Life history, ecology and management of blue sharks in the North Atlantic

Thesis submitted by

Sol Lucas

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School of Natural and Environmental Sciences
Newcastle University, Newcastle-upon-Tyne, NE1 7RU
United Kingdom

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Abstract

Overfishing has caused a decline of oceanic sharks and rays by over two thirds since 1970. Resilience to fishing pressure is informed by species-specific life history strategies, which are shaped by phylogeny, environment and individual energy budgets. Blue sharks (*Prionace glauca*) are potentially more resilient to fishing pressure, with their relatively high reproductive output compared to most other sharks. However, blue sharks are listed as Near Threatened on the IUCN red list, with declines of more than 50% across three generations in the North Atlantic. To support life history assessments and halt population declines, low-cost methods to assess blue shark growth and to mitigate fisheries bycatch are needed. In addition, the genetic population structure of blue sharks is unresolved, with contrasting evidence for panmixia and regional substructure, preventing effective conservation and management. This thesis aimed to investigate the relationship between shark life history strategies and conservation biology, assess blue shark genetic population structure, and test low-cost methods to assess body size and to reduce bycatch. The thesis starts by exploring the potential for sensory deterrents to reduce marine megafauna mortality in fisheries. The efficacy of sensory deterrents is context specific, depending on species biology, fishery and environmental characteristics. Next, life history strategies of 151 elasmobranch species are assessed using energy budget models. Elasmobranch life history strategies are structured along two axes: pace of life (the fast-slow continuum) and a reproductive strategy axis. Species' life history strategies, population growth rates and demographic resilience changed between a low and high feeding level. The thesis then develops and tests designs for low-cost stereo-video and laser photogrammetry systems. Stereo-video performed significantly better than laser photogrammetry in both pool and field trials, offering a cheap and accurate method to attain non-invasive length measurements of pelagic sharks. The thesis further assesses genetic structure of blue sharks for 307 individuals across eight global sampling locations. Subtle population substructure was found between one cluster in the eastern and southeastern Pacific and a second cluster for all other regions, which suggests they should be treated as independent management units. Finally, the thesis investigates behavioural response of blue sharks to ferrite magnet deterrents deployed on fishing lines. There was no significant difference in bait choices between control and magnet lines. Further development in sensory deterrents is required before implementation in fisheries. Overall, this thesis investigates conservation challenges and multidisciplinary assessment of blue sharks, with potential applications for fisheries management.

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Parts of the work described in this thesis have been presented in the following publications:

Publications & Author Contributions:

Thesis Chapter 1

Lucas, S. & Berggren, P., 2023. A systematic review of sensory deterrents for bycatch mitigation of marine megafauna. Reviews in Fish Biology and Fisheries 33:1-33. https://doi.org/10.1007/s11160-022-09736-5

Both authors contributed to the study conception, design and interpretation of data and writing of the manuscript. **Sol Lucas** acquired and analysed the data and wrote the original manuscript.

Thesis Chapter 2

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SL: Conceptualisation, Methodology, Formal analysis, Investigation, Validation, Data curation, Writing- Original draft preparation, Writing- Review & Editing, Visualisation; PB: Writing- Reviewing and Editing, Supervision; EB: Methodology, Formal analysis, Writing- Reviewing and Editing; IMS: Conceptualisation, Methodology, Formal analysis, Investigation, Validation, Data curation, Writing- Original draft preparation, Writing- Review & Editing, Visualisation, Supervision.

Thesis Chapter 2: Dataset

Smallegange, I.M. & **Lucas, S.**, 2024. DEBBIES Dataset to study Life Histories across Ectotherms. Sci Data 11 (153). https://doi.org/10.1038/s41597-024-02986-x

Isabel Smallegange - project conception – data acquisition – data validation – writing. **Sol Lucas** - data acquisition – data validation – proof reading.

Thesis Overview

Background and rationale

Marine megafauna (marine mammals, sea turtles, seabirds and elasmobranchs) play an important role in regulating and maintaining marine ecosystem health (Bjorndal and Jackson, 2002; Kiszka et al., 2015; Velarde et al., 2019; Heithaus et al., 2022). Effective conservation of these taxa are crucial, as their removal can cause serious detrimental impact on marine ecosystem balance, resilience and productivity (Daskalov, 2002; Myers et al., 2007; Heithaus et al., 2008). However, many species are highly threatened (Figure 0.1A), mainly due to mortality in fisheries as target catch and bycatch [Dias et al., 2019; Nelm et al., 2019; Dulvy et al., 2021; Fuentes et al., 2023; Figure 0.1B].

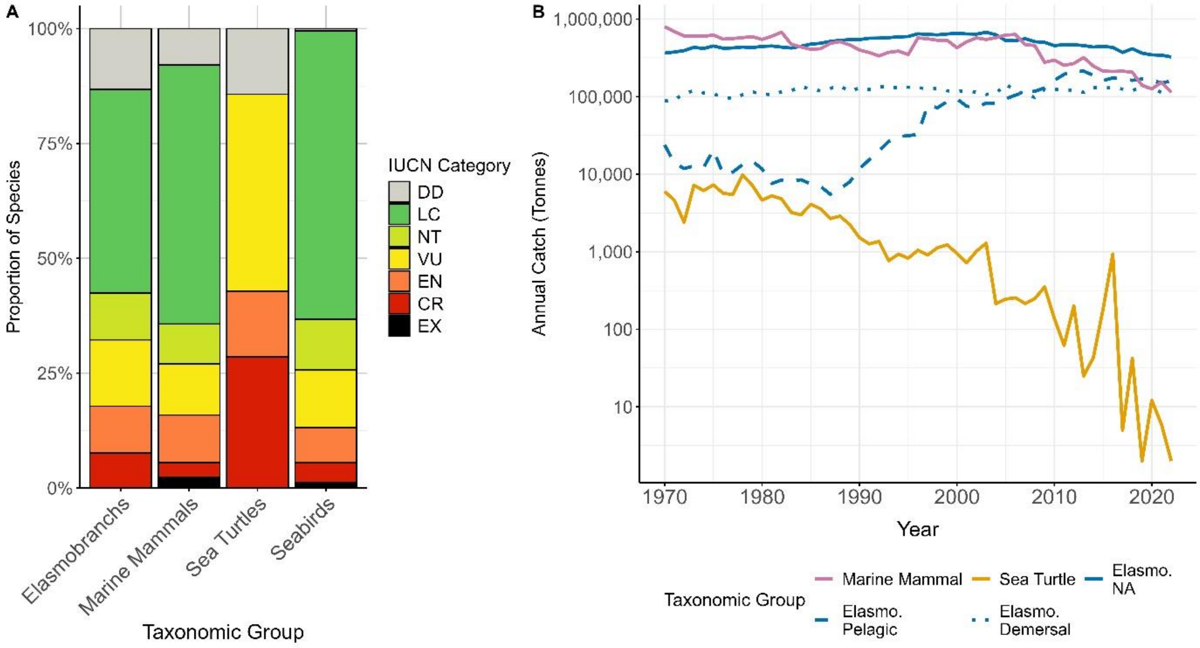


Figure 0.1 (A) Proportion of species in each conservation status category for elasmobranchs (n=1219), marine mammals (n=126), sea turtles (n=7) and seabirds (n=637) from the IUCN database (IUCN, 2025). (B) Total global fisheries catch (tonnes) of FAO landed catch FAO (2010-2022) by reporting country; (B) FAO landed catch (2010-2022) by taxonomic group for marine mammals (purple line), sea turtles (orange line) and elasmobranchs (seabird data were not available). FAO catch data were obtained using FishStatJ software (Version v4.04.00) (FAO, 2024) from the 'Global Capture Production' dataset to record total retained catch (for all fishing sectors but excludes discards). Elasmobranchs were split into pelagic (dashed blue line) and demersal (dotted blue line) species based on habitat types and descriptions of habitat

use on the IUCN red list database (IUCN, 2025) where available. Where species were not classified in FishstatJ, they were assigned to ‘Elasmobranch – NA’ (solid blue line).

Global catch figures show that landings of marine megafauna persists despite conservation concerns, and even increases in pelagic elasmobranchs (Figure 0.1B). Elasmobranchs are heavily exploited for their meat and fins, with an estimated 80 million individuals caught in fisheries each year (Worm et al., 2024). Over one third of elasmobranch species are threatened with extinction due to overfishing (Dulvy et al., 2021) and declines in shark abundance across coral reef (MacNeil et al., 2020; Sherman et al., 2023c), deep sea (Finucci et al., 2024) and pelagic (Pacoureau et al., 2021) ecosystems have prompted calls for catch restrictions. Efforts to regulate shark fishing practices have led to the establishment of national shark reserves and large no-take areas (Shiffman & Hammerschlag, 2016; Ward-Paige & Worm, 2017). Yet, sharks remain important commercial species and support fisheries globally (Dulvy et al., 2017). Legislation tackling the fin trade (e.g. Shiffman & Hammerschlag, 2016) has largely failed to reduce global shark mortality (Worm et al., 2024), and demand for shark meat has increased in some regions (Pincinato et al., 2022). Management and monitoring of fisheries and enforcement of regulations in large areas of open ocean is particularly challenging for the conservation of pelagic species (Letessier et al., 2017). Further, increases in fishing pressure over the last half century have led to steep declines (~71%) in the abundance of pelagic sharks and rays (Pacoureau et al., 2021). Despite declines in abundance, reports of landings for pelagic sharks have continued to increase (Figure 0.1B) highlighting the conservation challenge for these taxa.

The blue shark (*Prionace glauca*) is a globally distributed and highly migratory pelagic shark species. Blue sharks are the most frequently caught elasmobranch species worldwide and are common in the meat (Pincinato et al., 2022) and fin (Cardeñosa et al., 2018, 2020, 2022) trade, largely supplied by Spanish fisheries in the Atlantic (Figure 0.2A-B). Mainly caught in commercial longline fishing gear (Figure 0.2C), annual catch estimates are between 7-10 million individuals (Poseidon, 2022). While many sharks are vulnerable to high fishing pressure given their relatively slow life histories and low reproduction (Cortés, 2000), it is thought that blue sharks are resilient to exploitation (Cortés & Brooks, 2018) due to their relatively fast-paced life histories and fecundity (Nakano & Stevens, 2008; Aires-da-Silva et al., 2009; Smallegange & Lucas, 2024). Consequently, their IUCN conservation status is classified as Near Threatened globally (Rigby et al., 2019a). However, concerted fishing effort by pelagic longliners in the North Atlantic and Mediterranean has led to a regional assessment as Critically Endangered in the Mediterranean (Sims et al., 2016), and evidence suggests that they are

Endangered in the North Atlantic, with population declines exceeding 50% over the past three generations (Rigby et al., 2019b). Challenges in reconstructing fisheries catch data mean that actual catch rates may be higher than those reported (Pauly & Zeller, 2016), possibly exceeding the potential for biological removal of blue sharks in the North Atlantic (Aires-da-Silva et al., 2009). Accurate catch statistics, as well as basic life history data are essential for regional fisheries management organizations (RFMOS), such as the International Commission for the Conservation of Atlantic Tunas (ICCAT), to project population trajectories, assess exploitation risks, and develop effective management (Smith et al., 1998; Cortés, 2002; Winemiller, 2005; ICCAT, 2023a).

Blue sharks conduct annual trans-Atlantic migrations (Figure 0.3; Nakano & Stevens, 2008) following productivity (Druon et al., 2022) and sea surface temperature (Queiroz et al., 2016) fronts. Their movements are segregated by sex and maturity class, with females and juveniles occurring in cooler, higher latitudes compared to males (Maxwell et al., 2019; Fujinami et al., 2021). The North Atlantic and Mediterranean could represent distinct populations (Nikolic et al., 2023; Leone et al., 2024), as little movement is observed between ocean basins (e.g. Sippel et al., 2011; Kohler & Turner, 2019), leading to the suggestion that there is no mating between populations in the global north and south (da Silva et al., 2010). Nursery areas in the North Atlantic are thought to be located around seamounts in the central North Atlantic (e.g. near the Azores; (Aires-da-Silva et al., 2008; Vandeperre et al., 2014a; 2014b). These nursery areas and productivity fronts share a high spatial overlap with Spanish and Portuguese longline fishing hotspots (Queiroz et al., 2016). These fisheries are known to retain blue shark catch for trade (mainly to southeast Asia and South America; Poseidon, 2022), but approximately one third of the catch is discarded (Figure 0.2D). Effective management of blue sharks requires consideration of new evidence of their population structure, reduction of wasteful bycatch and addressing the impact of overlap with commercial longline fishing hotspots.

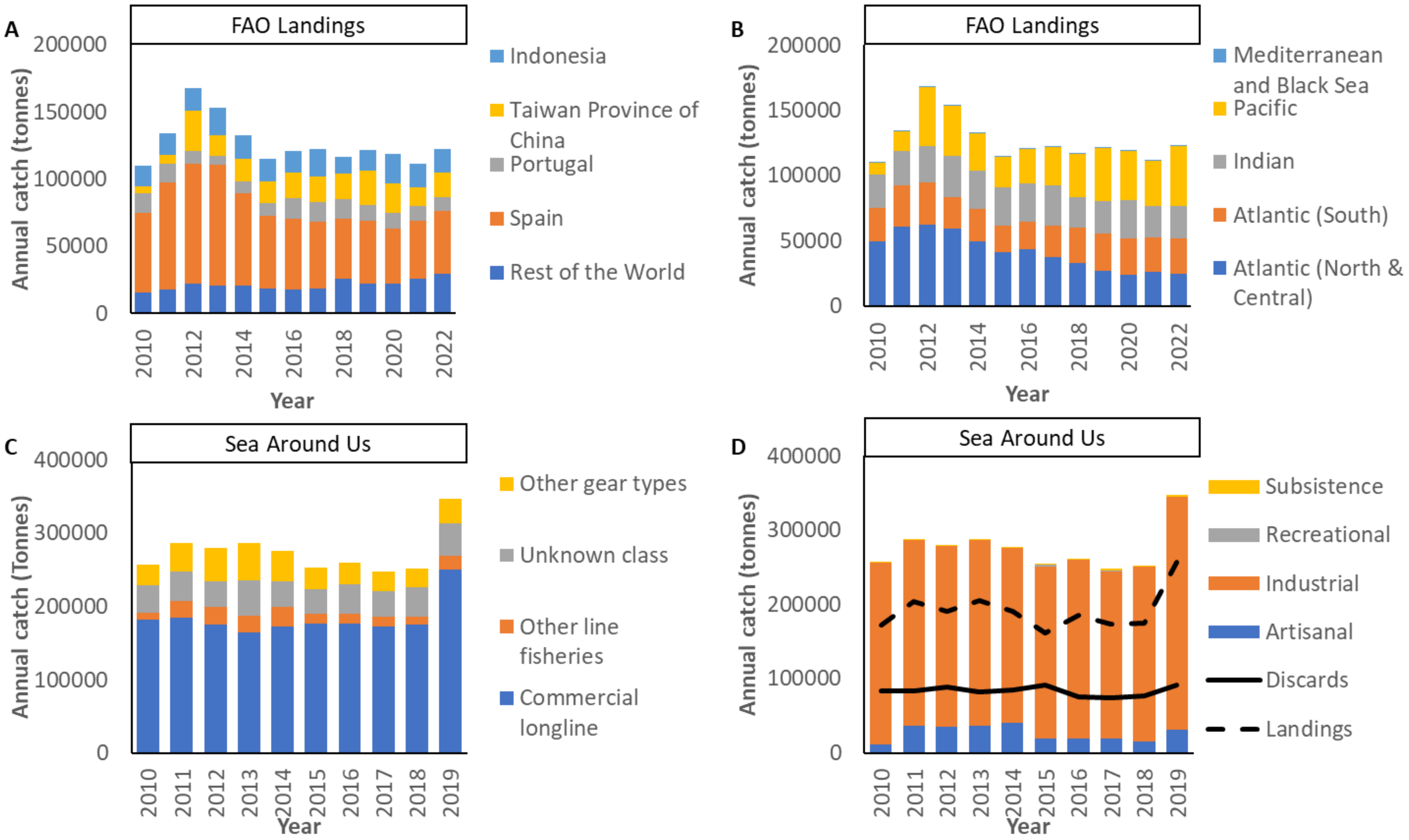

A
FAO Landings
Annual catch (tonnes)
0
50000
100000
150000
200000
2010
2012
2014
2016
2018
2020
2022
Year
Indonesia
Taiwan Province of China
Portugal
Spain
Rest of the World
B
FAO Landings
Annual catch (tonnes)
0
50000
100000
150000
200000
2010
2012
2014
2016
2018
2020
2022
Year
Mediterranean and Black Sea
Pacific
Indian
Atlantic (South)
Atlantic (North & Central)
C
Sea Around Us
Annual catch (Tonnes)
0
100000
200000
300000
400000
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year
Other gear types
Unknown class
Other line fisheries
Commercial longline
D
Sea Around Us
Annual catch (tonnes)
0
100000
200000
300000
400000
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year
Subsistence
Recreational
Industrial
Artisanal
Discards
Landings

Figure 0.2 Total global fisheries catch (tonnes) of blue shark from (A) FAO landed catch FAO (2010-2022) by reporting country; (B) FAO landed catch (2010-2022) by FAO major fishing areas; (C) Sea Around Us (2010-2019) reported catch by gear type; and (D) Sea Around Us total catch by fishing sector, with landings (dashed black line) and discards (solid black line) shown. FAO catch data were obtained using FishStatJ software (Version v4.04.00) (FAO, 2024) from the 'Global Capture Production' dataset to record total retained catch (for all fishing sectors but excludes discards) reported for blue sharks. Downloaded global Sea Around Us catch reconstruction data for blue sharks (reports by fishing sector and discard data; (Pauly et al., 2020).

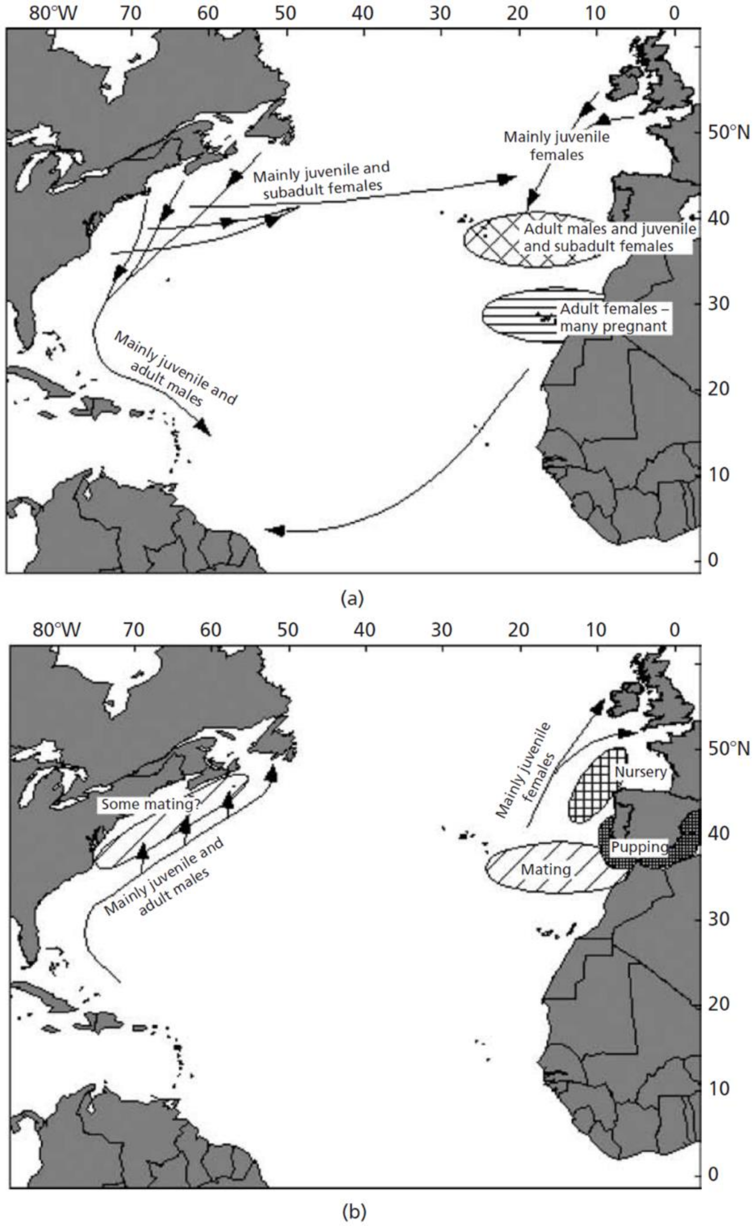


Figure 0.3 Map of migration pathway for blue sharks in the North Atlantic during (a) autumn–winter and (b) spring–summer, taken from Nakano & Stevens (2008).

Problem statement

Effective conservation and management of shark species require a holistic assessment of population health, including accurate catch estimates (Pauly & Zeller, 2016), demography (Winemiller, 2005), and population genetic structure to identify regional management units (Waples et al., 2008; Hohenlohe et al., 2021). Multidisciplinary research is essential to accurately assess the risks to blue sharks in the North Atlantic and develop strategies to reduce bycatch and promote the conservation of the most frequently caught shark species in the world.

The aim of this thesis is to investigate the relationship between elasmobranch life history strategies and conservation biology (Chapter 2), test low-cost methods to measure blue shark growth (Chapter 3) and mitigate their bycatch in fisheries (Chapter 1 and 5), to address information gaps in blue shark population structure (Chapter 4), and to provide recommendations for future research to enhance their conservation and management in the North Atlantic (Chapter 6) (Figure 0.4).

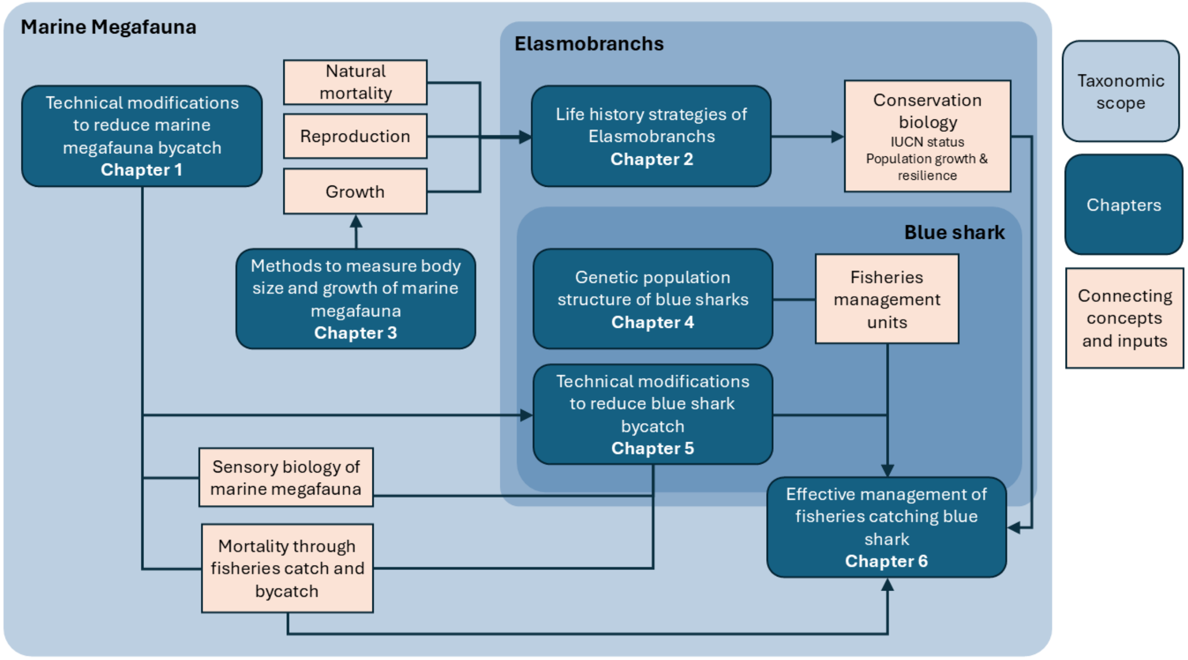


Figure 0.4 Conceptual framework diagram linking topics in this thesis together to provide a holistic understanding of blue shark conservation and fisheries management in the North Atlantic. The thesis starts with the broadest taxonomic scope, assessing the suitability of sensory deterrents to reduce bycatch of marine megafauna (Chapter 1). For effective fisheries management interventions, it is crucial to assess catch levels, methods to reduce bycatch and resilience to fisheries pressure. Therefore, next this thesis investigates how elasmobranch life history strategies link to conservation biology (Chapter 2). The models used in Chapter 2 are

parameterised by life history traits related to growth survival and reproduction. In Chapter 3, I develop a low-cost non-invasive measurement system to provide body size and growth data on marine megafauna. Next, the thesis investigates blue shark conservation and management, first, by assessing blue shark global genetic population structure (Chapter 4). Then in Chapter 5, after identifying a gap in the literature for sensory deterrents in Chapter 1, the thesis tests the efficacy of ferrite magnets as a deterrent for blue sharks in hook and line fisheries. Finally, Chapter 6 brings together findings from this thesis to provide specific recommendations for conservation and management of blue sharks in the North Atlantic.

Chapter 1. A systematic review of sensory deterrents for bycatch mitigation of marine megafauna

1.1 Abstract

Marine megafauna are critical for marine ecosystem health and their removal can cause food webs to collapse. Methods to reduce marine megafauna mortality can result in conflict between scientists, conservationists, fishers and fisheries management due to real or perceived effects on target catch, income and food security. Sensory deterrents have been used in attempts to mitigate bycatch and retain target catch quantity and quality. Here, we completed a systematic review of 116 papers, plus 25 literature reviews published between 1991 and 2022, to investigate potential for sensory deterrents to mitigate bycatch across four marine megafauna taxonomic groups (marine mammals, sea turtles, seabirds and elasmobranchs). Lights on gillnets are the only technology so far to result in significant bycatch reductions across all four taxonomic groups. It is difficult to make generalisations about the efficacy of sensory deterrents and their ability to deliver consistent bycatch reductions. The efficacy of each method is context dependent, varying with species, fishery and environmental characteristics. Further research is recommended for field studies assessing bycatch mitigation in all sensory deterrents, including combinations of deterrents, to assess effects on target and non-target species. The associated issues of habituation, habitat exclusion and foraging around fishing gear are important, although reducing mortality of vulnerable species should remain the highest priority for conservation and preserving ecosystems that fishers depend on. Multiple complementary measures will be required to achieve consistent bycatch reduction targets in many fisheries, of which sensory deterrents could play some part if implemented appropriately.

