.96; Shannon Diversity Index, t=6.5, $p < 0.0001$).

Table 2.1 Presence (+) or absence (-), species richness, International Union for the Conservation of Nature (IUCN) Red List conservation status, and IUCN Red List global population trend of shark and ray species observed on baited remote underwater video stations across different sampling reefs and regions in Tobago. Great hammerhead, scalloped hammerhead, and tiger sharks were grouped as large sharks (maturing at sizes > 1.5 m total length); smoothhound and sharpnose sharks were classified to genus and grouped as small sharks (maturing at sizes < 1.5 m total length).

Reef		**Atlantic**	**Charlotteville**	**Sisters**	**Caribbean**	**Buccoo**	**Canoe**		
Area (km^2)		9.1	2.4	3.4	8.6	5.1	7.8		
Stations usable (nS)		50	24	49	41	29	38		
Intensity (nS/km^2)		5.5	20.8	14.1	4.8	5.9	5.0		
Reduced stations (nR)		44	11	16	41	24	37		
Std. intensity (nR/ km^2)		4.8	4.6	4.7	4.8	4.7	4.7		
Region		NE	NE	NE	NE	SW	SW		
		MPA status						**IUCN Red List**	
Species	**Group**	-------------- Planned --------------				MPA	Open	**Status***	**Trend**
Nurse shark *Ginglymostoma cirratum*	n/a	+	+	+	+	+	+	VU	↓
Caribbean reef shark *Carcharhinus perezi*	n/a	+	+	+	+	+	+	EN	↓
Sharpnose shark *Rhizoprionodon* spp.	Small	+	+	+	+	-	-	VU	↓ **
Smoothhound *Mustelus* spp.	Small	-	+	+	+	-	-	NT	↓ ***
Tiger shark *Galeocerdo cuvier*	Large	+	+	+	-	-	-	NT	↓
Great hammerhead *Sphryna mokarran*	Large	-	+	+	-	-	-	CR	↓
Scalloped hammerhead *Sphyrna lewini*	Large	-	-	-	+	-	-	CR	↓
Southern stingray *Hypanus americanus*	n/a	+	+	+	+	+	+	NT	↓
Whitespotted eagle ray *Aetobatus narinari*	n/a	+	+	-	-	-	-	EN	↓
Species richness		6	8	7	6	3	3		
Total species richness		Northeast = 9				Southwest = 3		**Overall = 9**	

* NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered

** *Rhizoprionodon* identified only to genus, status presented here is Caribbean sharpnose shark (*R. porosus*)

*** *Mustelus* identified only to genus, status presented here is Dusky Smoothhound (*M. canis*)

2.4.2 All sharks and rays MaxN

The highest observed mean MaxN for sharks was in Caribbean (0.54±0.14) and the lowest was in Charlotteville (0.18±0.14), with little evidence for any difference among sites (Kruskal-Wallis, p = 0.08; Figure 2.2). When sharks were analysed without nurse sharks, there was a marked difference in mean MaxN among sites (Kruskal-Wallis, p = 0.002; Figure 2.2). Additionally, we found appreciable differences between the northeast and southwest of the island for sharks excluding nurse sharks (Kruskal-Wallis, p = 0.005; Figure 2.2), driven by increased mean MaxN in Caribbean and Sisters sites in the northeast region. Ray mean MaxN was highest in Canoe (0.57±0.11) and similar across other sites (0.13±0.09 [Sisters] – 0.24±0.08 [Caribbean]), with differences both among sites (Kruskal-Wallis, p = 0.006; Figure 2.2) and between the northeast and the southwest (Kruskal-Wallis, p = 0.007; Figure 2.2), driven by increased mean MaxN in Canoe in the southwest region.

2.4.3 Species and species groups MaxN

Large sharks were infrequently sighted in the northeast region and entirely absent in the southwest, such that large shark mean MaxN did not differ significantly among sites (Kruskal-Wallis, p = 0.64) or regions (Kruskal-Wallis, p = 0.19; Figure 2.2). Conversely we detected differences in small shark mean MaxN both among sites (Kruskal-Wallis, p = 0.02) and between regions (Kruskal-Wallis, p = 0.008), as small sharks were generally absent in the southwest region. We also detected differences in southern stingray mean MaxN both among sites (Kruskal-Wallis, p = 0.02) and between regions (Kruskal-Wallis, p = 0.02; Figure 2.2), driven by increased mean MaxN in Canoe in the southwest region.

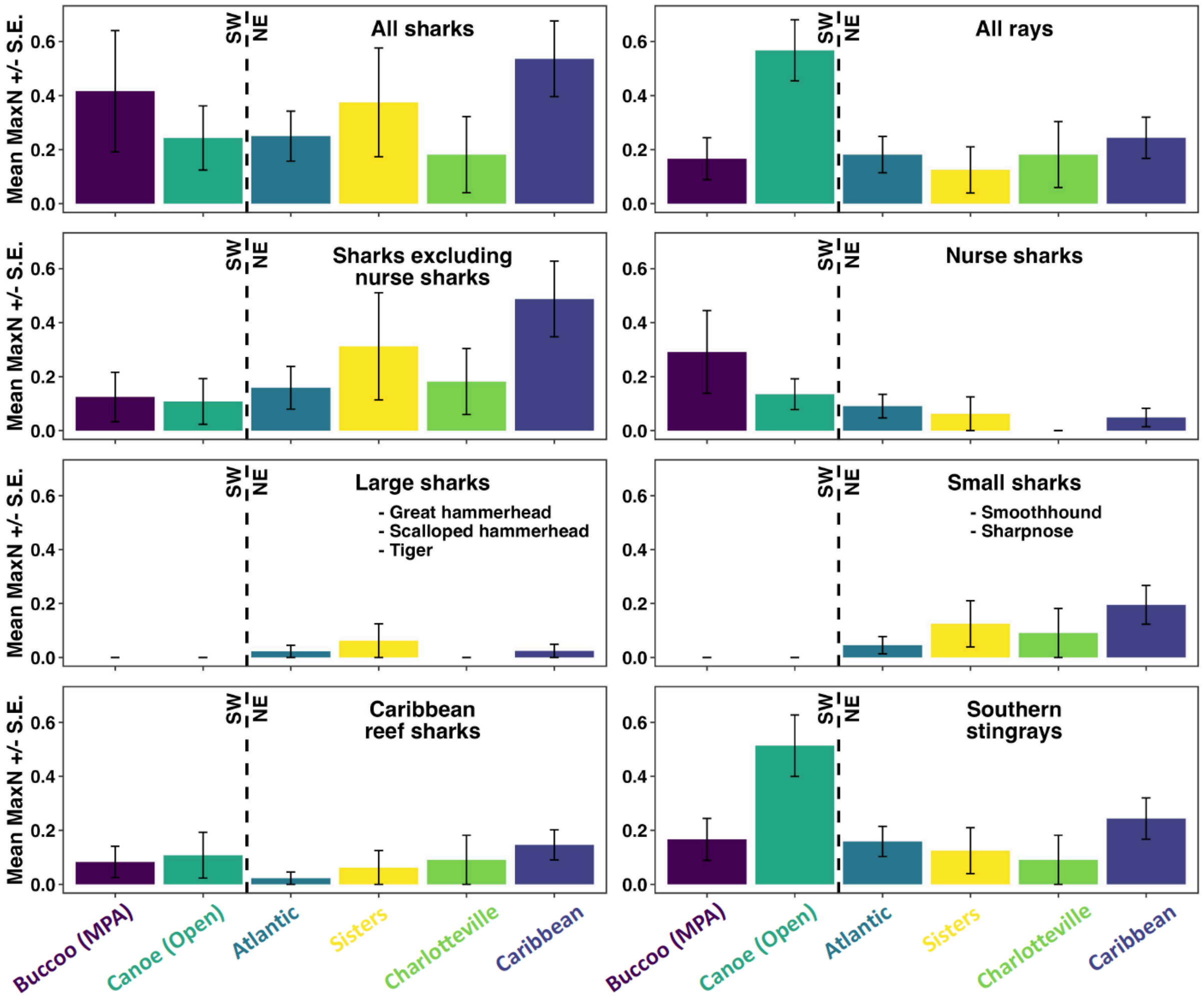


Figure 2.2 Mean MaxN (± S.E.) of all elasmobranch species groups (all sharks, all rays, sharks excluding nurse sharks, nurse sharks, large sharks, small sharks, Caribbean reef sharks, and southern stingrays) observed on baited remote underwater video sampling across all sites in Tobago, southern Caribbean. Note: great hammerhead, scalloped hammerhead, and tiger sharks were grouped as large sharks (maturing at sizes > 1.5 m total length); smoothhound and sharpnose sharks were classified to genus and grouped as small sharks (maturing at sizes < 1.5 m total length).

2.4.4 Influence of season, relief, depth, and water temperature on relative abundance

When sharks were analysed without nurse sharks, the AIC top model included depth, mean relief, and season as predictor variables; for large sharks the equivalent was mean relief, and for small sharks it was depth and season; for Caribbean reef sharks it was mean relief and season, and for nurse sharks it was depth and mean relief (Table 2.2). The AIC top model for southern stingrays included depth and mean relief (Table 2.2).

Table 2.2 Analysis of deviance tables for the best predictive model (ΔAIC = 0) for the association between environmental variables and MaxN observations of 1) sharks excluding nurse sharks, 2) large sharks, 3) small sharks, 4) Caribbean reef sharks, 5) nurse sharks, and 6) southern stingrays on baited remote underwater video stations in Tobago.

	df	**Deviance**	**Resid. df**	**Resid. Dev**	**Pr(>Chi)**	**% deviance expl.**
Response = Sharks excl. nurse MaxN						
NULL			170	79.54		
depth	1	3.30	169	76.24	0.07	4.15
mean relief	1	4.06	168	72.18	*< 0.05*	5.10
season	1	4.20	167	67.98	*< 0.05*	5.28
Response = large sharks MaxN						
NULL			170	24.26		
mean relief	1	4.41	169	19.85	*< 0.05*	18.18
Response = small sharks MaxN						
NULL			170	48.99		
depth	1	5.35	169	43.64	*< 0.05*	10.92
season	1	3.98	168	39.66	*< 0.05*	8.12
Response = Caribbean reef sharks MaxN						
NULL			170	59.59		
mean relief	1	3.04	169	56.55	0.08	5.1
season	1	2.6	168	53.95	0.11	4.4
Response = nurse sharks MaxN						
NULL			170	81.60		
depth	1	2.82	169	78.78	0.09	3.46
mean relief	1	19.47	168	59.32	***< 0.001***	23.86
Response = southern stingrays MaxN						
NULL			170	127.42		
depth	1	17.28	169	110.14	***< 0.001***	13.56
mean relief	1	4.22	168	105.91	*< 0.05*	3.31

Depth had a positive effect on small sharks but a negative effect on southern stingrays (p < 0.05, < 0.001, respectively; Table 2.2, Table 2.3). The onset of the dry season had a negative effect on both sharks excluding nurse sharks and on small sharks (p < 0.05, < 0.05, respectively; (Table 2.2, Table 2.3). Mean relief had a positive effect on both nurse sharks and sharks excluding nurse sharks (p < 0.001, p < 0.05, respectively; Table 2.2, Table 2.3), but a negative effect on both large sharks and southern stingrays (p < 0.05, < 0.05, respectively; Table 2.2, Table 2.3).

Table 2.3 Model-averaged coefficients from top models (ΔAIC < 2) predicting the association between environmental variables and MaxN observations of 1) sharks excluding nurse sharks, 2) large sharks, 3) small sharks, 4) Caribbean reef sharks, 5) nurse sharks, and 6) southern stingrays on baited remote underwater video stations in Tobago.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Response = Sharks Excluding Nurse Sharks MaxN				
Intercept	-1.25	3.71	0.34	0.74
Depth	0.06	0.03	2.16	< 0.05
Mean relief	0.57	0.24	2.40	< 0.05
Season	-0.78	0.61	1.27	0.20
Temperature	-0.08	0.14	0.54	0.59
Response = Large Sharks MaxN				
Intercept	-7.4×10^{-1}	5.8	0.13	0.90
Mean relief	-1.4×10^{2}	3.9×10^{4}	< 0.01	1.00
Temperature	-1.06×10^{-1}	2.2×10^{-1}	0.49	0.63
Depth	9.2×10^{-3}	3.2×10^{-2}	0.29	0.78
Response = Small Sharks MaxN				
Intercept	-4.2	1.44	2.89	< 0.01
Depth	0.06	0.05	1.32	0.19
Season	-1.63	1.21	1.34	0.18
Mean relief	0.14	0.28	0.48	0.63
Response = Caribbean Reef Sharks MaxN				
Intercept	-3.26	0.68	4.78	< 0.001
Mean relief	0.52	0.39	1.33	0.18
Season	-0.61	0.78	0.78	0.44
Depth	-0.003	0.02	0.19	0.85
Response = Nurse Sharks MaxN				
Intercept	-2.88	2.03	1.41	0.16
Depth	-0.03	0.04	0.98	0.33
Mean relief	1.09	0.29	3.74	< 0.001
Temperature	-0.01	0.07	0.15	0.88
Response = Southern stingrays MaxN				
Intercept	-0.47	2.04	0.23	0.82
Depth	-0.07	0.02	3.84	< 0.001
Mean relief	-0.36	0.18	1.93	0.05
Temperature	0.01	0.07	0.18	0.86

2.5 Discussion

Here we use BRUVS observations to establish a baseline of elasmobranch species richness, relative abundance, and diversity in Tobago, investigate the influence of season, relief, depth and water temperature on relative abundance, and investigate spatial variation in relative abundance. Reef shark abundance in Tobago is similar to other locations in the Caribbean (MacNeil et al. 2020), but the species richness recorded in northeast Tobago is comparable to BRUVS data in The Bahamas where targeted shark fishing has been effectively banned since the early 1990s (Brooks et al. 2011). This is both surprising, given historical and ongoing shark fishing, and encouraging in the context of the recent drafting of a Sustainable Shark and Ray Management Plan for Northeast Tobago and the declaration of the region as a UNESCO Man and the Biosphere Reserve. Identifying shark conservation potential in Tobago (MacNeil et al. 2020) therefore presents a timely opportunity to strengthen management through updated legislation such as gear restrictions and critical habitat protection.

The most common and widely distributed species were the southern stingray, nurse shark and Caribbean reef shark, while observations of aggregated large and small shark species were limited to the rural northeast region. A combination of habitat relief, depth, and season appear to be the best predictors of elasmobranch relative abundance, such that the variety of habitats available in the northeast (e.g. deep reefs, seamounts, offshore islands) may explain the higher species diversity. These habitats can support elevated abundance of predatory fish (Lester et al. 2022; Cresswell et al. 2023), rendering them suitable candidates for protection measures such as spatial or temporal fisheries exclusion within a broader management programme. The implementation of such measures in northeast Tobago, however, will require validation through further research, and should incorporate protection across depths around these habitats given potential species-specific depth preferences amongst sharks (Lester et al. 2022). Similarly, higher anthropogenic pressures emanating from larger population centres in the southwest may be a factor, since this has been negatively associated with predatory reef fish biomass (Valdivia et al. 2017), shark diversity (Bakker et al. 2017), and shark abundance (Clementi et al. 2021a). Indeed, sharks can be severely depleted within one hour travel time to human population centres (Juhel et al. 2018). This may indirectly promote northeast Tobago as a refuge by concentrating targeted pressure on shark populations in the southwest. Nevertheless, given both the major role of Trinidad and Tobago in the shark trade and the lack of fisheries management, the diversity of sharks recorded in the northeast was unexpected, particularly for large shark species that are among those most globally threatened by fishing (Queiroz et al. 2019). Notably, the scalloped hammerhead is a conservation priority (Dulvy et al. 2017), and our data represent the only confirmed sighting of this species in the largest BRUVS survey across 126 research sites in the Western Atlantic (MacNeil et al. 2020).

BRUVS are a widely accepted methodology for sampling reef-associated elasmobranchs (Bond et al. 2012; Goetze et al. 2018; Harvey et al. 2019; MacNeil et al. 2020), and using the MaxN metric is a conservative approach (Whitmarsh et al. 2017). As such, our finding that Tobago, and particularly the northeast region, exhibits unusually high shark diversity for the greater Caribbean (Bond et al. 2012; Bruns and Henderson 2020; MacNeil et al. 2020) warrants further research attention. Specifically, investigations into movement ecology may identify local habitat areas that are spatially or temporally important for sharks, and thus critical for effective management design. Typical dispersal distances of Caribbean reef sharks and nurse sharks necessitate a minimum no-take zone MPA coastline of 20 km and 50 km, respectively, to fully protect at least 50% of individuals (Dwyer et al. 2020). Therefore, at 7 km^2, the Buccoo Reef Marine Park is unlikely to provide sufficient coverage to benefit these species, and even well-enforced marine reserves close to human centres typically provide only limited benefits for apex predators (Cinner et al. 2018). Our findings are in line with this, as the shark and ray species observed in the southwest MPA are mesopredators rather than apex predators (Tilley et al. 2013; Bond et al. 2018).

Although similar regional observations have been made elsewhere (García 2017), the apparent robustness of Tobago shark assemblages to fishing pressure, certainly in terms of species richness, is relevant for regional management goals. The existing MPA in the southwest appears too small for effective shark and ray conservation, but the planned northeast MPA comprises over 600 km^2 and 50 km of coastline and could thus provide protection for site-attached and resident shark (Dwyer et al. 2020) and ray species. It could also reduce local fishing pressure on the migratory species, but further research on regional elasmobranch movement, habitat use, and shark fishery characteristics (i.e. gear types, target species and local fishing grounds) is needed to assess this possibility. Beyond the no-take MPA boundary it may also be possible to introduce additional regulations or management zones aimed at regulating shark fishing, such as restricting gear (e.g. longlines and/or gillnets; Chapman et al. 2005) or expanding no shark fishing zones (Flowers et al. 2022). Although success of local management will be largely influenced by political will, community buy-in and enforcement (Shiffman and Hammerschlag 2016), this has been achieved elsewhere in the Caribbean through combinations of incentives and penalties (Kaplan et al. 2015). With the presence of highly mobile species that will likely move outside the planned MPA (great hammerhead and scalloped hammerhead sharks), the national plan for sustainable shark management will be important. To mitigate fishing exposure beyond both MPA and national jurisdiction, Trinidad and Tobago should foster and maintain engagement with regional fisheries management organisations, policies such as the IUCN Marine Biodiversity of Areas Beyond National Jurisdiction, and international bodies including the Convention on International Trade in Endangered Species of Wild Fauna and Flora and the Convention on the Conservation of Migratory Species of Wild Animals. The MPA planned for northeast Tobago, together with the draft Sustainable Shark and Ray Management Plan and Fisheries Management Bill, present an opportunity to protect local populations of coastal species. As such, these could be the first steps towards the regional investments required to ultimately protect the full elasmobranch assemblage observed around this island.

Chapter 3: SPATIOTEMPORAL HABITAT PARTITIONING AMONGST SYMPATRIC DEMERSAL SHARK SPECIES IN THE CARDIGAN BAY SPECIAL AREA OF CONSERVATION, UK

3.1 Abstract

Global marine biodiversity declines require bold and ambitious plans in order to safeguard critical ecosystem services. Overfishing, habitat loss and projected climate impacts have yielded deleterious effects on marine predators, in particular, driving an ever increasing threat of extinction for many shark species with implications for ecosystem health. Identifying and protecting critical habitat areas for sharks is fundamental to their protection, and may allow for species recovery. Here we use nearshore baited remote underwater video stations to investigate spatial and temporal patterns of habitat use by sharks in a Special Area of Conservation (SAC) that is centrally important to the regional blue economy in the UK, the Cardigan Bay SAC. Our results show extensive habitat sharing between smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *S. stellaris*, with pronounced spatial and temporal trends. Nearshore reef habitats are substantially more important than non-reef habitats for both species. The relative abundance of each species, however, is roughly inversely seasonally proportional, with catshark and nursehound relative abundance highest in March and September, respectively. Temporal niche partitioning may be an important mechanism in marine systems, but has not been widely investigated in sympatric shark communities. Our methods rely exclusively on daytime sampling; therefore we cannot conclusively identify any diel component, but the apparent seasonal component of potential temporal niche partitioning warrants further research attention. These findings are directly relevant for ongoing development of the Welsh Marine Evidence Strategy (2019-2025) and the Welsh National Marine Plan, particularly to inform spatial planning to strengthen the role of SAC management design in protecting important shark areas.

3.2 Introduction

Marine predatory fish biomass has decreased extensively since the onset of industrialised fishing (Myers and Worm 2003,2005), with global elasmobranch (shark and ray) populations in a state of long-term decline (Myers and Worm 2003,2005; Dulvy et al. 2014; MacNeil et al. 2020; Dulvy et al. 2021; Pacoureau et al. 2021; Simpfendorfer et al. 2023). This has prompted widespread calls for conservation action, with popular approaches including the implementation of marine reserves or shark sanctuaries (Chapman and Frisk 2013; Worm et al. 2013; Chapman et al. 2021). Spatial protection may be effective and can facilitate population recovery for some species (Speed et al. 2018), but is linked both to ecological factors such as residency and movement ecology (Dwyer et al. 2020), and anthropogenic factors such as governance (MacNeil et al. 2020), compliance and enforcement (Kaplan et al. 2015). Moreover, success is heavily moderated by proximity to human pressures (Juhel et al. 2018; Letessier et al. 2019b). Shark species that receive attention tend to be large, charismatic, of high conservation value and/or heavily depleted (Shiffman et al. 2020). However, it is arguably important to also gain insights into population structure of less threatened species, particularly where depletion of other species has elevated their importance (trophic cascade) beyond what might be observed in a less exploited system. Amongst the research priorities identified are population status, movement ecology and critical habitat use, with temperate species relatively under-studied (Jorgensen et al. 2022).

Biodiversity action pathways in Wales include the Welsh Marine Evidence Strategy (2019-2025) and the Welsh National Marine Plan, and present an opportunity to align national with international objectives. The EU Green Deal (2019) and the EU Biodiversity Strategy for 2030 incorporate biodiversity and ecosystem protection targets for the European Union whilst, more widely, the Decade of Ocean Science for Sustainable Development (Ryabinin et al. 2019) identifies the following key goals:

“Goal 1: To generate the scientific knowledge and underpinning infrastructure and partnerships needed for sustainable development of the ocean.

Goal 2: To provide ocean science, data and information to inform policies for a well-functioning ocean in support of all Sustainable Development Goals of the 2030 Agenda.”

Current designations in Wales include a network of Special Areas of Conservation (SACs) and Special Protection Areas (SPAs) with objectives to safeguard species or habitats under the Habitats Directive (Habitats Directive 1992), and birds, respectively. Ambitious targets for marine spatial planning should seek to strengthen species and habitat protection, and incorporate restoration and recovery objectives (Santos et al. 2019; Harris et al. 2022; Holness et al. 2022; Manea et al. 2023). Given that the most vulnerable species to extinction in European continental shelf seas are typically long-lived and occupying upper trophic levels, with a substantial proportion also functionally distinct (Coulon et al. 2023), meeting these targets requires species ecology insights that are locally relevant and applicable.

The smallspotted catshark *Scyliorhinus canicula* is widespread and stable in its population. Yet it should be considered for species-level management attention given food web centrality (Wieczorek et al. 2018), genetically distinct populations within the UK (Gubili et al. 2014), and the important role of mesopredators in linking lower and upper trophic levels (Vaudo and Heithaus 2011). Furthermore, given widespread depletion of marine predatory biomass (Myers and Worm 2003,2005), the relative trophic position of mesopredators in exploited systems is likely to be higher than in unexploited systems (Prugh et al. 2009; Ritchie and Johnson 2009), thus potentially elevating the importance of species such as *S. canicula* in structuring marine communities. Despite high research attention (Table S3.1) key knowledge gaps remain, including the distribution of important habitat areas such as egg case nurseries that are critical for the design of oviparous elasmobranch conservation efforts (Kinney and Simpfendorfer 2009; Dodd et al. 2022) and, moreover, should be considered ecologically separate from juvenile nurseries (Hoff 2016). Conversely, and in comparison with the smallspotted catshark, the nursehound *Scyliorhinus stellaris* is listed as 'Vulnerable' by the IUCN Red List (Table 3.2), yet under-researched (Table S3.1). However, previous studies have shown refuging behaviour in both sheltered and exposed coastal environments, with a degree of philopatry (Sims et al. 2005), and it is prominent bycatch in Celtic Sea, Irish Sea, and Bristol Channel lobster and crab pot fisheries (Moore et al. 2023). Nevertheless, the paucity of ecological evidence is concerning given the trophic level, important role in the sports fishing blue economy (Hyder et al. 2021), and widespread availability of nursehounds in fishmongers and food takeaway establishments (Hobbs et al. 2019).

Baited remote underwater video stations (BRUVS) are a commonly used tool to investigate elasmobranch ecology (Bond et al. 2012; Unsworth et al. 2014; Bond et al. 2019; Sherman et al. 2020b; Clementi et al. 2021a; Jones et al. 2021). BRUVS sampling can yield estimates of species relative abundance using a maximum count of individuals seen simultaneously in the field of view (MaxN), which is a robust metric given it eliminates double counts. We therefore undertook, to our knowledge, the first standardised BRUVS sampling of the shark community assemblage in Cardigan Bay SAC, Wales, UK, with the following specific objectives to: 1) establish a baseline of species present; 2) investigate spatial and temporal variations in species relative abundance of shark species observed; and, 3) assess the influence of sampling month on regional spatiotemporal habitat use by sharks.

3.3 Methods

The Cardigan Bay Special Area of Conservation (SAC), west Wales, is a mixed use zone of approximately 1000 km^2 (JNCC, 2021), extending from Ceibwr Bay in Pembrokeshire to Aberath in Ceredigion (Figure 3.1). Its SAC status is based on seven qualifying features under Annex I and II of the Habitat's Directive, which include river lamprey, *Lampetra fluviatilis*, and the semi-resident population of bottlenose dolphins, *Tursiops truncates*, as well as the presence of submerged or partially submerged sea caves (JNCC, 2021). The bay is also used as a nursery ground for a wide range of demersal fish, some of which are commercially valuable (SAC, 2008). The area is important in the context of the regional blue economy, particularly wildlife watching tours. Sports fishing charters seasonally catch and release sharks including nursehound, *Scyliorhinus stellaris*, and tope, *Galeorhinus galeus*, while *S. canicula* can be bycatch in small scale local fisheries (Tim Harrison, personal comms.).

Three sampling sites were identified to represent different habitat types but with comparable distances from the closest human population centre (New Quay), and all frequently visited by wildlife watching boat trips (Sarah Perry, personal comms.). All sampling areas were approximately 1 km^2, within which GPS coordinates for sampling points (hereafter, stations) were randomly generated using the Cruise tool in Google Earth. Ten stations were generated per sampling site for 2021. For 2022, an additional three offshore sampling sites were added, with five stations then randomly generated per sampling site (Figure 3.1). Thus, each sampling period aimed to cover a total of 30 stations, although this was not always possible due to weather conditions. Sampling was conducted in May, July and September 2021, and March, May, July, and September 2022.