1.2 Introduction

Fisheries pose direct threats to marine megafauna (here defined as marine mammals, sea turtles, seabirds and elasmobranchs) through both targeted fishing and bycatch (Lewison et al., 2004, 2014; Žydelis et al., 2009). Given the k-selection life cycle of many megafauna species (low fecundity, slow growth rate, late maturity), populations face the risk of collapse if bycatch is not managed (Dent & Clarke, 2015). Marine megafauna provide vital ecosystem services, so their position in marine food webs must be safeguarded to ensure ecosystem and fishery health (Kiszka et al., 2015; Hammerschlag et al., 2019). The removal of apex predators can cause trophic cascades, leading to collapse or re-structuring of food webs (Daskalov, 2002; Heithaus et al., 2008), threatening the livelihoods of commercial and small-scale fishers, coastal communities that depend on them and potentially having widespread conservation impacts.

Given the consequences of marine megafauna mortality, bycatch mitigation is critical to preserving ecosystems and fisheries. Estimates for the annual mortality of marine megafauna in fisheries are shown in Table 1.1.

Table 1.1 Marine Megafauna estimated annual mortality in fisheries and data sources. Seabird data pooled for longlines and gillnets using two sources.

Megafauna Group	Annual mortality of individuals (millions)	Bycatch data period	Reference
Marine Mammals	0.53-0.82	1990-1994	(Read et al., 2006)
Sharks	63-273	2000-2010	(Worm et al., 2013)
Sea Turtles	0.85-8.5	1990-2008	(Wallace et al., 2010)
Seabirds	0.56-0.72	1980-2011	(Anderson et al., 2011; Žydelis et al., 2013)

The impact of bycatch in commercial fisheries is known to be substantial, exacerbating the pressures on populations from climate change, habitat degradation, pollution and ocean acidification (Barbraud et al., 2012; Senko et al., 2020). Estimates for the magnitude of bycatch (Table 1.1) have wide ranges and likely under-estimate true values, in part due to the threat of poorly understood small-scale fisheries (SSFs) (e.g. Worm et al., 2013). It is estimated that there are over 50 million fishers in SSFs (FAO, 2016), making up more than 95% of the fishers worldwide (Pauly, 2006). The SSF industry contributes multiple socio-economic benefits, including food security, development of coastal communities and poverty alleviation (Béné, 2006). Continued poor regulation and enforcement of policy make marine food webs vulnerable where SSFs exist (Pinnegar & Engelhard, 2008). Poor management of these fisheries means that highly destructive practices, such as dynamite fishing, still occur in some regions (Katikiro & Mahenge, 2016). Reliable catch data are difficult to obtain due to the presence of illegal, unregulated and unreported (IUU) catch (Gallic & Cox, 2006), which can occur in all fisheries, making it difficult to assess quantity and impact of fisheries and fisheries bycatch.

All major gear types contribute to bycatch, including line fisheries, gillnets, trawls, pots/traps and seines (Lewison et al., 2004). Line fisheries are defined here as any fishery using a line and baited hooks (e.g. longlines, pole and line). Gillnets include both capture fisheries (set nets and drift nets) and bather protection (beach nets). Pots and traps are varied, including lobster pots, fish traps and pound nets. Bycatch of marine megafauna occurs either by chance entanglement in passive gear (nets and some traps), chance entanglement in active gear (purse seines and trawls), or being attracted via sensory cues, such as olfaction from prey in and around gear or bait plumes on hooks, as well as visual attractants like fish aggregating devices (FADs) used in purse seines or lights in line and net fisheries (Chumchuen et al., 2019). The associated issue of depredation (herein referred to as ‘foraging around fishing gear’, as suggested in Bearzi and Reeves (2022)) occurs where animals feed on target catch already caught in gear. Foraging around fishing gear is a common recurring issue in some fisheries (Brill et al., 2009; Hamer et al., 2012; Guinet et al., 2015; Santana-Garcon et al., 2018; Lucchetti et al., 2019). Although this paper does not focus on foraging around fishing gear, the solutions are likely congruent with bycatch reduction. Indeed, foraging around fishing gear increases bycatch risk of animals coming into contact with gear, as well as impacting fishing efficiency by damaging gear and reducing target catch (Tixier et al., 2021).

Bycatch mitigation methods are designed to reduce incidental catch of non-target species. Reductions in fishing effort, catch limits and time-area closures offer alternatives to complete cessation of activity. Other methods to address mortality include changing gear type, gear-escape options, post-capture release by the fisher and technical devices that alert or deter animals from the gear to avoid entanglement (Werner et al., 2006). Changing gear can reduce bycatch, although the perceived potential for reducing target catch can make this unpopular with fishers (Lucchetti et al., 2019). Escape from gear can be facilitated by fisher behaviour in some cases (Basran et al., 2020), but is more common in the form of excluder devices on nets. These consist of turtle excluder devices (TEDs), seal exclusion devices (SEDs), sea lion exclusion devices (SLEDs) and devices for dolphins or other marine megafauna (Werner et al., 2006; Hamilton & Baker, 2019). Weakened rope is used in some pot/trap fisheries, where the line between the trap and the surface buoy is made such that a whale can break it (Trippel et al., 2008). Similarly, hooks in longline fisheries can be attached to weaker monofilament leaders so megafauna can break them and escape (Favaro & Côté, 2015). As with any interaction between marine megafauna and fishing gear, escape options can risk injury and affect post-release survival of individuals (Hamilton & Baker, 2015). Post-capture release can involve no change to the gear by simply releasing all non-target catch, or altering gear to increase the chance of survival while hooked to gear and after release. For example, circle hooks rather than J hooks have reduced mortality of sea turtles on longlines (Watson et al., 2005). Gear modifications have been effective in multiple contexts, but modifications may fail, cause mortality, injury, or remain on the animal after escape (Campana et al., 2016). Each of these methods must be researched further to evaluate long-term efficacy.

Technical strategies are intended to avoid contact with gear involve changing the behaviour of the animal by stimulating a sensory reaction which, if successful, renders exclusion and release unnecessary, as the animal would not interact with gear in the first place. Examples include the use of acoustic alarms (pingers), emitting sounds within the hearing range of odontocetes to alert and deter them from gear (Kraus et al., 1997), or the use of magnets to repel sharks (Robbins et al., 2011). By using technical adaptations designed to provide sensory cues to avert contact with gear (herein referred to as 'sensory deterrents'), the likelihood of entanglement or post-release mortality in non-target species may be reduced. In contrast to time-area closures, if used effectively in the right circumstances, sensory deterrents could allow fishers to continue fishing practises, receive income and provide food security for coastal communities.

Effective solutions for mitigating bycatch should (1) reduce mortality of at least one bycatch species without increasing mortality in other groups, (2) maintain target species catch quantity and quality where possible (without overfishing target catch), (3) be cost effective, (4) be viable for implementation in fisheries and (5) provide biologically relevant bycatch reductions, rather than small, but statistically significant reductions. The key challenge of reducing bycatch using sensory deterrents is that the capabilities of animals, both across and within groups, varies enormously and can overlap with target species.

By mitigating contact with gear, foraging around fishing gear may be addressed too, which reduces potential gear damage and can lead to increased target catch (Richards et al., 2018). However, animals can be highly motivated by the promise of food rewards and can be attracted by sensory cues where they are designed to deter other species, such as the 'dinner bell' effect of pingers, attracting pinnipeds to gillnets and increasing their risk of entanglement (Dawson et al., 2013). Neither escape options or post-capture release directly address foraging around fishing gear, and the risk of initial gear contact remains. This is in contrast to time-area closures or catch limits, where fishing activity is halted, so the fishers may lose out, which makes these solutions difficult to implement in many locations. The focus of this review is on bycatch mitigation using sensory deterrents, due to their potential for reducing animal contact with fishing gear, reducing bycatch and associated issues such as foraging around fishing gear.

All marine megafauna groups have the same core senses: vision, hearing, olfaction and touch. The senses are known to work in broadly the same way in all groups, with the exception of gustation (taste), which is poorly understood in marine species, so chemosensory detection is combined as olfactory for the purposes of this review (Southwood et al., 2008). Odontocetes, unlike other marine megafauna, can echolocate, using adapted tissue structures to produce and transmit click sounds (dorsal bursae complex, air sacs and melon) and lower mandibles to receive signals used in communication, navigation and foraging (Au, 1993). Elasmobranchs have two additional sensory specialisations, electrosensory and mechanosensory. The electrosensory system, facilitated by the jelly-filled ampullae of Lorenzini, can detect electrical and magnetic fields, used in prey detection and navigation (Kalmijn, 1982) and the mechanosensory lateral line for detecting pressure changes and vibrations in the water (Maruska, 2001).

Previous reviews on the topic of sensory technologies have mainly focused on single species or single groups of marine megafauna (e.g. Southwood et al., 2008; Friesen et al., 2017; Hamilton and Baker, 2019). Others identify multi-taxa mitigation options based on one taxonomic group and then generalise to other groups, or only focus on the effects of one technology across groups (e.g. Martin and Crawford, 2015; Gilman et al., 2020). In contrast, this review focusses on using sensory technologies in an attempt to avert contact and reduce mortality of multiple marine megafauna groups with fishing gear. The aim of this paper is to assess the potential of sensory deterrents for mitigating bycatch of marine megafauna in commercial and small-scale fisheries. The objectives of this study are (1) to summarise the development of sensory deterrents for reducing bycatch of marine megafauna in a systematic map, (2) to evaluate the efficacy of sensory deterrents and the potential for combining multiple technologies for maximum mitigation across taxa, and (3) to identify areas for future research in the field.

1.3 Methods

A literature search was completed using ROSES (RepOrting standards for Systematic Evidence Syntheses) protocols for systematic maps in conservation and environmental management (Haddaway et al., 2018). Scopus, WebOfScience and Proquest databases were searched up to and including 28/10/2021, then again up to and including 22/02/2022. The Title, Abstract and Keywords of each paper were searched using the string *((sense OR (sensory AND (biology OR ecology))) OR behavio*) AND (bycatch OR "incidental catch" OR "incidental capture") AND (mitigat* OR reduc*) AND ("marine mammal" OR cetacean* OR seal OR pinniped* OR elasmobranch* OR shark* OR ray* OR chondrichthy* OR seabird* OR "marine megafauna" OR turtle* OR reptile*)*. Duplicates were removed, then titles and abstracts screened, followed by a full text screening. Additional papers were sourced using unstructured citation checking. All papers that were excluded, could not be sourced, or could not be accessed were recorded in a CSV file. Authors of papers that could not be accessed were contacted via ResearchGate.

The screening process was documented using the ROSES Report (Online Resource 1; https://doi.org/10.1007/s11160-022-09736-5) is shown in Figure 1.1. Included papers had to focus on (1) bycatch (either field study, review or lab study testing a bycatch reduction technology), (2) sensory deterrents, (3) marine megafauna (marine mammal, sea turtle, elasmobranch, seabird) and additionally (4) be peer-reviewed in academic journals. Papers were excluded if they violated any inclusion criteria. Excluded papers were generally those that discussed foraging around fishing gear, habituation and/or other behaviour around gear or detection of gear, without mentioning one of the three inclusion criteria or linking them together. The addition of extra papers from unstructured citation checking was subjective, chosen to address the aim of this review and meeting the inclusion criteria. Papers containing sufficient evidence of false results, for example due to confounding variables or pseudo-replication, were included for the narrative, but excluded from the data extraction step. Review articles were included in this study for background information, but not in the data extraction step, to avoid duplication of results reported by these publications in the synthesis. Grey literature were sourced in the search but excluded from the synthesis, due to their variable quality, however, some key grey literature reports were retained for background information due to their importance in the development of sensory deterrents.

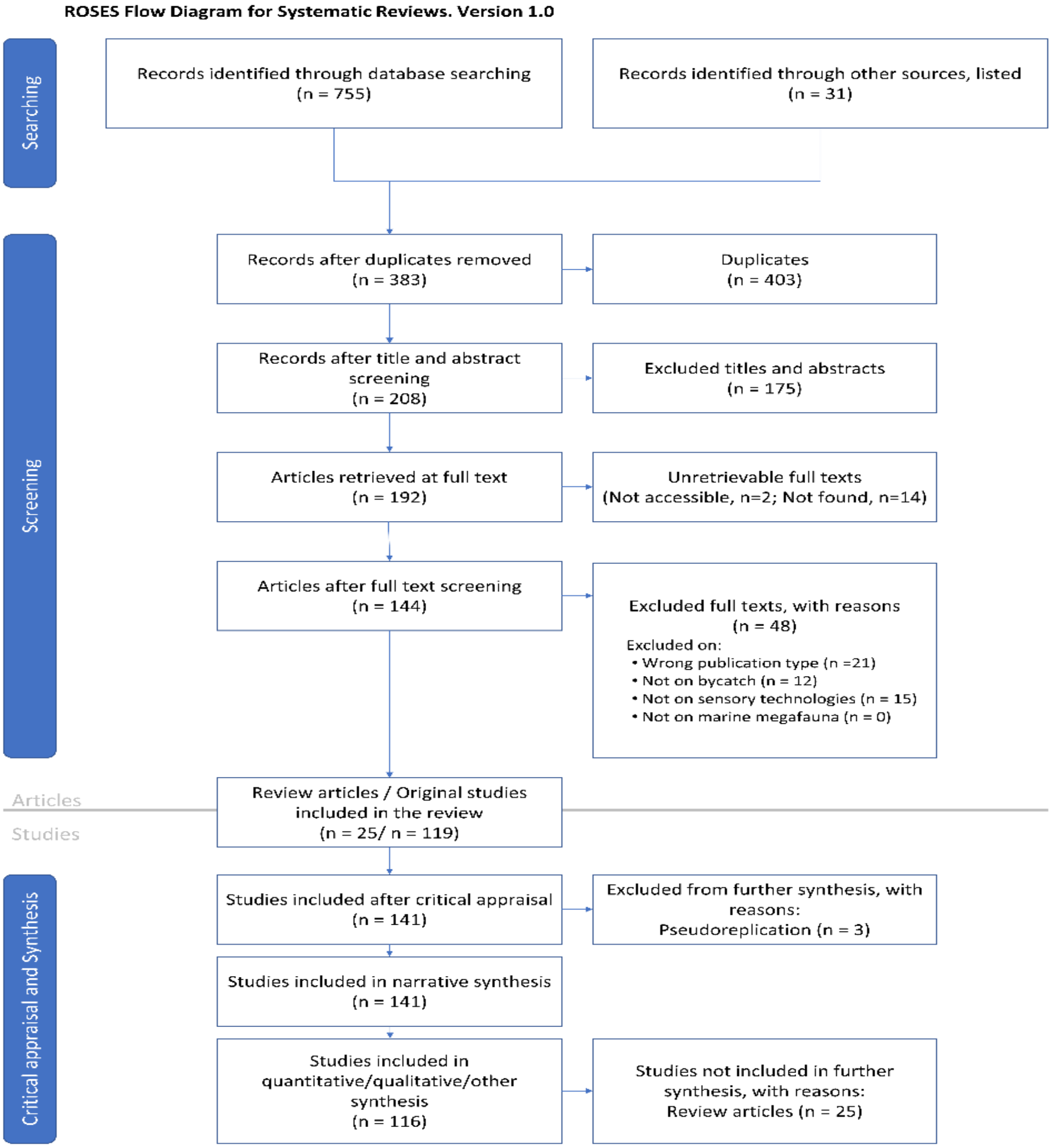


Figure 1.1 Flowchart detailing the literature screening process. Full details of the screening process can be found in (Haddaway et al., 2017, 2018). A report detailing the protocol for this study can be found in Online Resource 1 (https://doi.org/10.1007/s11160-022-09736-5). The outputs represent 116 studies investigating sensory bycatch mitigations in trials and 25 review papers, which are included in the narrative but excluded from the data extraction and analysis.

1.3.1 Data extraction

Data were extracted from all included papers into a CSV file (Online Resource 2; https://doi.org/10.1007/s11160-022-09736-5), which was imported into RStudio version 1.4.1106 for the synthesis (R Core Team, 2023; RStudio Team, 2023). Taxonomic information was recorded according to megafauna group (marine mammal, seabird, sea turtle, elasmobranch) to species, or the next lowest taxonomic level, and matched to the latest conservation status (IUCN, 2021). The study contexts were split into three categories: field, lab and desk study. Field studies were those using sensory deterrents compared to a control to measure bycatch directly, or behaviour of animals subject to bycatch risk around gear. Lab studies were those in captive conditions measuring a behavioural change to a sensory deterrent against a control, in the context of bycatch reduction. Desk studies were those indirectly assessing bycatch mitigation potential of a sensory deterrent by either conceptual or modelling means, including the design or suggestion of novel untested mitigation options.

Gear type was recorded for each study, including concept and proof of concept, for studies based on theory and studies completed in the lab without fishing gear, respectively. Study location details included continent, ocean and country. Mitigation details were recorded in four columns: mitigation sense, mitigation class, mitigation type and technology (e.g. acoustic, acoustic deterrent device, pinger, Aquatec PICE 50-100kHz). Potential for bycatch reduction was classed as Yes, No, Partial or Data Deficient based on study results, where Yes indicated support for the technology reducing bycatch, No indicated no support, Partial indicated some support or conflicting results and Data Deficient indicated a sample size too small to get a significant result. Significance level against controls were recorded as Yes, No, Data Deficient or Not Reported, where Yes indicated a significant result (p-value <= 0.05), No indicated a non-significant result, Data Deficient indicated a sample size too small and Not Reported indicated results where a significance level was not reported in the study. The basis of the results (e.g. bycatch reduction, avoidance response), any recorded effect on target catch and notes on the results were recorded, followed by basic bibliographic information and coding. Papers are identifiable in the extraction form by a Bibtex key, title, year and a unique paper number. Each paper was labelled as a Search or Addition, where Search papers were retrieved in the initial database search and Addition papers were sourced by unstructured citation checking.

1.3.2 Data and narrative synthesis

All papers from the data extraction step were included in the systematic mapping results by constructing graphs on study year, focal taxonomic group, fishing gear, mitigation method and a heatmap linking the number of studies for each sensory system against the marine megafauna groups to identify research gaps. The graph on study count by year was made up of the counts of individual papers. The other graphs and heatmap were made up of counts of each row entry on the data extraction sheet, representing trials, rather than the counts of individual studies (e.g.

if a study was on the response of three different species to two different models of pingers, there would be six rows in the data extraction form). This means that the count of entries in the data extraction form is a proxy for the coverage of studies and that a higher number of entries for one paper compared to another means a higher representation in the study coverage in the heatmap. The systematic mapping results were used in the narrative synthesis to describe the development of sensory bycatch mitigation technologies, which include the reviews from the literature search and key grey literature (sourced separately from the search). The synthesis of the results in two Venn diagrams were completed only using the field-based studies.

1.3.3 Mitigation types

A summary of the types of sensory technologies are shown in Table 1.2, as well as the sensory systems of each megafauna group. The technologies described in Table 1.2 are not separated by gear or target taxonomic group, but detail all available options retrieved from the literature search. Other sensory deterrents may exist in literature outside the search for this study, so those in the table may not represent an exhaustive list. Multiple options can potentially be used in conjunction with each other, as well as combination with non-sensory bycatch mitigation, such as time-area closures or catch limits. Tactile deterrents (including the mechanosensory lateral line) are recorded in Table 1.2 but are excluded from the rest of the review. All surfactants detailed in the literature search fit into olfactory chemical and semiochemical deterrents. No evidence of water jets or pre-net fences were described in peer-reviewed studies beyond reviews (e.g. Jordan et al., 2013). Physical barriers either fit into visual deterrents (such as artificial kelp in physical models) or are primarily used to prevent foraging around fishing gear rather than bycatch reduction, as is the case for hook sleeves (Hamer et al., 2012). Escape options are excluded because, despite some excellent results and promise for reducing bycatch of turtles (Cox et al., 2007), they are not designed to avert contact with marine megafauna, but rather to reduce mortality after contact with gear is made. Exclusions and unobtainable references are listed in Online Resource 3 (https://doi.org/10.1007/s11160-022-09736-5).

Table 1.2 All sensory technologies described in the peer reviewed literature in studies relating to bycatch reduction. Pooled across all taxa and gear types. Underneath see sensory modalities available to each megafauna group (indicated by an X).

	Sensory System					
	Acoustic	**Olfactory**	**Tactile**	**Visual**	**Echolocation**	**Electrosensory**
Mitigation Type	**Acoustic Deterrent Device (ADD):** an electronic device emitting pre-programmed sounds, including pinger or other artificial sound **Acoustic Harassment Device (AHD)**: similar to an ADD but designed to scare or harass, including loud electronic devices such as 'seal scarers', 'bombs', other explosives or air guns **Acoustic Reflection:** acoustic reflection devices (see Echolocation column) for creatures that cannot echolocate	**Semiochemical:** chemical extraction from an organism **Chemical:** manufactured or non-naturally extracted chemical **Alternative Bait Type:** bait on hooks (e.g. fish bait instead of squid) **Offal Discard Management:** Dumping waste from bait or fish while setting fishing gear	**Water Jet:** water hose or cannon deterrent **Escape Option:** physical exclusion, including turtle excluder device (TED), seal exclusion device (SED) or sea lion exclusion device (SLED) **Physical Barrier:** includes bait surround or shroud or physical model (see Visual column) **Surfactant:** Chemical deterrent reducing surface tension (see Olfactory column as repellent mechanism not fully understood)	**Lights:** LEDs in various wavelengths including UV, chemical lightsticks, strobes, vessel deck lights **Physical Model:** various structures providing a visual alert: predator cut-outs, shape models, piping, artificial kelp, looming eye buoys, high contrast panels, tori (bird scaring) lines **Gear Colour:** changes to standard gear colour including lines and nets **Bait Colour:** blue, yellow or red dye added to bait	**Acoustic Reflection Device:** an addition to gear designed to reflect biosonar, including net material alterations (barium sulfate, iron oxide, air filled tubes) and acrylic spheres	**Electropositive Metal (EPM) Alloy:** Rare earth metal alloy reacting with seawater and generating an electrical potential **Magnet:** pulsed magnetic field, permanent ferrite or rare earth magnet **Electrode Array:** pulsed electric field or microprocessor-controlled unit (MCU) **Modified Hook:** SMART (selective magnetic and repellent-treated with electropositive metal) hooks combining both EPMs and magnets
Odontocetes	X	X	X	X	X	
Other Mammals	X	X	X	X		
Elasmobranchs	X	X	X	X		X
Sea Turtles	X	X	X	X		
Seabirds	X	X	X	X		

1.4 Results

From the literature search 116 studies were included in the systematic map database and narrative synthesis. Additionally, 25 review articles were included in the narrative synthesis (Online Resource 4; https://doi.org/10.1007/s11160-022-09736-5). The 116 included studies resulted in 388 entry rows (trials) on the data extraction form, of which 312 were results taken from the field that were eligible for use in the Venn diagrams, corresponding to 90 unique papers. The number of papers published each year from the literature search are shown in Figure 1.2, showing the recent development of the field, the paucity of studies found before 2000 and the increase in study numbers after 2010. There were no studies sourced in the search from before 1991. The continent on which the field study papers were conducted are displayed in Figure 1.3, where NA indicates that the study was done in the lab. Of the studies in North America, 25 were in the USA or Canada. In Oceania all studies were in Australia or New Zealand. There is a general lack of studies in developing nations or locations where SSFs fleets are widespread. The gear type investigated in each study are shown in Figure 1.4, where ’proof of concept’ or ‘concept’ indicates that it was a lab experiment. Gillnets and longlines dominate the gear types in the field trials, with relatively little representation from other gears. For further context, see the data extraction form (Online Resource 2; https://doi.org/10.1007/s11160-022-09736-5).

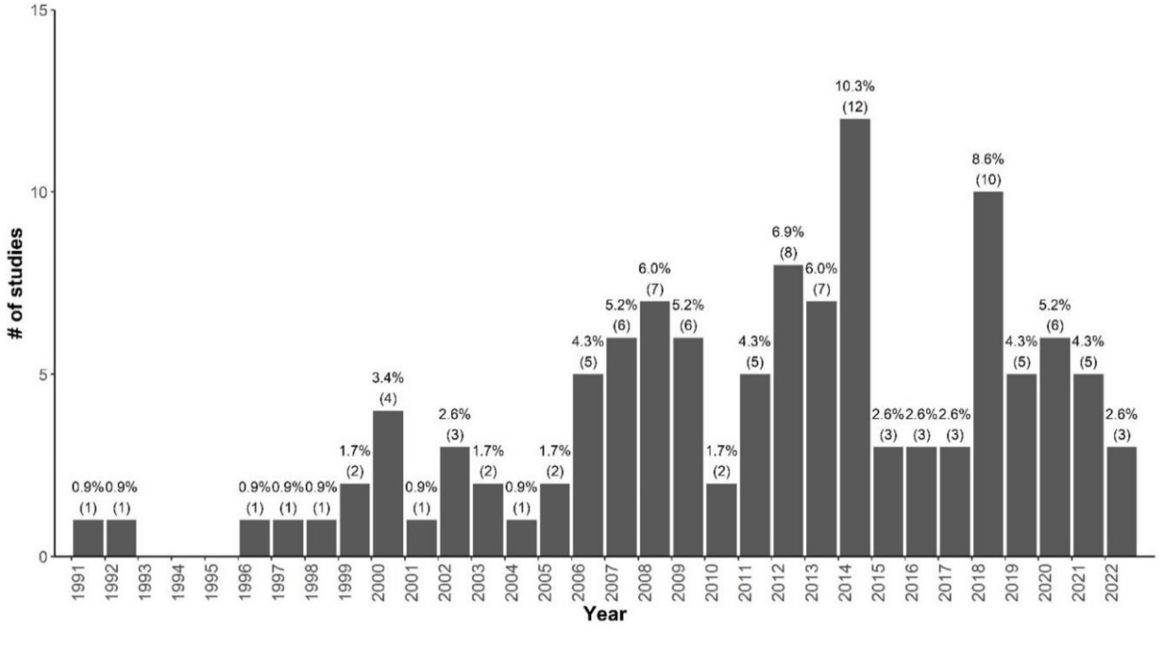


Figure 1.2 Study count by year for all 116 studies included from the literature screening process, which does not include the 25 review papers. Results range from 1991 to 2022.