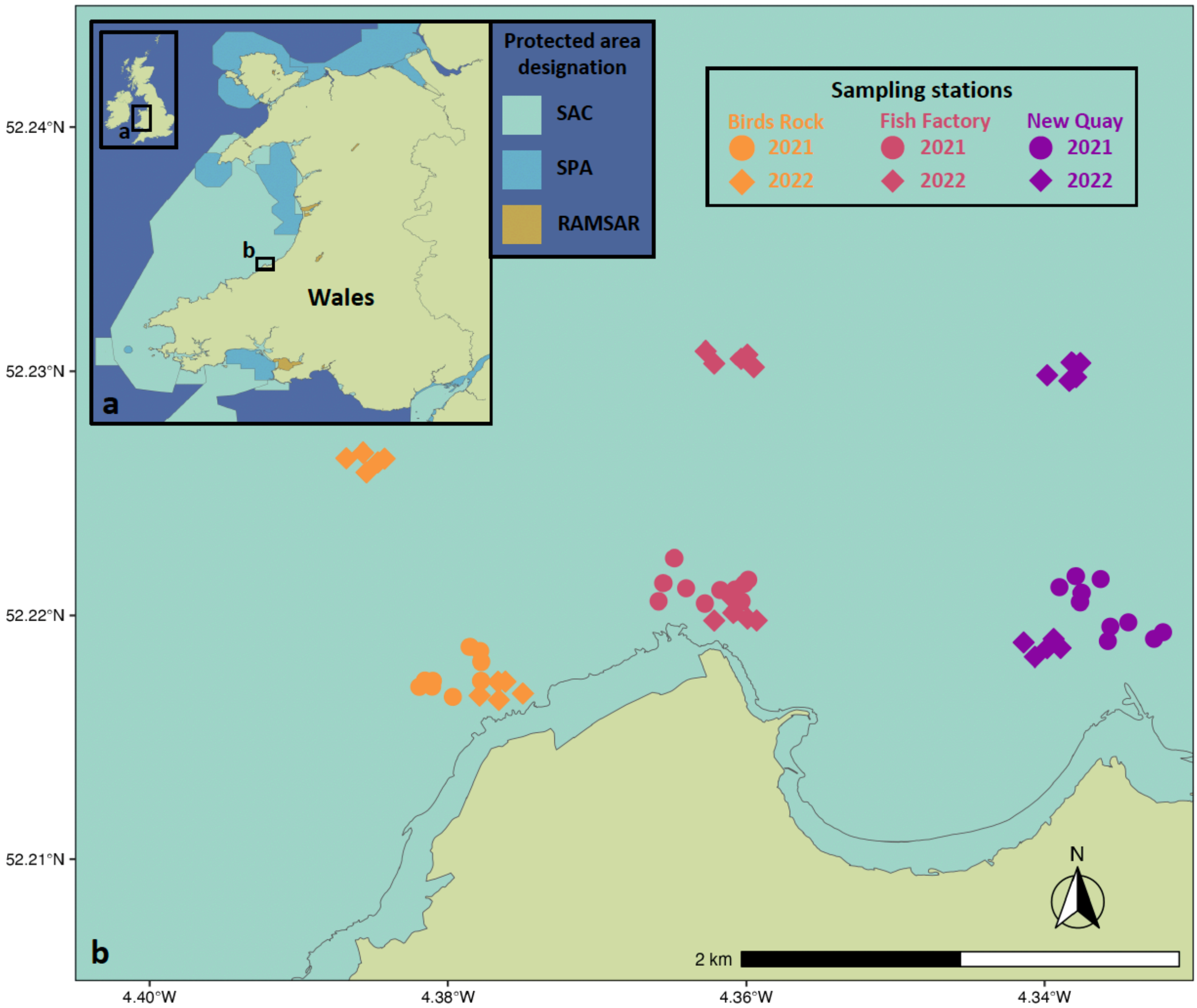


Figure 3.1 a) Wales, UK, showing the location of Special Areas of Conservation (SAC), Special Protection Areas (SPA), and Ramsar sites. b) Cardigan Bay SAC BRUVS sampling sites (Birds Rock, Fish Factory, New Quay) with stations therein, including spatially discrete offshore and nearshore stations sites sampled in 2021 and 2022.

The BRUVS setup comprised an aluminium frame (approximately 1 m x 0.6 m x 0.6 m) with a bait arm extending 1 m in front of the camera position and supporting a wire mesh cage in the middle of the field of view. A GoPro Hero7 Black camera was mounted in a GoPro SuperSuit housing (60 m depth rated), at approximately 40 cm from the base (Figure 3.2). The mesh cage was baited with approximately 1 kg of chopped oily fish, scad, *Trachurus trachurus*, or herring, *Clupea harengus*, to encourage bait plume dispersal (Dorman et al. 2012; Whitmarsh et al. 2017). A rope with sufficient scope to avoid toppling of the BRUVS was attached to a surface buoy to mark location (Murray et al. 2019).

Figure 3.2 Frames for mounting baited remote underwater video stations for this PhD (left) and camera field of view with the fish factory visible on New Quay Head, Cardigan Bay (right).

BRUVS were deployed between 09h00 and 17h00 to ensure sufficient light for video recording (Jones et al. 2021) and were left to record for a minimum of 60 minutes before retrieval, the minimum time required to sample 66% of fish species in nearshore North Atlantic waters (Unsworth et al. 2014). Up to 11 stations were sampled per day, and BRUVS that were deployed simultaneously were separated by a minimum of 1 km to ensure independent sampling (Harvey et al. 2019). A Garmin GPSMAP 86s handheld GPS was used to navigate to each station. Depth was either estimated using a rope marked at 50 cm intervals and weighted with a dive weight (in 2021), or measured using a Platimo Echotest II handheld depth sounder (2022). Additional data were recorded at both drop and haul time: Beaufort scale, cloud cover, and presence of boats.

Data recording began as soon as the BRUVS frame settled on the substrate. Video quality was first assessed using standardised criteria (Jones et al. 2021), with four rankings from excellent to unusable (Figure S3.1). This excluded a similar proportion of datasets from each site from analysis (Figure S3.1), yielding a total of 121 video datasets for full annotation (Table 3.1, Table S3.2). For the BRUVS sets retained for full annotation, sampling effort was standardised by watching all video files to 60 minutes. To further validate our choice of sampling effort, we recorded the time of first arrival for each species of shark observed for each BRUVS set. Next, we recorded MaxN, defined as the maximum number of individuals per species in the field of view at any given point in time throughout a BRUVS set. This eliminates the possibility of double counting individuals (Willis et al. 2000).

We first used generalised linear models to investigate the association between sampling month and site, and the relative abundance of each species (MaxN; response variable). We employed an information theoretic approach (Akaike's information criteria, AIC; Akaike 1998) to select the best error structure and link function (Poisson and log, respectively, for both *S. canicula* and *S. stellaris*), and then examined error structure using the R package 'DHARMa' (Hartig 2020) to check residual diagnostics for response variables (Table S3.3). Study design was to sample approximately equal areas of habitat with the same number of BRUVS, thereby standardising sampling intensity, but weather interferences prevented this and resulted in reduced numbers of usable BRUVS sets per site (Table 3.1). We therefore addressed the variation in the number of usable sets obtained from the nearshore and offshore sites (n = 100 and 21, respectively) by conducting two separate further analyses, one on the full dataset (total n = 121) and one on the nearshore sites only (n = 100). For both datasets we calculated mean MaxN ± standard error (SE) as the metric for relative abundance to standardise sampling effort among study sites (Goetze et al. 2018). For the full dataset, we calculated the number of stations required to standardise sampling intensity for each site, and thus ensure the same proportion of available habitat was sampled (Table 3.1). Next, we randomly selected the respective reduced number of stations from the complete dataset for each site, and repeated this for 2000 bootstrapped randomised subsets (Bond et al. 2012). We then extracted the median mean MaxN ± SE to report as the mean number of observations of each species per BRUVS deployed in each site. Similarly, we assessed spatial variation in relative abundance amongst the nearshore and offshore sites using a Kruskal-Wallis rank sum test repeated for 2000 bootstrapped randomised data subsets, again reporting the median p value extracted from the set of tests for each species. Thereafter, we calculated mean MaxN ± standard error (SE) for the nearshore datasets only. We then executed the same statistical tests, since reducing the dataset to standardise sampling intensity may have obfuscated any patterns in the nearshore data. Specifically, we used Kruskal-Wallis rank sum tests with Dunn *post-hoc* tests to assess pairwise differences in the relative abundance of both smallspotted catsharks and nursehounds, first between sites and then between months in order to identify specific variation in spatial and temporal relative abundance patterns, respectively. Lastly, we did not include *Mustelus* sp. in any analyses given it was only a single observation.

Table 3.1 Baited remote underwater video stations set in the Cardigan Bay Special Area of Conservation per year, site and habitat, the number of usable sets according to standardised criteria (Jones et al. 2021), and the reduced number of sets used in bootstrapped statistical analysis to standardise the sampling intensity and ensure equal proportions of available habitat sampled.

Site	**n sets**	**n usable sets**	
Birds Rock			
2021	27	25	
2022 offshore	10	5	
2022 nearshore	7	5	
Fish Factory			
2021	28	28	
2022 offshore	10	7	
2022 nearshore	13	6	
New Quay			
2021	28	28	
2022 offshore	15	9	
2022 nearshore	14	8	
Habitat	**n sets**	**n usable sets**	**n reduced sets**
Birds Rock nearshore	34	30	10
Birds Rock offshore	10	5	5
Fish Factory nearshore	41	34	10
Fish Factory offshore	10	7	5
New Quay nearshore	42	36	10
New Quay offshore	15	9	5

3.4 Results

We recorded sharks on 43 of 152 BRUVS deployed (28%; Figure 3.3). Total species richness was three: the smallspotted catshark, *Scyliorhinus canicula* (Figure 3.4), the nursehound, *S. stellaris* (Figure 3.4), and one individual of an unknown species of smooth hound shark, *Mustelus* sp. (Figure 3.3). The most frequently sighted species, *S. canicula*, was recorded on 19% of BRUVS (Table 3.2, Figure 3.3). Furthermore, of those BRUVS that yielded sightings, 75% recorded both *S. canicula* and *S. stellaris* within the first 40 minutes of recording (Figure 3.5), justifying our standardised 60 minutes sampling effort.

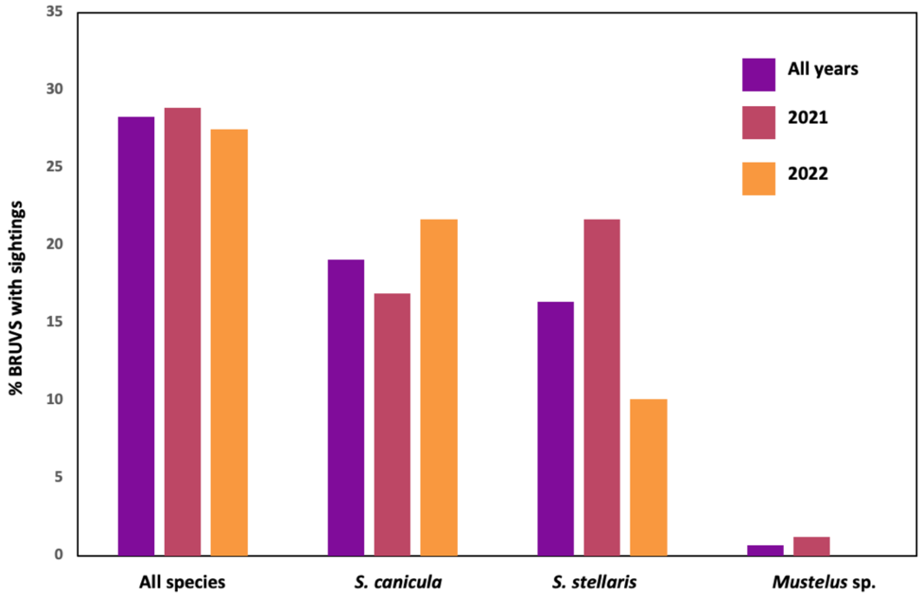


Figure 3.3 Annual variations in the percentage of deployments with sightings of smallspotted catsharks, *Scyliorhinus canicula*, nursehounds, *Scyliorhinus stellaris*, and smooth hound sharks, *Mustelus* sp., during BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK.

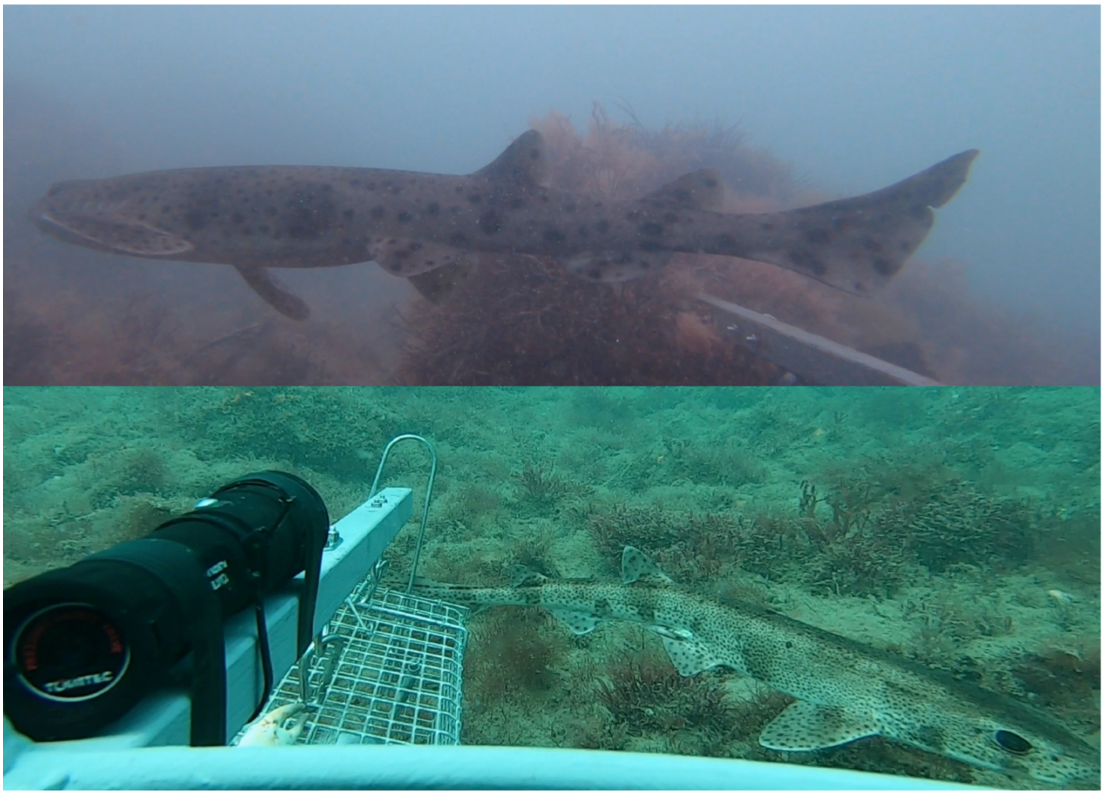


Figure 3.4 A smallspotted catshark, *Scyliorhinus canicula* (below), and nursehound, *Scyliorhinus stellaris* (above), observed during BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK. Note *S. stellaris* second dorsal fin origin well ahead of anal fin insertion, anal fin base equal or greater than interdorsal space, and longer than anal-caudal fin space, blotches on flank.

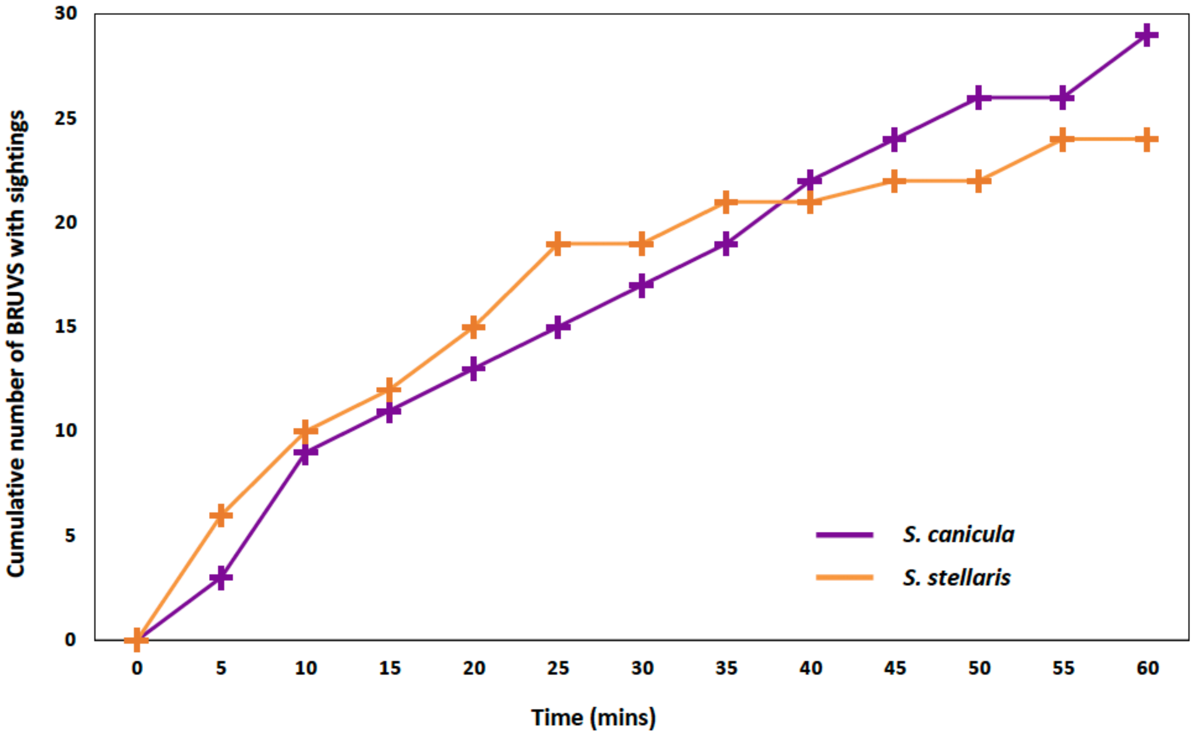


Figure 3.5 Species accumulation curve for smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *Scyliorhinus stellaris*, with deployment time for BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK.

Table 3.2 IUCN Red List status and sightings frequency of shark species recorded on BRUVS in the Cardigan Bay Special Area of Conservation.

Common name	Scientific name	IUCN Red List status	% BRUVS sighted
Smallspotted catshark	*Scyliorhinus canicula*	Least Concern	19
Nursehound	*Scyliorhinus stellaris*	Vulnerable*	16
Smoothhound	*Mustelus* sp.	Endangered**	0.7

*** Global status. ** Status for common smoothhound, *Mustelus mustelus.***

Spatial comparisons of relative abundance show it to be highest for both *S. canicula* and *S. stellaris* in the reef habitats of the New Quay site in the full dataset (0.8 ± 0.2 and 1.0 ± 0.29, respectively, Figure 3.6; Kruskal-Wallis rank sum $p < 0.01$; Table S3.4) and in the nearshore subset data (0.63 ± 0.32 and 1.25 ± 0.37, respectively, Figure 3.7; Kruskal-Wallis rank sum $p < 0.0001$; Table S3.4). Furthermore, within the full dataset analysis, catsharks were observed in all the offshore sites, with mean MaxN ± S.E. from 0.4 ± 0.24 (Fish Factory offshore) to 0.8 ± 0.2 (New Quay offshore), but only in the reef habitats of New Quay (0.6 ± 0.22) amongst the nearshore sites. In contrast, nursehounds were observed only in the New Quay sites, and particularly nearshore (1.0 ± 0.29; Figure 3.6). This demonstrates an association between site and MaxN for both *S. stellaris* and *S. canicula* (GLM $p < 0.0001$). Temporal trends in relative abundance were similarly apparent (Kruskal-Wallis rank sum $p < 0.01$; Table S3.4); mean MaxN was higher for *S. stellaris* in September (0.79 ± 0.21) than any other sampling month (Dunn post-hoc pairwise test; Figure 3.7; Table S3.5), and highest for *S. canicula* in March (0.5 ± 0.5) but varying between 0.07 ± 0.05 (July) and 0.41 ± 0.12 (May) for the other sampling months (Dunn post-hoc pairwise test; Figure 3.7; Table S3.5). This is reflected in evidence for an association between month and MaxN for *S. stellaris* (GLM $p < 0.001$) and moderate evidence for an association between month and MaxN for *S. canicula* (GLM $p < 0.05$; Table 3.3).

Table 3.3 Analysis of deviance table for generalised linear models used to investigate the association between month and site, and MaxN observations of smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *Scyliorhinus stellaris*, recorded on BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK.

	df	Deviance	Resid. df	Resid. deviance	Pr(>Chi)	% deviance expl.
Response: *S. canicula* MaxN						
NULL			120	100.18		
month	3	10.83	117	89.35	*< 0.05*	10.81
Site	5	41.83	112	47.53	*< 0.0001*	41.75
			Total deviance explained 52.56 %			
Response: *S. stellaris* MaxN						
NULL			120	127.89		
month	3	18.16	117	109.73	< 0.001	14.2
site	5	59.24	112	50.49	*< 0.0001*	46.32
			Total deviance explained 60.52 %			

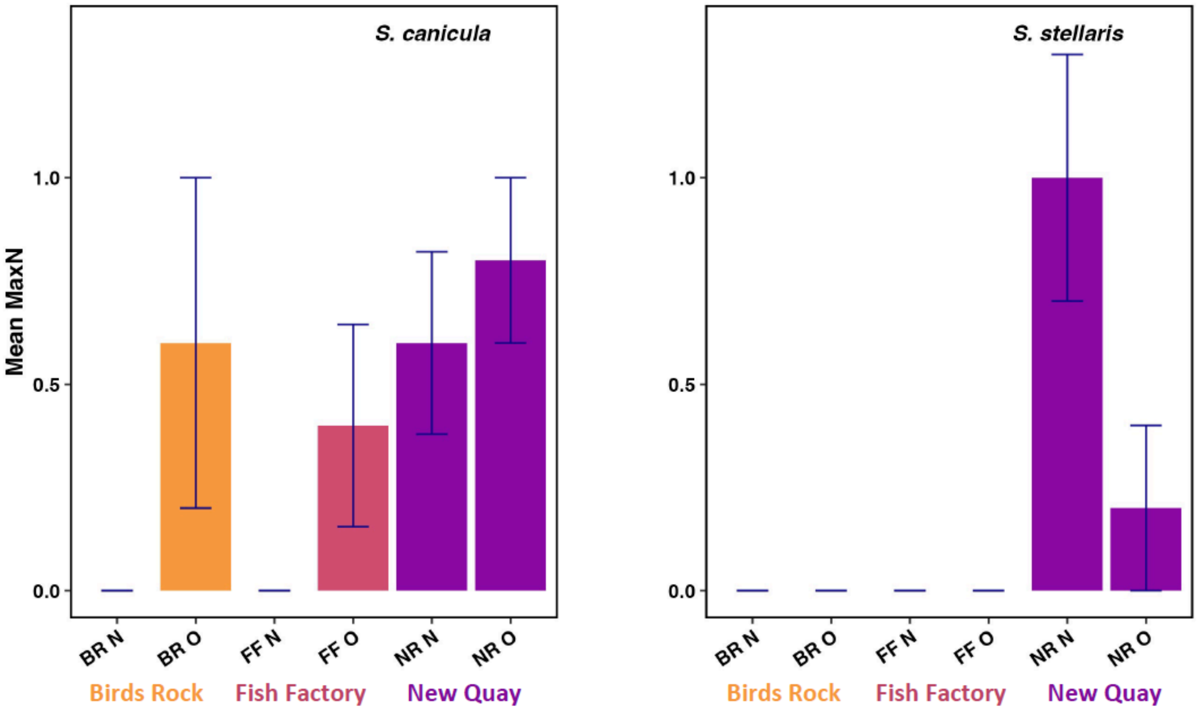


Figure 3.6 Median mean MaxN (± S.E.) value extracted from 2000 bootstrapped iterations for smallspotted catsharks, *Scyliorhinus canicula* (left), and nursehounds, *Scyliorhinus stellaris* (right), amongst all BRUVS sampling sites in the Cardigan Bay Special Area of Conservation, UK. Site codes: BR = Birds Rock, FF = Fish Factory, NR; "N" suffix = Nearshore, "O" suffix = Offshore.

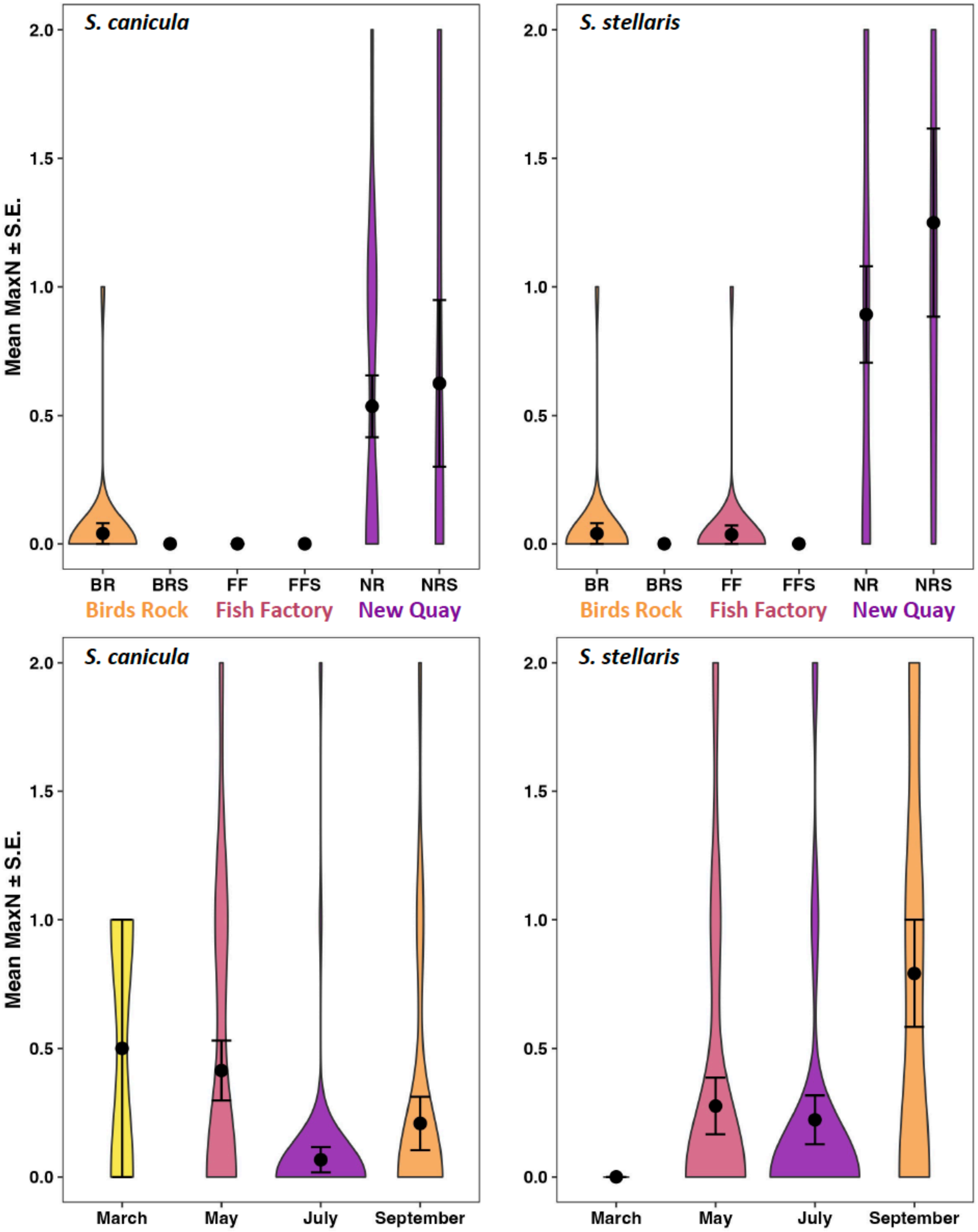


Figure 3.7 Mean MaxN (± S.E.) of smallspotted catsharks, *Scyliorhinus canicula* (left), and nursehounds, *Scyliorhinus stellaris* (right), per site (top) and sampling month (bottom) amongst nearshore BRUVS sampling sites in the Cardigan Bay Special Area of Conservation, UK. Site codes: BR = Birds Rock, FF = Fish Factory, NR = New Quay; "S" suffix = Nearshore (2022 sampling).

3.5 Discussion

Here we present results from the first standardised BRUVS sampling in the Cardigan Bay Special Area of Conservation (SAC), west Wales, UK. Within nearshore habitats close to New Quay, a regional centre for blue economy tourism, we observed three species of shark, including the nursehound, *Scyliorhinus stellaris*, classified as Vulnerable by the IUCN Red List of Threatened Species yet under-studied. Smallspotted catsharks, *Scyliorhinus canicula*, were observed from March to September, while nursehounds were observed from May to September. Furthermore, higher relative abundance of both species in reef habitat areas within the New Quay nearshore and offshore sites suggests elevated importance compared to non-reef habitats, although respective relative abundance was approximately seasonally inversely proportional. As such, we propose that potential temporal niche partitioning occurs and that this, together with potential critical habitat areas, should be further investigated in the context of strengthening shark conservation planning under the Welsh Marine Evidence Strategy (2019-2025) and the Welsh National Marine Plan.