Numbers on top of the bars in the format A(B) where A is the proportion of studies published out of all 116 studies found and B is the number of studies.

The following sections summarise the development of sensory technologies for marine megafauna by taxonomic group. The narrative includes papers sourced in the systematic search, highlighting some key grey literature which appeared before peer-reviewed studies in the development of technology, as well as seminal earlier work in peer-reviewed literature contributing to the development of deterrents. Comprehensive reviews on sensory technologies for each megafauna group exist. For seabirds see Gilman et al. (2005); Bull (2007); Martin and Crawford (2015); Friesen et al. (2017). For sea turtles see Southwood et al. (2008); Gilman et al. (2010); Echwikhi et al. (2011). For elasmobranchs see Cliff and Dudley (1992); O’Connell et al. (2011b); Jordan et al. (2013); O’Connell et al. (2014g); Favaro and Côté (2015); Hart and Collin (2015). For marine mammals see Dawson (1991); Jefferson & Curry (1996); Dawson et al. (1998, 2013); Hamer et al. (2012); Read (2013); Schakner & Blumstein (2013); Hamilton & Baker (2019). Mitigation of more than one taxonomic group are addressed in Werner et al. (2006); Cox et al. (2007); Martin & Crawford (2015); Gilman et al. (2020) In general, before the 1970s there was little published effort to reduce bycatch of marine megafauna, possibly because the problem was not well identified and ecological impacts were poorly understood.

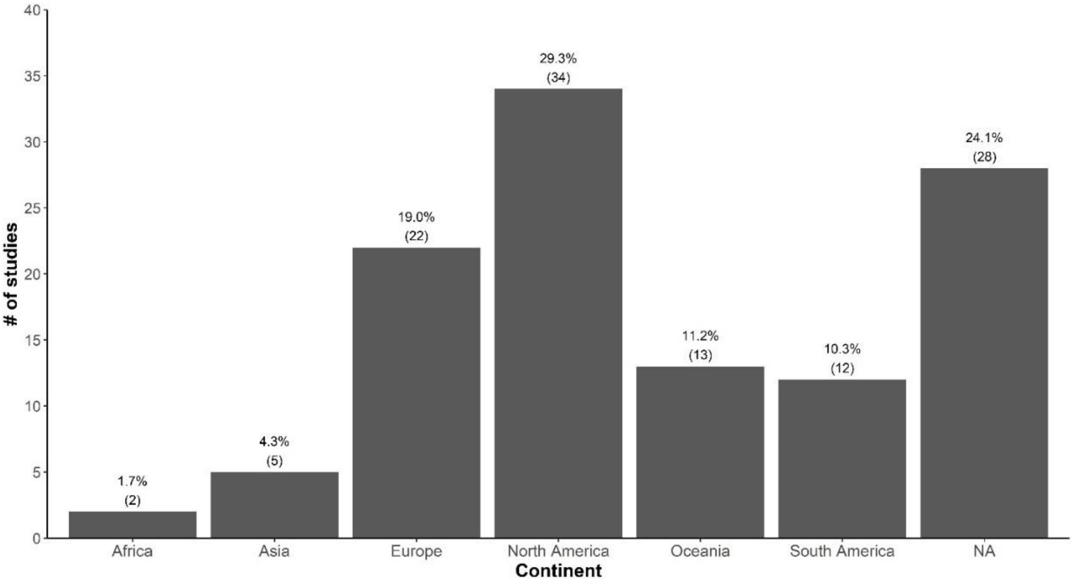


Figure 1.3 Study count by continent for the 116 field studies sourced in the literature screening process. All studies completed in a lab are shown as NA and review papers are not included. Study oceans and countries are detailed in Online Resource 1 (https://doi.org/10.1007/s11160-

022-09736-5). Numbers on top of the bars in the format A(B) where A is the proportion of studies published out of all 116 studies found and B is the number of studies.

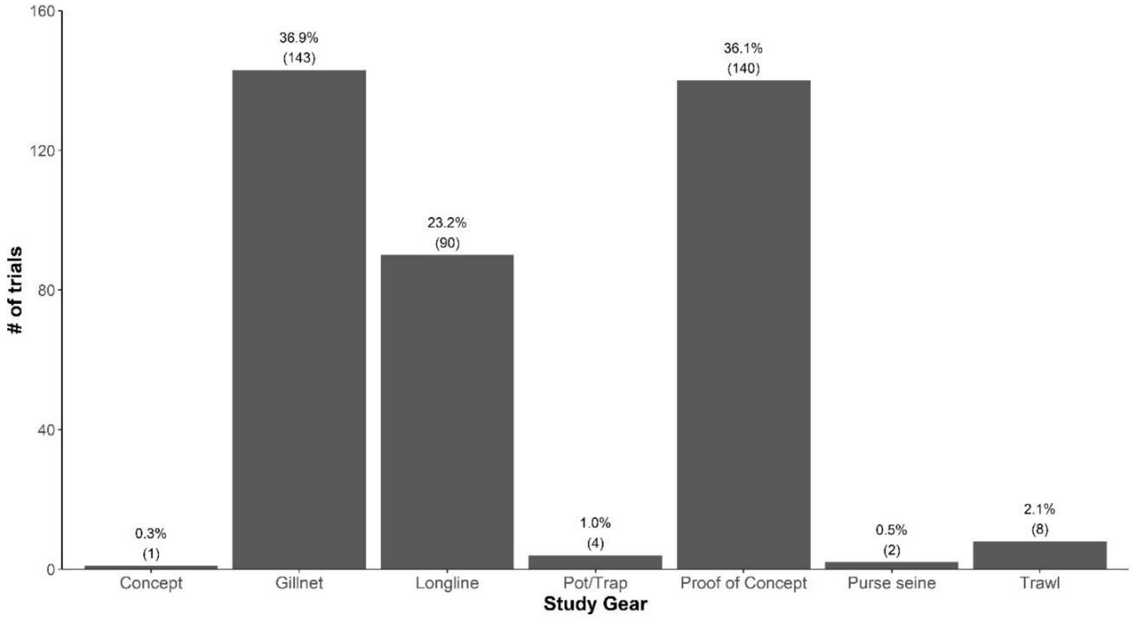


Figure 1.4 Trial count by gear for the 388 total trials in the 116 studies sourced in the literature screening process. All lab studies completed are shown as 'proof of concept' or 'concept'. Review papers are not included. Details can be found in Online Resource 1 (https://doi.org/10.1007/s11160-022-09736-5). Numbers on top of the bars in the format A(B) where A is the proportion of trials published out of all 388 trials found and B is the trial count.

1.4.1 Elasmobranchs

Acoustic

Acoustic shark deterrents have had little attention since initial experiments on the aversive responses of sharks to killer whale (*Orcinus orca*) calls in the 1970s (Myrberg et al., 1978). More recently, 'artificial sounds' (20Hz – 20kHz) have been trialled in combination with strobe lights, successfully deterring small shark species (*Heterodontus portusjacksoni* and *Hemiscyllium ocellatum*) from taking baits in a lab setting (Ryan et al., 2018). However, sound alone did not deter even the small species and neither stimulus, used on its own or in combination, caused significant behavioural change in wild white sharks (*Carcharodon carcharias)*. Chapuis et al. (2019) investigated the effects of playback of two distinct sound stimuli on eight shark species, using a modified baited remote underwater video systems (BRUVS) rig. They found that the 'artificial sound' (20Hz – 10kHz, with 95% of its energy under 1kHz) deterred all eight species, although this was only a partial deterrent effect on white sharks. A wild killer whale call, recorded in Australia, deterred the seven reef and coastal shark species tested in Australia but not white sharks in South Africa, although the authors noted that white sharks may be sensitive to regionally-specific killer whale calls (Chapuis et al., 2019). The authors also raised concerns about the effects anthropogenic noise could have on sharks, particularly given the deterrent effect of the artificial sound on reef and coastal species. Hearing, sound use and behavioural responses to acoustic cues are little studied in elasmobranchs, so this area calls for further investigation (Mickle & Higgs, 2022).

Olfactory

Elasmobranchs have highly sensitive olfactory systems which, although they vary between species, play a key role in prey detection and offer potential in commercial fisheries if a deterrent can be found that does not alter target species behaviour (Jordan et al., 2013). Early efforts were made to develop chemical shark repellent devices for military personnel during World War II. Decades of investigation produced conflicting results in semiochemicals from dead sharks (primarily ammonium acetate and copper acetate) and the apparent failure of tactile chemesthetic repellents (toxins), so research on these compounds was halted (Hart & Collin, 2015). Recent developments in chemical repellents have focused more on bycatch reduction than personal protection, involving the use of semiochemicals from dead sharks (’necromones’), which caused total cessation of feeding and temporary evacuation of shark species, without affecting teleost feeding behaviour (Stroud et al., 2014). Research for elasmobranch bycatch reduction in longlines has investigated effect of bait type, rather than chemical aversion. Replacing squid with fish baits reduced bycatch in elasmobranchs (Watson et al., 2005), as they did for turtles, although studies since have found species-specific bait preferences, with mixed results for fish and squid bait (Coelho et al., 2012).

Visual

The SharkSafe barrier, which combined permanent magnets with PVC pipe or artificial kelp, was presented as an alternative to gillnets used in fisheries or for bather protection on beaches (O’Connell et al., 2014a). Even on their own, the visual stimuli triggered increased avoidance responses and decreased entrance frequencies through the barrier in large species, including white sharks, bull sharks (*Carcharhinus leucas*) and great hammerheads (*Sphyrna mokarran*) (O’Connell et al., 2014a, 2014f; 2015). The use of lights to deter sharks has had mixed success. Strobe lights reduced bait strikes by small species in lab conditions but not wild white sharks (Ryan et al., 2018). In gillnet fishery trials, Mangel et al. (2018), Virgili et al. (2018) and Bielli et al. (2020) reported that green and UV-LEDs did not reduce elasmobranch catch. However, recently green LEDs caused a significant decrease of 95% in elasmobranch catch in Peruvian gillnets, although the study used a small sample size (28 paired sets) and measured change in biomass caught rather than individual animals (Senko et al., 2022).

Electrosensory

After the introduction of beach nets to protect bathers in South African waters in the late 1960s and early 1970s, initial experiments began to develop an electrical shark barrier to prevent human-shark interactions (Smith, 1974). Similar to the early chemical studies, electrical shark repellents were designed for personal use rather than bycatch mitigation in fisheries. The SharkPOD (Protective Oceanic Device) and Shark Shield Freedom7 began commercial marketing of repellents, although efficacy of these personal deterrent devices is questionable and results have been mixed (Huveneers et al., 2013, 2018).

Electrosensory bycatch mitigation research began in the 2000s by testing the effects of rare earth magnets, ferrite magnets and electropositive 'mischmetals' on elasmobranch foraging success, avoidance behaviour and bycatch levels. Rare earth metals and mischmetals exhibited mixed results from early lab and field trials (Kaimmer & Stoner, 2008; Stoner & Kaimmer, 2008; Brill et al., 2009; Tallack & Mandelman, 2009), whereas cheaper ferrite magnets were successful in causing avoidance responses in multiple species (Rigg et al. 2009; O'Connell et al. 2010). Initial promise of neodymium-based electropositive alloys in lab experiments (Jordan et al., 2011) did not translate to field studies, where bycatch of most species remained unchanged, with the exception of significantly reduced bycatch of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) (Robbins et al., 2011; Hutchinson et al., 2012; Godin et al., 2013; McCutcheon & Kajiura, 2013). Jordan et al. (2011) described that the presence of conspecifics may invoke competitive feeding behaviours which override any deterrent effect of magnets and that the magnetic field may actually attract individuals in these situations. Smith and O'Connell (2014) and Siegenthaler et al. (2016) both conducted controlled lab experiments using neodymium-based rare earth magnets to successfully deter foraging attempts of three elasmobranch species, conflicting with a later lab study on sand tiger sharks (*Carcharias taurus*) that showed no effect (Polpetta et al., 2021). Field trials of rare earth magnets have resulted in mixed responses of Australian swellshark (*Cephaloscyllium laticeps*) in trap fisheries (Westlake et al., 2018) and increased bycatch of blue shark (*Prionace glauca*) in longlines (Porsmoguer et al., 2015).

Meanwhile, SMART hooks (selective magnetic and repellent-treated with electropositive metal) were developed and tested on longlines, with nine recorded elasmobranch species caught (O'Connell et al., 2014d; Grant et al., 2018). Grant et al. (2018) reported that Greenland sharks (*Somnius microcephalus*) exhibited no behavioural response to SMART hooks and that their powerful inertial suction feeding may have negated any potential deterrent effects. In O'Connell et al. (2014d), skate bycatch was reduced when species were pooled together. At the species level, only spiny dogfish (*Squalus acanthias*) catch reduced significantly (28.2%), although bycatch was still high, with 930 individuals on SMART hooks and 1296 on controls. Favaro and Côté (2015) commented that statistically significant, but not sufficiently large bycatch reductions, combined with the challenges in implementing in commercials fisheries makes electrosensory deterrents unsuitable for widespread use, suggesting that monofilament nylon leaders, or raised longlines (for demersal species) are more effective ways to reduce elasmobranch bycatch in longline fisheries.

There have been multiple trials using ferrite magnets which show potential to reduce elasmobranch mortality in place of beach nets (O'Connell, et al., 2011a; 2014a; 2014e O'Connell & He, 2014). As mentioned, the development of the SharkSafe barrier, a combination of ferrite magnet and visual deterrents, triggered increased avoidance behaviours of several large shark species targeted by beach nets, including white, bull, lemon (*Negaprion brevirostris*) and great hammerhead sharks (O'Connell et al. 2014a, 2014c, 2014f, 2015). O'Connell and He (2014) report that efficacy of these barriers may not extend to rays and small shark species in nets, although alterations in barrier spacing may resolve this. However, the use of ferrite magnets could reduce bycatch of small shark species in trap fisheries, with an increase in target catch rates (Richards et al., 2018).

Recent developments involve use of pulsing electrical and magnetic signals to illicit aversive responses and reduce bait consumption (Howard et al., 2018; Polpetta et al., 2021). Howard et al. (2018) presented positive results in deterring feeding in sandbar sharks (*Carcharhinus plumbeus*) using electric fields from an electrode array, but bimodal bait consumption in groups of spiny dogfish, with either 0% or 100% of baits being taken during trials. Pulsed electrical or magnetic fields have triggered some aversive behaviour in captive largetooth sawfish (*Pristis pristis*) and sand tiger sharks respectively, although these subtle responses found in controlled conditions may not be sufficient to prevent capture in active fisheries (Abrantes et al., 2021; Polpetta et al., 2021).

Inconsistent results investigating magnetic deterrents across species and in various contexts can be due to multiple factors, including conspecific or heterospecific density, individual satiation, water visibility, salinity and the species tested (O’Connell et al., 2014g). Hutchinson et al. (2012) and Porsmoguer et al. (2015) argued that the limitations and cost of magnetic repellents make it challenging to establish generalisations about their efficacy, and therefore, they are currently unsuitable for implementation as bycatch reduction technologies. There is a consensus that further research in this area should be encouraged due to the unique sensory capabilities and potential for bycatch reduction of elasmobranchs found across multiple studies (e.g. Tallack and Mandelman, 2009; Jordan et al., 2013; O’Connell et al., 2014g; Hart and Collin, 2015; Polpetta et al., 2021), however in the meantime, it is necessary to pursue alternative bycatch mitigation options until electrosensory repellents are proven to be consistently effective in a variety of contexts (Favaro & Côté, 2015).

1.4.2 Seabirds

Acoustic

Pingers were tested alongside visual deterrents after initial trials of pingers with marine mammals. Melvin et al. (1999) found that bycatch of common murres (*Uria aalge*) was reduced by 50% with the introduction of pingers (1.5kHz), although there was no such reduction in bycatch of rhinoceros auklets (*Cerorhinca monocerata*).

Olfactory

Cherel et al. (1996) found that strategic offal discard was effective at deterring procellariiform birds from attempting to take bait or alighting on longlines. In factory stern trawlers where, unlike longlines, there is no olfactory or visual attraction from bait, offal discharge has caused increased contact rates with gear and consequent mortality (Sullivan et al., 2006; Kuepfer et al., 2022). As well as gear differences, discarding offal may have species-specific effects, by reinforcing the behaviour of birds attending vessels (Weimerskirch et al., 2000).

Pierre and Norden (2006), found that shark liver oil was successful at deterring flesh-footed shearwaters (*Ardenna carneipes*) and other seabird species (pooled) from diving behind vessels. In Norden and Pierre (2007), four chemicals were tested on procellariiform seabird assemblages in New Zealand. None of the chemicals had any significant effect on the behaviour of species in the family *Diomedea*, or on giant and cape petrels (*Macronectes giganteus, Macronectes halli, Daption capense*). However, ’fisher oil’ (directly extracted from school shark, *Galeorhinus galeus,* livers) significantly reduced numbers of birds gathering behind vessels and number of dives in flesh-footed shearwaters (Norden & Pierre, 2007). Fewer flesh-footed shearwaters and black petrels (*Procellaria parkinsoni*) were present behind vessels using fisher oil and commercial shark liver oil. Two commercial fish oils (Alaskan pollock and Peruvian anchovy) had the same effect in flesh-footed shearwaters only. These results highlighted the species-specific differences in deterrents, with repellent effects found on the burrow-nesting procellariiformes but not those with different life histories and ecology within the same order. Incidentally, this supports the indication that these chemicals work as olfactory deterrents rather than tactile chemesthesis (Norden & Pierre, 2007). Species specific differences in reaction to olfactory and visual stimuli are discussed in Friesen et al. (2017), who suggested multi-modal signals, by using multiple sensory cues, would have the greatest efficacy and broadest species coverage to mitigate seabird fishery interactions.

Visual

Cherel et al. (1996) commented that seabird bycatch was reduced when deck lights on longlining vessels were switched off during night sets, although not whether this was statistically significant. Night setting is believed to reduce bycatch because fewer birds are active at night or cannot locate baited hooks purely from olfactory cues alone (Cherel et al., 1996; Bull, 2007). Seabird scaring lines (herein referred to as tori lines), for use in longline fisheries, first appeared in grey literature reports in the early 1990s (Bull, 2007). Løkkeborg (1998) reported consistent significant reductions in seabird bycatch and interactions with Norwegian longline vessels using tori lines. Continued research provided further positive evidence (Lokkeborg & Robertson, 2002), although weather conditions, line quality and setting height (unique for each vessel) all affected performance (Brothers et al., 1999).

Meanwhile, in drift gillnet fisheries, Melvin et al. (1999) found that bycatch of common murres was reduced by 40-45% when the upper 20-50 meshes were replaced with mesh made of white twine, as a visual alert. Bycatch of rhinoceros auklets was significantly reduced (42%) when the upper 50 meshes were replaced with mesh made of white twine, with no significant change in bycatch by changing the upper 20 meshes only. Trippel et al. (2003) found significant bycatch reductions of great shearwaters (*Ardenna gravis*) using barium sulfate nets coloured blue, with 94 caught in 121 control nets and 11 in 72 test nets, although the authors note that this effect could be due to increased net stiffness. Blue-dyed bait trials successfully mitigated albatross interactions in swordfish and tuna longline fisheries (Gilman et al., 2005), although dyed bait may not be as effective as side-setting and underwater chutes, which attempt to prevent any contact with bait (Gilman et al., 2007a). Cocking et al. (2008) found that both blue-dyed fish and squid baits reduced strikes of birds in the family *Procellariidae* in Australian longlines, although the effect of blue-dyed fish diminished with time. It should be noted that the paired trial observations in this study may be non-independent due to the presentation of both blue and unaltered bait simultaneously, rather than each bait type being presented one at a time. Bait type may also mitigate procellariform bycatch too, although results have been conflicting, with some species preferring squid (Gonzalez et al., 2012), while others prefer fish (Li et al., 2012).

Deterrent lasers, such as the SeaBird Saver appear in grey literature (van Dam et al., 2014), but in no peer-reviewed studies. These devices may repel seabirds in the short term, but long-term efficacy is not known (Pierre, 2018) and the impact of lasers on bird eye health should be investigated before further implementation of this technology.

Research on tori lines continued with investigations of diversified methods, line and streamer designs in seabird bycatch reduction. Light streamer designs had no significant effect on bycatch of two albatross species in Japanese longlines, compared to traditional designs (Sato et al., 2012). However, Domingo et al. (2017) found that bycatch of six albatross and petrel species was not significantly different between tori line use and controls, although when pooled across all species, procellariiform bycatch was significantly reduced.

Recent visual deterrent investigations on gillnets have considered the use of lights, high contrast panels and gear colour on avoidance behaviour and bycatch (Hanamseth et al., 2018; Mangel et al., 2018; Field et al., 2019). Hanamseth et al. (2018) reported orange gillnets increased aversive reactions of little penguins (*Eudyptula minor*) compared to green and clear line, although these were in controlled lab conditions and did not measure effects on target catch. Studies on lights have described species-specific responses. Bycatch of long-tailed ducks (*Clangula hyemalis*) increased with the use of white LEDs in Baltic gillnets, while there was no significant difference in bycatch of velvet scoters (*Melanitta fusca*) and no significant difference in bycatch for either species with green LEDs (Field et al., 2019). Field et al. (2019) also showed that high contrast panels, as suggested in Martin & Crawford (2015), caused no significant change in duck bycatch compared with controls without panels. Further evidence of the effect of lights on ducks was presented in Cantlay et al. (2020), who found that long-tailed ducks were attracted by a white flashing LED, with no effect of three different wavelengths of light in lab trials. In contrast to the ineffectiveness of LEDs on ducks, Mangel et al. (2018) reported that Guanay cormorant (now *Leucocarbo bougainvilliorum*) bycatch was significantly reduced by 85.1% by using green LEDs in Peruvian gillnets. In the same area, Bielli et al. (2020) reported an 84% reduction in seabird bycatch using green LEDs, although statistical significance was not reported. Looming eye buoys (rotating panels with eye spots, attached to a buoy) are a promising development in deterring seabirds, with significant reductions of long-tailed duck abundance within 50m of the modified buoys compared to controls (Rouxel et al., 2021). In this study, habituation trials were confounded by the seasonal presence of migrating ducks, so further research was suggested to investigate the long-term deterrent capabilities of looming eye buoys (Rouxel et al., 2021).

1.4.3 Marine mammals

Acoustic

Sensory technologies designed to deter marine mammals emerged in the late 1970s and 1980s with the introduction of acoustic reflectors and pingers in gillnets (Dawson, 1991). Pinger studies began with research on Dall's porpoise (*Phocoenoides dalli*) bycatch in Japanese gillnets and entanglement of humpback whales (*Megaptera novaeangliae*) in Canadian cod traps (Lien et al., 1992; Hatakeyama et al., 1994). The efficacy of pingers was initially difficult to assess due to variable study designs, reporting standards and marginal results (Dawson, 1994; Dawson et al., 1998). Jefferson and Curry (1996) argued that despite promising results with pingers, small, but significant, bycatch reductions may be insufficient to address bycatch problems and consistent reductions would need to be achieved using independent observers before implementation in fisheries. Kraus et al. (1997) presented the first well-designed study in peer-reviewed literature, providing empirical evidence that bycatch of harbour porpoise (*Phocoena phocoena*) was significantly reduced by introducing 10kHz pingers to gillnets in the Gulf of Maine.

Field studies continued to present significant bycatch reductions in harbour porpoises, using pingers in various frequency ranges from 10-160kHz (Trippel et al., 1999; Gearin et al., 2000; Newborough et al., 2000). These were backed up by behavioural studies displaying harbour porpoise avoidance responses, however, no avoidance behaviour was witnessed in striped dolphin (*Stenella coeruleoalba*) in captive trials (Kastelein et al., 2000, 2001, 2006; Teilmann et al., 2006). Results from studies on other marine species were more variable. Pingers were determined to have a 'dinner-bell' effect on some species of pinniped, including harbour seal (*Phoca vitulina*) and South American sea lion (*Otaria flavescens*), both of which were attracted to or attacked nets significantly more when pingers were active (Melvin et al., 1999; Bordino et al., 2002). Other non-echolocating mammals, such as dugongs (*Dugong dugon*), exhibited no behavioural change when close to 4 or 10kHz pingers (Hodgson et al., 2007), highlighting that bycatch technologies should not be implemented in fisheries before thorough testing on bycatch species. Cox et al. (2004) reported no avoidance response from common bottlenose dolphins (*Tursiops truncatus*) around gillnets equipped with pingers, except reduced entry into a 100m buffer around nets when the alarms were active. The results from Cox et al. (2004) and

Kastelein et al. (2006) provided evidence that not all odontocetes avoid pingers, perhaps explained by behavioural flexibility in these species (Dawson et al., 2013). In contrast, Barlow and Cameron (2003) conducted a study on gillnets on the USA Pacific coast, where there were significant reductions in bycatch of odontocetes and pinnipeds (pooled across species – eight odontocetes and two pinnipeds), which were led by significant bycatch reductions of 85.1% and 68.9% in common dolphin and California sea lion respectively. Similar success was demonstrated with the Franciscana dolphin (*Pontoporia blainvillei*), where implementation of 10kHz pingers achieved a significant 85.7% bycatch reduction in Argentinian gillnets (Bordino et al., 2002).