We have obtained evidence for shared spatial use amongst catsharks and nursehounds, two important marine predators in nearshore UK marine environments, with comparable trophic levels (3.8 ± 0.3 SE and 4.0 ± 0.3 SE, respectively; Froese and Pauly 2000). This is important given that nursehound distribution estimates have, to date, predominantly relied on invasive trawl or fisheries-dependent sampling (Martin et al. 2010; Moore et al. 2023) rather than the *in situ* sampling used here. Nursehounds have also been under-reported compared to *S. canicula* for BRUVS set in the UK (Jones et al. 2021), and may be at risk of local extinction in parts of their distribution (Ragonese et al. 2013). Furthermore, the observed shared habitat use suggests that contamination impacting smallspotted catsharks (see Chapter 5) could also impact the nursehound, which has been documented to attenuate heavy metals in soft tissues (Squadrone et al. 2022). Given that nursehounds are retained by fisheries (Moore et al. 2023) and commonly available in fishmongers and takeaway food establishments in the UK (Hobbs et al. 2019), contaminant loading of this species should be investigated further. Opportunistic fisheries sampling has yielded important insights from vertebral chemistry in other shark species (Natanson et al. 2002; Harry et al. 2011; Smart et al. 2013; Coiraton et al. 2020; Jaureguizar et al. 2022), and therefore could be undertaken in this context to better understand risk levels associated with spatial consumption patterns.

Our results reveal spatial and temporal abundance variations amongst *S. canicula* and *S. stellaris* that may constitute temporal niche partitioning, although the influence of ecological drivers such as prey availability, reproduction or parturition remains unclear. For example, differential catshark relative abundance between March and May, although not statistically significant, could reflect the onset of dispersal behaviours that ultimately lead to ontogenetic and sexual segregation patterns (see Chapter 4). Notably, however, the highest seasonal relative abundance recorded for *S. stellaris* (September) correlates with bycatch peaks for this species in Welsh lobster and crab pot fisheries (Moore et al. 2023). Resource partitioning, whether for space, time, or diet, facilitates the co-existence of sympatric species (Bethea et al. 2004; Page et al. 2005; Dale et al. 2011; Fossette et al. 2017), and may be a key mechanistic driver of marine community composition (Kinney et al. 2011; Gavrilchuk et al. 2014). Trophic partitioning in sharks has been studied through dietary analyses (Papastamatiou et al. 2006; Sommerville et al. 2011; Vaudo and Heithaus 2011; Heithaus et al. 2013; Tilley et al. 2013) and, despite similar trophic levels, has been documented between *S. canicula* and *S. stellaris* (Yemisken et al. 2019). Temporal niche partitioning is less well documented, however, although distinct diel activity patterns have been recorded in coastal shark assemblages and may facilitate temporal partitioning of foraging times, potentially driving less dominant predators to suboptimal foraging times (Lear et al. 2021). Our BRUVS sampling was only conducted during daylight hours, therefore it was not possible to assess potential temporal niche partitioning in the context of either diel or nocturnal behaviours. To address this knowledge gap, acoustic telemetry could be used to investigate the period of partitioning behaviour, whether on a short cycle (days) or a long cycle (months/seasons).

Nursery habitat use has been documented in several shark species (Zanella et al. 2019; TinHan et al. 2020; LaFreniere et al. 2023), including *S. canicula* (Cau et al. 2013; Cau et al. 2017). These are areas where sharks are more commonly encountered than in other areas, have a tendency to remain or return for extended periods, and use the area repeatedly across years (Heupel et al. 2007), thus demonstrating the potential for habitat protection to safeguard critical life processes such as parturition and maturation. In this context, the separate analyses we undertook have yielded important considerations regarding whether our study sites constitute nursery habitats. First, analyses of both the full dataset and the subset of nearshore sites have shown the reef areas (New Quay nearshore and offshore sites) to be more important for both study species, with both a higher observation frequency and higher relative abundance than other areas. Additionally, *S. stellaris* was recorded during all sampling months except March, while *S. canicula* was recorded during every sampling month. Lastly, both species were observed during both sampling years, identifying a need for ongoing sampling to determine whether the ecological requirement for long-term habitat use across years is satisfied.

Spatial distribution away from core habitat areas (here, New Quay nearshore) is important in the context of elucidating spatial connectivity and migration corridors. Therefore, despite the need to subset data to standardise sampling intensities, the mean MaxN data obtained from full dataset analysis requires consideration; *S. stellaris* was only detected in the New Quay sites, while *S. canicula* was detected in both the New Quay sites as well as the offshore sites of both Birds Rock and Fish Factory. The sample size is small but suggests differential use of areas around the core habitat area that may reflect differential movement ecology, and should be further investigated. Smallspotted catsharks consistently use the same entry and exit areas between a marine protected area and surrounding waters in Northwest Spain (Papadopoulo et al. 2023), whereby repeated habitat use can identify candidate priority areas for protection under regional management.

The myriad threats to sharks illustrates the importance of elucidating the role of social groupings in structuring populations, particularly to strengthen assessment of species and habitat vulnerability (Jacoby et al. 2012b). Individual identification of sharks enables novel insights into social network structure (Mourier et al. 2012; Jacoby et al. 2021; Mourier and Planes 2021), and has been achieved with *S. canicula* in a laboratory setting (Hook et al. 2019). The use of the MaxIND metric in BRUVS analysis, being the number of different individuals recorded (Sherman et al. 2018), presents an alternative to the MaxN metric, which is inherently conservative and likely to underestimate high true abundance (Kilfoil et al. 2017; Sherman et al. 2018). Therefore, verifying *in situ* identification of individuals of both *S. canicula* and *S. stellaris* on BRUVS would not only provide a more accurate estimate of population size in the study sites, but also present a more affordable and non-invasive alternative to traditional tagging studies, that can nevertheless yield similar insights (Flowers et al. 2017; Cerutti-Pereyra et al. 2018). Additionally, the advancement of small camera technology, particularly in terms of image definition and recording rate, has considerably increased speciation capabilities, particularly amongst very similar species such as *S. canicula* and *S. stellaris*. As such, it appears likely that datasets collected with the earliest iterations of small camera models may have been subject to unintentional species misidentification. Whilst it is impossible to review all early datasets, we recommend adopting the inclusion of reference images for species identified in supplementary materials as standard protocol for future BRUVS studies. We did not undertake any BRUVS sampling between September and March, illustrating a temporal gap during which time there may be seasonal habitat use insights that are lacking in our data. BRUVS can reveal long-term shark population dynamics (Bond et al. 2012; Flowers et al. 2022), which is essential to determine criteria for shark nurseries.

Our findings demonstrate the potential for habitats already under Special Area of Conservation designation to be important areas for sharks. Standardised BRUVS sampling can yield comparable datasets and associated ecological and conservation insights on unprecedented scales (MacNeil et al. 2020; Simpfendorfer et al. 2023). Therefore we strongly recommend continued BRUVS monitoring of Cardigan Bay alongside engagement with other researchers to align broad objectives and standardise approaches. Specifically, future work should strive to elucidate intra- and inter-annual variation, particularly to determine whether regional habitats satisfy nursery criteria, are important shark areas, or serve as important migration corridors. These objectives are all directly relevant for conservation planning, not least the Welsh Marine Evidence Strategy (2019-2025) and Welsh National Marine Plan, but also towards the objectives of the international Decade of Ocean Science for Sustainable Development (Ryabinin et al. 2019), and could thus strengthen the evidence base for protection measures to promote regional shark recovery.

Chapter 4: VERTEBRAL ELEMENTAL COMPOSITION REVEALS LIFETIME PATTERNS OF HABITAT USE BY THE SMALLSPOTTED CATSHARK, *SCYLIORHINUS CANICULA*, IN THE UK

4.1 Abstract

An increasing number of shark species are threatened with extinction, and research priorities to mitigate these trends include identifying ontogenetic variations in spatial and temporal habitat use, as well as critical habitat areas to protect key life stages and processes. Here we use laser ablation inductively coupled plasma mass spectrometry with natural tags (barium, magnesium, manganese, strontium) to assess vertebral elemental composition as an indicator of habitat use by smallspotted catsharks, *Scyliorhinus canicula*, in the Bristol Channel and English Channel, UK. Throughout the sampling area, we identified broad-scale ontogenetic variations, with shared habitat use by young-of-year and sub-adults distinct from adult life stages. We found minimal sex segregation amongst young-of-year and sub-adults, compared with high levels amongst adults that appears to be driven by male dispersal. Finally, we found that distinct adult populations appear to use multiple birthing grounds which therefore are potentially critical habitats for population recruitment, but with differential importance according to usage. Together these findings present an important opportunity to integrate precautionary management into current conservation planning in the UK; the smallspotted catshark is centrally important to marine food webs, therefore strengthening population robustness against emerging fisheries and environmental perturbations should be a key objective. Furthermore, we identify a direction for regional research where *S. canicula* remains a significant component of fisheries and effective management should be prioritised.

4.2 Introduction

Global marine biodiversity declines threaten to undermine marine ecosystem function, with potentially far-reaching and catastrophic consequences, reflected in the declaration of 2021 to 2030 as an international Decade of Ocean Science for Sustainable Development (Ryabinin et al. 2019). Urgent challenges for conservation management remain the identification of priority species and the protection of critical habitats for recovery (Duarte et al. 2020), mitigation of anthropogenic impacts on natural systems, and promotion of a planetary health approach to human consumptive behaviours. Sharks are a conservation priority due to their ecological (Heithaus et al. 2008) and economic (Clua et al. 2011; Gallagher and Hammerschlag 2011; Vianna et al. 2012; Huveneers et al. 2017) importance. Yet important knowledge gaps remain regarding status, population and movement ecology, and effective management (Jorgensen et al. 2022), particularly for species that do not typically attract research interest (Simpfendorfer et al. 2011).

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) enables the use of fish vertebral elemental signatures as natural tags that reliably reflect environmental conditions. These include barium, magnesium, manganese, strontium, and zinc (McMillan et al. 2017); for example, the relative vertebral composition of barium and strontium can indicate the use of freshwater and saltwater habitats, respectively (Smith et al. 2013; McMillan et al. 2017). Hence, habitat use can be extrapolated from natural tags to yield movement and population structure insights (Smith et al. 2016; Mohan et al. 2018; Pistevos et al. 2019; Coiraton et al. 2020; Feitosa et al. 2020; TinHan et al. 2020; Feitosa et al. 2021; Livernois et al. 2021; LaFreniere et al. 2023). Unlike traditional acoustic tagging and telemetry, LA-ICP-MS analysis of natural tag signatures is not space-limited by acoustic array coverage. This approach can therefore strengthen broad-scale insights into elasmobranch population dynamics such as seasonal migration (Smith et al. 2016; Coiraton et al. 2020) and use of nursery habitats (McMillan et al. 2018; Feitosa et al. 2020; TinHan et al. 2020). Thus, opportunistic fisheries sampling can be exploited to address knowledge gaps (Coiraton et al. 2020; Feitosa et al. 2020; Livernois et al. 2021).

The UK is potentially important as both seasonal and year-round shark habitat (Colloca et al. 2019; Barker et al. 2022). Regionally, the smallspotted catshark, *Scyliorhinus canicula,* is centrally important to marine food webs, particularly given ongoing decline in other predatory species (Wieczorek et al. 2018). Despite there currently being no fishery in the UK it is an important target species elsewhere, and future fisheries trends could yet drive fishing pressure onto *S. canicula*. Population genetic structure in the Western English Channel shows long-term stability; this belies low dispersal capacity and thus may reflect population reduction, expansion and high gene flow in the Northeast Atlantic (Gubili et al. 2014). Aggregation behaviour in neonate and juvenile *S. canicula* may be driven by social preferences and familiarity, as well as habitat preference and predation risk reduction, with no clear patterns of sexual segregation (Jacoby et al. 2012a). Conversely, sexual segregation has been observed amongst adults within cave and boulder refuges (Sims et al. 2001; Wearmouth et al. 2012). Moreover, historical mercury concentrations suggest distinct adults populations throughout the Irish Sea (Leah et al. 1991), although single element analysis is inherently limited with lower resolution insights compared to the multi-element approach afforded by LA-ICP-MS. Notably, population biology has historically been a relative knowledge gap for *S. canicula* (Moore 2001). Hence it is important to understand regional population dynamics for effective population and potential fisheries management, and current conservation and biodiversity targets in the UK present an opportunity to incorporate species-level evidence into updated management objectives.

Scyliorhinus canicula is the most widely distributed nearshore shark species in the Northeast Atlantic shelf seas (Ellis and Shackley 1997) and therefore a suitable species for LA-ICP-MS proof of concept and optimisation. Importantly, lifetime insights obtained using this approach also have the potential to elucidate a key evidence gap regarding ontogenetic habitat use, and hence yield unprecedented broad-scale insights into sexual, ontogenetic and regional population structure. Accordingly, we hypothesise that adult populations of smallspotted catsharks are regionally spatially distinct, sexually segregated, and connected by birthing grounds that are essential habitats. To test this hypothesis, we assessed smallspotted catshark vertebral elemental composition across south and west Wales, and south Devon for (1) spatial variations; (2) ontogenetic variations; and, (3) the evidence for critical habitats.

4.3 Methods

A total of 49 *S. canicula* were used in this study (Table S4.1). Sampling was conducted during 2021 and 2022 at seven sites, with five on the south coast of Wales (three sampled in 2021, two in 2022) and two on the south coast of England (one sampled in 2021 and one in 2022), thereby ensuring comprehensive representation throughout the region (Figure 4.1). The Bristol Channel is a highly dynamic tidal environment between Wales and England. There are major human population centres in Bristol, Cardiff, and Swansea, and several Special Areas of Conservation (SAC), Special Protection Areas (SPA) and Ramsar sites (Figure 4.1). Individuals at all sites except Barry were recreational angling bycatch, fresh frozen. At the Barry site, dead samples were obtained several metres above the high tide line which, together with the presence of hooks in several, suggests angling discard. This is common practice with *S. canicula* landed by anglers in that location (S. Perkins, personal observ.). Precise date of landing was unknown for these specimens; some were highly desiccated but there was no evidence of scavenging, which suggests recent death.

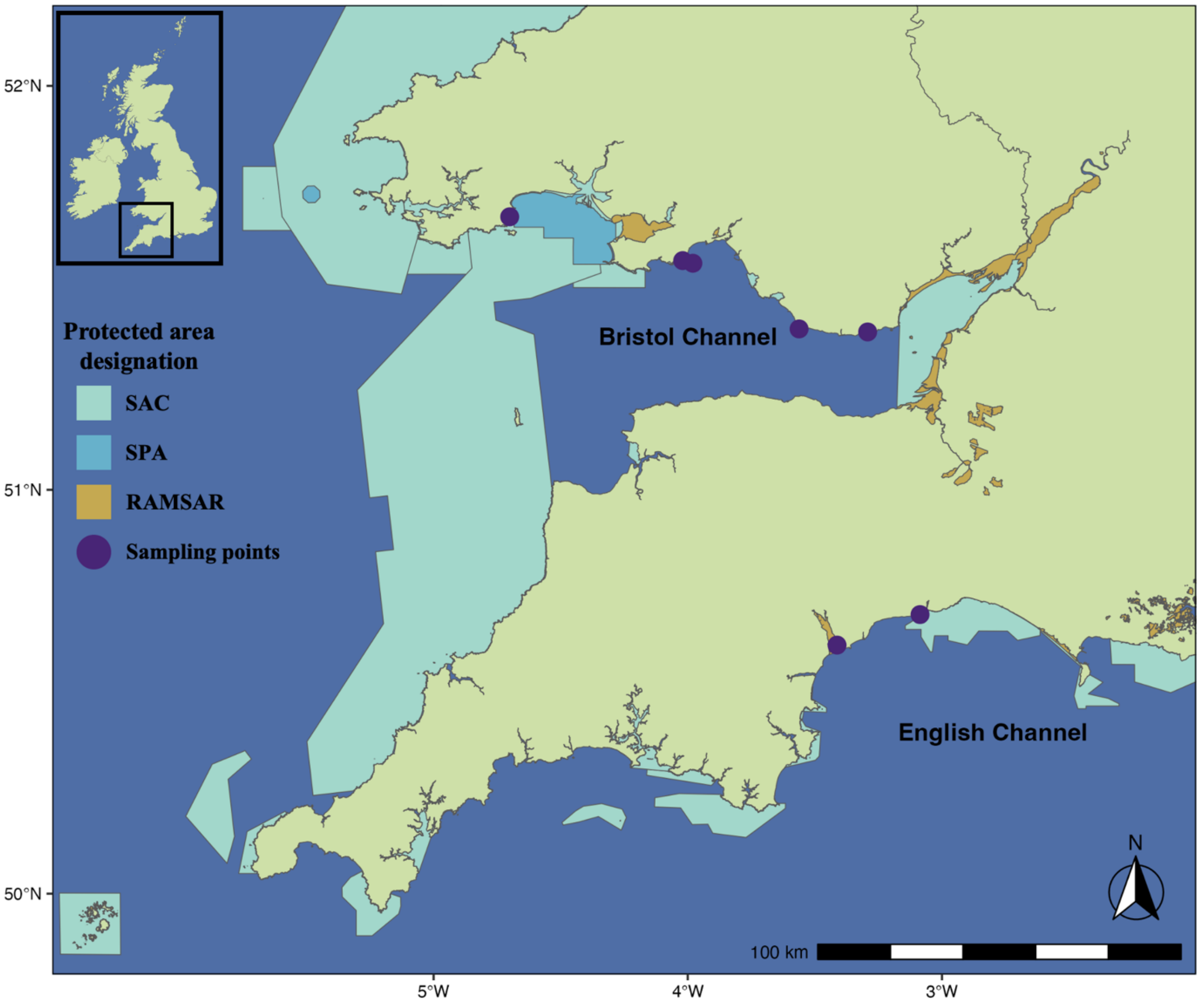


Figure 4.1 Study sampling locations for smallspotted catsharks, *Scyliorhinus canicula*, Special Areas of Conservation (SAC), Special Protection Areas (SPA) and Ramsar sites in the Bristol Channel and English Channel, UK.

Individuals were first stored at -20°C and later thawed for 24 hours in a laminar flow hood. Once thawed, the following standard body metrics were recorded: total length, fork length, body condition when collected (fresh or desiccated), and sex. It was not possible to accurately measure total length for the desiccated specimens. Therefore, we first used fresh frozen samples to validate historical findings that vertebral length is proportional to total length in *S. canicula* (see Ivory et al. 2004), then estimated total length from vertebral length measurements for desiccated specimens. Age estimates were extrapolated for each specimen using sex-specific Von Bertalanffy Growth Function parameters for *S. canicula*

(Table S4.2) and the following equation, where a is age, k is the growth coefficient, t_0 is the theoretical age when size is zero, and L_∞ is asymptotic size:

$$L(a) = L_\infty(1 - \exp(-k(a - t_0)))$$

A minimum of three post-cephalic vertebrae were removed from each individual and air dried for 24 hours in a laminar flow hood. The neural arch and extraneous tissue were removed with a scalpel and vertebrae were placed in 5% bleach for five minutes to remove any remaining tissue, then washed in Milli-Q water (Tillett et al. 2011; Mohan et al. 2017). Vertebrae were manually cleaned, dried again in a laminar flow hood, then stored at -20°C, following length measurement to the nearest 0.5 mm. Prior to mass spectrometry analysis, vertebrae were thawed then embedded in Araldite 2020 resin (Figure 4.2), ground longitudinally from one side with a diamond grinding wheel and smoothed with 1200 grit silicon carbide paper, then mounted on a glass slide with Araldite 2020 resin. Next, the exposed side was cut to a 1mm ‘bowtie’ section using a diamond saw, then ground to 300 µm with 800 and 1200 grit silicon carbide papers. Finally, this was polished using a 0.3 µm aluminium oxide slurry and washed in an ultrasonic bath (Figure 4.2).

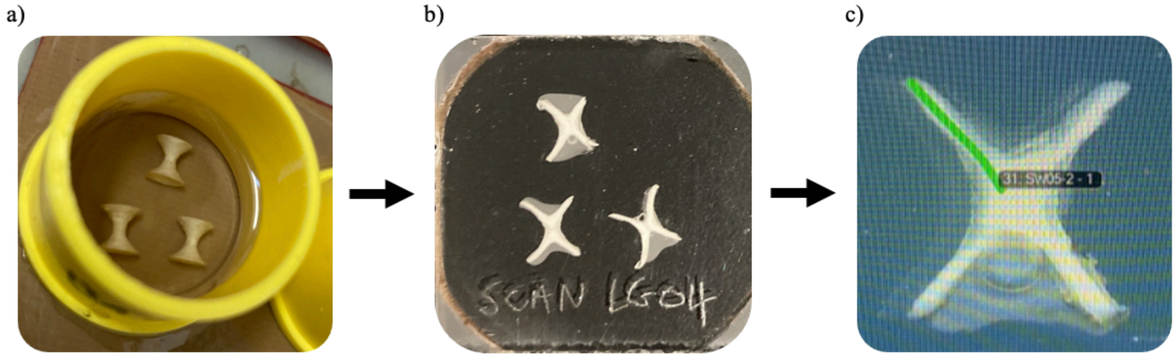


Figure 4.2 Preparation steps for smallspotted catshark, *Scyliorhinus canicula*, vertebrae isolated from the vertebral column, following cleaning and removal of connective tissue: a) embedded in resin; b) ground and polished, and; c) laser transect assigned along vertebral growth axis to incorporate chronological elemental signatures throughout specimen lifetime.

LA-ICP-MS analyses were undertaken using an ASI RESOlution 193 nm Excimer laser coupled to an Agilent-8900 triple quadrupole ICP-MS, with transects manually set along the corpus calcareum (Figure 4.2). For each specimen, one transect was run along each of three vertebrae to yield three replicates. Transects were ablated from the centre to the tips of the vertebrae, thereby incorporating chronological elemental signatures throughout specimen lifetime. Hence, the start and end of the transect represent embryonic and time of death elemental signatures, respectively. LA-ICP-MS settings were manually adjusted to optimise signal stability and sensitivity (Samperiz 2022). The laser was set at a shot frequency of 15 Hz and fluence of 3 J cm^{-2}, moving at a scan speed of 10 µm s^{-1} with an ablation spot size of 100 µm. Helium flow and Nitrogen flow were 350 mL min^{-1} and 3.5 mL min^{-1}, respectively, and National Institute of Standards and Technology (NIST) 612 and NIST 614 glass standards were ablated periodically between transects. The ICP-MS used nickel cones and radio frequency power of approximately 1230 W, nebuliser gas rate of 0.8 l min^{-1}, with a time resolved acquisition mode and time slice of 1.10 s.

Raw data were first corrected for background ratios and instrument drift, then converted to standardised element:calcium molar ratios in Python using the LAtools package (Branson et al. 2019). The three replicates per individual were visually aligned in QAnalySeries (Kotov and Pälike 2018) using strongly cyclical Mn:Ca peaks (Figure 4.3; Figures S4.4 - S4.9), which were additionally used to verify estimated age given the association between manganese incorporation and seasonal temperature fluctuations (Elsdon and Gillanders 2006; Smith et al. 2013). Finally, molar ratios were converted to concentration (ppm) using ^{43}Ca as the internal standard and with a 35 weight % for hydroxyapatite (McMillan et al. 2017; Mohan et al. 2018).

Investigating ontogenetic variation in contamination levels required assigning different portions of the vertebrae to the following life stages: pre-natal, young-of-year (to 1 year; YOY), sub-adult (1 year to 50% maturity), and adult. Smallspotted catsharks in the Bristol Channel (sex ratios 1.2♀ : 1♂) hatch at approximately 100 mm, with 50% maturity reached at 550 mm and 520 mm total length for females and males, respectively (Ellis and Shackley 1997). Despite regional variation in these characteristics (Kousteni et al. 2010; Capapé et al. 2014), parameters obtained from elsewhere in the UK are comparable (Henderson and Casey 2001). Therefore we used estimated age at 50% maturity, together with annual Mn:Ca peaks to assign a position on the vertebral transect corresponding to each life stage (Figure 4.3; Figures S4.4 - S4.9).

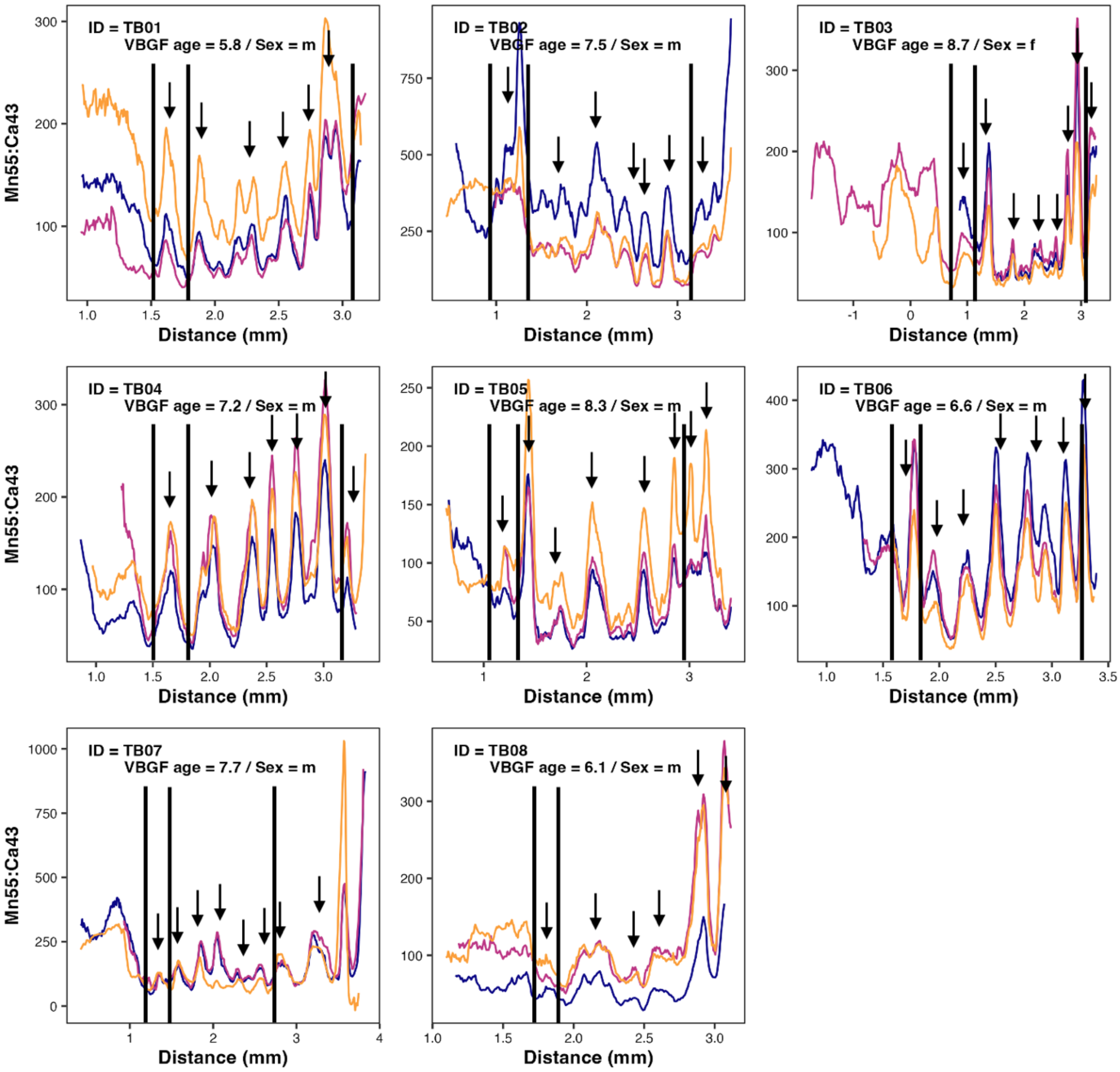


Figure 4.3 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Tenby sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

We used generalised linear models to investigate the association between region, site, sex and life stage, and single element vertebral composition (response variables), followed by an information theoretic approach (Akaike's information criteria, AIC; Akaike 1998) to select the best error structure and link function (Table 4.1). We used Kruskal-Wallis rank sum tests, first between sites to verify spatial variation and then between life stages to verify ontogenetic variation, followed by Dunn post-hoc tests on the latter to assess pairwise differences in elemental composition between life stage. We then used Wilcoxon rank sum tests to compare differences in elemental composition between sex, to test for sex-based dispersal, and regions (Bristol Channel and English Channel). Last, we investigated spatial population structure of both young-of-year and adult life stages from the Bristol Channel sites, using cluster analysis with median composition values as the response variable (Feitosa et al. 2021; LaFreniere et al. 2023). We selected linkage method according to agglomerative coefficient, with the Ward linkage method higher for both young-of-year (0.87) and adults (0.84) than any of the average, single or complete linkage methods. We then used average silhouette width to identify the optimum number of clusters for each life stage as a proxy for sub-populations. Data were analysed using R software (v4.2.2; R Core Team 2022) with the TropFishR (Mildenberger et al. 2017), vegan (Oksanen et al. 2022), MASS (Venables and Ripley 2002) and dendextend (Galili 2015) packages.