Some pinger studies investigating the behavioural responses of small odontocete cetaceans have been subject to pseudo-replication, leading to inflated sample sizes and potentially false results (Dawson & Lusseau, 2005, 2013). Culik et al. (2001) and Stone et al. (1997) found that active pingers significantly increased surfacing distances in harbour porpoise and Hector's dolphin (*Cephalorhynchus hectori*) respectively. Monteiro-Neto et al. (2004) described significant reductions in surfacing activity of Tucuxi (*Sotalia fluvatilis*) in quadrants close to active pingers, compared to trials using inactive pingers. However, the surfacing positions used in these three studies do not take into account individual animals or groups, so are not statistically independent (Dawson & Lusseau, 2005) and are therefore excluded from the data extraction step in this review.

Species-specific reactions to pingers continued to be demonstrated, with Carretta et al. (2008) reporting significant reductions in beaked whale bycatch using 10-12kHz pingers in gillnets (pooled across species). Bottlenose dolphin interaction with gillnets reduced with deployments of Aquatec pingers (5-160kHz) in field trials (Brotons et al., 2008). Further captive pingers trials on three pinniped species and three odontocete species displayed at least partial aversion in each (Bowles & Anderson, 2012), although it is important to consider that these trials in captive animals may not translate to real world scenarios. However, net interaction in three species was observed, including foraging attempts of harbour seals and California sea lions around gear, as well as agonistic behaviour towards gillnets by Commerson's dolphins (*Cephalorhynchus commersonii*) (Bowles & Anderson, 2012). Studies on harbour porpoises continued to produce positive significant results, either by directly measuring bycatch of individuals (Gönener & Bilgin, 2009), or increased avoidance behaviour (Carlström et al., 2009), each using 10-12kHz pingers. Trials of an alternative 40-120kHz acoustic alarm significantly reduced harbour porpoise bycatch in Danish gillnet fisheries (Larsen & Eigaard, 2014). Another alternative design, the Porpoise Alarm (PAL, 133kHz), imitating wild porpoise calls, triggered increased surfacing distance of harbour porpoises compared to controls by 19-30m, although with commercial pingers the surfacing distance was increased by at least 321m (Culik et al., 2015). Carretta and Barlow (2011) continued work in the same California fishery as Barlow and Cameron (2003), finding bycatch reductions of common dolphin and northern elephant seal (*Mirounga angustirostris*), but increases in bycatch of California sea lion. The increases in sea lion catch were attributed to behavioural changes during an El Niño year, reduction in fishing fleet size and a potential ’dinner-bell’ effect.

Hamer et al. (2012) suggested a toolbox of solutions may be needed to reduce bycatch, on a case-by-case basis for each fishery including technical mitigation options, fisher behaviour and management strategies, rather than a single technical gear modification, such as pingers, which may be ineffective at deterring some species. This approach was successful in the Gulf of Maine fishery, where a Take Reduction Plan paired time-area closures with pingers caused drastic reductions of porpoise bycatch from 1990 to 1999, to below target levels (Read, 2013). However, harbour porpoise bycatch in this region has fluctuated since 1999, with annual bycatch exceeding potential biological removal (PBR) since 2008 (Orphanides, 2012; Dawson et al., 2013). Harbour porpoise bycatch has dropped below PBR since 2017 (e.g. NOAA, 2021), however, this case study highlights the importance of continued engagement with fishers and management authorities.

Research into Australian shark nets, gill nets, traps and trawls tested pinger efficacy on a number of mammal species (Erbe & McPherson, 2012; Soto et al., 2013; Harcourt et al., 2014; Pirotta et al., 2016; Santana-Garcon et al., 2018). Erbe and McPherson (2012) calculated that humpback whales, dugongs and dolphin species should be able to detect both 3kHz and 10kHz pingers from at least 40m and 110m respectively, although detection of nets may not be sufficient to repel these animals. Indeed, pingers (2-5kHz) were ineffective at triggering avoidance responses of humpback whales during behavioural experiments (Harcourt et al., 2014; Pirotta et al., 2016), bottlenose dolphins from trawls (Santana-Garcon et al., 2018) and only minor behavioural responses in both Australian snubfin dolphin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphin (*Sousa chinensis*) (Soto et al., 2013). Meanwhile, studies on small odontocetes continued to display either positive results for potential bycatch reduction (Mangel et al., 2013; Clay et al., 2019; Kindt-Larsen et al., 2019), or inconclusive results (Bilgin & Kose, 2018). Despite potential bycatch reductions of small odontocetes, pingers could cause habitat exclusion (Carlström et al., 2002). Agent-based modelling has revealed that combinations with time-area closures could solve this for harbour porpoise populations and allow access to key foraging grounds (van Beest et al., 2017).

Acoustic harassment devices were found to be ineffective when humpback whale behaviour was unaffected by a ’seal scarer’ in an Icelandic purse seine fishery (Basran et al., 2020). In contrast, the authors reported that in two separate incidents, two humpback whales were encircled by the purse seine gear, but escaped through a 100m opening in the net while standard pingers were active (Basran et al., 2020). However, this combination of pingers and fisher behaviour (by leaving the net open to allow escape) would need verification in controlled trials to be confirmed as an effective and viable bycatch mitigation option for purse seines. Reviewing bycatch mitigation options for marine mammals, Hamilton and Baker (2019) concluded that pingers would be effective at deterring some species, but further research is required to address a range of taxonomic groups and fisheries. ‘Seal safe’ banana pingers (50-120kHz) increase avoidance responses in vulnerable Franciscana dolphins, although this effect is fairly small, with 19.4% reductions in surfacing frequency close to the pinger and 15% at 100m (Paitach et al., 2022). Significant reductions of bycatch and increased avoidance behaviour in harbour porpoises continue, adding to the evidence base that pingers are effective for at least some small odontocetes in gillnet fisheries globally (Chladek et al., 2020; Omeyer et al., 2020; Königson et al., 2021).

Olfactory

No marine mammal olfactory studies using primary data were sourced in the peer-reviewed literature. Discard management is discussed in Bonizzoni et al. (2022), referencing grey literature as a potential to reduce bycatch of both seabirds and marine mammals in Australian trawl fisheries.

Visual

Preliminary observations showed that cape fur seals (*Arctocephalus pusillus*) displayed little reaction to the artificial kelp SharkSafe barrier (O’Connell, 2014b), benefiting the case for removing entangling beach nets as these barriers may repel sharks but not impact non-target marine mammals, although further research is required to verify this. Recent developments in sensory technologies have indicated that visual deterrents may be effective at reducing marine mammal bycatch. Green LEDs resulted in a 70.8% and 66.7% reduction in small cetacean catch per unit effort (CPUE) in Peruvian surface driftnets and bottom set nets respectively (Bielli et al., 2020).

Echolocation Reflection

Early acoustic reflector research had contrasting results on dolphins and porpoises. Neither nickel bead chain or plastic tubing net attachments resulted in significant differences in dolphin bycatch (Hembree & Harwood, 1987). Au and Jones (1991) investigated net detection distances of bottlenose dolphin and harbour porpoise, with three alternative designs each resulting in theoretically greater detection distances in both species. Development of acoustically reflective gillnets continued with the introduction of barium sulfate fibres. Trippel et al. (2003) reported significant reductions of harbour porpoise bycatch in barium sulfate nets, however, it was not clear whether this was due to greater acoustic reflectivity or the greater net stiffness. Koschinski et al. (2006) reported reduced acoustic activity of harbour porpoises close to barium sulfate gillnets and suggested pairing these nets with acoustic tones, in an attempt to encourage use of biosonar and aversive responses. Both Larsen et al. (2007) and Trippel et al. (2008) found significantly reduced bycatch of harbour porpoises using stiff nets, but that the iron oxide nets in Larsen et al. (2007) also reduced target catch quantity. Mooney et al. (2007) tested barium sulfate and iron oxide nets in lab conditions to assess theoretical detection distances of harbour porpoise and bottlenose dolphin. They deduced that barium sulfate increases detection distances at a 0^{o} degree angle of incidence (horizontal to the sea surface and perpendicular to the net) for both species. However, detection distances for porpoises may be within 5m, and potentially only just above this distance for bottlenose dolphins, putting both species at risk of bycatch when travelling quickly near nets. Stiffness of all nets was found to reduce when soaked in seawater (Mooney et al., 2007). Neither stiff nylon nets, nor barium sulfate nets reduced bycatch of La plata dolphin in field trials (Bordino et al., 2013).

A longline echolocation disruptor (1-250kHz) was tested on a trained false killer whale (*Pseudorca crassidens*), resulting in an initial reduction in target location success, but with improved accuracy as the experiment progressed (Mooney et al., 2009). However, performance of a trained captive animal does not reflect real world fishing gear interactions with marine megafauna and the disruptor was not tested on wild animals. Acoustic reflection has been revisited with the addition of acrylic spheres to gillnets, which improve on net material additions by theoretically allowing net detection at any angle of approach (Kratzer et al., 2020). Promising pilot studies using this technology highlight the need for testing in large scale trials to make a judgement on efficacy in commercial fisheries (Kratzer et al., 2021).

1.4.4 Sea turtles

Acoustic

No sea turtle acoustic studies were sourced in the peer-reviewed literature.

Olfactory

Technologies targeting olfaction appear in grey literature (Swimmer & Brill, 2006) and peer-reviewed studies in the 2000s, with investigations into reducing bycatch on longlines (Southwood et al., 2008). Watson et al. (2005) investigated olfactory stimuli for bycatch prevention by testing the effect of alternative bait types. By replacing squid bait with mackerel bait, bycatch of both loggerhead and leatherback (*Dermochelys coriacea*) turtles were significantly reduced. Watson et al. (2005) combined the effects of bait type with non-sensory bycatch mitigation, finding further reductions in bycatch by using circle hooks. Replacing squid with fish bait has continued to exhibit bycatch reductions in all tested turtle species (Gilman et al., 2007b; Coelho et al., 2012). Effects of coloured baits have produced mixed results, often not translating to field studies. Replacing squid bait with fish has shown potential for reducing sea turtle bycatch on longlines, and is still being investigated (Echwikhi et al., 2011). Fish baits rather than squid are reported to be more effective at reducing bycatch, although there is potential to reduce target catch in teleost fishes using this method (Gilman et al., 2020).

Visual

Swimmer et al. (2005) tested altered squid bait colours on sea turtles in lab and field trials. In the lab, both loggerhead (*Caretta caretta*) and Kemp's Ridley turtles (*Lepidochelys kempii*) chose significantly more control bait than bait dyed blue. Interestingly, loggerheads also chose to strike control bait above red dyed bait, but Kemp's Ridley turtles chose red bait above controls significantly more frequently. However, in field trials using blue dyed squid on Costa Rican longlines, bycatch was not reduced in either species (Swimmer et al., 2005).

After initial studies on bait types, Southwood et al. (2008) described the similarities between turtle and target species reactions to olfactory cues, but noted key differences in visual capabilities. Crognale et al. (2008) explored visual differences between leatherback turtles and targeted swordfish in a theoretical study to find a longline deterrent. Differences in species biology mean green (*Chelonia mydas*) and loggerhead turtles have different visual capabilities to leatherbacks and swordfish, which both have similar spectral sensitivities. They concluded that light flickering at a rate of >16 Hz would be difficult to detect for the leatherbacks but viewed as flickering by swordfish (Crognale et al., 2008). Visual deterrents on gillnets developed with trials of green chemical lightsticks, green LEDs and predator models (shark cut-outs) in Mexico (Wang et al., 2010). All methods reduced bycatch of green turtles by at least 40%, although shark cut-outs also significantly reduced target catch. Wang et al. (2013) followed up the original study by trialling UV-LEDs in the same fishery, reporting a significant 39.7% reduction in green turtle bycatch and no effect on target catch, similar to previous results using lights. The authors also note that the efficacy of net illumination is dependent on the circumstances of use, commenting that lights may be ineffective when used in the day. Combinations of gear visibility from lights, UV-absorbent plastic and physical predator models have been suggested as effective bycatch mitigation options in gillnets (Gilman et al., 2010).

Research on visual deterrents continued in lab trials, where Piovano et al. (2013) investigated yellow, red and blue-dyed bait on loggerhead turtle behaviour. There was no clear overall preference for bait colour, with individuals choosing different colours to strike first and tending to repeatedly strike the same colour in subsequent trials, leading to the conclusion that bait colour would be ineffective at reducing bycatch in loggerheads (Piovano et al., 2013). Bostwick et al. (2014) found that 3D shark models and 3D sphere models had the potential to repel loggerhead turtles from striking at bait. Four and two out of six avoidance behaviours significantly increased for the shark and sphere model respectively, compared to control conditions. However, there is no record of a sphere model being tested in fisheries trials.

Recently, research efforts have been focused on reducing sea turtle bycatch in gillnets using lights. Virgili et al. (2018) found that UV-LEDs significantly reduced loggerhead turtle catch in the same Italian gillnet fishery, without reducing target catch quantity, also commenting that LEDs provide better light penetration through water than chemical lightsticks. Both Ortiz et al. (2016) and Bielli et al. (2020) came to similar conclusions investigating green LEDs in Peruvian gillnets, finding significant 63.9% reductions in green turtle and significant 74.4% reductions in all turtle species bycatch, respectively.

1.4.5 Multi-species sensory bycatch mitigation efficacy and study gaps

A summary of the efficacy of sensory technologies from the data extraction process is shown in Figure 1.5. Any technology with at least one significant result in favour of bycatch reduction is displayed in Diagram A. Any technology that would not be effective for reducing bycatch (indicated by non-significant or significant negative results in at least one study) is represented in Diagram B. In cases where there are conflicting results within or between studies, technologies appear in both diagrams.

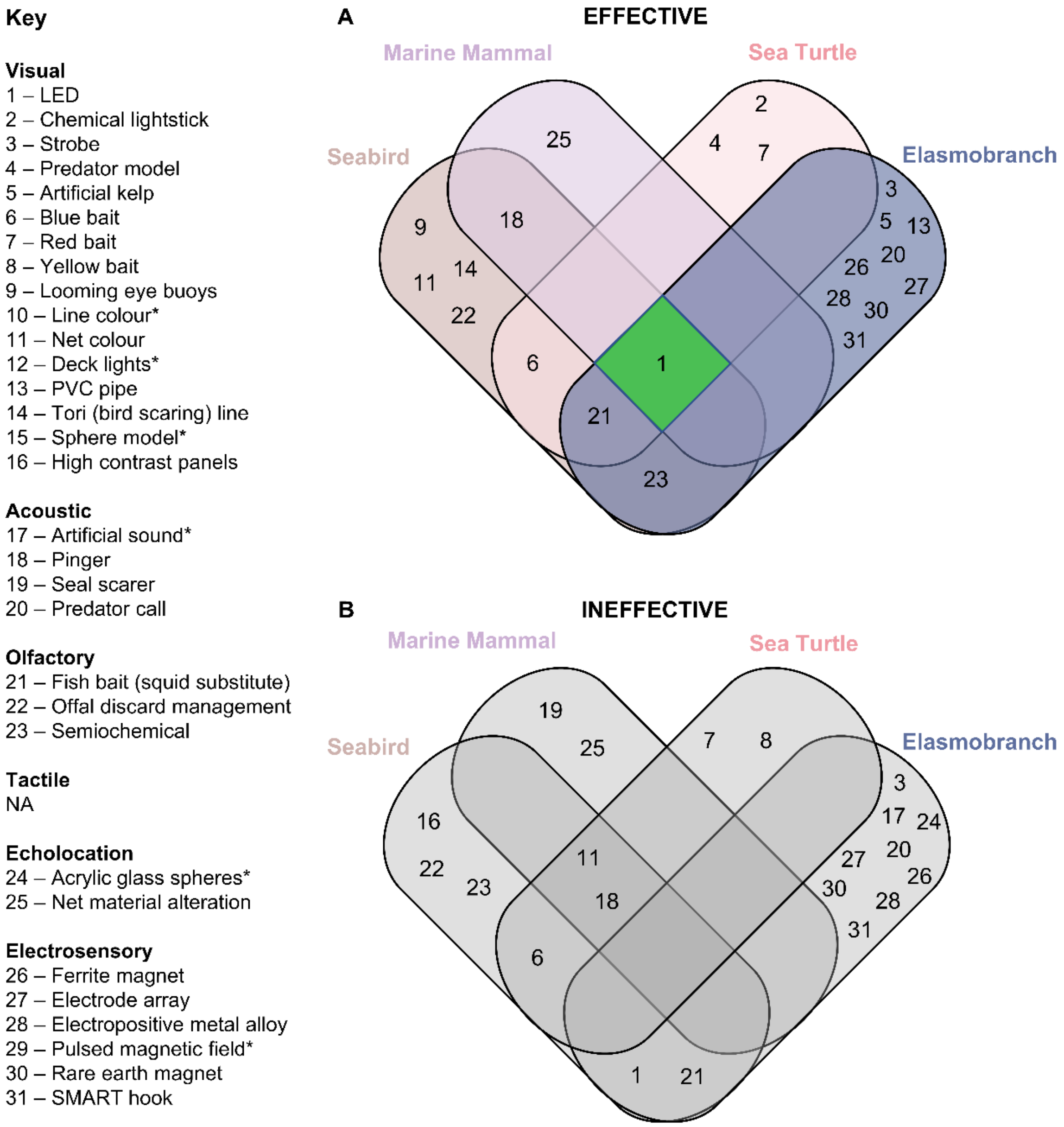
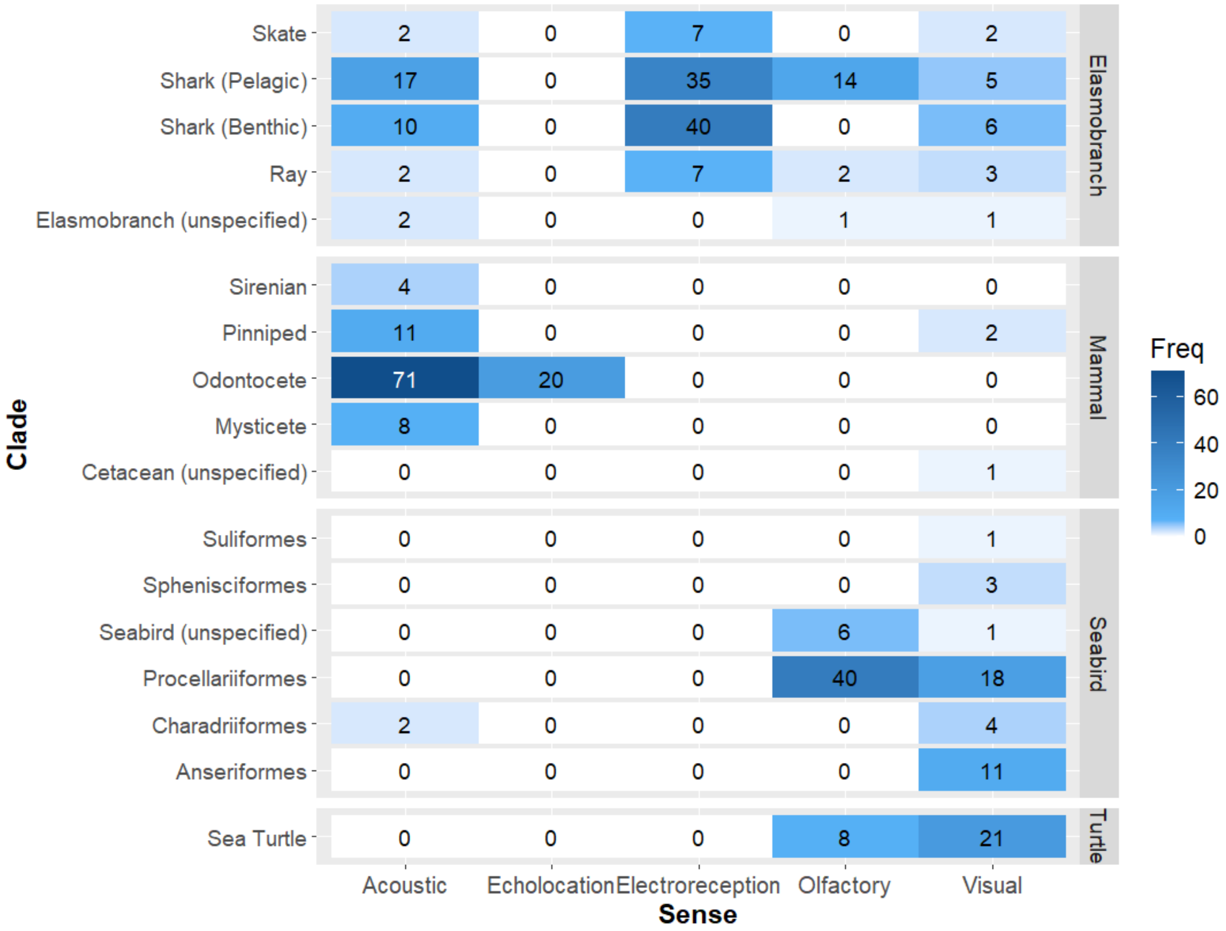


Figure 1.5 Effective and ineffective sensory deterrent Venn diagrams. (A) Technologies that have been shown to work on groups of marine megafauna in at least one study with statistically significant results. (B) Technologies that have been shown to have no significant effect, or a negative effect on marine megafauna groups. Some technologies appear in both diagrams. Asterisks (*) note technologies with partial efficacy, positive mitigation potential with no significant result, or where significance is not reported.

A heatmap displaying the number of trials found in the literature search relating to each sensory deterrent category and taxonomic group is shown in Figure 1.6. As some studies tested more than one method and included multiple megafauna species, the total number of trials in the table exceed the number of studies found in the literature. The heatmap represents counts of the number of trials, but not whether these trials were successful. Reviews are not included to avoid duplication of findings.



Clade	Acoustic	Echolocation	Electroreception	Olfactory	Visual
Skate	2	0	7	0	2
Shark (Pelagic)	17	0	35	14	5
Shark (Benthic)	10	0	40	0	6
Ray	2	0	7	2	3
Elasmobranch (unspecified)	2	0	0	1	1
Sirenian	4	0	0	0	0
Pinniped	11	0	0	0	2
Odontocete	71	20	0	0	0
Mysticete	8	0	0	0	0
Cetacean (unspecified)	0	0	0	0	1
Suliformes	0	0	0	0	1
Sphenisciformes	0	0	0	0	3
Seabird (unspecified)	0	0	0	6	1
Procellariiformes	0	0	0	40	18
Charadriiformes	2	0	0	0	4
Anseriformes	0	0	0	0	11
Sea Turtle	0	0	0	8	21

Figure 1.6 Heatmap showing the number of trials of each sensory deterrent system against the clade on which it was tested, including a separation of pelagic and benthic sharks, based on their habitat types and descriptions of habitat use on the IUCN red list database (IUCN, 2025). Number of trials (388 in total) exceeds the number of studies (116) due to multiple technologies or species being tested in each study.

1.5 Discussion

1.5.1 General principles in bycatch reduction

From a conservation perspective, time-area closures are an ideal and simple solution for reducing anthropogenic mortality of marine megafauna, if implemented and regulations are properly enforced. Changing gear may be a viable alternative in some situations, to reduce overlap with vulnerable populations. Where closures or gear changes are not currently possible (e.g. due to community dependence or lack of political support), bycatch reduction programmes must address bycatch of vulnerable marine megafauna to safeguard marine ecosystems, while attempting to maintain target catch quantity and quality. In such situations, sensory technologies may offer solutions, potentially enabling fisheries to continue operating while reducing bycatch, ideally in combination with other measures, such as periodical closures and catch limits. The efficacy of these technologies is dependent on the characteristics of the fishery and species composition in the area, meaning that management must be done on a context dependent basis (Jordan et al., 2013). Where only one marine megafauna group is present, there would be no need to address bycatch in all groups, but rather have a bespoke management programme based on that species group, as long as the programme does not cause attraction or increase entanglement risk of other potential bycatch species. Species and fishery-specific factors must be taken into account and technologies carefully tested in well-designed studies before wide-scale implementation in any fishery setting. It is not sufficient to infer that the results of one study with one gear type in one location will generalise and be applicable to other species, locations and gear. The nature of sensory deterrents is that results conflict, so proper well-designed trials are critical to success.

It is necessary to include a quantitative goal in bycatch reduction plans, ensuring that bycatch meets reductions required by the population biology of the species and demonstrating continued efficacy through time (Dawson et al., 2013). Sufficient statistical power is critical for assessing quantitative goals, to ensure that bycatch levels do not exceed set mortality limits, such as PBR (Dawson et al., 1998). Prior power analyses are useful for designing experiments to avoid inconclusive results due to insufficient sample size, leading to accepting potentially false null hypotheses of no effect of treatment (Type II error). However, only 6% (7) of the 116 studies in this review reported prior power analysis (see Online Resource 2 for further detail; https://doi.org/10.1007/s11160-022-09736-5). Further, statistical significance tests are important to assess outcomes of experiments such as mitigation trials. However, biologically relevant effect sizes are more important for conservation, rather than small, but significant, bycatch reductions. We encourage the use of resources which support the creation of bycatch reduction plans with quantitative bycatch reduction goals, monitoring and evaluation (FAO, 2020; Rogan et al., 2021). Compliance and ongoing efficacy of bycatch reduction technologies relies on affordable costs and effective bycatch monitoring and reduction programmes (Virgili et al., 2018; Bielli et al., 2020). Where technologies are unaffordable or logistically difficult to implement, compliance will likely be reduced. To support reductions through time, technologies should be re-usable where possible to save on replacement costs and waste (Wang et al., 2010).

Bycatch reduction requires close collaboration between fishing communities, scientists, fisheries management and environmental organisations. For programmes to work consistently through time, fisher and vessel behaviour must be in line with management plans (Roberson & Wilcox, 2022) and multiple measures are likely necessary to achieve sustained success (O'Keefe et al., 2014). Where management programmes or technologies are implemented inconsistently or fail, bycatch levels may increase (Palka et al., 2008; Carretta & Barlow, 2011). The dangers of poorly designed bycatch reduction programmes are that if they fail to reduce bycatch sufficiently, then advocacy from the fishing community is unlikely and subsequent adherence to policy may be poor in any current or future programmes (Palka et al., 2008). Cox et al. (2007) highlighted that collaboration, monitoring and compliance are critical and must have the support of the fishing community to be effective. Compliance may be achievable only through mandating the use of bycatch reduction technologies (Dawson et al., 2013) and combining sensory deterrents with additional measures to achieve success (Field et al., 2019). Observers may be effective at ensuring compliance on individual vessels, but observer coverage of entire fleets is often impractical, particularly in SSFs, where fisher buy-in is crucial. Remote electronic monitoring may offer an alternative with further improvements in automated analysis (Bartholomew et al., 2018), but until this technology matures, fishery-independent observations will be necessary to measure bycatch in trials (Jefferson & Curry, 1996). In SSFs all animals may be seen as having value as food or for sale and therefore there may be no concept of bycatch. In these situations the value of foraging around fishing gear and gear damage reduction could be leveraged, alongside legislation and enforcement measures, to encourage buy-in from the fishing community and achieve effective reductions in marine megafauna mortality. Quantifying the impacts and characteristics of bycatch in both commercial and SSFs is key to understanding the challenges and the potential solutions.

Habituation and habitat exclusion are important factors when using sensory technologies. Habituation to sensory deterrents has been recorded in empirical studies (Amano et al., 2017), and where it is not observed, this is perhaps due to the long time periods over which it could occur and difficulties in detecting it during short field studies which focus on immediate results (Königson et al., 2021). Habitat exclusion has been found in studies and derived in models when investigating some technologies, although evidence of the effects on populations are not clear (van Beest et al., 2017). Habituation may lead to increased bycatch or foraging attempts around fishing gear, and habitat exclusion could have impacts on population size, or act as barriers to key foraging grounds (Carlström et al., 2002), so both should be taken seriously and investigated in trials. Some papers argue that habituation could be beneficial because it may cause reduced, but still effective, avoidance distances (Teilmann et al., 2006; Omeyer et al., 2020). It is argued that these avoidance distances could reduce habitat exclusion while maintaining bycatch reductions (Kindt-Larsen et al., 2019). However, habituation would likely undermine the use of a technology eventually, and any short-term benefits of mild habituation may disappear quickly. This would result in wasted money spent on technologies, the original bycatch problem would return and the trust of the fisheries would be damaged. Modulation of sensory cues and combinations of mitigation options could alleviate potential habituation and habitat exclusion (Teilmann et al., 2006). Using technologies only in months of high bycatch could potentially reduce habituation effects (Amano et al., 2017), although effects of seasonal use would need to be tested before implementation and additional bycatch mitigation strategies would likely be required. Significant habituation and habitat exclusion may limit the ability of technologies to provide consistent bycatch reductions (O'Connell et al., 2015).

Bycatch and foraging around fishing gear are connected issues. Successful sensory technologies have the advantage of reducing initial contact between gear and marine megafauna, which therefore reduces the likelihood of foraging attempts around gear. However, it is important to note that the incentive of food reward may overcome deterrent stimuli during foraging attempts around fishing gear (Cantlay et al., 2020). Decreased bycatch and foraging around fishing gear have the benefit of sustaining levels of target catch, whilst reducing megafauna mortality and gear damage. Other mitigation types do not have the same benefits, for example, escape devices may still allow animal-gear contact in trawl nets. However, for some taxa and gear types, prevention of interactions and bycatch may not be possible. For these situations, or where fishery closure, movement of activity or gear changes are not possible, escape devices may be required to address bycatch and foraging around fishing gear (Lucchetti et al., 2019; Hamilton & Baker, 2019).

1.5.2 Sensory deterrents for bycatch mitigation across multiple taxonomic groups

LEDs are the only technology so far to produce significant positive results for bycatch reduction in all four marine megafauna groups (Figure 1.5A). Green LEDs (500nm) have empirically shown bycatch reductions across all groups in gillnet trials off the Pacific coasts of central and South America (Mangel et al., 2018; Bielli et al., 2020; Senko et al., 2022). These relatively recent findings are promising, although some important exceptions should be considered. Differences in vision between leatherback, green and loggerhead turtles highlight that results could be species specific and may not necessarily generalise within, or across, megafauna groups (Crognale et al., 2008). It appears that sea duck (family *Anatidae*) behaviour is not affected by lights, and ducks can even be attracted to light sources in the case of flashing white LEDs (Cantlay et al., 2020). It should also be noted that elasmobranch catch has either not changed significantly, or actually increased in some studies using green LEDs (Mangel et al., 2018; Virgili et al., 2018) and significant bycatch reductions were found in a study using a small sample size and measuring biomass reduction, rather than bycatch reduction of individual animals (Senko et al., 2022). Water turbidity was not reported in any of these studies and could potentially reduce efficacy of LED lights. In addition, the ecological impact of illuminating marine environments at night may cause different problems. Therefore, caution should be taken before assuming that green LEDs will reduce bycatch in gillnets for all marine megafauna species.

Sixteen sensory deterrents appear in both Figure 1.5A and Figure 1.5B, highlighting the variability of responses in different species and in different contexts. The six technologies appearing only in Figure 1.5A (chemical light stick, predator model, artificial kelp, looming eye buoys, PVC pipe, tori lines) also require further assessment before concluding their effectiveness, as they are relatively little studied. The exception to this is perhaps tori lines, which have encouraging results (Løkkeborg, 1998; Lokkeborg & Robertson, 2002).

Bait alterations have been effective on multiple megafauna groups in longlines. Blue bait has potential to reduce interactions with both seabirds and turtles (Swimmer et al., 2005; Cocking et al., 2008), while changing squid bait for fish bait can reduce seabird, elasmobranch and sea turtle bycatch (Watson et al., 2005; Gonzalez et al., 2012; Gilman et al., 2020). Fish bait in place of squid has promise for marine mammal fishery interactions too (Garrison, 2007), although will need testing in bycatch reduction trials, rather than assessing only foraging around fishing gear. Decreases in target catch and species-specific reactions of sharks and birds require attention, so catch composition of the fishery needs to be considered when changing bait type (Coelho et al., 2012; Li et al., 2012). Semiochemicals, such as shark liver oil and shark necromones have promise in repelling elasmobranchs and some seabirds, although this is species-specific (Pierre & Norden, 2006; Norden & Pierre, 2007; Stroud et al., 2014). Pingers have a strong track record for reducing bycatch in some odontocete cetaceans, especially neophobic species such as harbour porpoises (Dawson et al., 2013) and potentially some seabirds too (Melvin et al., 1999). However, significant bycatch reductions using pingers have not been found for elasmobranchs (Mangel et al., 2013).

More technologies have been trialled with success for one taxonomic group rather than multiple, generally due to species-specific biology, such as electrosensory systems in elasmobranchs (Jordan et al., 2013), echolocation in odontocetes (Trippel et al., 2008), or visual cues above the water for seabirds (Rouxel et al., 2021). Where multiple groups are caught, it may be appropriate to use multiple technologies in combination. Combinations of sensory deterrents can be effective across multiple groups, such as pingers reducing common murre and harbour porpoise bycatch (Kraus et al., 1997; Melvin et al., 1999). Alternatively combinations of non-sensory mitigation options with sensory deterrent may work. If areas are characterised by transient migrating populations and some permanent populations of different species, time-area closures when migrations pass through may be paired with sensory mitigation for the resident species or group. In cases where bycatch still occurs, post-release or escape mechanisms may be critical. For example, circle hooks combined with blue fish bait could support turtle post-release survival (Echwikhi et al., 2011).

A number of gaps in technologies tested in the literature are displayed in Figure 1.6. The gaps (represented by zeros) in echolocation and electrosensory options should be ignored, because only odontocetes can echolocate and elasmobranchs have specialised electrosensory systems. There is a lack of research on olfactory deterrents for marine mammals as they would likely be ineffective for odontocetes (Schakner & Blumstein, 2013). Recent findings suggest that offal discard management may reduce interactions and bycatch of odontocetes in trawls (Bonizzoni et al., 2022). These discards are unlikely to be detected by odontocetes using olfaction. Offal discard management was grouped within olfactory deterrents for the purposes of this study, although in reality the sensory deterrents in this review may be detected by different species using different sensory mechanisms.

Acoustic studies have mostly used pingers, with studies usually focusing on mammals, but other groups are also represented in bycatch. Four papers are exceptions to the pinger trials in the acoustic section. Basran et al. (2020) reported on seal scarers as an unsuccessful pinger alternative. Ryan et al. (2018) and Chapuis et al. (2019) investigated ’artificial sounds’ and orca calls on sharks, and Kratzer et al. (2021) reported on bycatch of sharks in acoustically reflective gillnets in a study on marine mammals. Incidentally, the 29 acoustic trials on sharks came from only nine papers. Culik et al. (2015) and Chladek et al. (2020) used synthetic porpoise calls, rather than conventional pingers, to deter wild porpoises. However, for the purposes of this review, these Porpoise Alarm devices were grouped with pingers for the data extraction and analysis, because they emit an acoustic signal in the hearing range of odontocetes, but not other megafauna species. Seabird and sea turtle sensory deterrents are most frequently focused on visual and olfactory cues. Olfactory studies revealed that bait type can influence both turtle and elasmobranch bycatch levels (Gilman et al., 2020) and semiochemicals such as dead sharks (or shark ’necromones’) have the potential to reduce gear interactions with both elasmobranchs and seabirds (Norden & Pierre, 2007). Visual deterrents have the broadest range of tested technologies, with LEDs the only technology so far tested (and found successful) in trials across all taxonomic groups (Bielli et al., 2020).

Few papers explicitly test the effects of technologies on multiple taxonomic groups (e.g. Bielli et al., 2020). However, many records on the effects of technologies focusing on single groups also record data on other taxa. For example, the effects of pingers and visible upper sections of gillnets on sharks and mammals in the Melvin et al. (1999) study on seabirds and the effects of pingers on sharks in the Barlow and Cameron (2003) study on marine mammals. Attempts by Martin and Crawford (2015) to generalise seabird bycatch mitigation technologies by designing high contrast panel attachments for gillnets were not successful when tested in field trials (Field et al., 2019), but the principles of attempting to reduce bycatch across multiple taxa should be encouraged. Recently studies are beginning to include cross-species mitigation options while attempting to retain target catch quantity and quality. For example, Bielli et al. (2020) found that lights can reduce bycatch in mammals, turtles and seabirds and Gilman et al. (2020) conducting a meta-analysis, concluded that changing bait from squid to fish reduces risk of blue shark and marine turtle bycatch, as also found in Watson et al. (2005).

1.5.3 Limitations of this review

A systematic search was used with the intention of providing reproducible methods and retrieving a representative sample of literature, rather than exhaustively sourcing all works related to the study aim. Other excellent databases exist for sourcing related papers (such as BMIS 2022), as well as other scholarly databases and comprehensive technical reports. This review is limited to the search terms and unstructured citation checking process described in the methods, but should offer a representative view of the field. Selection of grey literature for the narrative section is subject to bias. There are undoubtedly important grey literature reports and peer-reviewed academic papers that will have been missed from this search and therefore from the systematic map and the narrative synthesis. Inclusion criteria contains subjectivity when interpreting papers and this should be considered if repeating the search. Publication bias may present the peer-reviewed literature only with results deemed to be interesting enough for publication. Studies which test mitigation options that do not produce significant results are unlikely to be published. We recommend that anyone using this paper to find information relating to specific species should conduct further searches to ensure all relevant information is sourced.

Published results are often quantitative (e.g. level of bycatch reduction), making meta-analysis a tempting synthesis method. However, this method may be impractical for now, due to the variability in study design and reporting, which inhibits comparisons across studies on multiple mitigation types and species. Vote counting is not a solution to this problem, due to the variability in results. It was therefore decided to present the results in a Venn diagram with a minimum of one paper in support or against of a technology, alongside a narrative synthesis to summarise the previous research. For a more comprehensive understanding, we recommended reading the summary of results in Online Resource 2 (https://doi.org/10.1007/s11160-022-09736-5) and the referenced papers. Meta-analysis for each species or across groups would be useful future research, as long as reporting standards of field studies are consistent and list relevant confounding factors.

1.5.4 Recommendations for future research

A small number of well-studied sensory bycatch mitigation options were identified, such as pingers for harbour porpoises and magnetic deterrents for elasmobranchs (e.g. Chladek et al., 2020; Richards et al., 2018). However, there are few studies actually measuring bycatch reductions in the field, with many undertaken as proof of concept, by measuring a behavioural response rather than bycatch quantity. Even in field studies, there is often variability in results between regions, taxa and fisheries, meaning that additional research for promising mitigation options would be valuable.

General recommendations include reporting standards, study design, locations, study context and unintended effects on animals. Studies should detail key information that would support comparison (Cox et al., 2007). This includes reporting every species caught in the trials, if bycatch of each species (or pooled taxonomic group) was significantly increased, decreased or unaffected compared to controls (e.g. Carretta and Barlow, 2011). Consistent metrics should be reported, using number of individuals caught per unit effort (e.g. km net x hours or number of hauls) and normalised for abundance, where possible, rather than biomass (Gilman et al., 2005). Gear type, study location, technology used and technical specifications (e.g. 500nm lights, C8 barium ferrite magnet or 10-12kHz pinger) should be described in detail, including failure rates of the technology throughout the trials (e.g. Carretta and Barlow, 2011). Sample and effect sizes should be listed, as well as an interpretation of the evidence for bycatch reduction using the technology. Trials should be designed to achieve appropriate statistical power to assess the significance of results (Dawson et al., 1998), so pilot studies are recommended. Where possible, studies should be completed in the field, measuring actual bycatch quantities reported in CPUE, rather than measuring behaviour. However, experimental trials may involve substantial mortality of animals, so the vulnerability of each species affected by field trials must be considered. Modelling or behavioural responses may provide alternative or complementary metrics, particularly where bycatch trials are impractical or unethical (e.g. due to the presence of critically endangered species) (Jordan et al., 2013). Behavioural experiments must consider and mitigate pseudo-replication in study design (Dawson & Lusseau, 2005, 2013). New technologies could stimulate research of behaviour around gear in active fishery settings rather than in labs, such as the use of autonomous underwater vehicles equipped with video cameras (Poisson et al., 2021) or cameras deployed on fishing gear (Mitchell et al., 2019). Studies should attempt to measure and comment on initial observations, and if possible on the long-term effects, of the technology on habituation (Jefferson & Curry, 1996) and habitat exclusion (Larsen & Eigaard, 2014). Investigating new locations is encouraged (Figure 1.3), particularly in understudied regions where SSFs are present, such as in Asia, Africa and South America.

We encourage further research combining sensory deterrents to achieve bycatch reduction across taxonomic groups. Effective low-cost technologies that are easy to implement are likely to achieve the highest advocacy and compliance from the fishing industry. There is a further need for long-term trials in areas where CPUE of threatened species is low and efficacy of bycatch mitigation methods may take a long time to demonstrate. Combinations of deterrents should be used in commercial fishing trials to assess potential for large-scale bycatch reductions across species groups, for example combining LEDs and pingers on gillnets, which would test the efficacy of cost-effective lights with relatively established acoustic deterrents. Trials that combine technologies must consider that it may be difficult to identify which technologies cause bycatch reductions, where they occur, and technologies may interfere with each other. Despite limitations and poor performance in longline trials to date (Favaro & Côté, 2015), we also encourage continued research on electrosensory deterrents for elasmobranchs. The unique sensory capabilities of elasmobranchs present opportunities for selective bycatch mitigation, particularly use of ferrite magnets in place of beach nets (e.g. O'Connell et al., 2014a; 2014e) and the recent development of electrode arrays and pulsed magnetic fields (Howard et al., 2018; Polpetta et al., 2021). Combinations of sensory and non-sensory mitigation options should be trialled too. For details of non-sensory options, see e.g. Werner et al. (2006). It is important to stress that we do not support implementation of these technologies in fisheries where they have not been proved effective consistently over multiple years. As of yet, there are no technologies described in this review that are generalisable to all circumstances, or can be used as the sole solution to bycatch problems. Even in cases where technologies are successful, they must be accompanied by additional measures to ensure continued success (Dawson et al., 2013; Read, 2013).

We recommend further research of all sensory deterrents where there is mortality but no direct fishery application. The use of LED lights on gillnets should be investigated further, including the effects of water turbidity on results, and the ecological impacts of illuminating marine environments with LED lights. The use of cheap cut-out predator models in front of power station intakes or leaders for pound nets should be investigated for reducing sea turtle mortality (Wang et al., 2010) and further research into magnetic repellents in place of beach nets to reduce mortality across all groups, whilst still deterring potentially dangerous sharks from swimmers. Reduction of mortality here does not depend on maintaining a level of target catch as it does in fisheries, and the removal of beach nets would prevent the completely wasteful mortality of a wide variety of creatures. We hypothesise that there would be no significant increase in swimmer mortality if beach nets are removed without replacement, which would be the cheapest option, although scientific trials of this are open to potential ethical issues, community and political backlash.

1.5.5 Linking bycatch mitigation of marine megafauna to elasmobranch species vulnerability

In Chapter 1, I investigated broad scale methods to reduce bycatch of marine megafauna in fisheries, with a focus on sensory deterrents. Reduction of fisheries bycatch is not straightforward, requiring authorities to balance ecological and socio-economic needs. Sensory deterrents may offer solutions in some contexts, but are unlikely to serve as a panacea for large scale bycatch reductions. Therefore, it is crucial for fisheries managers to consider both measures to reduce fisheries mortality and the life history strategies of marine megafauna species, to understand their resilience to exploitation and if alternative management tools are required. Chapter 2 narrows the focus to elasmobranchs, a group disproportionately affected by fisheries mortality, to examine how their life history strategies influence their conservation biology and vulnerability to exploitation.

1.5.6 Conclusion

Sensory technologies have provided different results in a variety of contexts based on marine megafauna species composition, target catch biology, gear type, location and environmental conditions. Results do not always translate between lab and field studies. Avoidance behaviour does not always lead to permanent bycatch mitigation solutions, so directly measuring bycatch reduction in field trials is recommended. Effective non-sensory bycatch mitigation options exist, so combinations of technologies and management actions will be required to reduce bycatch in most areas. Lights on gillnets appears to be a particularly promising area for future research, as well as some electrosensory deterrents for elasmobranchs and the established acoustic deterrents for neophobic odontocetes. However, technical adaptations are insufficient to tackle bycatch on their own in most cases. Combinations of sensory deterrents should not be implemented without first proving consistently effective in field trials. Therefore, it is vital that complementary measures including time-area closures, quotas and modification of fisher behaviour should be considered in bycatch reduction programmes, alongside technical adaptations.

Advocacy and collaboration with the fishing community is critical to success. By leveraging fisher knowledge, bycatch may be reduced whilst maintaining target catch quantity and quality to support community income and food security. Sensory technologies have the potential to play some part in safeguarding marine megafauna populations and marine ecosystems, whilst preserving socioeconomic interests. The separate but associated issue of overfishing target catch is extremely important and must be addressed to prevent the collapse of entire ecosystems. However, by eliminating megafauna bycatch, the interests of science, conservation, management and the fishing community may be satisfied by conserving apex predators and keystone species to maintain balanced marine food webs. Sensory technologies are not perfect, and their success is dependent on the characteristics of the fisheries and species present. But, along with complementary measures, there are promising avenues for future research to reduce bycatch across multiple taxonomic groups.

Chapter 2. Changing feeding levels reveal plasticity in elasmobranch life history strategies

2.1 Abstract

Life history strategies are shaped by phylogeny, environmental conditions and individual energy budgets, and have implications for conservation biology. We structured life history traits of 151 elasmobranch species into life history strategies for two contrasting feeding levels. Elasmobranch life history strategies are structured along the fast-slow continuum and reproductive strategy axes. However, species' positions in this life history space were not fixed, but moved in an anticlockwise 'whirlpool' manner along the axes when feeding level increased. We also found that population growth rate does not necessarily inform on a species' demographic resilience. Finally, only at the higher feeding level does the fast-slow continuum predict IUCN conservation status, with the slowest species at the highest extinction risk. Our analyses reveal plasticity in species life history strategies and warn against extrapolating the life history strategy framework from one environment to another when predicting a species' response to (climate) change, perturbations, and (over)exploitation.

2.2 Introduction

Life history strategies of many animals and plants reflect "life history speed" or "pace of life" along a fast-slow continuum, and reproductive biology along a reproductive strategy axis (Gaillard et al., 1989; Salguero-Gómez et al., 2016; Capdevila et al., 2020a). Fast species mature early, grow fast and are short-lived and slow species are slow-growing and long-lived with low fecundity (Gaillard et al., 2016). The reproductive strategy axis is characterised by high lifetime reproductive output and high mortality at one end, and low reproductive output and low mortality at the other (Healy et al., 2019) (in some studies this second axis relates to development instead; Stearns 1983). These axes are shaped by trade-offs (Gaillard et al., 2016). For example, the fast-slow continuum represents the trade-off between reproduction versus survival (Stearns, 1983), often irrespective of body size or phylogenetic relatedness (Williams, 1966; Gadgil et al., 1970; Reznick, 1983). Yet, trade-offs that operate within individuals, such as trading off growth versus reproduction in the energy budget (Gadgil et al., 1970; Reznick, 1983), should be considered, as different dynamics can exist between populations or species with similar traits (Nilsen et al., 2009; Gamelon et al., 2021). Specifically, the classical association between life history strategies and population responses to environmental change breaks down when accounting for individual-level trade-offs and energy allocation in ray-finned fish (Rademaker et al., 2024). There is also limited understanding of how ecological and evolutionary factors, like phylogeny or habitat type, shape variation in life history strategies across species (Gaillard et al., 2016; Salguero-Gómez et al., 2016; Salguero-Gómez, 2017; Capdevila et al., 2020a). Identifying patterns in life history strategies across the tree of life is essential to predicting population growth rates and demographic resilience (herein ‘population performance’) (Salguero-Gómez et al., 2016). However, to do so requires in-depth understanding of how energy budgets, phylogeny and habitat structure life history strategies across species (Salguero-Gómez, 2017; Capdevila et al., 2020a; Romeijn & Smallegange, 2022).

Elasmobranchs (sharks, skates and rays) encompass a vast amount of life history variation. Longevity, for example, can range from five (e.g. *Carcharhinus sealei* and *Carcharhinus sorrah*; Ebert et al. 2021) to almost 400 years (*Somniosus microcephalus*; Nielsen et al. 2016). Reproduction is highly variable, including oviparity (skates and three families of shark), aplacental viviparity (in various forms; sharks and rays) and placental viviparity (some sharks) (Carrier et al., 2004; Miller et al., 2022). Elasmobranch population performance typically varies with body size, reproductive strategy and environmental temperature (Pardo & Dulvy, 2022; Barrowclift et al., 2023; Gravel et al., 2024), yet little is known about the impact of energy budgets. Here, we investigate how individual energy budgets, phylogeny and habitat structure elasmobranch life history strategies, and how the resulting fast-slow continuum and reproductive strategy framework links to their population performance, demographic resilience and conservation biology (Salguero-Gómez et al., 2016; Salguero-Gómez, 2017). We parameterise Dynamic Energy Budget Integral Projection Models (DEB-IPMs) for 157 elasmobranch species (Kooijman & Metz, 1984; Sousa et al., 2010; Ellner et al., 2016; Smallegange et al., 2017; Smallegange & Lucas, 2024). In DEB-IPMs, an energy budget model describes a species’ growth and reproduction, where energy intake is determined by setting an experienced feeding level (Kooijman, 2001; Kooijman et al., 2008). To identify life history strategies, we (objective 1) calculate, using the parameterised DEB-IPMs, a set of representative life history traits based on schedules of survival, growth and reproduction for a low and a high feeding level. We (objective 2) evaluate the variation in these traits along major axes using a phylogenetically-corrected principal components analysis (PCA). We then (objective 3) assess to what extent phylogenetic ancestry and habitat (water temperature) determine species position along these major axes. Finally, (objective 4) we test whether species position along these axes predicts population growth rate, speed of recovery from perturbations (demographic resilience) and IUCN conservation status. Our approach allows us to investigate whether feeding level influences life history strategies and the resulting conservation biology of ectotherm species.

2.3 Methods

2.3.1 Brief description of the DEB-IPM

A DEB-IPM describes the dynamics of a population comprising cohorts of females of different sizes as a result of their survival, growth and reproduction (Smallegange et al., 2017; Smallegange & Lucas, 2024). Specifically, denoting the number of females at year *t* by $N(L,t)$ gives the dynamics of the body length number distribution from year *t* to *t*+1 as:

$$N(L',t+1) = \int_\Omega \left[D(L',L(t))R\big(L(t)\big) + G(L',L(t))S(L(t))\right]N(L,t)dL \qquad \text{eqn 1}$$

where the closed interval Ω denotes the length domain. The survival function $S(L(t))$ in equation (1) is the probability that an individual of length L survives from time *t* to *t* + 1:

$$S(L(t)) = \begin{cases} e^{-\mu_\mathrm{j}} & \text{for } L_b \leq L < L_p \;\; \& \;\; L \leq L_m E(Y)/\kappa\,, \\ e^{-\mu_\mathrm{a}} & \text{for } L_p \leq L \leq L_m \;\; \& \;\; L \leq L_m E(Y)/\kappa\,, \\ 0 & \text{otherwise} \end{cases} \qquad \text{eqn 2}$$

where $E(Y)$ can range from zero (empty gut) to one (full gut), L_b is length at birth, L_p length at puberty and L_m maximum attainable length (Figure 2.1). Individuals die from starvation at body lengths at which maintenance requirements exceeds the total amount of assimilated energy, which occurs when $L > L_m \cdot E(Y)/\kappa$ and hence, $S\big(L(t)\big) = 0$ (e.g. an individual of length L_m will die of starvation if $E(Y)<\kappa$, where κ is the fraction of assimilated energy allocated to respiration, with $1 - \kappa$ allocated to reproduction [Figure 2.1]). Juveniles and adults often have different mortality rates, and thus, juveniles ($L_b \leq L < L_p$) that do not die of starvation (i.e. $L \leq L_m \cdot E(Y)/\kappa$) have a mortality rate of μ_j and adults ($L_p \leq L \leq L_m$) that do not die of starvation (i.e. $L \leq L_m \cdot E(Y)/\kappa$) have a mortality rate of μ_a (Figure 2.1).