4.4 Results

Scyliorhinus canicula used in this study comprised 25 females and 24 males (1♀ : 0.96♂ sex ratio). All seven sites along the Bristol and English channels yielded individuals from all life stages, except Swansea with no adults. Mean total length varied between 456 mm and 590 mm from the Barry and Beer sites respectively, corresponding to a mean age range of 5.3 to 9 years (Table S4.1).

Site influenced the composition of all target elements (GLM and Kruskal-Wallis rank sum $p < 0.0001$), and explained the most deviance for barium (35.03%), magnesium (34.52%) and manganese (6.95%; Table 4.1, Table S4.3; Figure S4.1), suggesting the existence of spatially discrete populations. Life stage similarly influenced the composition of all target elements (GLM and Kruskal-Wallis rank sum $p < 0.0001$), and explained the most deviance for strontium (20.45%; Table 4.1). Furthermore, *post-hoc* pairwise tests revealed ontogenetic trends in elemental composition; barium increased consistently from young-of-year to adults, whereas magnesium and strontium both decreased consistently, while manganese decreased from young-of-year to sub-adults and increased from sub-adults to adults (Table 4.2, Table S4.4; Figure S4.2). This suggests spatial segregation of life stages, with shared use of offshore or deeper habitat areas by young-of-year and sub-adults, followed by dispersal with increasing maturity to nearshore shallow areas. We also identified associations between sex and the composition of all target elements (GLM $p < 0.0001$); barium, magnesium and manganese were all lower in females (Wilcoxon rank sum testing, alternative = less, $p < 0.0001$; Table

S4.5), while strontium was lower in males (Wilcoxon rank sum testing, alternative = greater, $p < 0.0001$; Table S4.5; Figure S4.3). This further suggests that adult males are the primary driver of the extrapolated dispersal patterns. Barium, magnesium and strontium levels were higher in the Bristol Channel than the English Channel, while manganese levels were lower (Table S4.6).

Table 4.1 Analysis of deviance table for generalised linear models used to investigate the association between region, site, sex and life stage, and single element response variables (barium, magnesium, manganese and strontium) within the vertebral composition of smallspotted catsharks, *Scyliorhinus canicula*, in the Bristol Channel and English Channel, UK.

	Df	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(>Chi)**	**% deviance explained**
Response: Barium		**Family: Inverse gaussian**			**Link: Inverse**	
NULL			35348	517.13		
Region	1	0.244	35347	516.89	< 0.001	0.05
Site	5	181.162	35342	335.73	< 0.0001	35.03
Sex	1	11.633	35341	324.10	< 0.0001	2.25
Life stage	2	0.868	35339	323.23	< 0.0001	0.17
Response: Magnesium		**Family: Inverse gaussian**			**Link: Log**	
NULL			35348	0.42		
Region	1	0.004	35347	0.42	< 0.0001	0.95
Site	5	0.145	35342	0.27	< 0.0001	34.52
Sex	1	0.006	35341	0.26	< 0.0001	1.43
Life stage	2	0.035	35339	0.23	< 0.0001	8.33
Response: Manganese		**Family: Inverse gaussian**			**Link: Identity**	
NULL			35348	307.14		
Region	1	0.459	35347	306.68	< 0.0001	0.15
Site	5	21.356	35342	285.32	< 0.0001	6.95
Sex	1	0.498	35341	284.82	< 0.0001	0.16
Life stage	2	12.132	35339	272.69	< 0.0001	3.95
Response: Strontium		**Family: Gamma**			**Link: Inverse**	
NULL			35348	277.64		
Region	1	4.556	35347	273.08	< 0.0001	1.64
Site	5	24.174	35342	248.91	< 0.0001	8.71
Sex	1	3.313	35341	245.59	< 0.0001	1.19
Life stage	2	56.777	35339	188.82	< 0.0001	20.45

Table 4.2 Dunn post-hoc test results of pairwise life stage comparisons of single element vertebral composition in smallspotted catsharks, *Scyliorhinus canicula*, in the Bristol Channel and English Channel, UK (YOY = young-of-year).

Element	**Pairwise comparison**	**Z**	**p. unadj**	**p. adj**
Barium (^{138}Ba)	Adult vs Sub-adult	3.32	< 0.001	< 0.001
	Adult vs YOY	5.24	< 0.0001	< 0.0001
	Sub-adult vs YOY	3.72	< 0.001	< 0.001
Magnesium (^{25}Mg)	Adult vs Sub-adult	-0.96	> 0.1	> 0.1
	Adult vs YOY	-39.49	0.00	0.00
	Sub-adult vs YOY	-58.56	0.00	0.00
Manganese (^{55}Mn)	Adult vs Sub-adult	28.07	< 0.0001	< 0.0001
	Adult vs YOY	14.54	< 0.0001	< 0.0001
	Sub-adult vs YOY	-13.55	< 0.0001	< 0.0001
Strontium (^{86}Sr)	Adult vs Sub-adult	-60.71	0.00	0.00
	Adult vs YOY	-83.00	0.00	0.00
	Sub-adult vs YOY	-48.72	0.00	0.00

Multi-element non-metric multidimensional scaling using sex as a factor revealed tight clustering and little segregation amongst young-of-year and sub-adults (Figure 4.4), but increasingly pronounced sex segregation within adult life stages (Figure 4.4). This suggests that the influence of sex on elemental composition is largely driven by adults. Furthermore, using life stage as a factor yielded clustering of young-of-year and sub-adults, which together were more distinct from adult life stages (Figure 4.4). Again, this suggests shared habitat use by young-of-year and sub-adults, and that spatial variation in elemental composition is driven by dispersal of adults. This is further supported by cluster analysis of multi-element vertebral composition; we identified eight population clusters for young-of-year compared to six population clusters for adults using the average silhouette width method to determine optimum number of clusters (Figure 4.5). This suggests our specimens from the Bristol Channel comprise six spatially discrete adult populations that utilise at least eight birthing grounds.

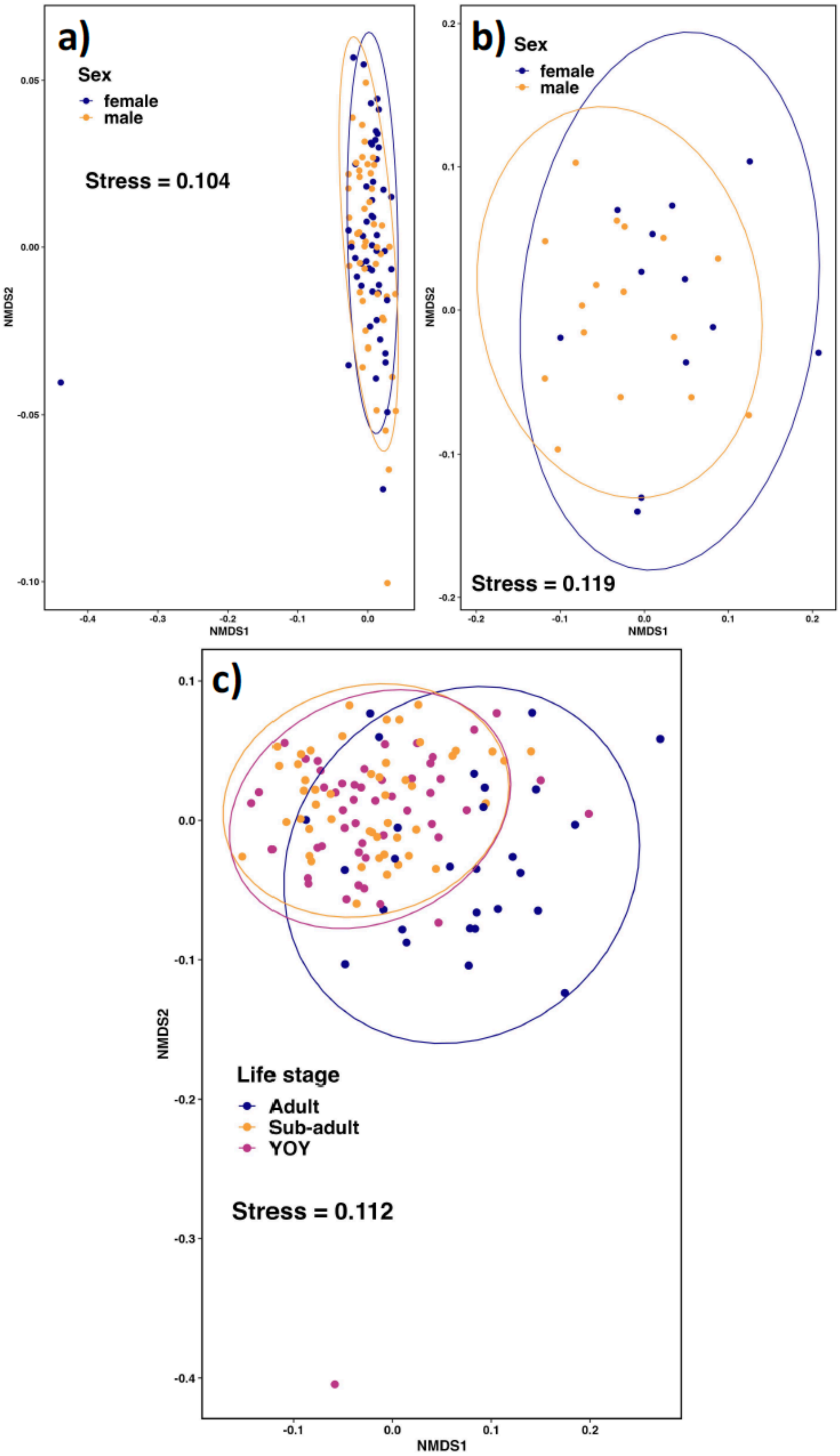
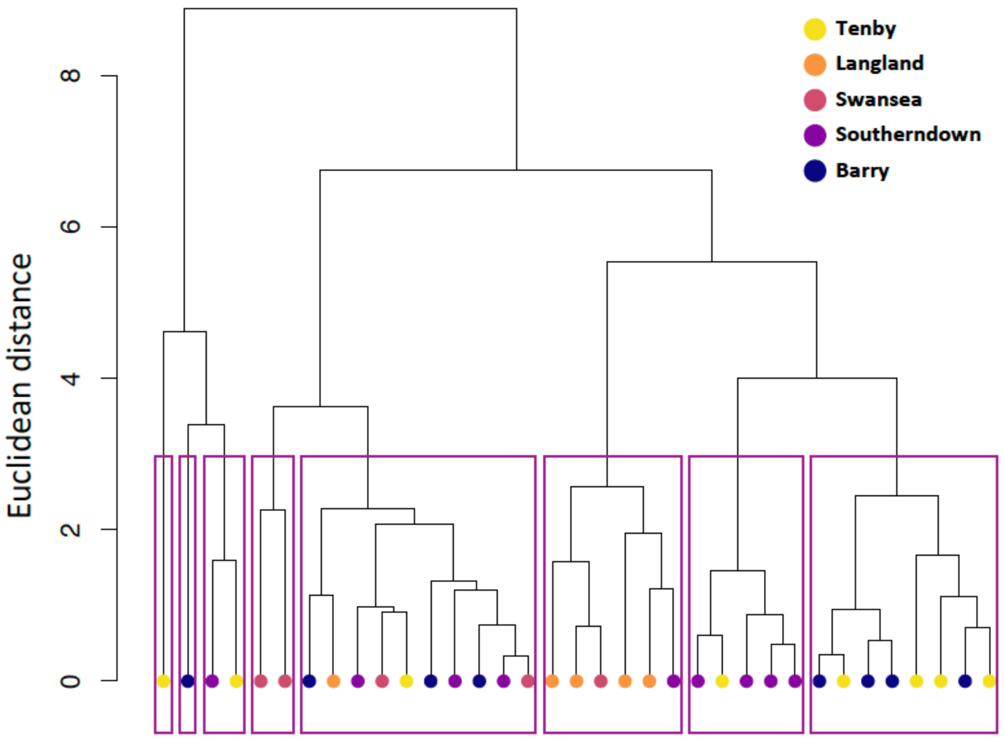
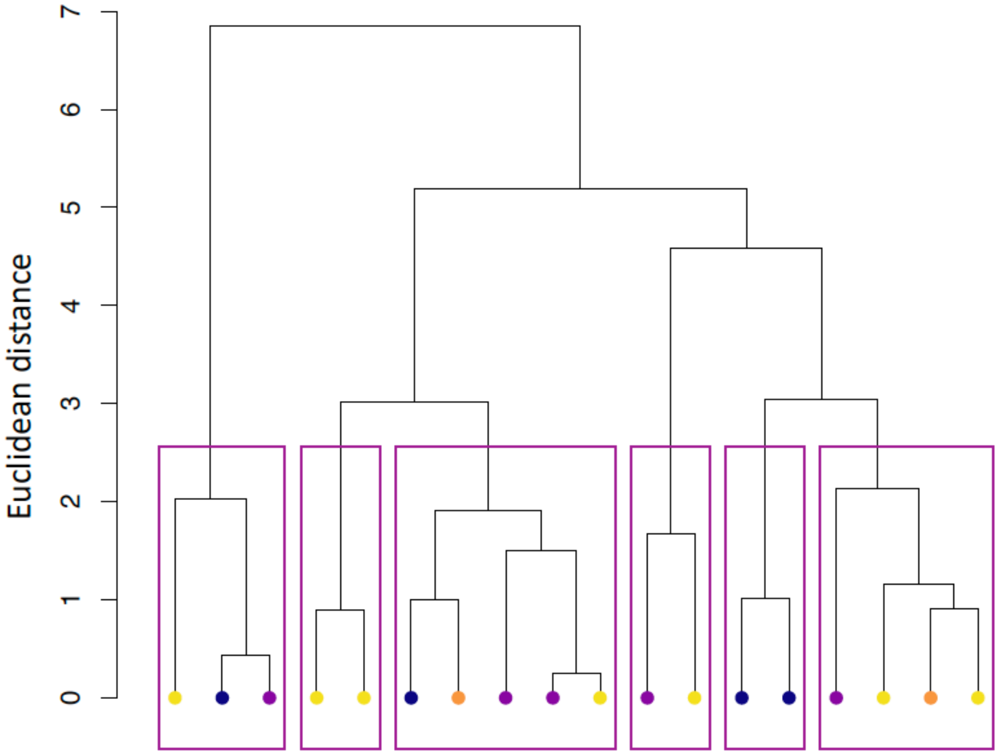


Figure 4.4 Multi-element (barium, magnesium, manganese, strontium) non-metric multidimensional scaling plot of smallspotted catshark, *Scyliorhinus canicula*, vertebral composition in the Bristol Channel and English Channel, UK; a) young-of-year and sub-adult life stages, with sex as a factor; b) adult life stages, with sex as a factor; and, c) with life stage as a factor.



Young-of-year smallspotted catsharks *Scyliorhinus canicula*



Adult smallspotted catsharks *Scyliorhinus canicula*

Figure 4.5 Cluster analysis for multi-element (barium, magnesium, manganese and strontium) vertebral composition in young-of-year (top) and adult (bottom) smallspotted catsharks, *Scyliorhinus canicula*, in the Bristol Channel; eight population clusters identified for young-of-year and six population clusters identified for adult life stages. Each node represents an individual, with colour according to sampling site. Note: fewer adult nodes reflects immature individuals sampled.

4.5 Discussion

Here we apply laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to investigate spatial and ontogenetic population structure in the smallspotted catshark, *Scyliorhinus canicula*, sampled from seven sites across the Bristol Channel and English Channel, UK. Its abundance and widespread distribution renders *S. canicula* a suitable model species to validate the use of LA-ICP-MS in regional population studies. Using natural tags, we identify evidence both for spatial segregation of adult and non-adult life stages, and for shared habitat use by young-of-year and sub-adults. Additionally, we found evidence for sexual segregation amongst adults, but not amongst young-of-year or sub-adults. These findings are in line with current knowledge, and thus not only support this application of LA-ICP-MS but present an opportunity to establish standardised protocols for regionally comparable studies. Finally, we used cluster analysis to identify six population clusters amongst adults, but eight population clusters amongst the young-of-year. This suggests that adult populations may utilise multiple birthing grounds, which adds to the ecological evidence base for this species. Identifying critical habitat areas is a research priority for sharks, therefore this study has relevance for conservation planning in the UK including the Welsh Marine Evidence Strategy (2019-2025), and presents an opportunity to incorporate and strengthen regional shark management.

Our findings suggest the persistence of young-of-year and sub-adults in shared habitat post-hatching, with little sexual segregation (Figure 4.4). With ontogenetic development there appears to be range expansion, culminating in reduced habitat overlap between adults and pre-maturity life stages, and more pronounced sexual segregation amongst adults (Figure 4.4). Spatial and ontogenetic population structure are important ecological considerations for the design of marine protected areas (MPAs) to protect sharks (Gilmour et al. 2022). Despite long-term increases in UK abundance that contrast with observed declines in other elasmobranch species (McHugh et al. 2011), *S. canicula* warrants management attention in its own right given central importance to marine food webs (Wieczorek et al. 2018). Furthermore, abundance trends likely reflect the fact there is currently no target fishery for *S. canicula* in the UK, since overfishing is a key driver of shark population decline (Myers and Worm 2003; MacNeil et al. 2020; Dulvy et al. 2021). There are few sustainably managed shark fisheries globally (Simpfendorfer and Dulvy 2017) and fisheries pressure can drive long-term

S. canicula decline (Barausse et al. 2014). However, MPAs may be an effective tool for protection and population recovery in exploited stocks (Rodríguez-Cabello et al. 2008), albeit potentially more so for females given less dispersal and higher philopatry (Gubili et al. 2014; Papadopoulo et al. 2023). Shark protection and fisheries management success are closely linked to strong governance and highly protected areas in wealthy nations (Simpfendorfer et al. 2023), therefore *S. canicula* in the UK presents such an opportunity and our findings should be a key consideration for spatial planning. Future fisheries pressure, together with potential climate-driven impacts (Pegado et al. 2020; Ripley et al. 2021), illustrate the importance of incorporating species-level evidence into wider regional management programmes to strengthen population robustness.

Several shark species utilise coastal nursery areas (Jennings et al. 2008; Heupel and Simpfendorfer 2011; Marie et al. 2017), where sharks are more commonly encountered than in other areas, have a tendency to remain or return for extended periods, and use the area repeatedly across years (Heupel et al. 2007). Here we identify habitat overlap between young-of-year and sub-adult *S. canicula* prior to maturity, with no evidence of sexual segregation (Figure 4.4). Importantly, this comprises several age classes that were sampled simultaneously, demonstrating that mixing of immature life stages is repeated across years. As natural tags, strontium and barium both serve as proxies for freshwater influence, while magnesium and manganese reflect temperature fluctuations (Smith et al. 2013). Taken together, the elemental trends we observed (lower strontium and magnesium but stable or higher barium and manganese, with ontogenetic development) suggest young-of-year and sub-adult shared use of offshore or deeper habitat areas, followed by dispersal and sexual segregation with increasing maturity to nearshore shallow areas. It is unclear what drives this behavioural transition and when, but it may be related to male-biased dispersal (Gubili et al. 2014), differential sex-based foraging habits (Kimber et al. 2009), or female avoidance of males (Wearmouth et al. 2012; Micarelli et al. 2020). Contrasting observations of size and sex distributions amongst *S. canicula* throughout its range (Rodríguez-Cabello et al. 2007; Finotto et al. 2015; Cau et al. 2017) highlight the need for local ecological evidence to design locally-adapted management. Our findings, therefore, are important new ecological insights for regional *S. canicula* populations insomuch that shared habitats may be critical for maintaining connectivity between more widely dispersed adults. This has direct implications for recruitment to adult stocks and thus the design of management; higher philopatry in female *S. canicula* (Gubili et al. 2014), together with shared habitat use identified in this study, demonstrate sex- or age-biased vulnerability to localised fishing pressure and therefore the potential for MPAs that limit fishing to safeguard recruitment to adult stock.

Multi-element dissimilarity and cluster analysis of our data suggests the existence of at least eight birthing grounds within our sampling area that may meet the criteria for shark nurseries (Heupel et al. 2007). Further work would be needed to investigate these patterns throughout UK waters but, together with migration corridors, nurseries can be important habitat areas for sharks (Heupel et al. 2018; Zanella et al. 2019; LaFreniere et al. 2023). This is likely to be even more pronounced for *S. canicula* given embryogenesis is particularly important for oviparous species, due to high mortality rates in early life stages (Ripley et al. 2021). These should therefore be priorities for research attention, particularly given shark nursery research trends that disproportionately target tropical coastal species (Heupel et al. 2018). Interestingly, and of direct relevance for management planning, the different sizes of the identified clusters suggests these birthing grounds potentially offer differential importance for regional adult stock recruitment. Additionally, adults likely make periodic returns to mating grounds or nursery habitats for depositing egg cases, but such movements might not be sufficiently protracted to be reflected in vertebral microchemistry. Therefore the evidence we obtained that adult populations utilise multiple birthing grounds should be investigated further, particularly given potentially differential importance for regional populations and the fact that LA-ICP-MS fine-scale resolution limits remain largely untested. Mediterranean nursery grounds for *S. canicula* have been identified in black coral, *Leiopathes glaberrima,* habitats during underwater video surveys (Cau et al. 2013; Cau et al. 2017), while acoustic telemetry can yield high resolution movement ecology insights within the confines of an acoustic array (Papadopoulo et al. 2023) and archival depth telemetry studies can reveal putative egg-laying behaviour (Wearmouth et al. 2013). The distribution of preferred egg-laying habitat such as the pink sea fan, *Eunicella verrucosa,* (Hiscock et al. 2019), together with citizen science records of egg case sightings that likely reflect broad patterns of birthing ground distribution, could inform telemetry study design that may elucidate precise locations of critical habitats. Nevertheless, LA-ICP-MS is relatively new technology, such that advancement and refinement should seek to increase the resolution of spatial ecology insights.

LA-ICP-MS allows broad-scale insights into spatial population structure, yet important questions remain regarding the applicability of LA-ICP-MS to different elasmobranch species (Pistevos et al. 2019) and capacity to elucidate fine scale resolution. However, our findings suggest that contiguous sampling at higher spatial resolution could elucidate connectivity within regional populations of *S. canicula*. Smallspotted catsharks can be negatively impacted by fisheries and human coastal impacts (Navarro et al. 2016), but potentially present a rare opportunity to develop sustainable shark fisheries management. As such, identifying birthing and nursery grounds for incorporation into existing conservation infrastructure, including Special Areas of Conservation and Special Protection Areas, should inform marine spatial planning. Areas should be prioritised that may serve as refuges under future projected ocean warming conditions that can disrupt physiological homeostasis (Pegado et al. 2020) and predator avoidance behaviours in *S. canicula* (Ripley et al. 2021). Sharks can be a divisive and emotive subject (Casola et al. 2022). Yet, despite considerable ecological importance, *S. canicula* is often perceived as an overabundant pest species (personal comms.) and is frequently dumped by recreational sea anglers in at least one of our sampling locations (S. Perkins, personal observ.). Sharks are typically slow to recover from depletion, therefore this pattern of behaviour could elicit chronic long-term negative population impacts and be exacerbated within important habitat areas. However, addressing these practices could mitigate the impacts. New regulations for land-based shark fishing in Florida were introduced in 2019, arising from engagement and the design of science-based solutions to mitigate unnecessary and potentially harmful angling practices (Shiffman 2020). Therefore, efforts to strengthen conservation management in the UK should consider addressing social perceptions of sharks, including *S. canicula*. Given population decline in many shark species, conservation should target not only those species at risk of extinction but also those for which precautionary management could yet strengthen and safeguard persistence. The urgency of marine conservation demands ambitious and comprehensive action. Legislative developments and revision of biodiversity objectives present an important opportunity to incorporate species action plans for the smallspotted catshark, which remains an important marine predator in UK nearshore coastal environments.

Chapter 5: SENTINEL SHARKS: SMALLSPOTTED CATSHARKS *SCYLIORHINUS CANICULA* REVEAL CONTAMINATION HOTSPOTS IN THE BRISTOL CHANNEL, UK

5.1 Abstract

Anthropogenic pollution in the marine environment can potentially impact species physiology, wider ecosystem functioning, and human health. Here we apply laser ablation inductively coupled plasma mass spectrometry to investigate lifetime vertebral composition in smallspotted catsharks *Scyliorhinus canicula* as a model for heavy metal contamination in the UK. We identified higher levels of all target elements (arsenic, cadmium, chromium, copper, lead, uranium, zinc) in the Bristol Channel compared to the English Channel, with potential contamination hotspots in Barry and Tenby. Moreover, median composition values exceed European Union and/or World Health Organization recommended soft tissue limits for safe consumption; arsenic (3.07 ppm), copper (4.1 ppm), lead (0.99 ppm), and uranium (0.05 ppm). This identifies potential human risk and important future work objectives to elucidate the relationship between vertebral and soft tissue composition. Lifetime trends for all contaminants followed a similar trajectory, with higher levels in pre-natal life stages, lower but generally consistent levels throughout young-of-year and sub-adult life stages, and increasing levels following maturation to adult life stages. Consistent life-time exposure implies a high possibility of bioaccumulation processes in soft tissues for all elements. This suggests that similar patterns could be observed in sympatric mesopredator species, with associated risk implications for human consumption. Further research is needed to investigate this, but in the first instance our work identifies the potential use of *S. canicula* as a sentinel species for food contamination mitigation and marine management.

5.2 Introduction

The declaration of 2021 to 2030 as an international Decade of Ocean Science for Sustainable Development (Ryabinin et al. 2019) illustrates the importance of oceans as indicators and regulators of planetary health (Myers 2017; Borja et al. 2020; Damanaki et al. 2020; Laffoley et al. 2021). Anthropogenic marine pollution is globally widespread with associated system impacts at all levels (Ivanina and Sokolova 2015; Busbee et al. 2020), and hence the potential to fundamentally undermine ecosystem functioning. Thus, an urgent challenge remains to link pollution hotspots with causal factors, and identify potential repercussions for species, including humans, and ecosystem health. Although pollutant contamination has been extensively studied in teleost fish (Has-Schön et al. 2006; Castro-González and Méndez-Armenta 2008; Jezierska et al. 2009) and marine mammals (Stuart-Smith and Jepson 2017; Brown et al. 2018; Busbee et al. 2020), relatively little research has focused on pollutant contamination in sharks and rays. This remains a key knowledge gap for understanding both the physiological impacts of marine pollution on elasmobranchs, and the implications for humans of consuming shark products.

Ecological characteristics including slow growth, late maturity, low fecundity and high trophic level render elasmobranchs potential bioaccumulators (Jeffree et al. 2006b; Pethybridge et al. 2010; Maz-Courrau et al. 2012), bioindicators (Alves et al. 2016), and toxic sinks (De Boeck et al. 2010). Pollutant research in sharks has focused mainly on the North Atlantic and North Pacific regions and much of the analysis has targeted soft tissues, most frequently liver and muscles (Tiktak et al. 2020). However, soft tissue analysis insights are restricted to contemporary contamination, with no capacity to investigate lifetime patterns. Conversely, trace element composition analysis of shark vertebrae can target elements both for population studies (McMillan et al. 2018; Coiraton et al. 2020; Feitosa et al. 2020), and for examining heavy metal contamination (Mohammed and Mohammed 2017; Raoult et al. 2018). Importantly, this approach enables examination of patterns over lifetime scales, which are likely driven by the interrelationships between habitat, size, age, trophic level, life strategy and diet. Therefore, historical insights obtained from vertebral pollutant signatures could reveal temporal variations in pollutant exposure, and differential associated human consumption risk.

The smallspotted catshark *Scyliorhinus canicula* (hereafter “catshark”) is a benthic-dwelling shark, widely distributed throughout the Northeast Atlantic and is the most frequently observed shark species on baited remote underwater videos in the UK (Jones et al. 2021). It is listed as ‘Least Concern’ by IUCN Red List with an increasing population trend for its European population (Finucci et al. 2021), and is therefore an appropriate sentinel species for investigating pollutant exposure patterns and as a proxy for species of commercial and conservation importance. Here we apply laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to quantify lifetime variations in vertebral composition of smallspotted catsharks as sentinel species for heavy metal contamination (arsenic, cadmium, chromium, copper, lead, uranium, zinc) in the Bristol Channel and the English Channel, UK. We hypothesise that spatiotemporal variation in industrial heavy metal trace element composition is linked to pollutants from human activity, and where heavy metal presence is detected this has direct implications for consumption of fisheries target species. To test this hypothesis, we assessed (1) spatial variations in catshark vertebral elemental composition in historically industrialised areas (Bristol Channel: south and west Wales region), and compared it to less historically industrialised areas (English Channel: south Devon region); (2) ontogenetic trends in pollutant attenuation; and, (3) comparability between our findings and international guidelines for food safety.