In equation (1), the function $G(L',L(t))$ is the probability that an individual of body length L at time *t* grows to length L' at *t* + 1, conditional on survival, following a Gaussian distribution:

$$G(L',L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{\frac{-(L'-E(L(t+1))^2}{2\sigma_L^2(L(t+1))}} \qquad \text{eqn 3}$$

with growth realised by a cohort of individuals with length $L(t)$ equalling:

$$E\big(L(t+1)\big) = \begin{cases} L(t)e^{-\dot{r}_B} + \big(1 - e^{-\dot{r}_B}\big)L_m E(Y) & \text{for } L \leq L_m E(Y) \\ L(t) & \text{otherwise} \end{cases}, \qquad \text{eqn 4}$$

and the variance in length at time *t* + 1 for a cohort of individuals of length L as:

$$\sigma^2(L(t+1)) = \begin{cases} (1 - e^{-\dot{r}_B})^2 L_m^2 \sigma^2(Y) & \text{for } L \leq L_m E(Y) \\ 0 & \text{otherwise} \end{cases} \qquad \text{eqn 5}$$

where *E(Y)* is the standard deviation of the expected feeding level, and where $\dot{r}_B$ is the von Bertalanffy growth rate (Figure 2.1).

The reproduction function $R(L(t))$ in equation (1) gives the number of offspring produced between time *t* and *t* + 1 by an individual of length L at time *t*:

$$R(L(t)) = \begin{cases} 0 & \text{for } L_b \leq L < L_p \\ E(Y)R_m L(t)^2/L_m^2 & \text{for } L_p \leq L \leq L_m E(Y) \\ \frac{R_m}{1-\kappa}\left[E(Y)L(t)^2 - \frac{\kappa L(t)^3}{L_m}\right] & \text{for } L_m E(Y) < L \leq L_m E(Y)/\kappa \end{cases} \qquad \text{eqn 6}$$

Individuals are mature when they reach puberty at body length L_p and only surviving adults reproduce; thus, only individuals within a cohort of length $L_p \leq L \leq L_m Y/\kappa$ reproduce.

Finally, the probability density function $D(L', L(t))$ gives the probability that offspring of an individual of body length L are of length L' at time *t* + 1, and hence describes the association between parent and offspring character values:

$$D\big(L', L(t)\big) = \begin{cases} 0 & \text{for } L < L_p \\ \frac{1}{\sqrt{2\pi\sigma_{L_b}^2(L(\,t))}} e^{\frac{-(L' - E_{L_b}(L(t)))^2}{2\sigma_{L_b}^2(L(\,t))}} & \text{otherwise} \end{cases} \qquad \text{eqn 7}$$

where $E_{L_b}\big(L(t)\big)$ is the expected size of offspring produced by a cohort of individuals with length *L*(*t*), and $\sigma_{L_b}^2(L(t))$ the associated variance. For simplicity, $E_{L_b}\big(L(t)\big)$ is set to be constant and associated variance, $\sigma_{L_b}^2\big(L(t)\big)$ is assumed to be very small.

DEB-IPMs were parameterised using the DEBBIES database of ectotherms for 157 elasmobranch species, from 11 orders and 37 families (Smallegange & Lucas, 2024).

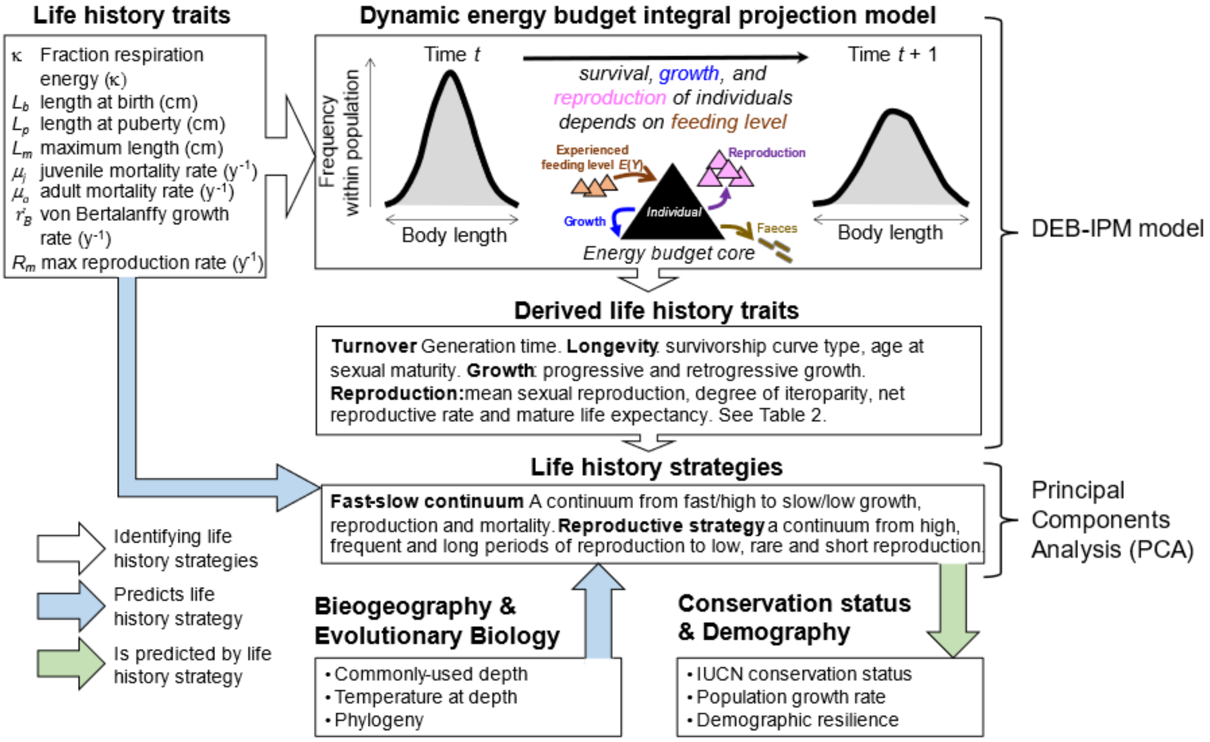


Figure 2.1 Workflow of parameterising a DEB-IPM using the DEBBIES database (Smallegange & Lucas, 2024), using the derived life history traits to plot elasmobranch life history strategies in a Principal Components Analysis (PCA). Species biogeography and phylogeny were used to estimate position on PCA axes, and the PC scores were used to predict conservation status, population growth rates and demographic resilience. White arrows indicate parameterisation of models or calculation of traits. Blue arrows represent metrics used to predict life history strategies and green arrows indicate the use of life history strategies to make predictions of conservation status and demography.

2.3.2 Life history strategies

Nine representative life history traits were calculated based on schedules of survival, growth and reproduction (Table 2.1) (Salguero-Gómez et al., 2016; Salguero-Gómez, 2017; Capdevila et al., 2020a) in MATLAB Version 9.12 (The MathWorks Inc., 2022) using the code in Smallegange & Lucas (2024) (objective 1). For each species, this was done for a low and high feeding level, $E(Y)$= 0.6 and $E(Y)$= 0.9, respectively. Feeding levels lower than $E(Y)$= 0.6 were not explored because these were too low for individual growth and reproduction to occur for many species. To identify life history strategies along major axes (objective 2), we performed a varimax-rotated, phylogenetically corrected principal component analysis (pPCA) (Revell, 2012), using the *phy.pca* function in the R library *phytools* (Revell, 2012; Chamberlain & Szöcs, 2013; Salguero-Gómez et al., 2016; Paniw et al., 2018; R Core Team, 2023). Traits were log-transformed and scaled to adhere to PCA assumptions (m= 0 and SD= 1).

To correct for phylogenetic relatedness among species, a pool of 10,000 possible phylogenetic trees were obtained from Stein et al. 2018, available at Vertlife.org. These trees represented 500 root node ages combined with 20 scenarios for infilling taxon with no genetic data. We randomly selected twenty trees and ran the pPCA for each, on both the high and low feeding levels ($E(Y)= 0.6$ and $E(Y)= 0.9$). Each rooted phylogenetic tree had its branch lengths scaled proportionally based on time of separation of clades and species, using the *rotl* package (Michonneau et al., 2016). In the tree, branch length informs on phylogenetic relatedness. The pPCA links the phylogeny to the life-history traits via a modified covariance matrix and estimated Pagel's λ, a scaling parameter for the phylogenetic correlation between species, expected under Brownian motion (Freckleton et al., 2002). Pagel's λ was estimated using the *ape* package (Paradis & Schliep, 2019) and varies between 0 (phylogenetic independence) and 1 (species traits covary proportionally to their shared evolutionary history) (Revell, 2010). The loadings for each axis were consistent across all trees (Online Resource S1; https://doi.org/10.1101/2024.07.11.601909) and Pagel's λ was either consistently above or below our cut-off value of $\lambda>0.25$ (Online Resource S2; https://doi.org/10.1101/2024.07.11.601909), above which we assumed the phylogenetic signal is strong for both feeding levels. Therefore, we report results from one single tree, randomly selected from the subsample of twenty trees (Appendix A: Figure S2.1). Three species (*Squalus hawaiiensis*, *Aetobatus narutobiei* and *Maculabatis ambigua*) were not in the Vertlife.org database and thus excluded from the phylogenetic tree and analyses. Two species, *Etmopterus granulosus* and *Aetomylaeus bovinus*, were removed because they did not have an associated polygon shapefile on the IUCN database (see below). After visual inspection of the PCAs, *Somniosus microcephalus* was identified as an outlier and removed, because of its extreme life history trait values compared to all other species in the dataset.

Table 2.1 Demographic quantities and their loadings onto the Principal Components axes. To calculate life history traits, we discretised each DEB-IPM (Eqn 1) by dividing the length domain Ω into 200 very small-width discrete bins, resulting in a matrix **A** of size $m \times n$, where $m = n = 200$, and which dominant eigenvalue equals λ. Mean lifetime reproductive success R_0 is the dominant eigenvalue of the matrix $\mathbf{F} = \mathbf{V}(\mathbf{I} - \mathbf{G}\boldsymbol{S})^{-1}$, where **I** is the identity matrix and **V**= **DR**, with **D** as the parent-offspring association, **R** the reproduction, **G** the growth and **S** the survival matrix48; this gives generation time $T = \log(R_0)/\log(\lambda)$ (Caswell, 2001). The mean life expectancy, η_e, is calculated as $\eta_e = 1^T\mathbf{N}$, where 1 is a vector of ones of length m and **N** is the fundamental matrix $\mathbf{N} = (\mathbf{I} - \mathbf{S})^{-1}$. The longevity of an individual of length L is η_L, which means we can calculate age at sexual maturity $\boldsymbol{L_\alpha} = \boldsymbol{\eta_{L_b}}$ and mature life expectancy $\boldsymbol{L_\varpi} = \boldsymbol{\eta_{L_p}}$ so that $\boldsymbol{\eta_e} = \boldsymbol{L_\alpha} + \boldsymbol{L_\varpi}$ (Caswell, 2019, eqn 4.21). l_x is the probability of surviving to age at least x, and m_x is the average fertility of age class x (cf. Tuljapurkar et al., 2009), $\overline{\mathbf{G}}$ is the mean of G, $\overline{\mathbf{V}}$ is the mean of V, and i and j are the row and column entries of the matrix, respectively. The vital rates included in the studied set of demographic quantities (progressive growth γ, retrogressive growth ρ, and sexual reproduction φ) were averaged across the columns j (the length bins), weighted by the relative contributions of each stage at stationary equilibrium. For example, to calculate mean sexual reproduction φ, we summed the values in the columns j of the **V** matrix and multiplied each φ_{ij} by the corresponding jth element w_j of the stable stage distribution w, calculated as the right eigenvector of **A**.

		Feeding level		$E(Y)$= 0.6			$E(Y)$= 0.9		
		Number of species in analysis		63			151		
Demographic quantity	**Symbol**	**Definition**	**Equation**	**PC1**	**PC2**	**PC3**	**p-PC1**	**p-PC2**	**p-PC3**
Generation time	T	Number of days required for the individuals of a population to be fully replaced by new ones	$T = \frac{\log(R_0)}{\log(\lambda)}$	**0.532**	-0.215	-0.007	**0.942**	-0.234	0.147
Survivorship curve	H	Keyfitz' entropy (H < 1 denotes increasing mortality rate with age, H > 1 denotes decreasing mortality rate with age, (H)= 1 denotes a constant mortality rate with age) (Keyfitz & Caswell, 2005).	$H = -\frac{\sum_{x=0}^{x=\eta_e} \log(l_x) l_x}{\sum_{x=0}^{x=\eta_e} l_x}$	0.281	0.110	**0.772**	0.086	0.083	**0.987**

Age at maturity	L_a	Number of days that it takes an average individual in the population to become reproductive	$L_{\alpha} = \eta_{L_b}$	0.274	0.048	**-0.538**	**0.828**	0.384	-0.228
Progressive growth	g	Mean probability of growing to a larger length across the length domain W.	$\gamma = \sum_{i}^{m} \bar{\mathbf{G}}_{i,j}\vert_{i<j}$	**0.511**	0.006	-0.007	**0.869**	-0.004	0.043
Retrogressive growth	r	Mean probability of growing to a smaller length across the length domain W.	$\rho = \sum_{i}^{m} \bar{\mathbf{G}}_{i,j}\vert_{i>j}$	-0.161	**-0.462**	0.042	-0.138	**-0.898**	-0.066
Mean recruitment success	φ	Mean per-capita number of recruits across the length domain W.	$\varphi = \sum_{i}^{m} \bar{\mathbf{V}}_{i,j}$	-0.210	**0.521**	0.043	**-0.720**	**0.643**	0.092
Degree of iteroparity	S	Coefficient of variation in age at reproduction	$S = \bar{m}_x/\sigma(m_x)$	-0.045	**0.451**	0.169	-0.228	**0.734**	0.059
Net reproductive rate	R_0	Mean number of recruits produced during the mean life expectancy of an individual in the population.	$R_0 = \sum_{x=0}^{x=\eta_e} l_x m_x$	0.097	**0.474**	-0.287	0.344	**0.870**	-0.028
Mature life expectancy	L_w	Number of days from the mean age at maturity (L_α) until the mean life expectancy (η_e) of an individual in the population.	$\boldsymbol{L_{\varpi} = \eta_{L_p}}$	**0.469**	0.162	-0.023	**0.899**	0.264	0.187
Axis				**Fast-slow**	**Repro**	**Longevity**	**Fast-slow**	**Repro**	**Longevity**
Proportion of variance explained				42.1%	31.2%	14.9%	43.1%	31.0%	12.0%
Cumulative proportion of variance explained				42.1%	73.3%	88.2%	43.1%	74.1%	86.1%
Kaiser criterion				3.79	2.80	1.34	15.05	7.78	1.17
Pagel's lambda (for the pPCA)				-			0.303		

We checked the influence of phylogeny and body mass on the structuring of life history strategies (see Jeschke & Kokko, 2009 for a detailed discussion) by running PCA analyses with and without a phylogenetic correction, and with and without a body mass correction. Body mass was corrected for by computing the residuals for linear models between the $\log_{10}$-transformed life history traits (Table 2.1) and body mass for each species for both the PCA and the pPCA (Jolicoeur et al., 1984; Gaillard et al., 1989; Revell, 2009). Body mass values were extracted from Fishbase (Froese & Pauly, 2023) using the *rfishbase* package (Boettiger et al., 2012). Where available, we used the maximum mass given on Fishbase. For species without mass records, we employed length-weight relationships to infer maximum body mass. If the length-weight relationship used a length type that was not in the database, length-length conversions were conducted prior to length-weight conversions (e.g. converting fork length to pre-caudal length). Data were not available for all species. The total number of species included in each PCA are summarised in Table S2.1 (Appendix A). We assessed the significance of PC axes using Kaiser's criterion, retaining PC axes with eigenvalues greater than unity (Kaiser, 1960).

To compare if and how species position changed between the low and high feeding levels, we took the standardised score (z-score) of each principal component for all species in each analysis (n= 63 for $E(Y)$= 0.6, n= 151 for $E(Y)$= 0.9). The standardised scores were plotted only for the 63 species that were in both analyses.

2.3.3 Effect of phylogenetic ancestry and habitat (water temperature) on life history patterns

For each feeding level, we assessed if habitat and phylogenetic clade affect elasmobranch life history variation (objective 3). We sourced habitat information (water depth and environmental temperature) for each species. Continuous variable 'commonly used depth' was sourced for each species from the Fishbase database (Boettiger et al., 2012; Froese & Pauly, 2023). If commonly used depth was unavailable, median depth was sourced from the IUCN database (IUCN, 2021). For temperature, we used 'temperature-at-depth' following the methodology of (Barrowclift et al., 2023). To this end, shape files containing polygons of known depth ranges for each species were taken from the IUCN database (IUCN, 2021). These were overlaid onto the International Pacific Research Center's mean annual ocean temperatures across 27 depth levels (0-2000m), based on a dataset from the Argo Project (available at http://apdrc.soest.hawaii.edu/projects/Argo/data/statistics/On_standard_levels/

Ensemble_mean/1x1/m00/index.html). Median temperature-at-depth was calculated using values at the nearest depth level to each species' commonly used depth (or the IUCN median depth where commonly used depth was unavailable). For mesotherm species (family *Lamnidae*) a correction factor of 3.5^{o}C was applied to their median temperature.

We tested collinearity between depth, temperature and clade using visual inflation factor (threshold value VIF>10) in the *faraway* R package (Faraway, 2022). Depth, temperature and clade were all colinear. Therefore, we separately assessed the effect of temperature at depth (as the representative variable for habitat) and clade on the PC scores of the first and second axis of the best fitting (p)PCA for each feeding level. We used four general linear models (LMs) for each feeding level, where the predictor variable was either temperature at depth or phylogenetic clade, and the response variable was either PC1 or PC2 score. For each LM, the model assumptions of Gaussian errors, homoscedasticity and collinearity were confirmed by inspecting the probability plots and error structures in R (Lüdecke et al., 2021; Faraway, 2022; R Core Team, 2023).

2.3.4 Life history strategies as predictors of population growth rate, demographic resilience and conservation status

We used LMs to test, for each feeding level, if the PC scores (continuous variables) of the first and second axis of the best fitting PCA, and their interaction, predict population growth rate (λ) and demographic resilience across species (objective 4). To calculate λ, we discretised each DEB-IPM (Eqn 1) by dividing the length domain Ω into 200 very small-width discrete bins, resulting in a matrix **A** of size $m \times n$, where $m = n = 200$, and which dominant eigenvalue equals λ (Table 2.1). Demographic resilience was calculated as the damping ratio ξ, with $\xi = \lambda/||\lambda_2||$, where λ_2 is the highest subdominant eigenvalue of matrix **A** (Caswell, 2001; Capdevila et al., 2020b). To investigate predictive links between life history strategies and conservation status, global conservation statuses for each species were sourced from the IUCN database (IUCN, 2021), where LC indicates Least Concern, NT indicates Near Threatened, VU indicates Vulnerable, EN indicates Endangered, CR indicates Critically Endangered and DD indicates Data Deficient. We used an ordinal regression to assess if PC scores predict species IUCN conservation status (excluding Data Deficient species).

All LMs, ordinal regression analyses and plots (Wickham, 2016; Attali & Baker, 2023; Hijmans, 2023; Slowikowski, 2023) were performed in R version 4.3.2 (R Core Team, 2023) in Rstudio (RStudio Team, 2023), using the *dplyr* and *tibble* packages for data manipulation

(Wickham et al., 2022; Müller & Wickham, 2023). For each LM, the model assumptions of Gaussian errors, homoscedasticity and collinearity were confirmed by inspecting the probability plots and error structures in R (Faraway, 2022; Lüdecke et al., 2021; R Core Team, 2023).

2.4 Results

2.4.1 Elasmobranch life history strategies structure along three axes (objective 1 & 2)

At the low feeding level (E(Y)= 0.6), we found that elasmobranch life history traits structure along three separate PC axes that cumulatively explain 88.2% of the total variance in life histories (Table 2.1: PC1: 42.1%, PC2: 31.2%, PC3: 14.9%). Pagel's λ was lower than our cut-off value of 0.25 (Pagel's $\lambda < 0.001$) (Table 2.1), so the phylogenetic signal did not impact the results. Correcting for body mass did not qualitatively change the results either (Appendix A: Table S2.1) and we thus continued with the PCA results. Generation time (T), progressive growth (γ) and mature life expectancy (L_{ω}) loaded positively onto PC1 (Figure 2.2A) (Table 2.1). As PC1 scores move from negative to positive, individuals increase their allocation to progressive growth and mature life expectancy (longevity) at the expense of population turnover (i.e., greater generation time), suggesting an axis analogous to the fast-slow continuum (Gaillard et al., 2016) (Figure 2.2A). Degree of iteroparity (S), mean recruitment success (φ) and net reproductive rate (R0) were loaded positively onto PC2 and retrogressive growth (ρ) negatively (Figure 2.2A) (Table 2.1). These life history traits are all associated with reproductive strategies. Thus, as PC2 scores move from negative to positive, elasmobranchs attain greater lifetime reproductive success while their retrogressive growth decreases (Figure 2.2A). Finally, survivorship curve type (H) and mean age at maturity (L_{α}) were positively and negatively, respectively, loaded onto PC3 (Table 2.1). This means that as age at maturity increases (high L_{α}), senescence rates increase (mortality rate increases with age, corresponding to low H).

Like the low feeding level, at the high feeding level ($E(Y)= 0.9$), we found that elasmobranch life history traits structure along three separate pPC axes that cumulatively explain 86.1% of the total variation in life histories (Table 2.1: pPC1: 43.1%, pPC2: 31.0%, pPC3: 12.0%). Pagel's λ was higher than our cut-off value of 0.25 (Pagel's $\lambda = 0.31$), indicating the phylogenetic signal was significant. Correcting for body mass did not qualitatively change the results (Appendix A: Table S2.1) and thus we continued with the pPCA results. Generation time (T), progressive growth (γ), mature life expectancy (L_{ω}) and age at maturity (L_{α}) were loaded positively onto PC1 and mean recruitment success (φ) negatively (Figure 2.2B) (Table 2.1). Like the low feeding level, as PC1 score increases, individuals increase their allocation to progressive growth and mature life expectancy at the expense of longer generation times and later maturity. Therefore, again, PC1 most closely represents the fast-slow continuum (Figure 2.2B). Degree of iteroparity (S), mean recruitment success (φ) and net reproductive rate ($R0$) were loaded positively onto PC2 and retrogressive growth (ρ) negatively, respectively (Figure 2.2B) (Table 2.1). As PC2 score increases, elasmobranchs attain greater lifetime reproductive success (iteroparity and net reproductive rate) and an increased number of breeding females (recruitment success), again representing the reproductive strategy axis (Figure 2.2B). Only survivorship curve type (H) was loaded positively onto PC3 (Table 2.1), so for higher PC3 scores, senescence rates decrease (decreasing mortality with age).

Comparing the position of each species at each feeding level showed that species move along each PC axis in particular ways (Figure 2.2C). For example, at the low feeding level, species that are fast paced but have a low reproductive strategy score (e.g. *Mobula birostris*), increase mostly in life history speed with increasing feeding level (Figure 2.2C: bottom left-hand corner). But, at low feeding level, species that are fast paced and also have a high reproductive strategy (e.g. *Anoxypristis cuspidata*), move to a lower reproductive strategy with an increase in feeding level (Figure 2.2C: top left-hand corner). Likewise, species that are slow paced with a low reproductive strategy at low feeding level (e.g. *Beringraja binoculata*), show a higher reproductive strategy as feeding level increases (Figure 2.2C: bottom right-hand corner). But species that are slow paced with a high reproductive strategy (e.g. *Prionace glauca*) tend to show faster life history speeds with increasing feeding level (Figure 2.2C: top right-hand corner). Together, these shifts create an anticlockwise ‘whirlpool’ effect as species move across the life history strategy space in response to an increase in feeding level (Figure 2.2C).

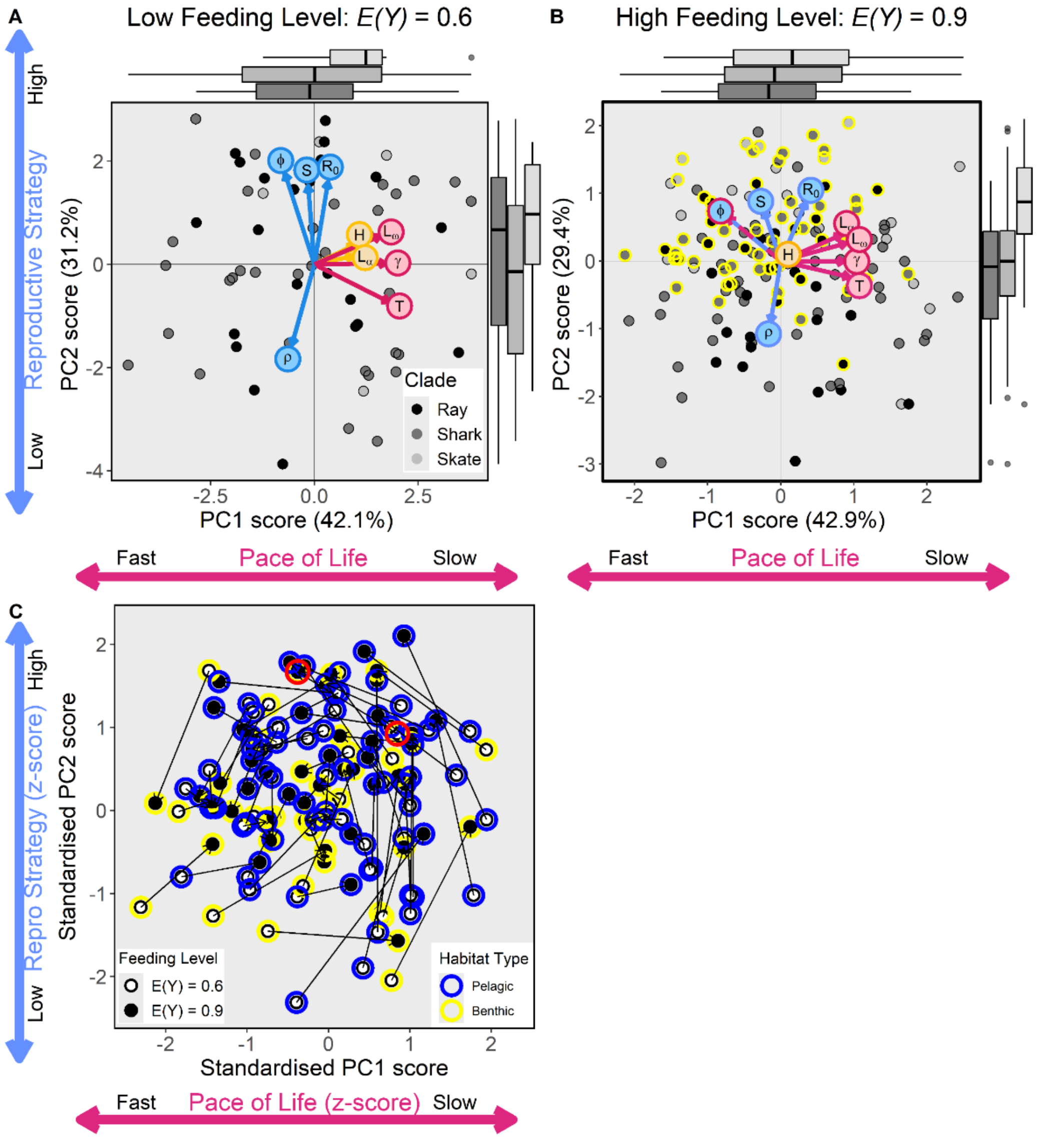


Figure 2.2 (p)PCA plots for the 0.6 (A) and 0.9 (B) feeding levels, representing 63 and 151 species respectively. Marginal boxplots of the split by clade (Shark, Skate and Ray) are included for each principal component. Species present in A are highlighted in yellow in B. Labelled arrows correspond to the variables used in the PCA analysis and show the magnitude and direction of the loadings. Red arrows align with the fast-slow continuum, blue arrows align with the reproductive axis and the orange arrow does not align with either of the primary two principal components. The dashed blue/red arrow aligns with both the Slow-Fast continuum and the reproductive axis in plot B. (C) the change standardised (z-scored) PC scores plotted for the 63 species in both low (white points) and high (black points) feeding level. The change in life history strategies between low and high feeding level creates a ‘whirlpool’ effect. Benthic shark species are highlighted in yellow and pelagic shark species are highlighted in

blue, in line with habitat types and descriptions of habitat use on the IUCN red list database (IUCN, 2025). The blue shark is further highlighted by a red circle.

2.4.2 Habitat type shapes life history strategies differently for different feeding levels and clades (objective 3)

For the low feeding level *E*(*Y*)= 0.6, neither temperature at depth (p= 0.350) nor clade (p= 0.320) significantly affected species position on the PC1 (fast-slow) axis. Similarly, neither temperature at depth (p= 0.924) nor clade (p= 0.336) significantly affected species position on the PC2 (reproductive strategy) axis.

At the high feeding level *E*(*Y*)= 0.9, phylogenetic clade did not significantly affect PC1 score (fast-slow continuum) (p= 0.445). There was a significant effect of temperature at depth on PC1 score ($F_{1,149}$= 23.93, adjusted-R^2= 0.13, p= <0.001). PC1 scores decreased in value (and pace of life increased) with increasing temperature at depth, indicating faster pace of life in warmer waters (Figure 2.3A). PC2 scores (reproductive strategy) decreased with increasing temperature at depth ($F_{1,149}$= 4.86, adjusted-R^2= 0.03, p= 0.029: Figure 2.3B). This suggests that across all elasmobranchs, species with lower reproductive outputs occur in warmer waters. PC2 scores were higher for skates than sharks and rays, indicating that skates have a high reproductive output ($F_{2,148}$= 6.97, adjusted-R^2= 0.11, p= <0.001, Figure 2.2B).

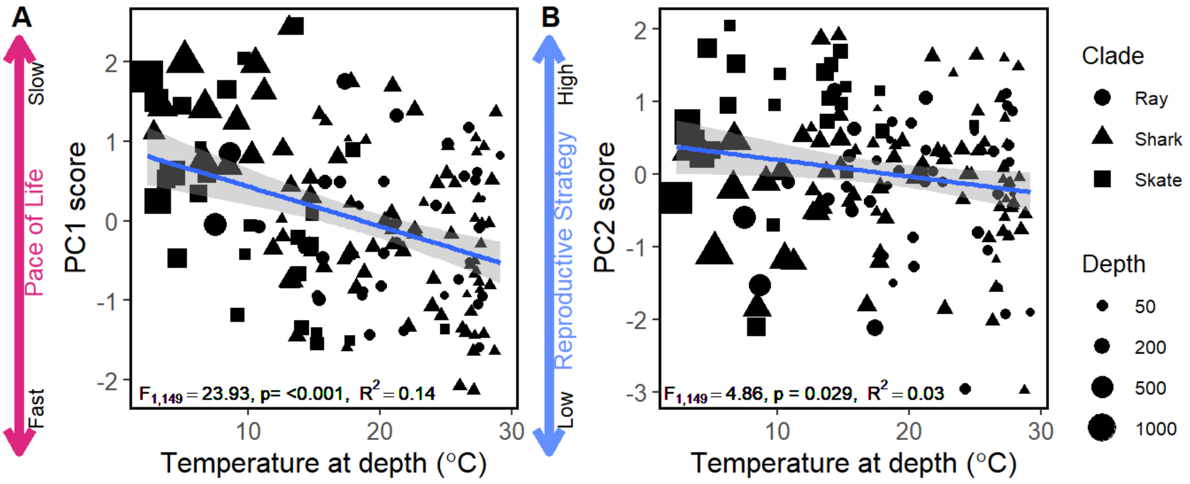


Figure 2.3 For the high feeding level E(Y)= 0.9. (A): The relationship between temperature-at-depth and PC1 (fast slow axis). Warmer temperatures relate to negative PC1 scores (faster paces of life). (B) PC2 score decreased for increasing temperature-at-depth. Reproductive output was greater for species inhabiting cooler waters. F-statistics, p-values and R^2 for each

analysis are in each plot window. The grey band around the fitted models shows the 95% confidence intervals.

2.4.3 Life history strategies as predictors of population performance and IUCN status depends on feeding level (objective 4)

At the low feeding level *E(Y)*= 0.6, population growth rate significantly increased with increasing PC1 scores (fast-slow axis) and increasing PC2 scores (reproductive strategy axis) (Table 2.2), showing that slower paced species and species with higher reproductive outputs have higher population growth rates (Figure 2.4A: e.g. *Raja montagui*, *Leucoraja ocellata*, *Squalus acanthias*). Resilience to perturbations (damping ratio) was significantly affected by the interaction between PC1 and PC2 scores (Table 2.2). Damping ratio significantly increased with both decreasing PC1 scores and increasing PC2 scores, showing that faster paced species with higher reproductive outputs have increased resilience to perturbations (Figure 2.4C: e.g. *Scoliodon laticaudus*, *Urolophus paucimaculatus*, *Rhizoprionodon acutus*). There was no significant association of PC1 scores, PC2 scores, or their interaction on the IUCN category of species (Table 2.2, Figure 2.4E).

Table 2.2 General linear models for population growth rate (λ) and demographic resilience (damping ratio, ξ), as well as ordinal regression models for IUCN conservation status, as a response to PC1 (fast-slow axis) and PC2 (reproductive strategy) scores, for both the low (*E(Y)*=0.6) and high (*E(Y)*=0.9) feeding levels.

Variable	**Axes**	**Estimate**	**df**	**Std. Error**	**p**	**R^2**
		Feeding Level E(Y)= 0.6				
$\lambda \sim PC1 * PC2$	Intercept	1.010		0.008	**<0.001**	0.674
	PC1	0.042	1	0.004	**<0.001**	
	PC2	0.031	1	0.005	**<0.001**	
	PC1:PC2	0.002	1	0.003	0.402	
	Error term	0.067	59			
$\xi \sim PC1 * PC2$	Intercept	1.164		0.011	**<0.001**	0.590
	PC1	-0.034	1	0.006	**<0.001**	
	PC2	0.053	1	0.007	**<0.001**	
	PC1:PC2	-0.009	1	0.004	**0.029**	
	Error term	0.092	59			

as.factor(IUCN) ~ PC1 * PC2	PC1	0.019		0.116	0.869	0.012
	PC2	-0.128		0.133	0.336	
	PC1:PC2	0.088		0.073	0.227	
Feeding Level E(Y)= 0.9						
$\lambda \sim PC1 * PC2$	Intercept	1.215		0.007	<**0.001**	0.826
	PC1	-0.068	1	0.007	<**0.001**	
	PC2	0.167	1	0.007	<**0.001**	
	PC1:PC2	-0.082	1	0.007	<**0.001**	
	Error term	0.086	147			
$\xi \sim PC1 * PC2$	Intercept	1.237		0.012	<**0.001**	0.544
	PC1	-0.151	1	0.013	<**0.001**	
	PC2	-0.041	1	0.013	**0.001**	
	PC1:PC2	0.037	1	0.013	**0.004**	
	Error term	0.151	147			
as.factor(IUCN) ~ PC1 * PC2	PC1	0.483		0.151	**0.001**	0.030
	PC2	-0.095		0.150	0.526	
	PC1:PC2	-0.160		0.150	0.287	

R^2 values are adjusted-R^2 for the linear models and pseudo-R^2 for the ordinal regression on conservation status. McFadden's pseudo R^2 was calculated for the ordinal regression models using the equation $R^2 = 1 - \frac{residual\ deviance}{null\ deviance}$.

At the high feeding level *E(Y)*= 0.9, population growth rate was significantly affected by the interaction between PC1 scores (fast-slow axis) and PC2 scores (reproductive strategy) (Table 2.2). Population growth rate increased with increasing PC2 scores, but this increase was steeper for species with high, negative PC1 scores (faster species) than for species with high, positive PC1 scores (slower species) (Figure 2.4B: e.g. *Rostroraja eglanteria*, *Raja microocellata*, *Raja montagui*). Resilience to perturbations (damping ratio) was significantly affected by the interaction between PC1 scores and PC2 scores (Table 2.2). Damping ratio increased with decreasing PC1 (increasing pace of life) at a higher rate at low PC2 scores than at higher PC2 scores (Figure 2.4D). Overall, faster species with intermediate reproductive outputs show the highest resilience to perturbations (Figure 2.4D: e.g. *Scoliodon laticaudus*, *Rhizoprionodon acutus*, *Anoxypristis cuspidata*). There was a significant positive association between PC1 scores (fast-slow axis) and IUCN category, but not with PC2 scores or their interaction (Table 2.2). Species with a higher PC1 score (slower pace of life) were more likely to be in a higher threat category than species with a lower PC1 score (faster pace of life) (Figure 2.4F).

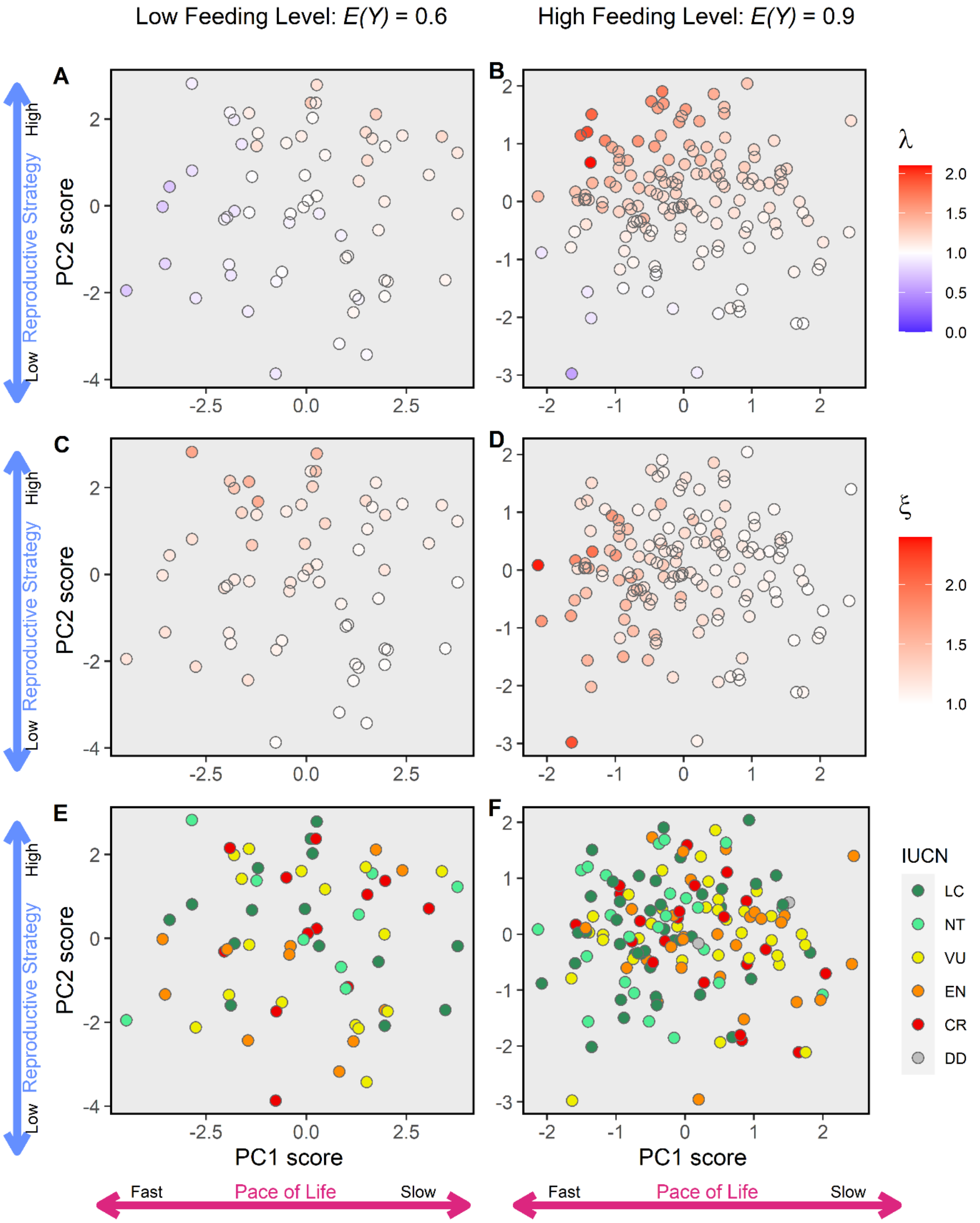


Figure 2.4 Overlays on the PCA figures for both feeding levels: E(Y)= 0.6 (A,C,E) and E(Y)= 0.9 (B,D,F). Population growth rate (A,B), damping ratio (C,D), IUCN conservation status (E,F).

2.5 Discussion

Our aim was to investigate how individual energy budgets, phylogeny and habitat type structure elasmobranch life history variation, and if this structured variation can predict population performance, resilience and conservation biology. Elasmobranch life histories are primarily structured along a fast-slow continuum and reproductive strategy axes at both a low and high feeding level. Interestingly, we found that as feeding level increased, species moved along the life history axes in an anticlockwise manner. Regardless, the two life history strategies (the fast-slow continuum and reproductive strategy) predicted species' population growth rate and demographic resilience for both feeding levels, and IUCN conservation status in the higher feeding level.

2.5.1 The impact of feeding level on quantifying and applying life history strategies

Typically, most variation in animal life history strategies, including the elasmobranchs studied here, is captured with two axes: the fast-slow continuum and reproductive strategy axis (Gaillard et al., 1989, 2016; Salguero-Gómez et al., 2016). For many taxa, including elasmobranchs, these strategies are influenced by phylogeny and habitat (Capdevila et al., 2020a), likely due to distinct environmental selective pressures. In this study, we captured the phenomenon that species move in life history space in an anticlockwise 'whirlpool' manner as feeding level changes. As feeding levels increase, faster-paced species (on the fast end of the fast-slow continuum) with low reproductive output speed up, whilst those with high reproductive output shift to lower reproductive output. Slower-paced species with low reproductive output increase their reproductive output, whilst those with high reproductive output increase their pace of life. The mechanism that underpins this 'whirlpool' effect is not immediately obvious, but possibly related to species-specific energy budget structure. Such plasticity in life history strategies can be adaptive when developing organisms adjust their allocation decisions in response to their local (feeding) environment, following evolved rules that maximise expected fitness in different ecological conditions (McNamara & Houston, 1996). The consequences of such feeding level effects can be far-reaching. Like other studies (Salguero-Gómez et al., 2016; Salguero-Gómez, 2017), we found that the two life history strategy axes predict species population growth, resilience and even conservation status. But plasticity in life history strategies highlights how predictions on performance, resilience and conservation status *specific to a species* will depend on feeding level, and thus, the environment it inhabits. One should therefore be cautious when extrapolating how species-specific life history strategies predict responses to (climate) change and perturbations in one environment, to another.

Although we find qualitatively the same two life history strategy axes as in other studies (Appendix A: Table S2.1; Salguero-Gómez et al., 2016; Salguero-Gómez, 2017; Healy et al., 2019; Capdevila et al., 2020a), there is one notable difference in the traits that comprise these strategies. One would expect that investment into development, i.e. high progressive growth, is characteristic of species with a faster life history speed. But in our analyses, progressive growth was higher for species with slower life history speeds, not faster (e.g. Salguero-Gómez et al., 2016; Salguero-Gómez, 2017) (Appendix A: Table S2.1). We surmise that this is due to high variation in the von Bertalanffy growth rate between species, driving a positive correlation between generation time and progressive growth (cf. van Noordwijk & de Jong 1986). For example, the values of progressive growth and generation time change with different values of von Bertalanffy growth rate and feeding level. The relationship between generation time and progressive growth for the reef manta ray, *Mobula alfredi,* can be plotted for a range of feeding levels and values of von Bertalanffy growth rate (Appendix A: Figure S2.2). For the same von Bertalanffy growth rate value, generation time increases with decreasing feeding level and progressive growth decreases. At the same time, generation time decreases with increasing von Bertalanffy growth rate values. The result is that, at the same feeding level (black solid lines in Appendix A: Figure S2.2), progressive growth increases with decreasing values of von Bertalanffy growth rate, and simultaneously, generation time increases. Because our dataset covers a wide range of von Bertalanffy growth rate values, this would explain why we found that the slower a species' life history speed, the higher its apparent progressive growth. These findings highlight the need for careful interpretation of correlations between life history traits calculated from demographic datasets (our objective 1 and e.g. Salguero-Gómez et al., 2016; Salguero-Gómez, 2017; Paniw et al., 2018; Healy et al., 2019; Capdevila et al., 2020a), and how these are used to predict population characteristics (van Noordwijk & de Jong, 1986).

2.5.2 Consequences for elasmobranch conservation

For many oceanic species, demographic data are sparce or lacking (Bradshaw et al., 2007; Pardo et al., 2016a; Temple et al., 2020). This often means the only measure available to evaluate a species relative risk to perturbations like fishing or environmental change, is an estimate of its maximum intrinsic rate of population increase, r_{max} (Myers et al., 1997, 1999; Dulvy et al., 2004; Pardo et al., 2016b). Typically, species with higher r_{max} values are assumed to have higher resilience to perturbations (cf. Cortés 2016; Pardo et al. 2016b, a). The intrinsic rate of population increase, r, is related to population growth rate ($\lambda = e^r$). We found that species with the highest population growth rates do not necessarily show the highest resilience. Particularly at the high feeding level, those species where populations grow at relatively low rates show the highest resilience. This highlights the importance of exercising caution when using summary metrics such as r_{max} to predict species' resilience (cf. Smallegange et al. 2020). Our approach presents a more mechanistic methodology that can be applied to data-sparce elasmobranchs to understand and predict their resilience and conservation status. For example, we found that faster-paced elasmobranchs show higher resilience. We also found that these faster-paced species generally live in warmer waters. Faster paced elasmobranchs might thus be better able to deal with the current rise in sea temperatures than slower species (Rosa et al., 2014; Osgood et al., 2021). However, some species living in warmer, shallower waters are more intrinsically vulnerable to exploitation (based on their r_{max} values) (Barrowclift et al., 2023), and may experience higher mortality due to their proximity to densely populated areas with fisheries (Letessier et al., 2019, 2024) compared to those living in colder and deeper waters (Dulvy et al., 2021). Additionally, global (sea water) warming is linked to poorer hunting performance in sharks (Pistevos et al., 2015). Warming can thus reduce the sharks' experienced feeding level, population growth rate and ultimately their resilience. Understanding how elasmobranch life histories, their habitats and feeding translate into differences in resilience is crucial to informing management decisions and predicting conservation status. Given that the most immediate threat to sharks, skates and rays is overfishing (Dulvy et al., 2021; Pacoureau et al., 2021; Worm et al., 2024), further study using an energy budget, demographic approach like ours could examine the effects of different fisheries mortalities (either by empirical measures or by derived estimates; Smith et al. 1998) on population performance of threatened or highly fished species.

2.5.3 Use of practical conservation tools to inform life history trait variation

Chapter 2 revealed plasticity in elasmobranch life history strategies, depending on experienced feeding level. Shifts in life history strategy between low and high feeding levels have implications for population growth and resilience. For example, the blue shark exhibited population growth at both low ($E(Y)$= 0.6: λ= 1.12, ξ = 1.05) and high ($E(Y)$= 0.9: λ= 1.52, ξ = 1.11) feeding levels (Figure 2.2C). Despite substantial fisheries pressure, the fast life history and high reproductive output of the blue shark may buffer against high mortality from bycatch and target catch. To link life history strategies to conservation biology, the models presented in Chapter 2 depend on accurate life history traits related to body size, growth, reproduction and survival. However, for species with broad distributions, like the blue shark, these traits may vary across locations and over time. Therefore, accurate measurement and monitoring of these traits through time is essential for generating reliable demographic predictions. In Chapter 3, I develop an accurate low-cost system to measure body length and growth of blue sharks, with potential applications for parameterising the demographic models used in Chapter 2.

2.5.4 Conclusion

Studies have shown that population responses to future environmental change and perturbations depend on species-specific life-history strategies. Further research should explore if variations in environmental conditions fuel plasticity of life history strategies in a range of taxa, and how these impact population performance and responses to change. Our analyses reveal that feeding level can cause plasticity in life history strategies, impacting how the fast-slow continuum and reproductive strategy framework can be used to predict population responses to change and perturbations. For elasmobranchs, we provide strong support for the expansion of the classical use of maximum intrinsic rate of population increase, r_{max}, to the fast-slow continuum and reproductive strategy framework, and highlight how our approach can be used to explore different scenarios of (over)fishing to quantify sustainable levels of exploitation.

Chapter 3. Design and comparison of underwater stereo-video and paired-laser photogrammetry to estimate size (body length) of blue sharks (*Prionace glauca*)

3.1 Abstract

Stereo-video and paired-laser photogrammetry provide non-invasive, cost-effective methods for measuring marine megafauna. This study compared the accuracy of a custom designed and built, low-cost, snorkeler-operated stereo-video system with paired-laser photogrammetry in both pool and field trials. Measurements were taken of a pole of known length and analysed using the StereoMorph package in R and Adobe Photoshop. Stereo-video was more accurate (mean error: 0.78% in the pool, 0.67% in field trials) compared to laser photogrammetry (mean error: 1.73% in the pool, 2.78% in field trials) at angles up to 20°. The stereo-video was then tested to collect length measurements of six blue sharks (*Prionace glauca*; pre-caudal length 1088-1501mm, mean ± SD = 1359 ± 155mm) in the English Channel and the Celtic Sea, during snorkel surveys. Length measurements combined with individual shark identification could be used to develop a long-term understanding of the transient UK population of blue sharks. Designs of the system are provided for use with open-source software, along with recommendations for deployment. This study demonstrates that a low-cost (£1,161, about half the cost of an 'off-the-shelf' setup) stereo-video system can effectively and accurately measure free-swimming marine megafauna. The system could benefit researchers and other users with limited resources to conduct research on marine megafauna.

3.2 Introduction

Body size measurements are critical to the study of population structure (Cubbage & Calambokidis, 1987; Meekan et al., 2006; Morisaka et al., 2022; Letessier et al., 2024), ageing (e.g. Natanson & Cailliet, 1986; Pauly, 2002; Frisk & Miller, 2006) and life histories (Francis & Duffy, 2005; Beldade et al., 2012; Harasti et al., 2019) of threatened marine fish and megafauna species. While direct measurements of captured animals offer accuracy, restraining large animals is often impractical (Sequeira et al., 2016) and capture can lead to stress, injury or mortality, as well as risk to researchers (Siegfried et al., 2021; Weber et al., 2021). Non-invasive techniques have been developed to accurately measure body size of marine species, including stereo-video and photogrammetry (Klimley & Brown, 1983; Harvey et al., 2002; Wehkamp & Fischer, 2014) and paired-laser photogrammetry (Deakos, 2010; Rohner et al., 2011). Published literature includes guides on general principles of these methods (e.g. Harvey

& Shortis, 1998; Shortis & Harvey, 1998), but few open-source designs have been shared for low-cost systems (e.g. for movement tracking; Dunkley et al., 2023). There is a need for publication of 'open-design' drawings, as well as suggestions for end-to-end manufacture and implementation of these systems with open-source software, for researchers with limited resources (Raasch et al., 2009; Boisseau et al., 2018).