5.3 Methods

A total of 49 catsharks were used in this study, collected from recreational angling bycatch at seven locations. Five sampling sites were selected along a presumed pollution gradient with differential proximity to anthropogenic stressors in the Bristol Channel region (Figure 5.1), with major human population centres (> 50k) in Bristol, Cardiff, and Swansea. Furthermore, South Wales in particular has a heavily industrialised history with major steel and historic coal ports in Cardiff, Barry and Port Talbot. These sites therefore likely also reflect legacy industrial contamination linked not only to salt marsh erosion (French 1993) but also both aeolian and watershed transport and sediment reworking by strong tidal currents (Nickless et al. 1972; Duquesne et al. 2006). Three sites were sampled in 2021 and two in 2022. Additionally, two sites in the English Channel region served as references (Figure 5.1), selected based on their location between South Devon and East Devon, with low human population density, and lack of historical heavy industry. One site was sampled in 2021 and one in 2022.

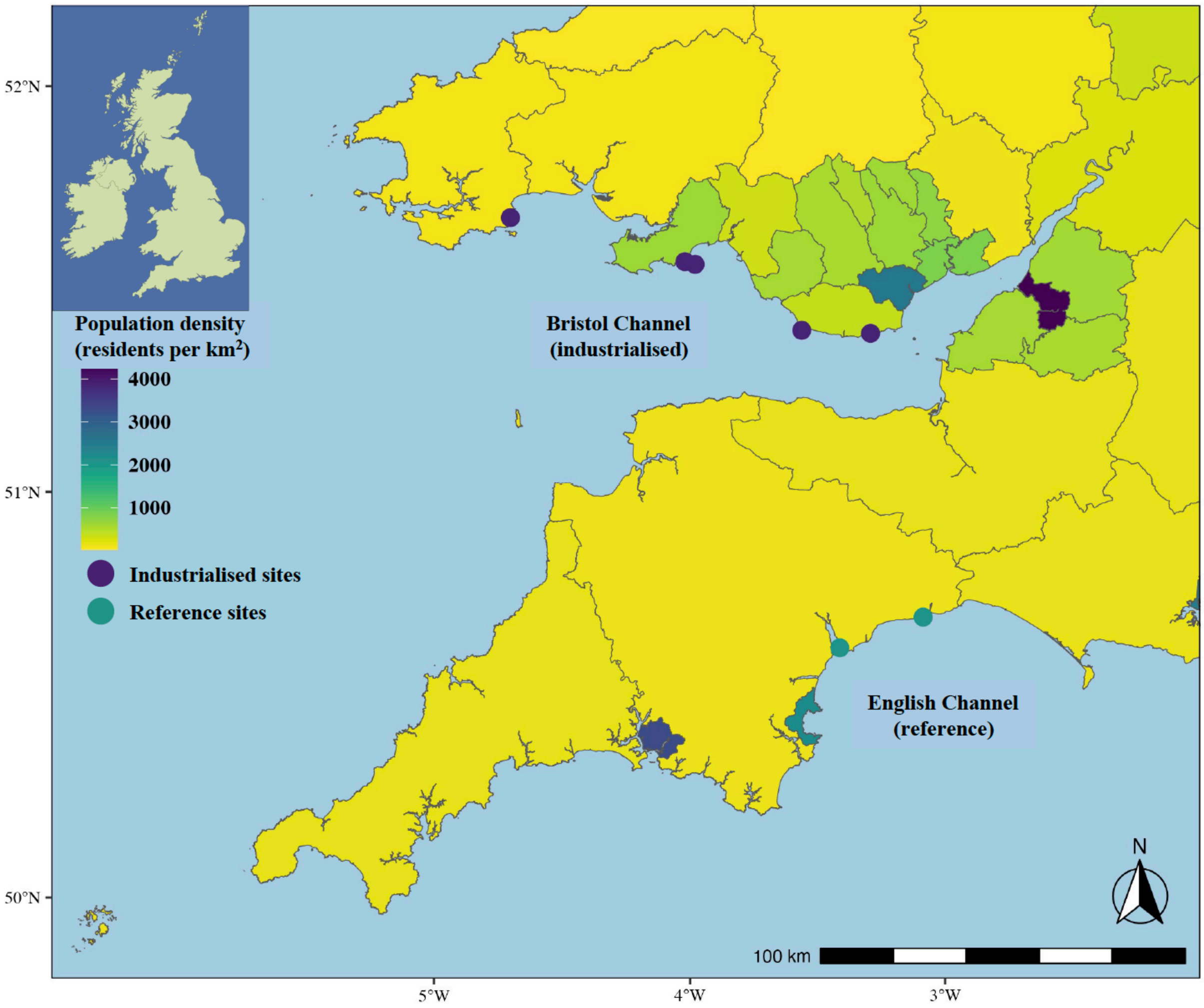


Figure 5.1 Spatial variation in human population density, and sampling locations for *Scyliorhinus canicula* in the Bristol Channel and English Channel study regions.

Samples were prepared for LA-ICP-MS analysis (see Chapter 4 for full sampling and sample preparation protocols) of growth axis transects across the corpus calcareum (Figure 5.2) to measure lifetime vertebral elemental composition of the following elements: arsenic, cadmium, chromium, copper, lead, uranium, zinc. The LA-ICP-MS setup comprised an ASI RESOlution 193 nm Excimer laser coupled to an Agilent-8900 triple quadrupole ICP-MS; laser shot frequency was 15 Hz and fluence was 3 J cm^{-2}, with a scan speed of 10 µm s^{-1} and ablation spot size of 100 µm. Helium and Nitrogen flow rates were 350 mL min^{-1} and 3.5 mL min^{-1}, respectively, and National Institute of Standards and Technology (NIST) 612 and NIST 614 glass standards were ablated periodically between transects. The ICP-MS used nickel cones and radio frequency power of approximately 1230 W, nebuliser gas rate of 0.8 l min^{-1}, with a time resolved acquisition mode and time slice of 1.10 s. Raw data were corrected and standardised to element:calcium molar ratios in Python using the Latools package (Branson et al. 2019), and replicates from individuals were visually aligned in QanalySeries (Kotov and Pälike 2018) with seasonal Mn:Ca peaks (Elsdon and Gillanders 2006; Smith et al. 2013). Lastly, molar ratios were converted to concentration (ppm) using ^{43}Ca as the internal standard and a 35 weight % for hydroxyapatite (McMillan et al. 2017; Mohan et al. 2018), thereby allowing comparison with previous research (LaFreniere et al. 2023).

Figure 5.2 Transect placement along corpus calcareum of *Scyliorhinus canicula* (SW05-2-1 = replicate 2 of individual 5 from Swansea sampling site).

We used generalised linear models (GLMs) to investigate the association of region (Bristol Channel vs English Channel), site, sex and life stage with single element vertebral composition (response variables), followed by an information theoretic approach (Akaike's information criteria, AIC; Akaike 1998) to select the best error structure and link function (Table 5.1). We used Wilcoxon rank sum tests to compare differences in pollutant concentrations both between regions (Bristol Channel experimental and English Channel reference) and sex. We then used Kruskal-Wallis rank sum followed by Dunn *post-hoc* tests to assess differences in pollutant concentrations across sites within the Bristol Channel region and identify pollution hotspots. To investigate ontogenetic trends and any association between maturity and pollutant attenuation we combined Von Bertalanffy Growth parameters (Table S5.1; see Ivory et al. 2004) and length at 50% maturity estimates (see Ellis and Shackley 1997) for catsharks in the UK with annual Mn:Ca peaks to assign transect points for the following life stages: pre-natal, young-of-year (to 1 year; YOY), sub-adult (1 year to 50% maturity), and adult (see Chapter 4 for full methods). Next, we used Kruskal-Wallis rank sum followed by Dunn *post-hoc* tests to assess pairwise differences in pollutant concentrations between life stages, with median elemental composition values as the response variable (Feitosa et al. 2021; LaFreniere et al. 2023). We visualised variations in elemental composition with non-metric multidimensional scaling in the vegan package (Oksanen et al. 2022) using the metaMDS function on a matrix of Bray distances, where we extracted three dimensions. Data were analysed using R software (v4.2.2; R Core Team 2022) with the MASS (Venables and Ripley 2002), TropFishR (Mildenberger et al. 2017) and FSA (Ogle et al. 2023) packages.

5.4 Results

Sampling comprised 25 female and 24 male catsharks, with 14 specimens collected from the English Channel and 35 specimens from the Bristol Channel (Table S5.2). Total length ranged from 350 mm to 646 mm (mean ± SD = 533 ± 61 mm), while estimated age ranged from 3 years to 12 years (mean ± SD = 7.3 ± 1.7 years).

We found evidence (GLM $p < 0.001$; Wilcoxon rank sum testing $p < 0.001$) supporting our hypothesis that contamination in the Bristol Channel is higher than the English Channel for all heavy metals analysed (Table S5.3); region explained between 2.09% (arsenic) and 15.72% (zinc) of elemental composition deviance (Table 5.1). The composition of all seven target elements also varied significantly between sites (GLM $p < 0.001$), with potential pollution hotspots at Barry and Tenby in the Bristol Channel (Figure 5.3; Kruskal-Wallis rank sum $p < 0.0001$; Table S5.4, Table S5.5). Chromium, copper, uranium and zinc levels were all highest in Tenby and Barry. Tenby also yielded the second highest levels of arsenic, behind the Swansea site, while Barry yielded the second highest levels of both cadmium and lead, behind the Southerndown site, reflected in non-metric multidimensional scaling of multi-element composition amongst sites (Figure 5.4). The greatest similarity in multi-element composition is seen between Barry and Tenby; together these sites were similar to Langland which in turn was similar to Swansea, while Southerndown was the most distinct. Overall, site explained between 4.97% (uranium) and 40.23% (arsenic), of elemental composition deviance (Table 5.1).

Table 5.1 Analysis of deviance table for generalised linear models used to investigate the association between Region, Site, Sex and Life Stage on single element response variables (arsenic, cadmium, chromium, copper, lead, uranium and zinc) within the vertebral composition of smallspotted catsharks *Scyliorhinus canicula* (Sig: NS = not significant; ** = $p < 0.01$, *** = $p < 0.001$)

	Df	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(>Chi)**	**% deviance explained**
Response: Arsenic		**Family: Gamma**			**Link: Log**	
NULL			35381	37321		
Region	1	780.5	35380	36540	< 0.001	2.09
Site	5	15015.1	35375	21525	< 0.001	40.23
Sex	1	5.5	35374	21520	< 0.01	0.01
Life stage	2	923.4	35372	20596	< 0.001	2.47
Response: Cadmium		**Family: Gamma**			**Link: Identity**	
NULL			35381	55300		
Region	1	4417.6	35380	50882	< 0.001	7.99
Site	5	8115.7	35375	42767	< 0.001	14.68
Sex	1	16.0	35374	42751	< 0.001	0.03
Life stage	2	209.6	35372	42541	< 0.001	0.38
Response: Chromium		**Family: Inverse gaussian**			**Link: Log**	
NULL			35381	1064.95		
Region	1	39.021	35380	1025.93	< 0.001	3.66
Site	5	222.528	35375	803.40	< 0.001	20.89
Sex	1	15.174	35374	788.23	< 0.001	1.42
Life stage	2	2.272	35372	785.96	< 0.01	0.21
Response: Copper		**Family: Gamma**			**Link: Sqrt**	
NULL			35381	43861		
Region	1	4318.3	35380	39543	< 0.001	9.85
Site	5	16153.8	35375	23389	< 0.001	36.83
Sex	1	57.0	35374	23332	< 0.001	0.13
Life stage	2	264.8	35372	23068	< 0.001	0.60
Response: Lead		**Family: Gamma**			**Link: Identity**	
NULL			35381	22388		
Region	1	705.48	35380	21682	< 0.001	3.15
Site	5	2148.62	35375	19533	< 0.001	9.59
Sex	1	24.03	35374	19509	< 0.001	0.11
Life stage	2	1390.42	35372	18119	< 0.001	6.21
Response: Uranium		**Family: Gamma**			**Link: Identity**	
NULL			35381	19422		
Region	1	879.04	35380	18542	< 0.001	4.53
Site	5	964.52	35375	17578	< 0.001	4.97
Sex	1	202.67	35374	17375	< 0.001	1.04
Life stage	2	1306.61	35372	16069	< 0.001	6.73
Response: Zinc		**Family: Gamma**			**Link: Identity**	
NULL			35381	21694		
Region	1	3409.5	35380	18284	< 0.001	15.72
Site	5	5637.7	35375	12646	< 0.001	25.99
Sex	1	82.7	35374	12564	< 0.001	0.38
Life stage	2	1611.1	35372	10953	< 0.001	7.43

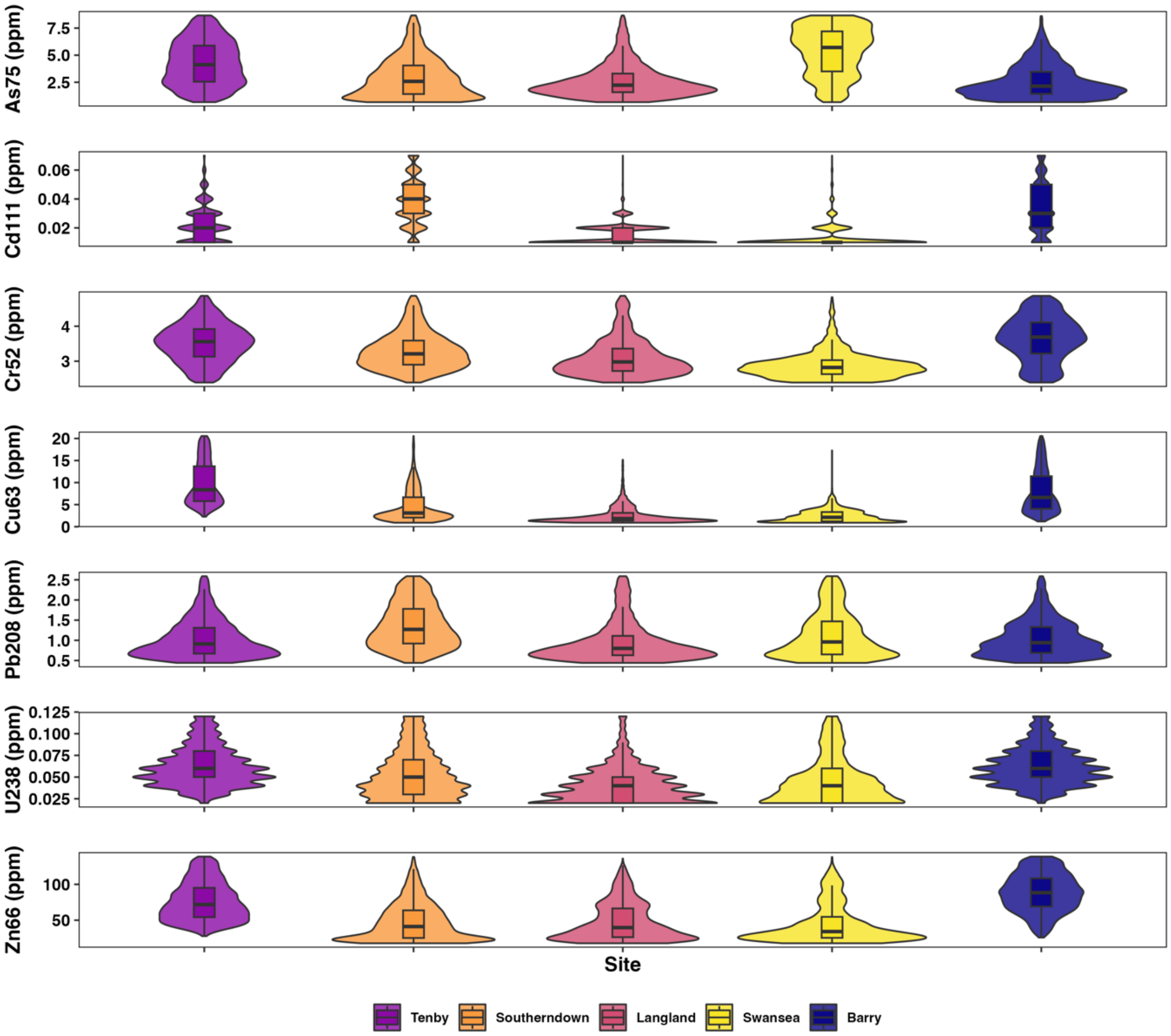


Figure 5.3 Differential vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* amongst contaminated Bristol Channel sites (from top to bottom: arsenic, cadmium, chromium, copper, lead, uranium, and zinc. Boxes represent interquartile range, horizontal line represents median, whisker length = 1.5 * interquartile range, outliers removed). English Channel reference sites are not included so as not to obfuscate pollution hotspot patterns emanating from more contaminated Bristol Channel sites. Note different y axis scales.

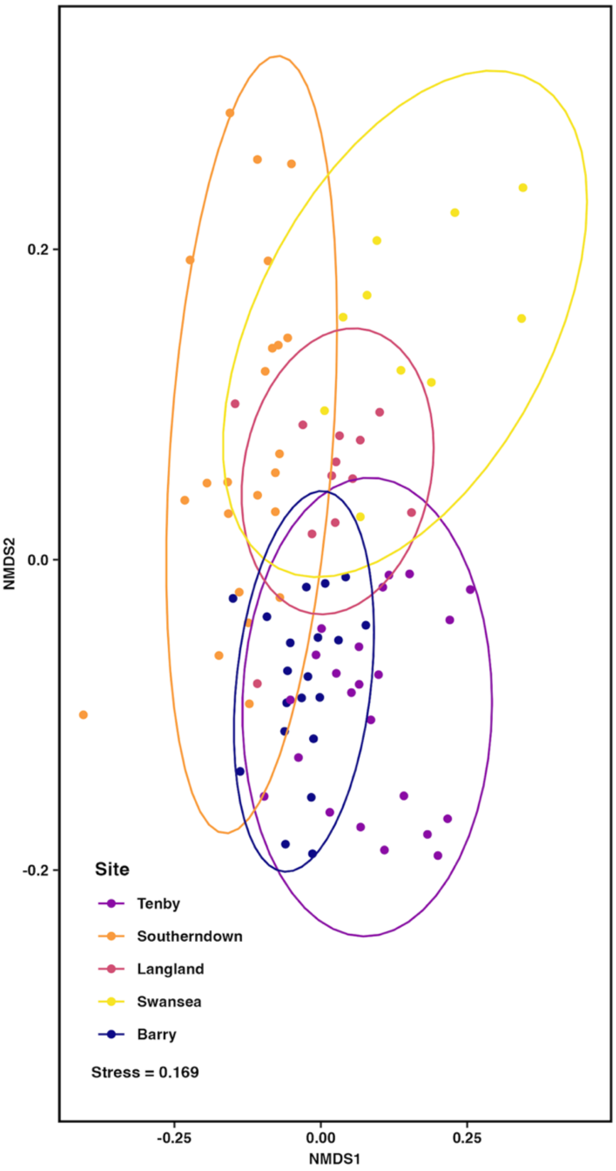


Figure 5.4 Differential vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* amongst contaminated Bristol Channel sites represented with multi-element non-metric multidimensional scaling obtained through Bray distance matrices. English Channel reference sites are not included so as not to obfuscate pollution hotspot patterns emanating from more contaminated Bristol Channel sites. Points represent individual sharks and colours denote sampling site.

Life stage also influenced the composition of all elements, with patterns of vertebral heavy metal composition characterised by three general trends in all individuals, regardless of location; young-of-year composition was generally lowest, with moderate increase during sub-adult stages, and more pronounced increase towards maturity and in adults (Figure 5.5). Ontogenetic trends are supported by differential composition amongst life stages for all elements (Kruskal-Wallis rank sum $p < 0.0001$; Table S5.4). This is further strengthened by post-hoc pairwise tests that showed that all elements varied significantly between all life stages ($p < 0.001$), with four exceptions; we found no significant difference between zinc levels in young-of-year and adults ($p < 0.1$), copper levels between adults and either sub-adults or young-of-year, and cadmium levels between adults and sub-adults ($p > 0.1$; Table S5.6).

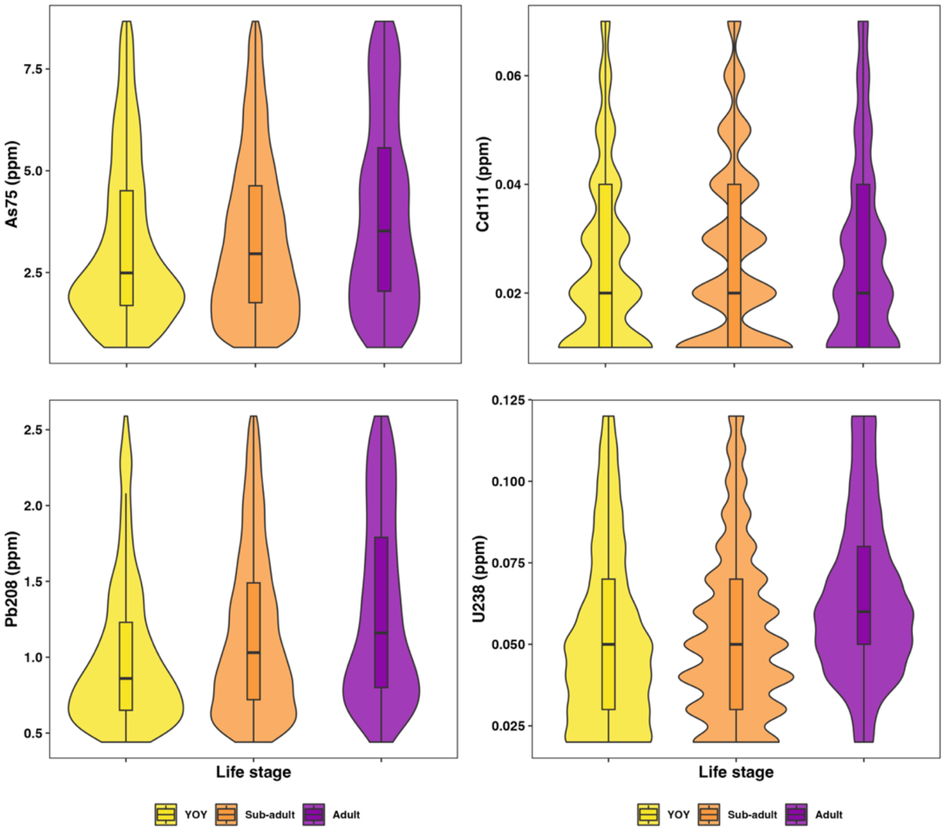


Figure 5.5 Differential life stage (YOY = young-of-year) vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* amongst contaminated Bristol Channel sites (left to right, top to bottom: arsenic, cadmium, lead and uranium. Boxes represent interquartile range, horizontal line represents median, whisker length = 1.5 * interquartile range, outliers removed) Note different y axis scales.

Cadmium, chromium, lead and uranium levels were significantly higher in females than males (Wilcoxon rank sum testing, alternative = greater, $p < 0.0001$; Table S5.7), while arsenic, copper and zinc were significantly lower in females (Wilcoxon rank sum testing, alternative = less, $p < 0.0001$; Table S5.7).

5.5 Discussion

Heavy metals linked to human activity are frequently found in the marine environment and can be bioavailable (Bryan and Langston 1992; Vicente-Martorell et al. 2009; Castillo et al. 2013). Furthermore, a combination of lifetime accumulation (bioaccumulation) and trophic transfer (biomagnification) can culminate in higher concentration of pollutants in older individuals and at higher trophic levels (Atwell et al. 1998; Lee et al. 2019). Here we use LA-ICP-MS to investigate spatial and lifetime temporal trends in pollutant contamination in the vertebrae of catsharks in the UK, successfully identifying a number of heavy metals (arsenic, cadmium, chromium, copper, lead, uranium, zinc). We detected higher concentrations of all metals in Bristol Channel sites compared to reference sites in the English Channel. Furthermore, there was distinct spatial variation across the Bristol Channel, with two potential pollutant hotspots amongst our sampling sites. Additionally, we observed ontogenetic trends of increasing contamination levels for arsenic, chromium, lead and uranium, and thus robust evidence for bioavailability and potential bioaccumulation of these pollutants. This lifetime effect has potential physiological implications not only for catsharks, but also other species at similar trophic levels and in polluted habitats.

We detected median levels of arsenic between 2.24 and 8.6 ppm. Levels up to 0.027 ppm have been detected in the muscles of the freshwater green chromide, *Etroplus suratensis*, and up to 4.732 ppm in the kidneys of the climbing perch, *Anabas testudineus*. This compares to muscle and liver values of 3.96 – 12.8 ppm and 5.67 – 10.1, respectively, for the Caribbean sharpnose shark, *Rhizoprionodon porosus*, in Brazil (Maciel et al. 2021), and 121.07 ppm in muscle tissue of the blackmouth catshark, *Galeus melastomus*, in the northern Tyrrhenian Sea (Gallo et al. 2023). The limits for food safety set by Australia and New Zealand are 2 ppm, while the WHO has replaced an earlier maximum permissible limit in food of 1 ppm with a recommendation that no arsenic intake is completely safe for human consumption (World Health Organization 2019).

Our measured levels of cadmium (median 0.01 – 0.04 ppm) were below European Union (EU) limits for human consumption of 0.05 ppm wet weight in fish muscles (Perera et al. 2016). Our observations were also comparable to levels of 0.01 – 0.4 ppm amongst six fish species from the Caspian Sea (Basim and Khoshnood 2016) and 0.04 ppm recorded in muscle tissues of the bamboo shark, *Chiloscyllium plagiosum*, in Hong Kong (Cornish et al. 2007).

Nevertheless, levels of 0.0045 ppm in seawater are potentially hazardous to marine life (Kumar and Singh 2010).

Strikingly, we recorded median levels of lead between 0.78 and 1.57 ppm. This exceeds not only concentrations recorded in Caspian Sea fish (0.01 – 0.55 ppm; Basim and Khoshnood 2016) and the blackmouth catshark in the northern Tyrrhenian Sea (0.16 ppm; Gallo et al. 2023), but both EU limits of 0.3 ppm for fish muscle meat and FAO / WHO limits of 0.2 ppm in prepared foods for babies or young children. Furthermore, our levels exceed those previously recorded in the liver, gonads, spleen, skin and kidney, and are comparable to those recorded in the muscle (1.8 ppm) of *S. canicula* in Liverpool Bay and the Irish Sea (Vas 1991).

Dietary exposure to uranium from foodstuffs in European countries is estimated to be 0.009 – 0.04 mg per kg body weight per day, which is below the WHO tolerable daily intake of 0.06 mg/kg body weight per day. However, the WHO limits for drinking water are 0.03 ppm, which is comparable to our recorded median levels of uranium (0.04 – 0.06 ppm), which in turn exceed levels of 0.03 ppm measured in oysters (Pearson and Ashmore 2020). There is a relative paucity of research into uranium concentrations in European food and the potential health impacts, therefore it has been identified as priority for future work (Alexander et al. 2009).

We recorded median levels of copper between 1.47 and 14.72 ppm, the latter exceeding blackmouth catshark muscle (1.75 ppm; Gallo et al. 2023) and liver (8.2 ppm for males, 9.9 ppm for females; Gaion et al. 2016) loading in the northern Tyrrhenian Sea, and muscle loading in bamboo sharks in Hong Kong (2.37 ppm; Cornish et al. 2007). Our highest median concentrations were for zinc (95.51 ppm), which is not always present as a contaminant and can be important as an essential metal for physiological development, with high rates of pre-natal deposition (Raoult et al. 2018) and variable composition across species; muscle composition of zinc has been recorded at levels of 16.96 ppm in the Pacific Sharpnose shark, *Rhizoprionodon longurio* (see Frías-Espericueta et al. 2014), 20.8 ppm in bamboo sharks (Cornish et al. 2007), and 104 ppm in scalloped hammerhead sharks (Ruelas-Inzunza and Paez-Osuna 2007). Similarly to zinc, chromium is not an exclusively toxic heavy metal and has been recorded at 28.6 ppm in bamboo catsharks (Cornish et al. 2007), an order of magnitude higher than our highest measured median value (3.72 ppm).

Heavy metal contamination can exceed safe limits for human consumption in both freshwater (Has-Schön et al. 2006) and marine fish (McKinney et al. 2016; Kim et al. 2019), including *S. canicula* (Marques et al. 2021; Filice et al. 2023). It is therefore not unprecedented that we detected a number of heavy metals in the vertebrae of Bristol Channel smallspotted catsharks at levels that may be of risk to consumers. Nevertheless, the levels of both arsenic and lead we recorded exceeded EU limits for food safety, while cadmium and uranium were comparable with limits. Importantly, however, the values we obtained relate to vertebral rather than soft tissues, and composition can vary between organs in the same species (Vas 1991). Given that soft tissue loading is the relevant component for human consumption, the levels we recorded warrant investigation of the compositional relationship between different organs. This is further demonstrated in the lifetime data yielded by our LA-ICP-MS approach that reveal temporally consistent compositional signals, that in fact increase with ontogenetic development for several of our target elements. This suggests a strong possibility of bioaccumulation that could manifest in elevated soft tissue loading. This is particularly important with respect to toxic heavy metals such as arsenic, which is suggested to bioaccumulate in sharks so that larger or mature individuals may present elevated consumer risk. Shark meat is widely sold for consumption in the UK, often under misleading umbrella terms (Hobbs et al. 2019), and exposure to arsenic can have potentially significant public health implications (Kite-Powell et al. 2008; Horta et al. 2011). Our findings, namely that several target elements were found at levels approaching, or exceeding, safe environmental, food or drinking water limits as set by the European Food Safety Authority (EFSA) or the World Health Organization (WHO), raise an important concern for regional fisheries and human consumption and warrant further investigation.

The most vulnerable species to extinction in European continental shelf seas are typically long-lived and occupying upper trophic levels, with a substantial proportion also functionally distinct (Coulon et al. 2023). Catsharks are an important component of nearshore marine ecosystems owing to central importance in marine food webs (Wieczorek et al. 2018), therefore potential future depletion and loss of these species could yet undermine ecosystem functioning. Heavy metal contamination can impact catshark physiology, such as through oxidative stress (Filice et al. 2023) and changes to haematological parameters (Tort and Torres 1988; Tort and Hernández-Pascual 1990). Accordingly, the spatial variations in pollutant contamination that we recorded present important considerations, particularly in the context of spatial population discreteness and connectivity. Both biomagnification and species mobility have the potential to spatially transfer pollution impacts away from point source. Therefore, spatial connectivity could indirectly expose populations to pollutant impacts, even if they are spatially discrete, which may in fact also apply to ontogenetic connectivity. Maternal offloading of contaminants has been recorded in several shark species (Lyons et al. 2013; Lyons and Lowe 2013; Frías-Espericueta et al. 2015; Lyons and Adams 2015), and although catsharks are oviparous, catshark egg cases are sufficiently permeable to allow embryonic absorption of radio-isotopes (Jeffree et al. 2006a). As such, pollutant contamination in mature females could be offloaded prior to egg case deposition, after which embryonic exposure would be determined by environmental conditions. Thereafter, any pollutant exposure would likely be exacerbated following developmental opening of egg case seawater slits, and thus direct seawater exchange (Ballard et al. 1993). Elucidating this link for *S. canicula*, therefore, could provide important insights into the impacts of contaminant offloading on other oviparous shark species, as well as the potentially differential risk factors associated with critical habitat areas such as parturition grounds, migration corridors, and nurseries. Different pathways of contaminant uptake include both direct absorption and trophic transfer, and the latter may explain the compositional increases we recorded with maturity and increasing influence of biomagnification relative to bioaccumulation. Ultimately, chronic exposure to heavy metal contamination may have direct and profound repercussions on fitness and metabolic functioning, as can projected climate impacts such as impaired predator avoidance (Ripley et al. 2021). Therefore our findings present an important consideration to mitigate the potential synergy of human pressure impacts on species ecology.

An important question for environmental pollution management relates to the longevity of impacts. Hence, the lifetime signals we obtained provide important insights into this, particularly given our data incorporate the Covid-19 Anthropause period (Table S5.2) that was an almost unique opportunity to examine human-wildlife interactions and perturbations (Rutz et al. 2020; Gaiser et al. 2022; Perkins et al. 2022). Subsequently, a variety of changes in human-wildlife interactions and wildlife behaviour have been associated with Anthropause (Kough et al. 2022; Raymond et al. 2023; Walters et al. 2023). However, we did not detect any appreciable declines in pollutants. Rather, the fact that we observed almost the opposite effect to that which might have been expected, with consistent or increasing signals, suggests several things; notably, heavy metal contamination of the marine environment is likely to be both chronic and legacy in its nature, impacts may include a considerable lag effect, and reduced human activity during Anthropause was not sufficiently prolonged to be reflected in environmental signals. This raises several considerations for environmental management, not least regarding rates of deposition and uptake of chronic pollutants in marine habitats.

There is currently no commercial fishery for catsharks in the UK, therefore any contemporary consumption is likely to be small-scale. However, active regional fisheries for human consumption continue to operate elsewhere (Marques et al. 2021). Nevertheless, other shark species are consumed in the UK, including nursehound, *S. stellaris*, spiny dogfish, *Squalus acanthias*, and several species sold under umbrella terms (Hobbs et al. 2019). Hence, catsharks have potential use as a proxy and bioindicator for other sharks that are currently consumed in the UK, and could elucidate pollutant hotspot areas of concern. This has implications for human health, with respect both to contemporary fisheries that target species occupying similar niches to catsharks, and more directly for human consumption under potential future fisheries pressure. Mercury is an important pollutant and the most widely studied in recent years (Tiktak et al. 2020). It has been recorded in Portuguese catshark fisheries at levels exceeding guidelines for human consumption (Marques et al. 2021), but is not detected by LA-ICP-MS equipment. This highlights an important gap in our knowledge, particularly given that mercury presents a number of potential health risks for consumers and has been historically recorded in catshark populations in the Irish Sea (Leah et al. 1991). Here we identify a potential public health concern that warrants further research attention to understand the potential implications for species of fisheries interest, and engagement between relevant health authorities and fisheries organisations. Aside from this, smallspotted catsharks remain an important component of nearshore marine environments, therefore elucidating potential impacts of future perturbation on species fitness, resilience, and wider ecosystem function should also remain a priority for research.

Chapter 6: GENERAL DISCUSSION

6.1 Discussion and main findings

This thesis seeks to address some of the knowledge gaps that are currently prohibitive to the implementation of regionally relevant and species-specific shark management measures. A mixed methods approach using BRUVS and LA-ICP-MS shows capacity to yield ecological insights at both the individual and population level, and across spatial scales, particularly in the context of identifying potentially important habitat areas for sharks that could be central to management measures to strengthen their protection. This is timely and could contribute to current biodiversity conservation planning; Northeast Tobago has recently been declared a UNESCO Man and the Biosphere Reserve, with additional plans to implement a large MPA and newly designed shark fisheries management regulations. Cardigan Bay was formally designated with SAC status in 2004, while the Welsh Marine Evidence Strategy (2019-2025), the Welsh National Marine Plan, and the Well-being of Future Generations Act (Wales) have shared objectives of sustainable marine resource management.

In Chapter 2, I use standardised BRUVS sampling to investigate the shark and ray assemblages around Tobago. Species richness was comparable to Caribbean regions where sharks are protected, and included species of conservation interest including Critically Endangered scalloped and great hammerhead sharks. This contradicted a prior hypothesis that elasmobranch communities would be comparable to elsewhere in the wider Caribbean where shark management is absent, given there is historical and ongoing shark fishing in Trinidad and Tobago. The observed patterns may be seasonal, and are likely linked to the availability of particular habitats in Northeast Tobago.

In Chapter 3, standardised BRUVS sampling across two years in the Cardigan Bay SAC yielded the first regional *in situ* insights into spatiotemporal habitat use amongst nursehounds, as well as a strong possibility of temporal niche partitioning between congeneric nursehounds and smallspotted catsharks. There was also a single sighting of a smoothhound of unknown species despite significant proportions of data rendered unusable by adverse weather conditions; this suggests that further BRUVS research would be warranted, since favourable conditions could generate important ecological insights that were not possible to capture with the sample size here.

In Chapter 4, LA-ICP-MS analysis of vertebral elemental composition was used to analyse regional lifetime patterns of habitat use in presumed spatially distinct populations of smallspotted catshark throughout the Bristol Channel. Shared habitat use amongst young-of-year and juvenile suggests the existence of juvenile nurseries with dispersal behaviour towards maturation, particularly amongst males. These nurseries may constitute critical habitat areas that would be directly relevant for marine spatial planning.

In Chapter 5, LA-ICP-MS analysis of vertebral elemental composition revealed spatial patterns of heavy metal contamination within the Bristol Channel, as well as evidence of bioaccumulation and biomagnification which may have physiological implications for sharks. Some heavy metals, including arsenic and lead, were detected above safe limits for human consumption. Although further analysis is required to elucidate the relationship between vertebral and soft tissue contamination levels, this highlights potential risk in the context of regional fisheries for human consumption.

6.2 Conservation implications and next steps

Sharks are globally depleted (MacNeil et al. 2020; Dulvy et al. 2021; Pacoureau et al. 2021; Simpfendorfer et al. 2023). Furthermore, the ongoing speed and extent of decline suggest that the coming years could be determinant in either observing or averting an elasmobranch extinction crisis. The considerable importance of sharks for marine ecosystem functionality suggests that such an outcome could elicit as yet poorly understood trophic cascades and system-wide impacts, averting which should be a priority. A broad horizon scan of future research priorities identifies two important themes: wider trophic impacts of ongoing depletion, and public perceptions and support for shark conservation.

6.2.1 Host-parasite communities of Caribbean and western Atlantic sharks

Overfishing has depleted reef sharks to functional extinction on nearly 20% of reefs globally (MacNeil et al. 2020) and driven a 70% decline in oceanic shark species since 1970 (Pacoureau et al. 2021). Demonstrably, commercial and unsustainable fishing can influence community structure and food web organisation (Marcogliese 2002). Fisheries that deplete high trophic levels can drive changes in community diversity and composition (Simpfendorfer et al. 2023). Consequently, this community shift can induce predatory release by which range expansion, increased abundance, and spatial and dietary overlap is seen in lower trophic levels. The feeding and movement ecology of sharks are key determinants of parasite composition, particularly in the intestine where it is linked to trophic transmission (Preti et al. 2020). Since movement patterns of free-living hosts can spatially link food webs, this may reduce the distinctiveness of compositional parasite assemblages (Marcogliese 2002). Conversely, the breakdown of linkage through depletion of key free-living hosts may in turn disrupt wider regional food web structure and thereby undermine ecosystem robustness and resilience.

Parasites are the most species rich mode of animal life (Carlson et al. 2020) and the dominant links within food webs, where single predator-prey interactions can support numerous host-parasite links (Poulin 2010). Furthermore, parasite diversity is intrinsically linked to the centrality and connectedness of a host within a community network (Anderson and Sukhdeo 2011), so that parasitism can be used to infer trophic ecology and feeding behaviour of host species. Given their importance, parasites are likely to be significantly impacted by biodiversity loss and the disturbance and restructuring of host species networks. The ecological significance of parasites determines that phase shifts to alternative stable states are likely to elicit ecosystem-wide impacts on parasitism and community structure.

Shark fisheries are widespread in the Caribbean and Western Atlantic, and sharks are now so depleted that they are seldom sighted except under strong fisheries management or large MPA networks (Ward-Paige et al. 2010; MacNeil et al. 2020; Simpfendorfer et al. 2023). Therefore, understanding wider ecosystem and trophic impacts of continued fisheries exploitation and population collapse is a research priority. Network theory and modelling can provide important insights into community-wide responses to external pressures such as species removal by fishing, and host-parasite networks can be used to model predicted impacts of ecological perturbation. Interrogation of open source host-parasite databases and the literature on shark-parasite interactions, therefore, could enable construction of a novel host-parasite network for shark communities in the Caribbean and Western Atlantic. This could be used to investigate potential trophic impacts of continued shark decline, specifically through the following objectives:

1) Identify parasite diversity associated with host species;
2) Determine which host species support highest parasite diversity;
3) Identify potential knowledge gaps according to temporal sampling bias or host species with low observed parasite diversity;

4) Identify geographical trends in prevalence of generalist and specialist parasites;
5) Simulate fishing pressure via network perturbation and host removal to predict how network structure and robustness would be affected by the extinction of endangered and critically endangered shark species.

6.2.2 Social perceptions and shark conservation in the UK

The ongoing decline in global shark populations as a result of overfishing (MacNeil et al. 2020; Dulvy et al. 2021; Pacoureau et al. 2021) has precipitated widespread establishment of MPAs to safeguard their economic (Vianna et al. 2012; Huveneers et al. 2017) and ecological (Heithaus et al. 2008) value. Proximity to human populations, however, limits MPA effectiveness (Juhel et al. 2018; Letessier et al. 2019b), demonstrating an intrinsic connectedness between human and shark communities. Yet there remains a research knowledge deficit regarding the values and attitudes of communities that are dependent on sharks, compared with more traditional biological and ecological research areas (Simpfendorfer et al. 2011).

Public perceptions of sharks are highly variable. The perpetuation of negative perceptions can be attributed to media coverage and misinformation, particularly regarding their anthropogenic threat, but documentaries remain an important source of information on sharks (Giovos et al. 2021). Conversely, improved knowledge elicits positive attitudes towards sharks (Gallagher et al. 2015), and support for shark conservation (O'Bryhim and Parsons 2015; Drymon and Scyphers 2017). This polarity of public opinion has the potential to undermine conservation efforts, particularly regarding enforcement and compliance, despite some evidence of positive changes in public perceptions of sharks (Whatmough et al. 2011). The United Nations declaration of the Decade of Ocean Science for Sustainable Development, 2021-2030 (Ryabinin et al. 2019) presents an opportunity to improve societal relationships with the ocean. Addressing ocean literacy and enhancing marine stewardship should be prioritised as important determinants of the extent to which UN objectives can be achieved. This is reflected in a burgeoning body of social sciences research evidence, and the incorporation of perceptions research into management design (Jefferson et al. 2021).

In the UK, there are approximately 40 species of sharks. The use of sharks as a resource is both extractive and non-extractive across scales, including commercial fisheries (Hobbs et al. 2019; Silva and Ellis 2019), recreational angling (Scotts et al. 2023), and nature-based tourism such as shark watching (Topelko and Dearden 2005). Knowledge of UK perceptions of sharks is, however, outdated and limited in scope (Friedrich et al. 2014; Giovos et al. 2021). With calls to strengthen shark conservation in the UK, not least through the identification of possible refuges for the Critically Endangered angelshark, *Squatina squatina* (Barker et al. 2022), the potential for misconceptions to preclude societal shifts in support of conservation should be addressed.

6.2.3 Pathways to shark population recovery

Increased research attention, a slowly building but definite groundswell of support for shark conservation (Whatmough et al. 2011; O'Bryhim and Parsons 2015; Drymon and Scyphers 2017; Shiffman 2020), and the ongoing development of improved monitoring and regulatory systems such as satellite surveillance (Kurekin et al. 2019; Rowlands et al. 2019), are reasons for optimism. Crucially, internationally coordinated efforts could yet see a reversal of decadal trends, and lead to shark recovery, and current global biodiversity programmes (Chapter 1) present a critical opportunity to pursue these objectives. Specific goals should be ambitious, and their success will require the availability of relevant and applicable ecological insights. Together, our findings strengthen the evidence base required to implement specific management measures to protect sharks in marine managed areas, in both the southern Caribbean and the UK.

In Tobago, the evidence of broad spatial use by sharks is encouraging, but in reality this observation is only the first step towards strengthening any benefits conferred by existing protection measures. Crucial information is yet to be gathered, particularly regarding the degree of seasonality of habitat use. A long-term BRUVS monitoring programme would fill intra-annual temporal gaps in our dataset and elucidate inter-annual habitat use patterns. Repeated use across years is one of the key criteria for shark nursery habitats (Heupel et al. 2007), and may therefore provide important clues about the potential for habitat protection to afford long-term benefits for sharks. The success of any such measures would also be closely linked to the local and regional movement ecology of wide-ranging species observed in our dataset, which have the capacity to travel distances beyond that which all except the largest MPA benefits can extend (Dwyer et al. 2020). A satellite archival tagging programme could be considered, to better understand both local and long-distance migratory patterns, and investigate regional population connectivity. Lastly, LA-ICP-MS natural tag analysis of vertebral samples (Chapter 4) already opportunistically obtained from landing sites for *S. lewini* and the smalltail shark, *Carcharhinus porosus*, could be used for future analysis to gain insights into population structure within the fisheries stock in both Trinidad and Tobago. This, together with satellite tracking, would help to better understand the degree of connectivity between the two islands and how likely management measures implemented in Tobago are to offer protection to sharks locally, nationally, and regionally. Engaging local knowledge, particularly that of fishers, could yield anecdotal evidence to support the design of empirical studies to maximise the chances of success. Local engagement would also provide an avenue for outreach to foster support for any regulations that are passed by the Sustainable Shark and Ray Management Plan, which could be pivotal to its success given the importance of community buy-in and self-enforcement for such measures (Kaplan et al. 2015).

The BRUVS and LA-ICP-MS analyses conducted in the UK represent an effort that should be made to address ecological knowledge deficits for sharks, beyond the species that attract research bias (Shiffman et al. 2020). The congeneric nursehound and smallspotted catshark are likely to be important predators in UK marine ecosystems given long-term trends of the decline in regional fish stocks (Kemp et al. 2023b). Therefore, identifying critical habitat areas for incorporation into revamped management plans should be prioritised. BRUVS sampling has provided important initial insights into spatiotemporal shark assemblages in Cardigan Bay SAC, but several developments should be explored to further strengthen these. First, stereo analysis of BRUVS footage will enable insights into population structure as well as biomass estimates. The feasibility of *in situ* individual identification of both nursehounds and smallspotted catsharks should be explored, particularly given it has been achieved in a laboratory setting for the latter (Navarro et al. 2018) and would enable the construction of social networks of habitat use by both species; these networks could be fundamental to better understanding potential temporal niche partitioning between both species. Long-term objectives should match the recommendations for a BRUVS programme in Tobago, which would allow for the assessment of nursery habitat criteria. However, given the importance of protecting all life stages of sharks to achieve conservation success (Kinney and Simpfendorfer 2009), in particular for oviparous species for which egg nurseries and juvenile nurseries may be distinct (Hoff 2010; Hoff 2016), BRUVS sampling should also be complemented by tagging studies using a regional acoustic array within the SAC. This would address the movement ecology knowledge gap inherent in BRUVS studies, and thus enable the identification of movement patterns, critical habitat areas and spatial connectivity, and in turn specific locations where management measures could have the most impact.

The broad-scale *S. canicula* population structure identified by LA-ICP-MS should be complemented by contiguous sampling, particularly targeting areas already under some form of conservation designation. With emerging and cutting edge capacity of this technology, increasing the fine scale resolution of ecological insights would significantly increase its application potential and strengthen its credentials as a stock management tool. Given its wide distribution and stable population status, the smallspotted catshark is a viable model species for the development of sustainable shark fisheries management, therefore this approach could allow similar insights for other species using opportunistic fisheries sampling, not least for the nursehound which is widely available from UK fishmongers (Hobbs et al. 2019). Regarding human fisheries consumption, an important next step is to use LA-ICP-MS to investigate the relationship between smallspotted catshark vertebral heavy metal contamination, and contaminant loading in soft tissues and organs. This will help to determine the extent of the health risks associated with regional fisheries and the viability of this species as a bioindicator.

Time is increasingly critical for the implementation of effective biodiversity management interventions that could address the global trends of recent decades. Regarding specifically the potential capacity of UK marine habitats to protect sharks, research should focus on critical habitat connectivity with wider Northeast Atlantic populations. A unique opportunity to reassess and redesign marine resource management in the UK has been afforded by the political departure of the UK from the EU. This is all the more important, given the alignment of national and international objectives with the Decade of Ocean Science for Sustainable Development, 2021-2030 (Ryabinin et al. 2019).

APPENDICES

Chapter 2 Appendix

Table S2.1 Residual diagnostics returned by the R package 'DHARMa' (Hartig 2020) to validate GLM model selection used to investigate the association between environmental variables and MaxN observations of 1) all sharks, 2) sharks excluding nurse sharks, 3) large sharks, 4) small sharks, 5) Caribbean reef sharks, 6) nurse sharks, 7) all rays, and 8) southern stingrays on baited remote underwater video stations in Tobago. Error family for each response variable is shown in brackets (NB = negative binomial, P = Poisson).

Response variable	**KS test**	**Dispersion test**	**Outlier test**	**Residual vs predicted**
All sharks (NB)	0.97	0.74	1	No significant problems
Sharks excluding nurse sharks (NB)	0.83	0.9	1	No significant problems
Large sharks (P)	0.27	0.99	1	No significant problems
Small sharks (NB)	0.72	0.99	1	No significant problems
Caribbean reef (P)	0.69	0.1	0.44	No significant problems
Nurse (NB)	0.97	0.99	1	No significant problems
All rays (NB)	0.77	0.93	0.7	No significant problems
Southern stingrays (P)	0.12	0.51	1	No significant problems

Table S2.2 Top models (ΔAIC < 2) retained for model averaging to investigate the association between environmental variables and MaxN observations of 1) all sharks, 2) sharks excluding nurse sharks, 3) large sharks, 4) small sharks, 5) Caribbean reef sharks, 6) nurse sharks, 7) all rays, and 8) southern stingrays on baited remote underwater video stations in Tobago.

	df	**ΔAIC**	**weight**
Response = All sharks			
mean relief + season	4	0.00	0.11
mean relief + season + year	4	0.00	0.11
mean relief	3	0.07	0.10
mean relief + year	3	0.07	0.10
temp + mean relief	4	0.51	0.08
temp + mean relief + year	4	0.51	0.08
depth + mean relief	4	1.21	0.06
depth + mean relief + year	4	1.21	0.06
depth + mean relief + season	5	1.40	0.05
depth + mean relief + season + year	5	1.40	0.05
temp + mean relief + season	5	1.48	0.05
temp + mean relief + season + year	5	1.48	0.05
depth + temp + mean relief	5	1.61	0.05
depth + temp + mean relief + year	5	1.61	0.05
Response = Sharks excluding nurse sharks			
depth + mean relief + season	5	0.00	0.28
depth + mean relief + season + year	5	0.00	0.28
depth + temp + mean relief + season	6	1.62	0.12
depth + temp + mean relief + season + year	6	1.62	0.12
depth + temp + mean relief	5	2.00	0.10
depth + temp + mean relief + year	5	2.00	0.10
Response = Large sharks			
mean relief	2	0.00	0.23
mean relief + year	2	0.00	0.23
temp + mean relief	3	0.83	0.15
temp + mean relief + year	3	0.83	0.15
depth + mean relief	3	1.50	0.11
depth + mean relief + year	3	1.50	0.11
Response = Small sharks			
depth + season	4	0.00	0.19
depth + season + year	4	0.00	0.19
depth + mean relief + season	5	0.50	0.15
depth + mean relief + season + year	5	0.50	0.15
season	3	1.51	0.09
season + year	3	1.51	0.09
depth	3	1.88	0.07
depth + year	3	1.88	0.07
Response = Caribbean reef sharks			
mean relief + season	3	0.00	0.19
mean relief + season + year	3	0.00	0.19
mean relief	2	0.53	0.15

mean relief + year	2	0.53	0.15
(Null)	1	1.52	0.09
year	1	1.52	0.09
depth + mean relief + season	4	1.80	0.08
depth + mean relief + season + year	4	1.80	0.08
Response = Nurse sharks			
depth + mean relief	4	0.00	0.25
depth + mean relief + year	4	0.00	0.25
mean relief	3	0.80	0.16
mean relief + year	3	0.80	0.16
depth + temp + mean relief	5	1.99	0.09
depth + temp + mean relief + year	5	1.99	0.09
Response = Rays			
depth	3	0.00	0.16
depth + year	3	0.00	0.16
depth + mean relief	4	0.02	0.16
depth + mean relief + year	4	0.02	0.16
depth + season	4	1.78	0.06
depth + season + year	4	1.78	0.06
depth + temp	4	1.86	0.06
depth + temp + year	4	1.86	0.06
depth + temp + mean relief	5	1.88	0.06
depth + temp + mean relief + year	5	1.88	0.06
Response = Stingrays			
depth + mean relief	4	0.00	0.37
depth + mean relief + year	4	0.00	0.37
depth + temp + mean relief	5	1.99	0.13
depth + temp + mean relief + year	5	1.99	0.13

Table S2.3 Model-averaged coefficients for top models (ΔAIC < 2) predicting the association between environmental variables and MaxN observations of 1) all sharks, 2) sharks excluding nurse sharks, 3) large sharks, 4) small sharks, 5) Caribbean reef sharks, 6) nurse sharks, 7) all rays, and 8) southern stingrays on baited remote underwater video stations in Tobago.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Response = All sharks MaxN				
Intercept	-0.72	2.65	0.27	0.79
Mean relief	0.65	0.18	3.64	< 0.001
Season	-0.21	0.35	0.61	0.54
Depth	-0.05	0.09	0.5	0.61
Temperature	0.01	0.01	0.43	0.67
Response = Sharks Excluding Nurse Sharks MaxN				
Intercept	-1.25	3.71	0.34	0.74
Depth	0.06	0.03	2.16	< 0.05
Mean relief	0.57	0.24	2.40	< 0.05
Season	-0.78	0.61	1.27	0.20
Temperature	-0.08	0.14	0.54	0.59
Response = Large Sharks MaxN				
Intercept	-7.4×10^{-1}	5.8	0.13	0.90
Mean relief	-1.4×10^{2}	3.9×10^{4}	< 0.01	1.00
Temperature	-1.06×10^{-1}	2.2×10^{-1}	0.49	0.63
Depth	9.2×10^{-3}	3.2×10^{-2}	0.29	0.78
Response = Small Sharks MaxN				
Intercept	-4.2	1.44	2.89	< 0.01
Depth	0.06	0.05	1.32	0.19
Season	-1.63	1.21	1.34	0.18
Mean relief	0.14	0.28	0.48	0.63
Response = Caribbean reef sharks MaxN				
Intercept	-3.26	0.68	4.78	< 0.001
Mean relief	0.52	0.39	1.33	0.18
Season	-0.61	0.78	0.78	0.44
Depth	-0.003	0.02	0.19	0.85
Response = Nurse sharks MaxN				
Intercept	-2.88	2.03	1.41	0.16
Depth	-0.03	0.04	0.98	0.33
Mean relief	1.09	0.29	3.74	< 0.001
Temperature	-0.01	0.07	0.15	0.88
Response = All rays MaxN				
Intercept	-0.55	1.86	0.29	0.77
Depth	-0.07	0.02	3.98	< 0.001
Mean relief	-0.09	0.15	0.63	0.53
Season	-0.02	0.12	0.18	0.86
Temperature	0.02	0.07	0.22	0.82
Response = Southern stingrays MaxN				
Intercept	-0.47	2.04	0.23	0.82
Depth	-0.07	0.02	3.84	< 0.001
Mean relief	-0.36	0.18	1.93	0.05

Temperature	0.01	0.07	0.18	0.86

Table S2.4 Analysis of deviance tables for the best predictive model (ΔAIC = 0) for the association between environmental variables and MaxN observations of 1) all sharks, 2) sharks excluding nurse sharks, 3) large sharks, 4) small sharks, 5) Caribbean reef sharks, 6) nurse sharks, 7) all rays, and 8) southern stingrays on baited remote underwater video stations in Tobago.

	df	**Deviance**	**Resid. df**	**Resid. Dev.**	**Pr(>Chi)**	**% deviance expl.**
Response = all sharks MaxN						
NULL			170	116.06		
mean relief	1	13.84	169	102.22	***< 0.001***	11.9
season	1	2.18	168	100.04	0.14	1.88
Total deviance explained 13.78 %						
Response = Sharks excluding nurse MaxN						
NULL			170	79.54		
depth	1	3.30	169	76.24	0.07	4.15
mean relief	1	4.06	168	72.18	*< 0.05*	5.10
season	1	4.20	167	67.98	*< 0.05*	5.28
Total deviance explained 14.53 %						
Response = large sharks MaxN						
NULL			170	24.26		
mean relief	1	4.41	169	19.85	*< 0.05*	18.18
Total deviance explained 18.18 %						
Response = small sharks MaxN						
NULL			170	48.99		
depth	1	5.35	169	43.64	*< 0.05*	10.92
season	1	3.98	168	39.66	*< 0.05*	8.12
Total deviance explained 19.04 %						
Response = Caribbean reef sharks MaxN						
NULL			170	59.59		
mean relief	1	3.04	169	56.55	0.08	5.1
season	1	2.6	168	53.95	0.11	4.4
Total deviance explained 9.5 %						
Response = nurse sharks MaxN						
NULL			170	81.60		
depth	1	2.82	169	78.78	0.09	3.46
mean relief	1	19.47	168	59.32	***< 0.001***	23.86
Total deviance explained 27.32 %						
Response = all rays MaxN						
NULL			170	139.07		
depth	1	18.38	169	120.70	***< 0.001***	13.22
Total deviance explained 13.22 %						
Response = southern stingrays MaxN						
NULL			170	127.42		
depth	1	17.28	169	110.14	***< 0.001***	13.56
mean relief	1	4.22	168	105.91	*< 0.05*	3.31

Total deviance explained 16.87 %

Chapter 3 Appendix

Table S3.1 Results from Web of Science "All Fields" interrogation for species-specific shark search terms, including smallspotted catshark, *Scyliorhinus canicula*, and nursehound, *Scyliorhinus stellaris* (both bold; correct on 25th August 2023).

Search term	Common name	All results	Results since 2003
"Scyliorhinus canicula"	Smallspotted catshark	1335	695
"Prionace glauca"	Blue shark	749	634
"Carcharodon carcharias"	White shark	719	603
"Sphyrna lewini"	Scalloped hammerhead shark	519	455
"Galeocerdo cuvier"	Tiger shark	450	414
"Carcharhinus longimanus"	Oceanic whitetip shark	78	67
"Scyliorhinus stellaris"	Nursehound	124	51

Table S3.2 The number of deployments and usable datasets from BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK.

Sampling year	Sampling month	Deployments	Usable datasets
2021	May	30	29
	July	30	30
	September	23	22
2022	March	17	8
	May	9	2
	July	30	28
	September	13	2

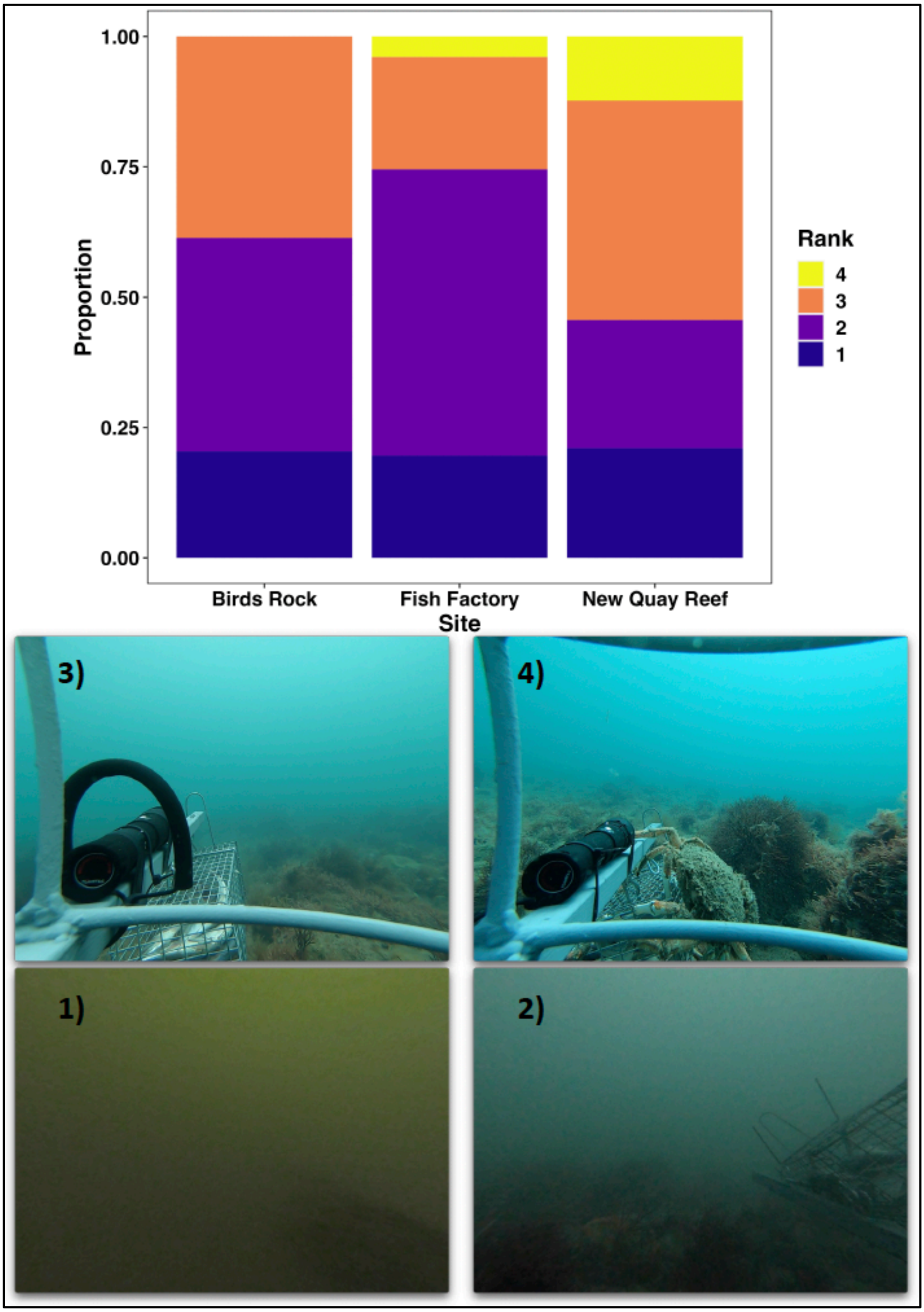


Figure S3.1 Top: the proportion of dataset image quality in each study site during BRUVS sampling in Cardigan Bay Special Area of Conservation, ranked according to standardised criteria (Jones et al. 2021); and, bottom: examples of datasets from this study assigned each rating (1) unusable, 2) poor, 3) good, and 4) excellent).

Table S3.3 Residual diagnostics returned by the R package 'DHARMa' (Hartig 2020) for generalised linear models used to investigate the association between month and site, and MaxN observations of smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *Scyliorhinus stellaris*, recorded on BRUVS in the Cardigan Bay Special Area of Conservation, UK.

Response	Error family	Link	KS test	Dispersion test	Outlier test	Residual vs predicted
S. canicula	Poisson	Log	0.20	0.07	1	No sig. problems
S. stellaris	Poisson	Log	0.55	0.58	1	No sig. problems

Table S3.4 Kruskal-Wallis rank sum test results for differences in the relative abundance of smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *Scyliorhinus stellaris*, amongst sampling sites in the full dataset, and both sampling sites and sampling months in the nearshore sites data subset, from BRUVS sampling in the Cardigan Bay Special Area of Conservation, UK.

	Dataset: full dataset		
Factor: sampling site	**chi-squared**	**df**	**p-value**
S. canicula	15.59	5	< 0.01
S. stellaris	20.33	5	< 0.01
	Dataset: nearshore sites subset		
Factor: sampling site	**chi-squared**	**df**	**p-value**
S. canicula	29.89	2	< 0.0001
S. stellaris	42.49	2	< 0.0001
Factor: sampling month			
S. canicula	12.17	3	< 0.01
S. stellaris	12.07	3	< 0.01

Table S3.5 Dunn post-hoc test results of pairwise site and month comparisons of the relative abundance of smallspotted catsharks, *Scyliorhinus canicula*, and nursehounds, *Scyliorhinus stellaris*, amongst nearshore BRUVS sampling sites and sampling months in the Cardigan Bay Special Area of Conservation, UK.

Factor: sampling site	**Pairwise comparison**	**Z**	**p. unadj**	**p. adj**
S. canicula	Birds Rock vs Fish Factory	0.34	0.7	0.7
	Birds Rock vs New Quay	-4.42	< 0.0001	< 0.0001
	Fish Factory vs New Quay	-4.92	< 0.0001	< 0.0001
S. stellaris	Birds Rock vs Fish Factory	0.03	0.9	0.9
	Birds Rock vs New Quay	-5.48	< 0.0001	< 0.0001
	Fish Factory vs New Quay	-5.69	< 0.0001	< 0.0001
Factor: sampling month	**Pairwise comparison**	**Z**	**p. unadj**	**p. adj**
S. canicula	July vs March	-1.58	0.1	0.5

	July vs May	-3.29	< 0.01	< 0.01
	March vs May	0.49	0.6	0.6
	July vs September	-1.26	0.2	0.6
	March vs September	1.12	0.3	0.5
	May vs September	1.68	0.1	0.5
S. stellaris	July vs March	0.44	0.6	0.6
	July vs May	-0.63	0.5	1
	March vs May	-0.64	0.5	1
	July vs September	-3.32	< 0.001	< 0.01
	March vs September	-1.57	0.1	0.5
	May vs September	-2.5	< 0.05	0.06

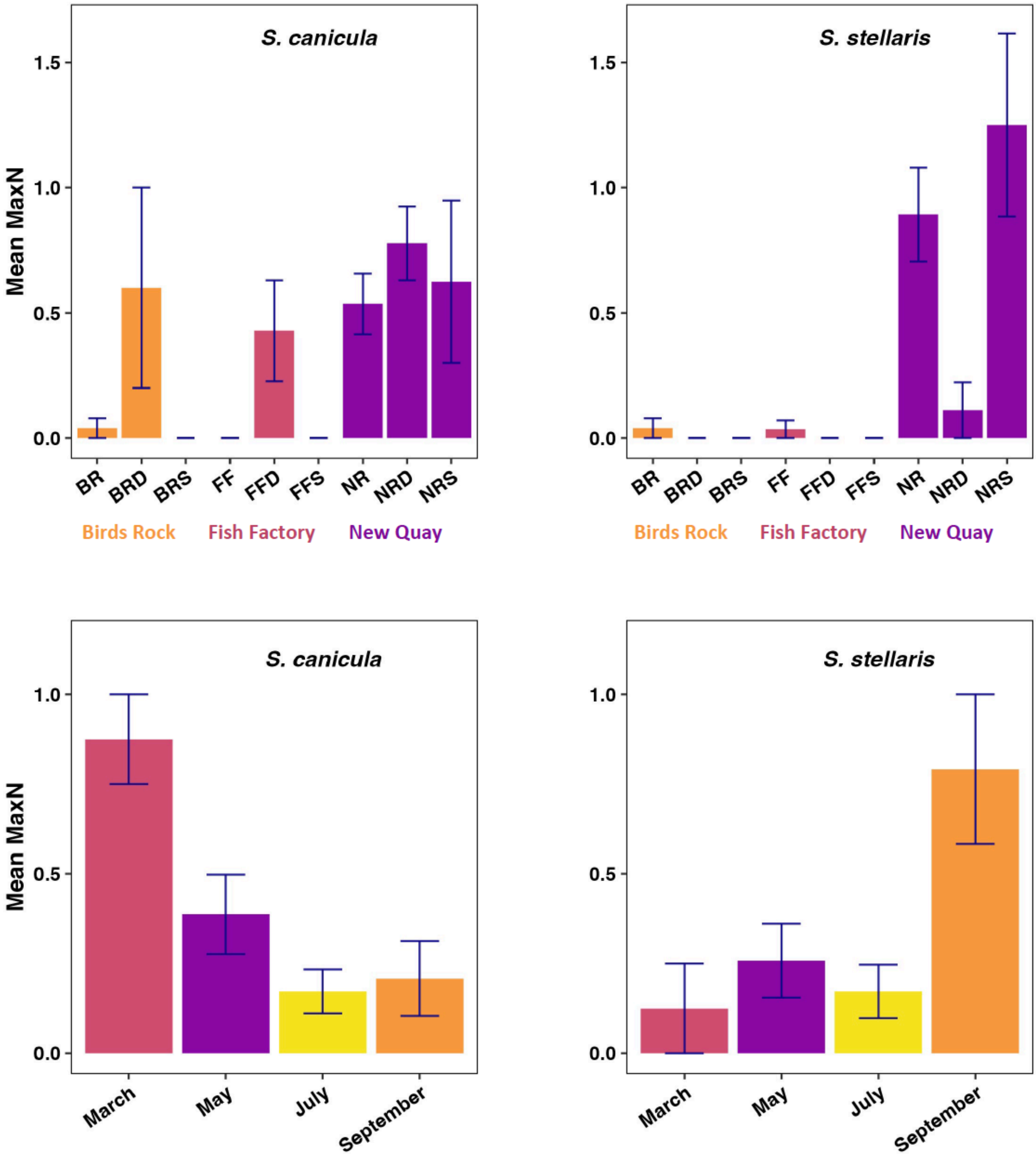


Figure S3.2 Overall mean MaxN (± S.E.) of smallspotted catsharks, *Scyliorhinus canicula* (left), and nursehounds, *Scyliorhinus stellaris* (right), amongst all BRUVS sampling sites (top) and sampling months (bottom) in the Cardigan Bay Special Area of Conservation, UK.

Chapter 4 Appendix

Table S4.1 Sampling year, sex demographics, mean total length (tl.mean) and standard deviation (tl.sd), and mean age (age.mean) and standard deviation (age.sd) of smallspotted catshark, *Scyliorhinus canicula*, recreational fishing bycatch collected from the Bristol Channel and English Channel, UK.

	Year	n females	n males	tl.mean (mm)	tl.sd (mm)	age.mean (y)	age.sd (y)
Region = English Channel							
Beer	2022	3	2	590	30.7	9	1.3
Exmouth	2021	7	2	568	34.9	8.4	1.5
Region = Bristol Channel							
Barry	2021	4	4	456	63.8	5.3	1.3
Langland	2022	0	5	545	27.9	7.2	0.7
Swansea	2021	1	4	471	64.4	5.6	1.4
Southerndown	2022	9	0	555	30.5	8.1	1.1
Tenby	2021	1	7	542	36	7.2	1

Table S4.2 Von Bertalanffy growth parameters for smallspotted catsharks, *Scyliorhinus canicula*, in the UK (see Ivory et al. 2004).

	Male	Female
L_∞ (cm)	87.42	75.14
K	0.118	0.15
t0	-1.09	-0.96

Table S4.3 Kruskal-Wallis rank sum test results of the influence of site on vertebral elemental composition in smallspotted catsharks, *Scyliorhinus canicula*, in the Bristol Channel and English Channel, UK.

Element	chi-squared	df	p-value
Barium (^{138}Ba)	13648	6	< 0.0001
Magnesium (^{25}Mg)	14030	6	< 0.0001
Manganese (^{55}Mn)	2528	6	< 0.0001
Strontium (^{86}Sr)	3925	6	< 0.0001

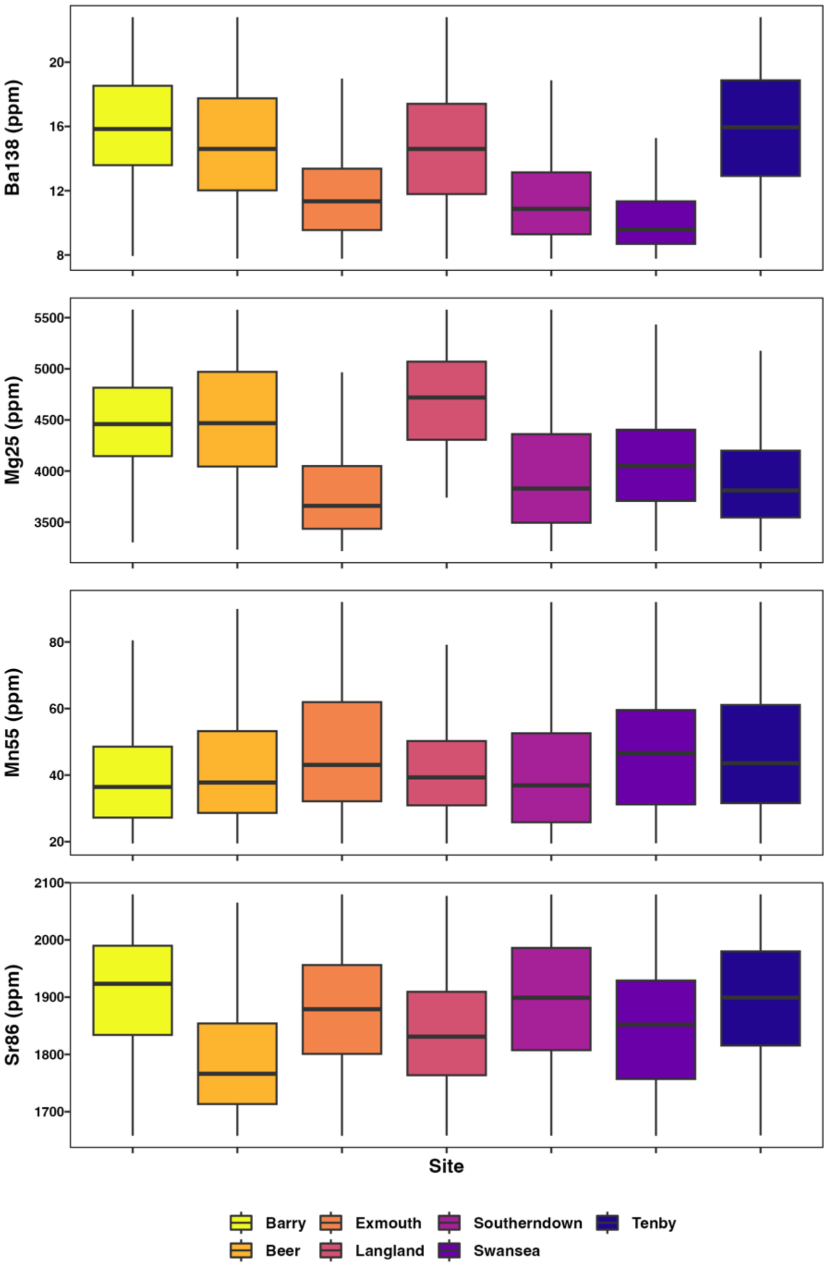


Figure S4.1 Smallspotted catshark, *Scyliorhinus canicula*, vertebral elemental composition within different sites in the Bristol Channel and English Channel, UK; top to bottom: barium, magnesium, manganese, and strontium. Boxes represent interquartile range, horizontal line represents median, whisker length = 1.5 * interquartile range (outliers removed). Note different y axis scales.

Table S4.4 Kruskal-Wallis rank sum test results of the influence of life stage on vertebral elemental composition in smallspotted catsharks, Scyliorhinus canicula, in the Bristol Channel and English Channel, UK.

Element	**chi-squared**	**df**	**p-value**
Barium (138Ba)	28.364	2	< 0.0001
Magnesium (25Mg)	3497.5	2	< 0.0001
Manganese (55Mn)	891.25	2	< 0.0001
Strontium (86Sr)	6898.3	2	< 0.0001

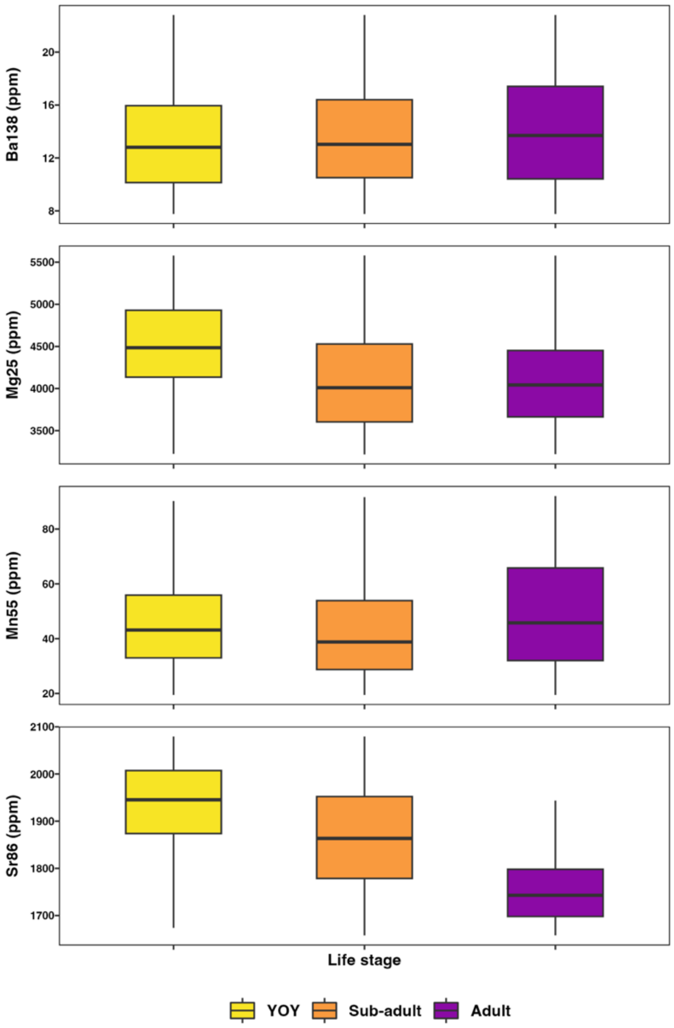


Figure S4.2 Ontogenetic variation in smallspotted catshark, *Scyliorhinus canicula*, vertebral elemental composition across sampling sites in the Bristol Channel and English Channel, UK; top to bottom: barium, magnesium, manganese, and strontium. Boxes represent interquartile range, horizontal line represents median, whisker length = 1.5 * interquartile range (outliers removed). Note different y axis scales.

Table S4.5 Wilcoxon rank sum sex-based comparison of smallspotted catshark, *Scyliorhinus canicula*, vertebral elemental composition in the Bristol Channel and English Channel, UK.

Wilcoxon rank sum test with continuity correction		
	W	**p-value**
Data = Ba138_ppm by Sex (alternative = less)		
	128031992	< 0.0001
Data = Mg25_ppm by Sex (alternative = less)		
	131992996	< 0.0001
Data = Mn55_ppm by Sex (alternative = less)		
	135274179	< 0.0001
Data = Sr86_ppm by Sex (alternative = greater)		
	176556774	< 0.0001

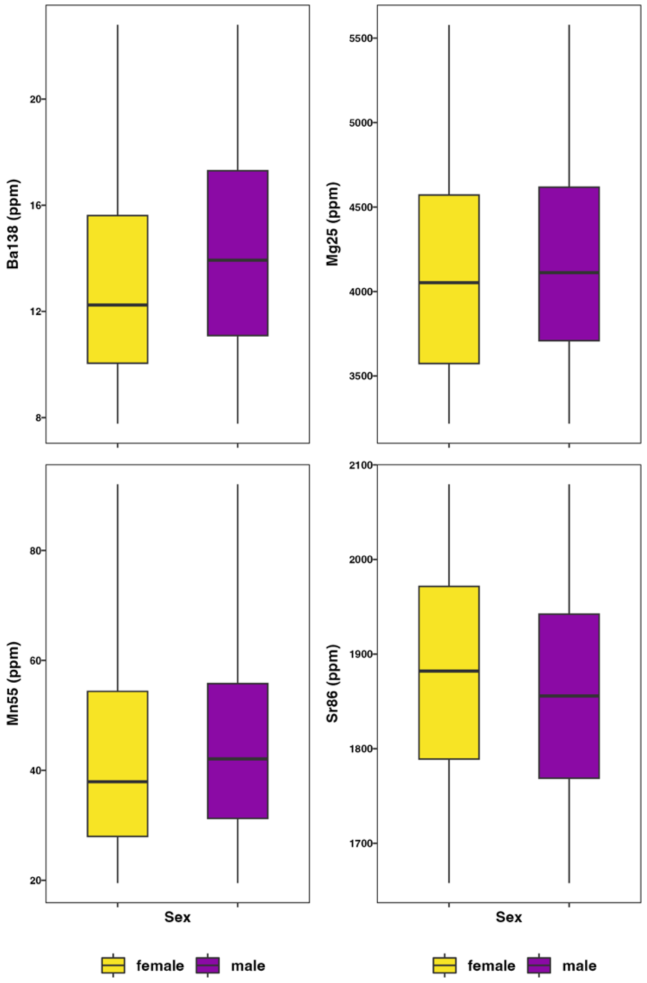


Figure S4.3 Vertebral elemental composition recorded for female and male smallspotted catsharks, *Scyliorhinus canicula*, across sampling sites in the Bristol Channel and English Channel, UK; top left: barium, top right: magnesium, bottom left: manganese, and bottom right: strontium. Boxes represent interquartile range, horizontal line represents median, whisker length = 1.5 * interquartile range (outliers removed). Note different y axis scales.

Table S4.6 Wilcoxon rank sum regional comparison of smallspotted catshark, *Scyliorhinus canicula*, vertebral elemental composition in the Bristol Channel and English Channel regions, UK.

Wilcoxon rank sum test with continuity correction		
	W	**p-value**
Data = Ba138_ppm by Region (alternative = greater)		
	154497564	< 0.0001
Data = Mg25_ppm by Region (alternative = greater)		
	160744849	< 0.0001
Data = Mn55_ppm by Region (alternative = less)		
	136000000	< 0.0001
Data = Sr86_ppm by Region (alternative = greater)		
	163024036	< 0.0001

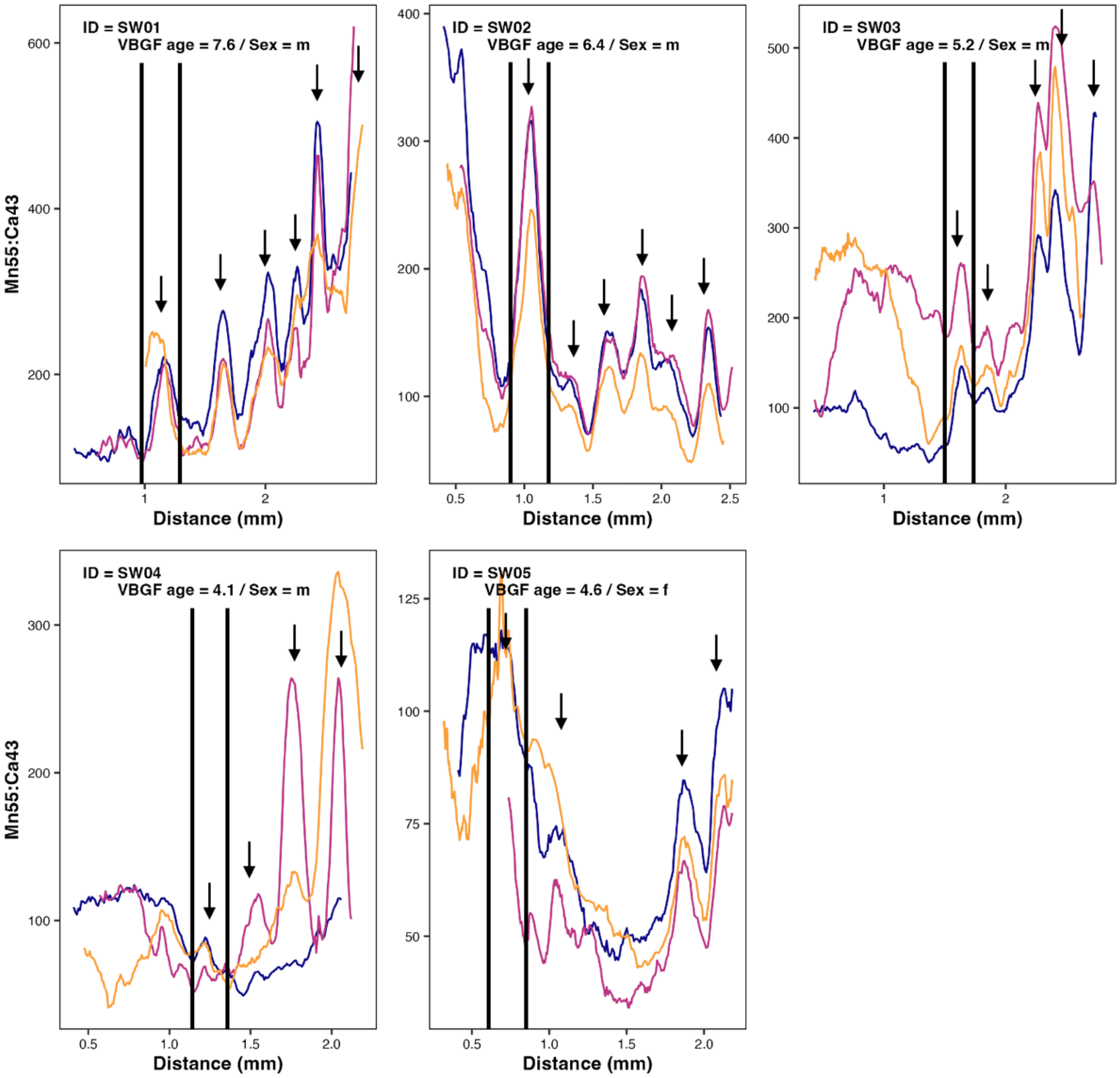


Figure S4.4 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Swansea sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

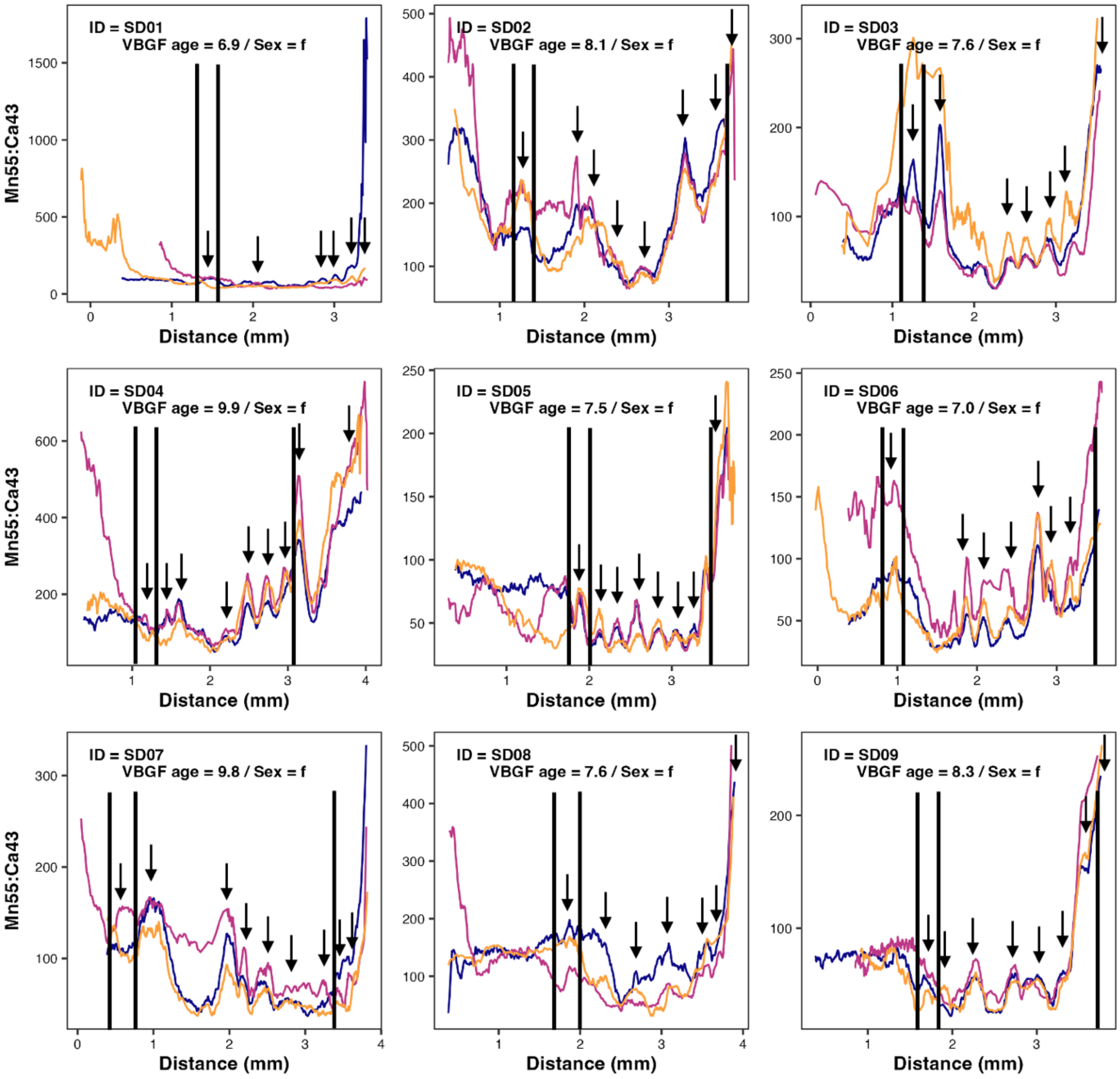


Figure S4.5 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Southerndown sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

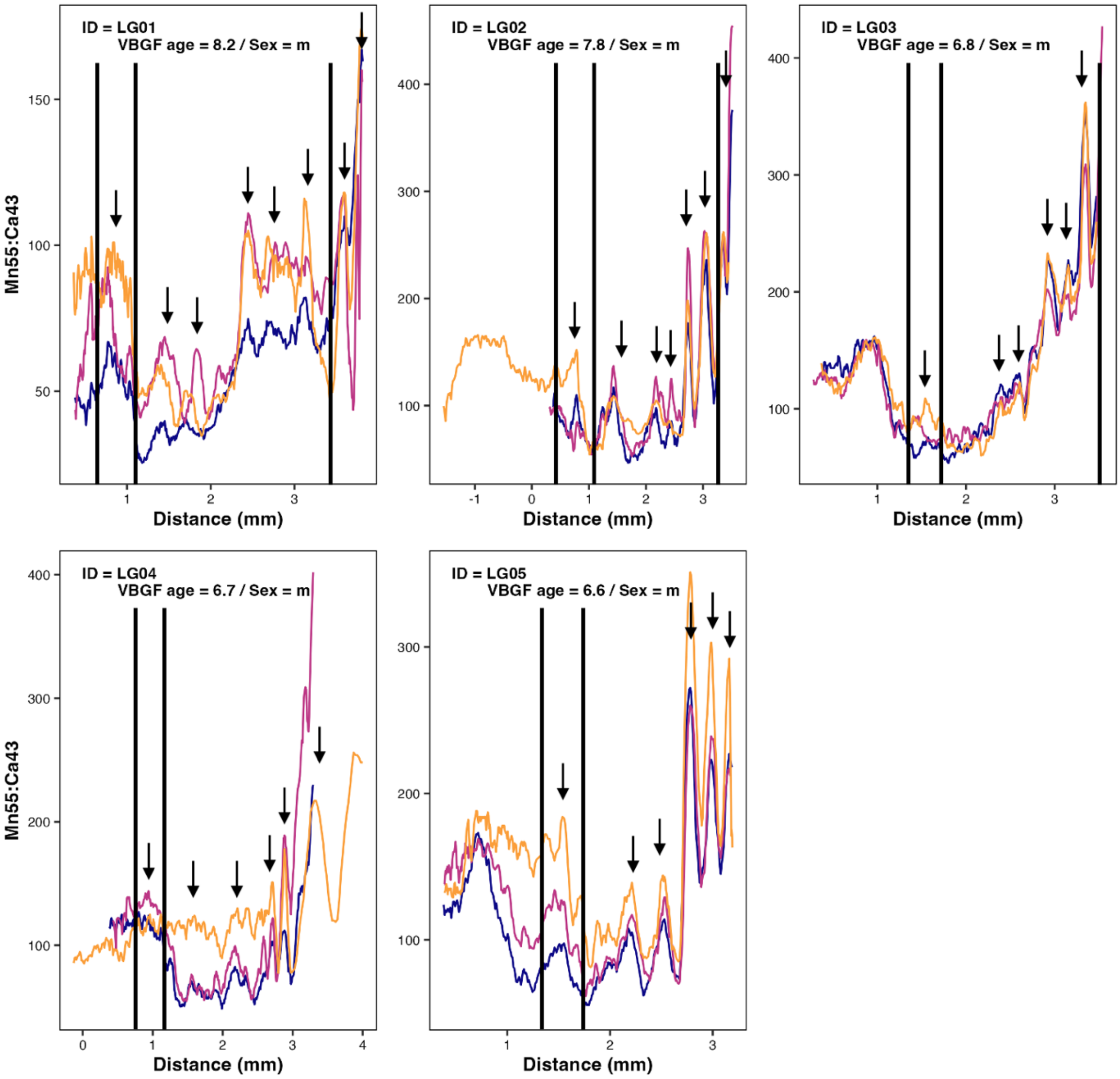


Figure S4.6 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Langland sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

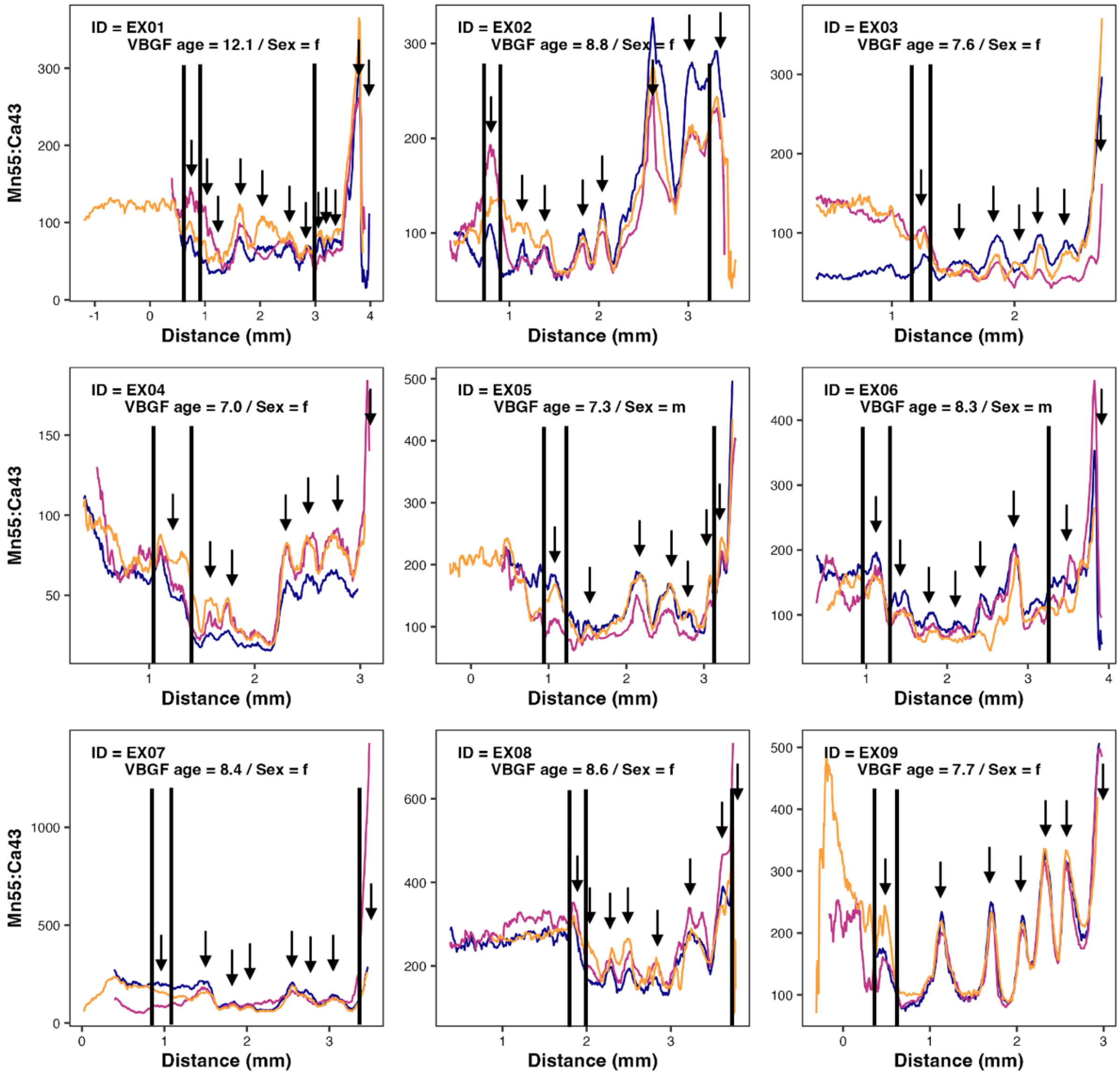


Figure S4.7 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Exmouth sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

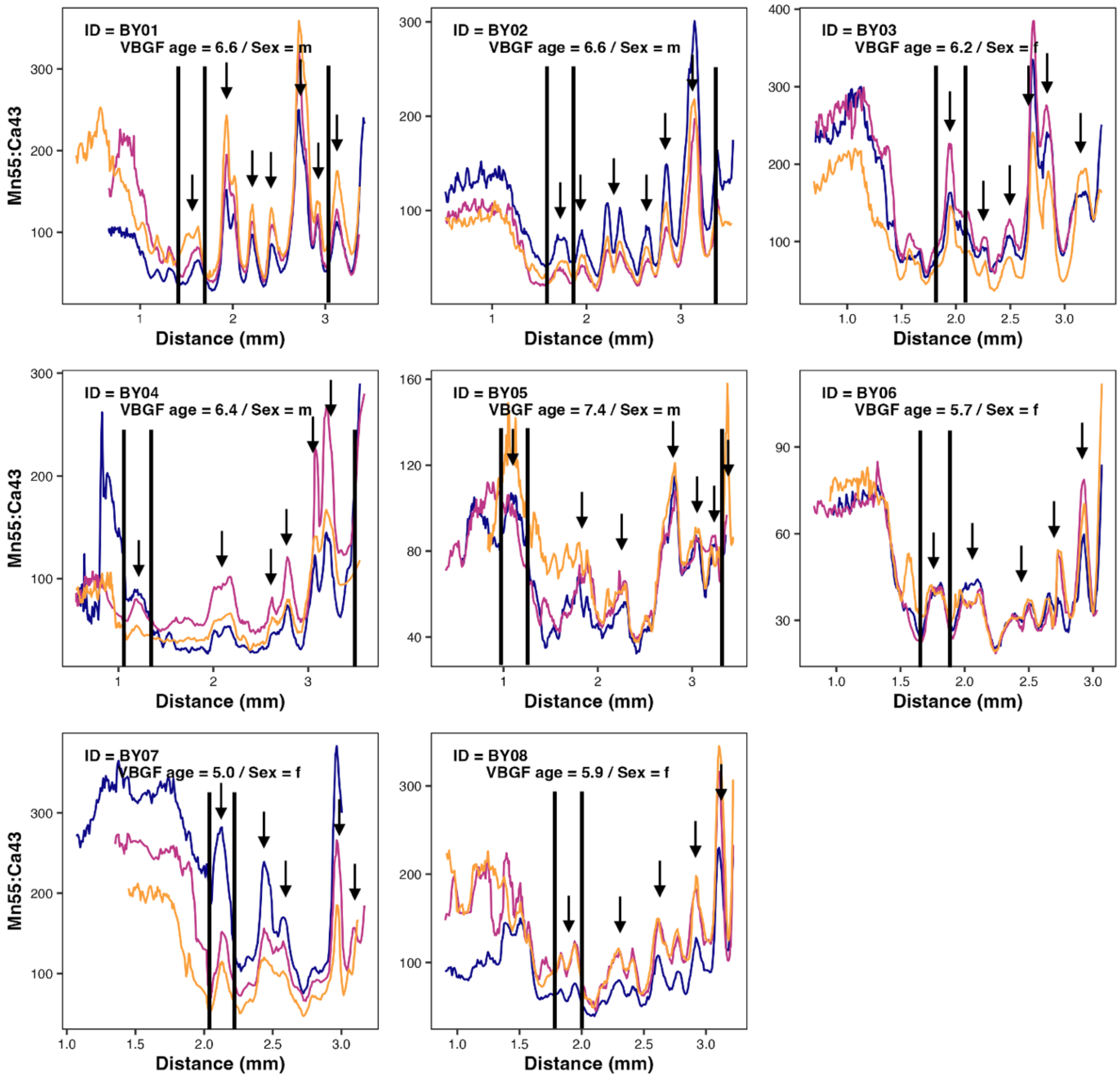


Figure S4.8 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Barry sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

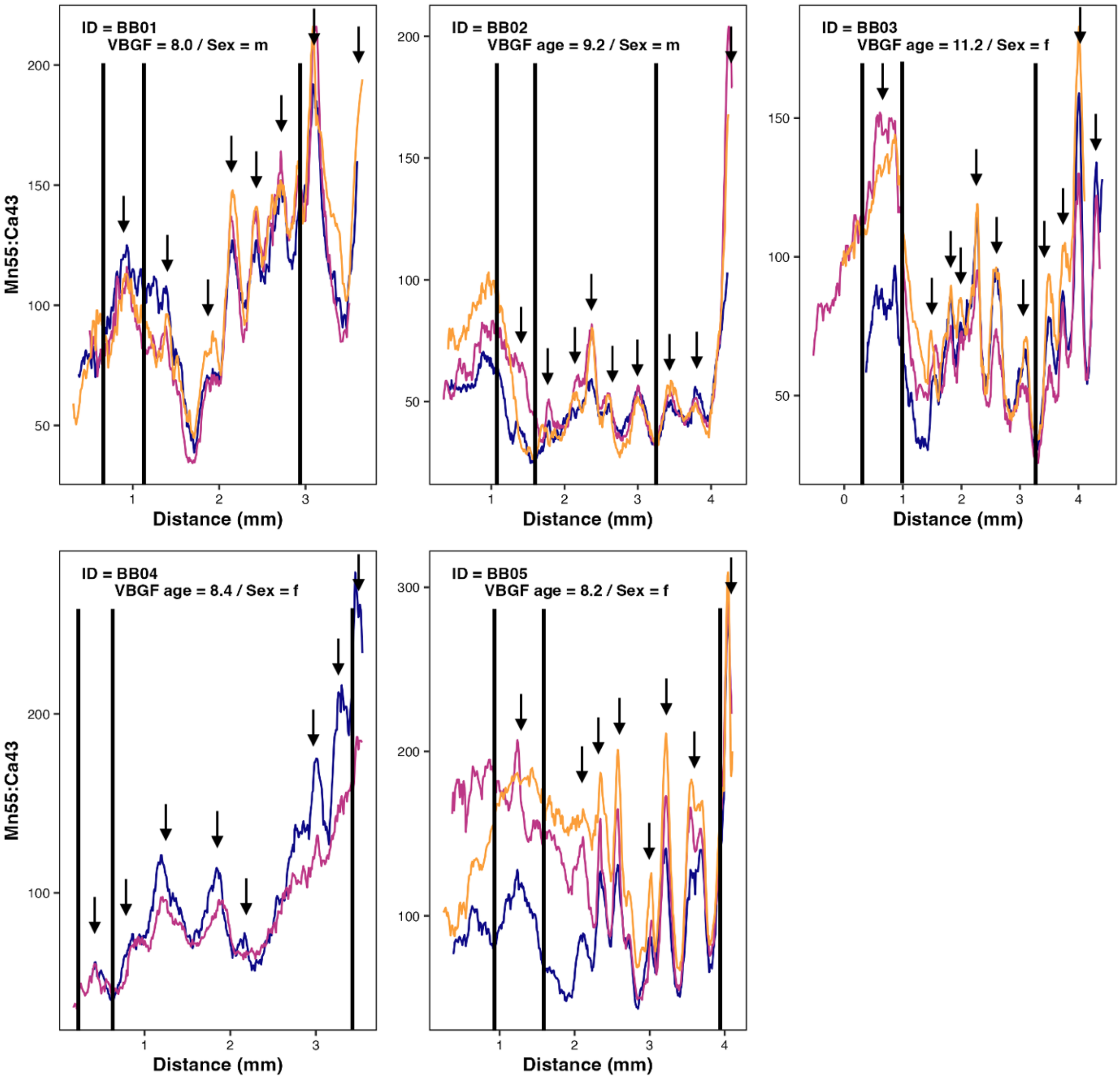


Figure S4.9 Annual vertebral manganese peaks (arrows) analysed using laser ablation inductively coupled plasma mass spectrometry for smallspotted catshark, *Scyliorhinus canicula*, individuals from the Beer sampling site. ID = Specimen ID, VBGF = Von Bertalanffy Growth Function age estimate. Vertical bars represent, from left to right: hatching point, year 1, and 50% maturity. Note: some panels do not have 50% maturity bar.

Chapter 5 Appendix

Table S5.1 Von Bertalanffy growth parameters for smallspotted catsharks *Scyliorhinus canicula* in the UK (see Ivory et al. 2004)

	Male	**Female**
L∞ (cm)	87.42	75.14
K	0.118	0.15
t0	-1.09	-0.96

Table S5.2 Sampling year, sex demographics, mean total length (tl.mean) and standard deviation (tl.sd), and mean age (age.mean) and standard deviation (age.sd) of *Scyliorhinus canicula* recreational fishing bycatch collected from the Bristol Channel and English Channel, UK

	Year	**females**	**males**	**tl.mean (mm)**	**tl.sd (mm)**	**age.mean (y)**	**age.sd (y)**
Region = English Channel (reference)							
Beer	2022	3	2	590	30.7	9	1.3
Exmouth	2021	7	2	568	34.9	8.4	1.5
Region = Bristol Channel (experimental)							
Barry	2021	4	4	456	63.8	5.3	1.3
Langland	2022	0	5	545	27.9	7.2	0.7
Swansea	2021	1	4	471	64.4	5.6	1.4
Southerndown	2022	9	0	555	30.5	8.1	1.1
Tenby	2021	1	7	542	36	7.2	1

Table S5.3 Wilcoxon rank sum test results of regional comparison of vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* in the Bristol Channel and English Channel regions

Wilcoxon rank sum test with continuity correction		
	W	**p-value**
Data = As75_ppm by Region (alternative = greater)		
	142650628	< 0.001
Data = Cd111_ppm by Region (alternative = greater)		
	194107949	< 0.0001
Data = Cr52_ppm by Region (alternative = greater)		
	181958876	< 0.0001
Data = Cu63_ppm by Region (alternative = greater)		
	165966506	< 0.0001
Data = Pb208_ppm by Region (alternative = greater)		
	175326932	< 0.0001
Data = U238_ppm by Region (alternative = greater)		
	179466094	< 0.0001
Data = Zn66_ppm by Region (alternative = greater)		
	204974272	< 0.0001

Table S5.4 Kruskal-Wallis rank sum test results of the influence of site (left column) and life stage (right column) on vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* in the Bristol Channel

	Kruskal-Wallis rank sum test for all target elements					
	Factor = Site			**Factor = Life stage**		
	chi-squared	**df**	**p-value**	**chi-squared**	**df**	**p-value**
Response variable: As75						
	7134.5	4	< 0.0001	332.17	2	< 0.0001
Response variable: Cd111						
	10080	4	< 0.0001	34.214	2	< 0.0001
Response variable: Cr52						
	4764.5	4	< 0.0001	162.12	2	< 0.0001
Response variable: Cu63						
	12679	4	< 0.0001	26.469	2	< 0.0001
Response variable: Pb208						
	4652.6	4	< 0.0001	830.41	2	< 0.0001
Response variable: U238						
	3234.9	4	< 0.0001	743.21	2	< 0.0001
Response variable: Zn66						
	11901	4	< 0.0001	606.29	2	< 0.0001

Table S5.5 Dunn post-hoc test results of pairwise site comparisons of vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* in the Bristol Channel

Sites compared	**Z**	**p.unadj**	**p.adj**	**Z**	**p.unadj**	**p.adj**
Response variable:		**Arsenic**			**Cadmium**	
Barry v Langland	-0.115	0.91	1	53.206	0	0
Barry v Southerndown	0.097	0.92	0.92	-18.045	< 0.0001	< 0.0001
Langland v Southerndown	0.221	0.83	1	-76.031	0	0
Barry v Swansea	-62.513	0	0	55.439	0	0
Langland v Swansea	-60.925	0	0	9.013	< 0.0001	< 0.0001
Southerndown v Swansea	-67.293	0	0	74.253	0	0
Barry v Tenby	-43.989	0	0	37.023	< 0.0001	< 0.0001
Langland v Tenby	-42.268	0	0	-19.869	< 0.0001	< 0.0001
Southerndown v Tenby	-49.598	0	0	60.776	0	0
Swansea v Tenby	28.141	< 0.0001	< 0.0001	-26.602	< 0.0001	< 0.0001
Response variable:		**Chromium**			**Copper**	
Barry v Langland	43.234	0	0	60.174	0	0
Barry v Southerndown	24.704	< 0.0001	< 0.0001	51.877	0	0
Langland v Southerndown	-24.018	< 0.0001	< 0.0001	-16.648	< 0.0001	< 0.0001
Barry v Swansea	62.159	0	0	58.519	0	0
Langland v Swansea	24.027	< 0.0001	< 0.0001	6.113	< 0.0001	< 0.0001
Southerndown v Swansea	46.785	0	0	20.818	< 0.0001	< 0.0001
Barry v Tenby	16.813	< 0.0001	< 0.0001	-22.928	< 0.0001	< 0.0001
Langland v Tenby	-28.934	< 0.0001	< 0.0001	-84.915	0	0
Southerndown v Tenby	-7.257	< 0.0001	< 0.0001	-80.762	0	0
Swansea -v Tenby	-50.271	0	0	-79.407	0	0
Response variable:		**Lead**			**Uranium**	
Barry v Langland	16.748	< 0.0001	< 0.0001	42.451	0	0
Barry v Southerndown	-43.087	0	0	15.817	< 0.0001	< 0.0001
Langland v Southerndown	-59.815	0	0	-31.677	< 0.0001	< 0.0001
Barry v Swansea	4.388	< 0.0001	< 0.0001	32.656	< 0.0001	< 0.0001
Langland v Swansea	-9.914	< 0.0001	< 0.0001	-4.109	< 0.0001	< 0.0001
Southerndown -v Swansea	39.686	0	0	22.274	< 0.0001	< 0.0001
Barry v Tenby	-0.182	0.86	0.86	-2.019	< 0.05	< 0.05
Langland -v Tenby	-17.659	< 0.0001	< 0.0001	-46.263	0	0
Southerndown v Tenby	45.446	0	0	-19.030	< 0.0001	< 0.0001
Swansea v Tenby	-4.682	< 0.0001	< 0.0001	-35.392	< 0.0001	< 0.0001
Response variable:		**Zinc**				
Barry v Langland	71.108	0	0			
Barry v Southerndown	84.192	0	0			
Langland v Southerndown	2.284	< 0.05	< 0.05			
Barry v Swansea	65.847	0	0			
Langland v Swansea	3.998	< 0.0001	< 0.001			
Southerndown -v Swansea	2.472	< 0.05	< 0.05			
Barry v Tenby	15.619	< 0.0001	< 0.0001			
Langland -v Tenby	-59.184	0	0			
Southerndown v Tenby	-71.628	0	0			
Swansea v Tenby	-55.068	0	0			

Table S5.6 Dunn post-hoc test results of pairwise life stage comparisons of vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* in the Bristol Channel (YOY = young-of-year).

Response variable	Pairwise comparison	Z	P.unadj	P.adj
Arsenic	Adult vs Sub-adult	14.263	< 0.0001	< 0.0001
	Adult vs YOY	18.222	< 0.0001	< 0.0001
	Sub-adult vs YOY	9.684	< 0.0001	< 0.0001
Cadmium	Adult vs Sub-adult	-0.877	0.38	0.38
	Adult vs YOY	2.809	< 0.01	< 0.01
	Sub-adult vs YOY	5.845	< 0.0001	< 0.0001
Chromium	Adult vs Sub-adult	11.086	< 0.0001	< 0.0001
	Adult vs YOY	12.613	< 0.0001	< 0.0001
	Sub-adult vs YOY	4.985	< 0.0001	< 0.0001
Copper	Adult vs Sub-adult	-1.786	0.07	0.15
	Adult vs YOY	1.504	0.13	0.13
	Sub-adult vs YOY	4.994	< 0.0001	< 0.0001
Lead	Adult vs Sub-adult	21.694	< 0.0001	< 0.0001
	Adult vs YOY	28.752	< 0.0001	< 0.0001
	Sub-adult vs YOY	16.428	< 0.0001	< 0.0001
Uranium	Adult vs Sub-adult	25.139	< 0.0001	< 0.0001
	Adult vs YOY	26.387	< 0.0001	< 0.0001
	Sub-adult vs YOY	7.674	< 0.0001	< 0.0001
Zinc	Adult vs Sub-adult	16.306	< 0.0001	< 0.0001
	Adult vs YOY	1.784	0.07	0.07
	Sub-adult vs YOY	-20.155	< 0.0001	< 0.0001

Table S5.7 Wilcoxon rank sum test results of comparison by sex of vertebral heavy metal composition in smallspotted catsharks *Scyliorhinus canicula* in the Bristol Channel and English Channel regions

Wilcoxon rank sum test with continuity correction		
	W	**p-value**
Data = As75_ppm by Sex (alternative = less)		
	137385867	< 0.0001
Data = Cd111_ppm by Sex (alternative = greater)		
	191602558	< 0.0001
Data = Cr52_ppm by Sex (alternative = greater)		
	162464654	< 0.0001
Data = Cu63_ppm by Sex (alternative = less)		
	124828146	< 0.0001
Data = Pb208_ppm by Sex (alternative = greater)		
	192972992	< 0.0001
Data = U238_ppm by Sex (alternative = greater)		
	165727225	< 0.0001
Data = Zn66_ppm by Sex (alternative = less)		
	120775947	< 0.0001

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