Common applications of non-invasive measurement techniques include benthic and pelagic baited remote underwater videos systems (stereo-BRUVS) (e.g. Letessier et al., 2013; Bouchet & Meeuwig, 2015; Whitmarsh et al., 2017; Bouchet et al., 2018; Langlois et al., 2020), handheld stereo-video (Davis et al., 2015; Delacy et al., 2017; Siegfried et al., 2021) and paired-laser photogrammetry systems (Rohner et al., 2015; Cheney et al., 2017; Rogers et al., 2017; Wong & Auger-Méthé, 2018), which are typically operated by divers or snorkellers. Stereo-video and photogrammetry systems use two aligned and calibrated cameras (Harvey & Shortis, 1998; Shortis & Harvey, 1998; Shortis, 2015), where the overlap of the resulting images is used to calculate length measurements. These methods have been applied successfully across a range of marine megafauna including sharks (Klimley & Brown, 1983; Sequeira et al., 2016; Harasti et al., 2019; Lewis et al., 2023), mammals (Cubbage & Calambokidis, 1987; Hillcoat et al., 2021; Morisaka et al., 2022) and sea turtles (Siegfried et al., 2021; Piacenza et al., 2022). Paired-laser photogrammetry uses images from a single camera, positioned between two fixed lasers that project a scale bar onto the body of the animal, with a simple calculation to obtain body length. This technique has predominantly been applied in studies on marine megafauna such as whale sharks (*Rhincodon typus*) (Rohner et al., 2011; Araujo et al., 2014; Rohner et al., 2015; Robinson et al., 2016; Perry et al., 2018), reef manta rays (*Mobula alfredi*; Deakos, 2010), white sharks (*Carcharodon carcharias*; Leurs et al., 2015), long-finned pilot whales (*Globicephala melas*; Wong & Auger-Méthé, 2018) and green sea turtles (*Chelonia mydas*; Araujo et al., 2016, 2019). However, accuracy of non-invasive measurement systems can vary due to misalignment of cameras or lasers after calibration, diffraction (internal or external) of the lasers, non-perpendicular alignment of the target animal relative to the cameras, distance to the animal, image distortion, or improper calibration (Harvey & Shortis, 1998; Shortis & Harvey, 1998; Deakos, 2010; Letessier et al., 2015; Rohner et al., 2015; Delacy et al., 2017). Therefore, it is crucial to evaluate system accuracy in controlled trials and field checks using objects of known length.

The design of stereo-video systems include 'off-the-shelf' hardware and software (e.g. https://www.seagis.com.au/ and https://www.blueabacus.org/), or bespoke low-cost alternatives (Letessier et al., 2015; Delacy et al., 2017; Dunkley et al., 2023). Off-the-shelf setups offer high accuracy, but are relatively expensive. SeaGIS diver-operated stereo diver systems cost ~£1,170 and pelagic BRUVS cost ~£1,300 each (including base bar, housings and handles, but not cameras; costs converted from AUD to GBP). SeaGIS CAL software costs a minimum ~£640 (student price) and EventMeasure for a minimum of ~£620 (Student price). In addition, 3D calibration hardware is minimum ~£1,490 (500x500x300mm calibration cube and scale bar). Blue Abacus pelagic BRUVS (coming pre-calibrated and including downlines and leashes, but not cameras) cost ~£2,300 each. Alternatively, paired-laser photogrammetry systems require software to measure pixel distances and are commonly made using bespoke systems to fix lasers in place. Given the potential price barriers, low-cost and open-source designs for these systems could benefit researchers with limited budgets.

Low-cost alternatives to off-the-shelf systems include small action cameras (Letessier et al., 2015), 2D calibration checkerboards instead of a 3D cube (Boutros et al., 2015), open-source software (Olsen & Westneat, 2015) and bespoke or open-designs (Deakos, 2010; Rohner et al., 2015; Delacy et al., 2017). Excellent guides exist on the design (Shortis & Harvey, 1998; Bouchet & Meeuwig, 2015; Bergshoeff et al., 2017; Dunkley et al., 2023), deployment (Santana-Garcon et al., 2014; Bouchet et al., 2018; Langlois et al., 2020), validation (Deakos, 2010; Boutros et al., 2015; Letessier et al., 2015; Rohner et al., 2015; Delacy et al., 2017; Siegfried et al., 2021) and comparison (López-Macías et al., 2023; O'Connell et al., 2023) of non-invasive body length measurement methods. However, there is currently limited published guidance on end-to-end design of these systems and no direct comparison between methods using ground truth measurements for verification.

Here, a low-cost stereo-video and paired-laser photogrammetry system is developed and tested. The aim of the study is to design and build an accurate low-cost non-invasive system for measuring marine megafauna. The objectives are to first (1) design and build snorkeller-operated stereo-video and laser photogrammetry systems, (2) compare the accuracy of ground truth measurements for the two systems, using objects of known length. Then using the more accurate system to (3) check the consistency of measurement accuracy when used throughout a field season (five months) using objects of known length, (4) check the effect of target object angle and distance on the accuracy of results, suggesting a cutoff angle and distance for taking measurements, (5) estimate the lengths of blue sharks (*Prionace glauca*) in field trials and (6) share the designs of the more accurate system.

3.3 Comparing stereo-video and stereo-laser photogrammetry

3.3.1 Equipment & design of the stereo-video and laser photogrammetry systems (objective 1)

A handheld aluminium rig was designed and built to test and compare stereo-video and paired-laser photogrammetry systems (Figure 3.1a). Two rigs were built to identical specifications to simultaneously collect stereo-video and laser data across two field locations (rig_1 used in Cornwall and rig_2 used in Pembrokeshire, UK) and to compare accuracy in controlled pool trials. Each rig was equipped with two waterproof green pointer lasers (Tauchsport Oceama Underwater Green Laser) mounted 300mm apart in parallel using adjustable clamps. Three GoPro Hero 9^{TM} cameras were mounted on the frame inside standard GoPro dive housings. The central camera was positioned between the lasers, with the optical axis aligned parallel to the laser beams. The other two cameras were set 800 mm apart and converged inwards at 8^{o} on custom 3D-printed mounts, following established protocols for stereo measurements (Boutros et al., 2015; Letessier et al., 2015; Delacy et al., 2017). All cameras were configured to a linear field of view (94^{o}) to avoid fisheye distortion, recording at 2.7k video resolution and 120 frames per second.

3.3.2 Stereo-video calibration

Stereo-camera calibration followed the protocol described in Delacy et al. (2017). A checkerboard pattern of 9 × 5 squares (checkerboard dimensions: 570.8 × 317.1 mm, square: 63.4 × 63.4 mm) was filmed in a clear pool. A hand clap was recorded in view of both cameras, to synchronise the video frames and set a common start time. The *calibrateCameras* function performed checkerboard corner detection (Appendix B, Figure S3.1), undistortion coefficient estimation, and calibration coefficient estimation from up to 100 frames of the calibration videos (Olsen & Westneat, 2015). Calibration was performed using the Stereomorph package in R version 4.0.4 cameras (R Core Team, 2023), with detailed guidance available in the StereoMorph user guide (https://aaronolsen.github.io/software/stereomorph.html)).

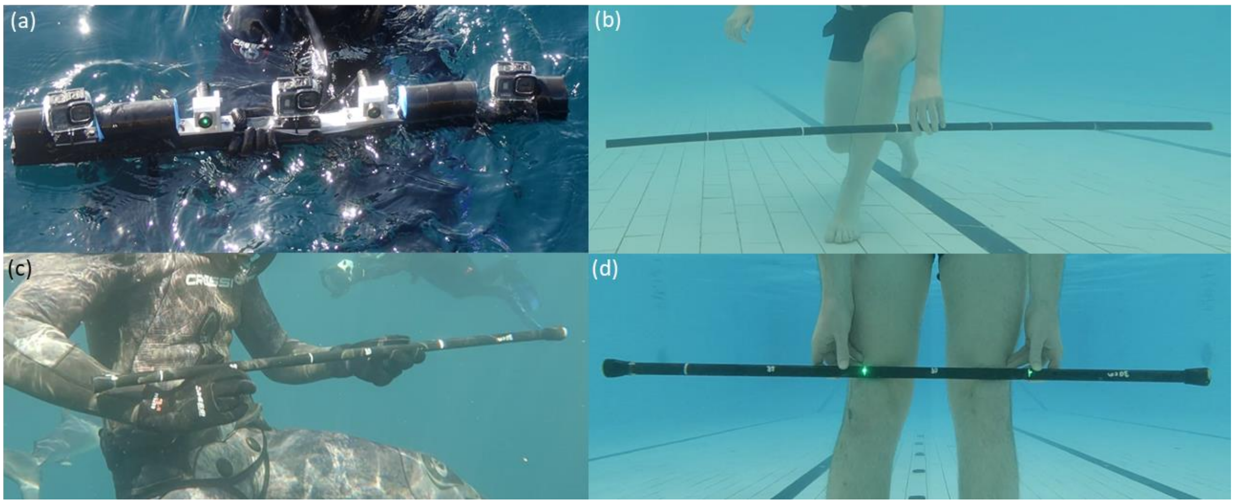


Figure 3.1 The stereo-video and laser photogrammetry system used in the pool and field to obtain measurements of sharks and a pole of known length. (a) Foam pieces were attached to the aluminium frame and wrapped in black duct tape for buoyancy in field trials. The left and right cameras collected data for the stereo-video measurements and the central camera collected data for the laser measurements. The two green laser pointers were fixed in place, parallel to each other, by adjusting the mounts. (b) Pole of known length (1500mm) filmed from the left view camera, showing the seven evenly-spaced landmarks with measurement distances of 250, 500, 750, 1000 and 1500mm. (c) and (d) show the 1000mm pole used in pool trials and field checks, with five landmarks at distances of 300, 600, 900 and 1000mm. Uneven spacing of the landmarks was used so the lasers could be projected onto a known object of 300mm, at the intended separation distance of the lasers.

3.3.3 Laser photogrammetry calibration

Calibration and assessment of the laser photogrammetry setup was conducted following methods outlined by Deakos (2010), Rohner et al. (2015) and Araujo et al. (2016).

Non-parallel alignment of lasers

Non-parallel alignment of the lasers would cause variation in point spacing with changes in distance to the target, causing inaccurate measurements. To ensure parallel alignment, the lasers were calibrated on land at intervals of 1, 3 and 5m against a parallel surface (either a wall or two targets set 300mm apart) before each deployment. If lasers were non-parallel, the clamps were re-positioned until they consistently hit the targets at 300mm at each distance.

Image distortion

Image distortion may occur due to diffraction between the wide-angle lens, housing and water. To account for this, a 13x9 checkerboard pattern (different to the stereo system checkerboard, total dimensions of 387.4mm × 268.2 mm with each square 29.8 × 29.8 mm) was photographed underwater (Appendix B, Figure S3.2). The horizontal pixel length of the central square was measured using Adobe Photoshop® version 22.0.0 and used as the reference for undistorted dimensions. The pixel lengths for 3, 5, 7, 9, 11 and 13 squares were measured and plotted against the expected values using a regression curve (Figure 3.2a). All measurements were corrected using the function:

$$L_{expected} = (-7.77 \times 10^{-5}) {L_{actual}}^2 + 1.05 L_{actual} - 9.34 \qquad \text{eqn 1}$$

Where, $L_{expected}$ is the expected pixel distance and L_{actual} is the measured pixel distance on the distorted photograph. Horizontal distortion was chosen over diagonal correction methods used in other studies (Deakos, 2010; Rohner et al., 2015; Araujo et al., 2016), because the targets measured in the pool and field were predominantly oriented horizontally in the images.

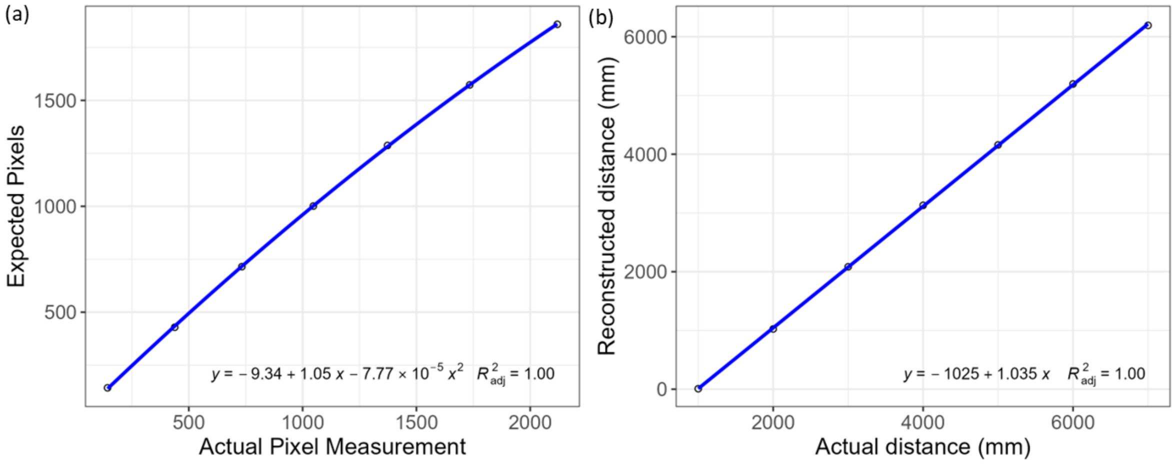


Figure 3.2 (a) Actual pixel measurements from images of a 13x9 square checkerboard, plotted against expected pixel values. Actual pixel values were measured using images taken with a wide-angle lens. Expected pixel distances were calculated by multiplying the number of squares measured by the pixel distance in the centre square of the image. The measurements of squares of the checkerboard were all taken horizontally, as that matched the orientation of the pole of known length and most sharks in the footage. All measured pixel distances in the analysis of the laser footage were transformed using the resulting linear regression equation.

Stereo-video footage was not transformed, as the camera calibration step accounts for image distortion. (b) Actual distance to reconstructed distance conversion measured in the pool trials from the stereo-video footage.

3.3.4 Comparing ground truth measurements

Pool trials

To assess the accuracy of both the paired-lasers and stereo-video measurements, controlled trials were conducted in a clear pool, using two objects of known length: a 1500mm plastic pole was initially used (before the field season), but after it was lost during the field season it was replaced with a 1000mm painted steel pole (used during and after the field season). Multiple measurements were made for each pole from ten video clips, with the poles presented between 0° and ~65° to the optical axis and up to ~7m from the cameras.

Videos were synchronised by identifying frames where the hand clap occurred in Shotcut version 24.02.29 and ten clips of ten frames each were extracted from each video for measurement using FFmpeg version 2022-05-26. Frames were extracted and labelled in the RStudio Stereomorph package (Olsen & Westneat, 2015; RStudio Team, 2023). Length measurements were obtained by labelling landmarks on the poles, made visible by contrasting white lines and the laser points (Figure 3.1b). For clips where laser points were visible, pixel distances were measured using the Photoshop ‘Ruler Tool’. These pixel measurements were then used to estimate actual length measurements on the 1000mm pole and the distance between the lasers (Figure 3.1c-d), using the following equation:

$$L_{pole,mm} = \frac{L_{pole,pixels} \times L_{lasers,mm}}{L_{lasers,pixels}} \qquad \text{eqn 2}$$

Where $L_{pole,mm}$ is the length of the pole in millimetres, $L_{pole,pixels}$ is the distance between length landmarks on the pole in pixels, $L_{lasers,mm}$ is the known distance between the lasers (300mm), and $L_{lasers,pixels}$ is the distance between the lasers in pixels.

Accuracy was calculated as the proportional percentage error of the estimated length compared to the known length of pole landmarks. Distance and angle of the target relative to the frame were calculated using the 3D positions of the pole in Stereomorph (Olsen & Westneat, 2015; RStudio Team, 2023). An angle to the target of 0^{o} indicated a perpendicular orientation to the optical axis (Garner et al., 2021). This approach for measuring the angle was chosen over the angle of incidence to the optical axis (Letessier et al., 2015), because the frame could be pointed at the shark, minimising the angle of incidence to the optical axis, but the angle of the shark to the pole could not be controlled. Distance to the target was estimated using the 3D reconstructions of the image space in StereoMorph. Markers were placed from one to seven metres in the pool and a general linear model (LM) was used to estimate the relationship between reconstructed distance and true distance to the pole. The relationship between the actual distance and reconstructed z_distance explained 100% of the variance ($y = -1025 + 1.035x$, df=5, $p<0.001$, Adjusted_$R^2 = 1.00$, Figure 3.2b). A one-way ANOVA was used to determine the number of labelled frames required per clip, using the pre-field season pool clips. ANOVA model assumptions of linearity, homogeneity of variance and normality of residuals were verified using the *check_model* function in the *Performance* package in R version 4.4.1 (Lüdecke et al., 2021; R Core Team, 2023). There was no difference in the log(error) value between measurements from one up to ten frames for rig_1 ($F(9, 770) = 0.033$, p=1.00) or rig_2 ($F(9, 790) = 0.088$, p=1.00). To account for the potential for human error in pixel labelling, three frames per video were used to take measurements of the pole and sharks.

Field trials

The 1000mm steel pole was used in a field check at the study site in Cornwall, UK. Length measurements were taken from seven landmarks marked with contrasting white tape, as well as the laser positions on the pole (Figure 3.1d). The angle of the pole relative to the frame was calculated using the mean angle between two measurements and the distance to the pole was estimated using the average of distance along the z-axis for each landmark in the stereo image 3D reconstruction. Proportional errors were calculated in the same way as the pool trials.

Performance comparison of laser and stereo systems (objective 2)

The accuracy of both laser and stereo systems is influenced by the distance and angle of the target to the optical axis (Deakos, 2010; Letessier et al., 2015; Rohner et al., 2015; Delacy et al., 2017; Garcia-Baciero et al., 2024). A visual check was performed to assess the errors compared to the distance and angle of incidence to the camera (Figure 3.3), resulting in the exclusion of angle of incidence of greater than 20^{o} from the analysis comparing laser and stereo-video systems.

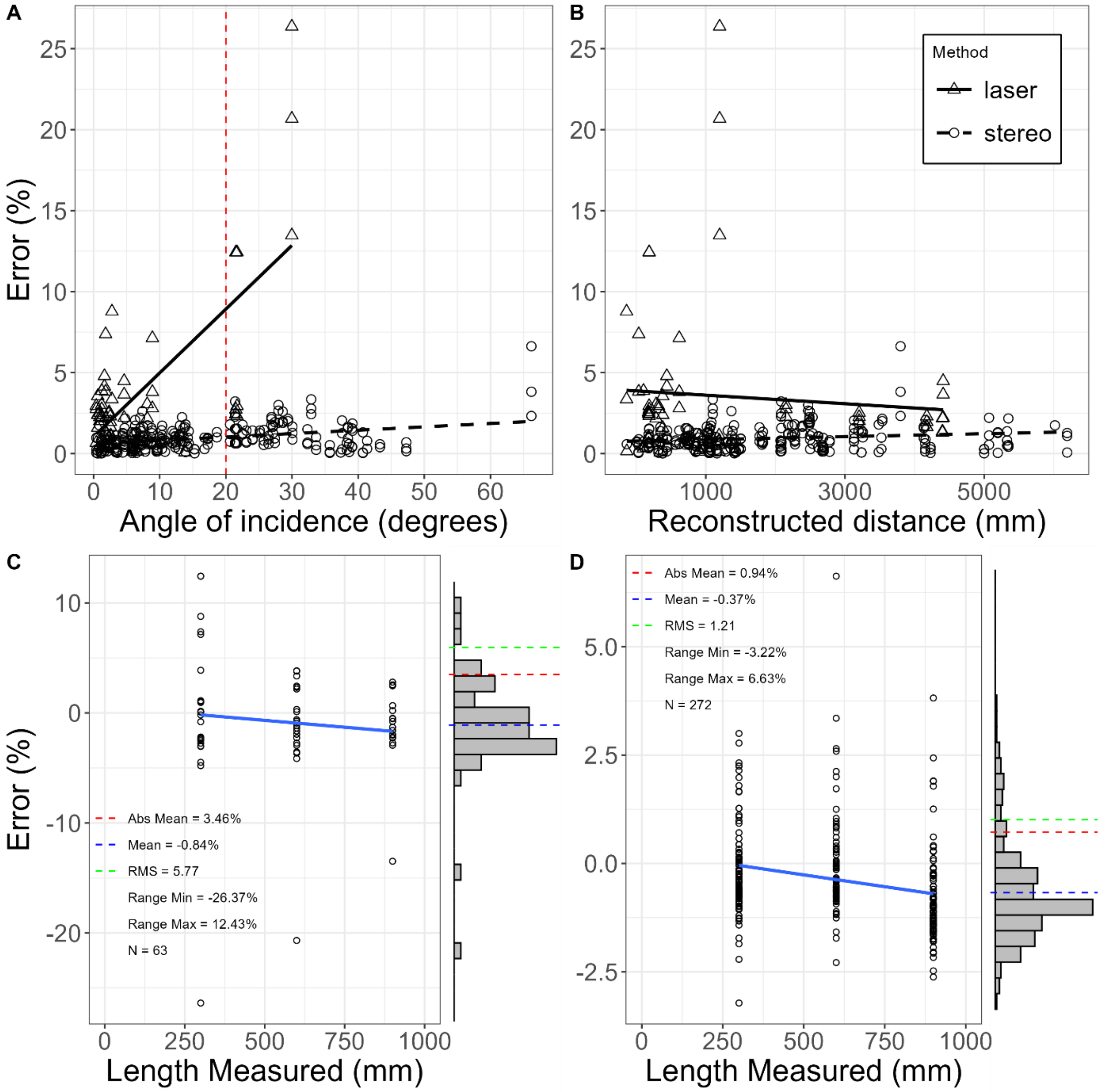


Figure 3.3 The effect of angle (A) and distance (B) on the absolute proportional percentage error for the stereo-video (circles and dashed line) and laser photogrammetry (triangles and solid line) systems. Angles of greater than 20^{o} were excluded from the analysis comparing the two systems (red dashed vertical line in plot A). (C-D) Absolute proportional percentage error (= measured length * 100 / ground truth length) plotted against known target length measurement for (C) lasers and (D) stereo-video.

A one-way ANOVA was conducted to determine if absolute proportional errors were different between field and pool measurements for the stereo-video and laser photogrammetry systems. Due to the heavy right skew of the histogram of absolute proportional percentage error, the analyses used natural-log value of the absolute proportional errors to meet the model assumptions (Lüdecke et al., 2021). For the stereo-video system, errors were analysed separately for each frame to test whether rig selection influenced accuracy. No ground truth measurements were available for rig_2 in the field, so error measurements were compared across five groups: stereo-video in the pool for rig_1 and rig_2, stereo-video in the field for rig_1, laser measurements in the field and laser measurements in the pool. Laser measurements were not split by rig number because calibrations must be performed before each deployment, whereas each stereo-video system has a unique calibration file.

The ANOVA indicated a significant main effect of group on log(error), $F(4, 456) = 52.67$, $p < 0.001$). Tukey post hoc analysis revealed significantly lower errors in the stereo-video group for rig_1 in the pool compared to lasers in both the pool ($p < 0.001$) and field ($p < 0.001$), as well as compared to the stereo-video for rig_2 in the pool ($p < 0.001$) (Table 3.1). Similarly, proportional errors were significantly lower in the stereo-video group for rig_1 in the field compared to lasers in the pool ($p < 0.001$) and field ($p < 0.001$), and for the stereo-video for rig_2 in the pool ($p < 0.001$). No other group comparisons were statistically significant. The stereo-video system (rig_1) performed significantly better than the paired-laser photogrammetry system in both field and pool trials, so the stereo-video system was used to measure blue sharks.

Table 3.1 Descriptive statistics for the absolute proportional error of ground truth measurements for the stereo-video and laser photogrammetry systems, using poles of known length in a controlled pool environment and in field trials. The two different rigs were split up for stereo-video, but not for the laser measurements, as the calibration files are different for each stereo-video system, but calibration is the same for the laser photogrammetry system.

System	**Field or Pool**	**n**	**Absolute error range**	**Mean absolute error**	**SD error**	**Max reconstructed distance from cameras (mm)**	**Max angle (degrees)**
Stereo Rig_1	Field	33	0.01-1.63%	0.67%	0.40%	618	14.4
	Pool	146	0.02-2.62%	0.78%	0.54%	6193	18.6
Stereo Rig_2	Pool	76	0.10-8.63%	4.01%	2.06%	5529	18.4
Laser photogrammetry	Field	29	0.08-8.77%	2.78%	2.18%	618	13.8
	Pool	24	0.11-4.48%	1.73%	1.12%	4411	6.6

Stereo-video measurement consistency (objective 3)

The stereo-video system was designed to maintain the GoPro cameras in a fixed position for the duration of the season. A one-way ANOVA was conducted and assumptions verified (Lüdecke et al., 2021) to determine if the natural logarithm of the absolute proportional error changed between pool trials at the beginning and end of the season for rig_1 and rig_2 using stereo-video. Each rig used a separate calibration file, made in the pool trials at the beginning of the season. Error measurements were compared across four groups: two sets of measurements per rig, one taken before the field season and one after the field season in pool trials.

There was a significant main effect of group on log(error), F(3, 519) = 115.2, $p < 0.001$). Tukey post hoc analysis revealed that errors were significantly lower in rig_1 before the field season compared to rig_2 after the field season ($p < 0.001$). Similarly, errors in rig_2 were significantly lower before the field season than after ($p < 0.001$). Additionally, errors in rig_1 after the field season were significantly lower than those in rig_2 before ($p = 0.016$) and after the season ($p < 0.001$). No other differences between groups were statistically significant. Rig_1 exhibited consistent performance in trials both before (absolute percentage error mean = 1.13%, max = 2.86%) and after the field season (mean = 0.80%, max = 3.53%). However, errors for rig_2 were higher after the field season (mean = 4.15%, max = 8.68%) than before (mean = 1.20%, max = 2.47%). It was not possible to determine when in the field season these increased errors occurred, so the data for rig_2 were excluded from further analyses. Consequently, only measurements from the rig_1 stereo-videos were used for blue shark measurements and analyses on the effect of distance and angle on measurement error.

Effect of angle and distance on results (objective 4)

A general linear model (LM) was used to investigate the influence of angle and distance on the absolute proportional percentage error for rig_1 of the stereo-video system. Errors were transformed using the natural logarithm due to presence of zero-inflated data. LM model assumptions of Gaussian errors, homoscedasticity and collinearity were verified by inspecting the probability plots and error structures in R version 4.4.1 (Lüdecke et al., 2021; Faraway, 2022; RStudio Team, 2023). The interaction between angle and distance from the rig significantly influenced the error (estimate = 7.2×10^{-6}, SE = 2.5×10^{-6}, $p = 0.005$; Figure 3.3). Therefore, angles exceeding 25^{o} and ~5m (4000mm reconstructed) distance were excluded from further analyses. Mean absolute proportional error of the remaining measurements was 0.92% and maximum error was 3.53% (Figure 3.4).

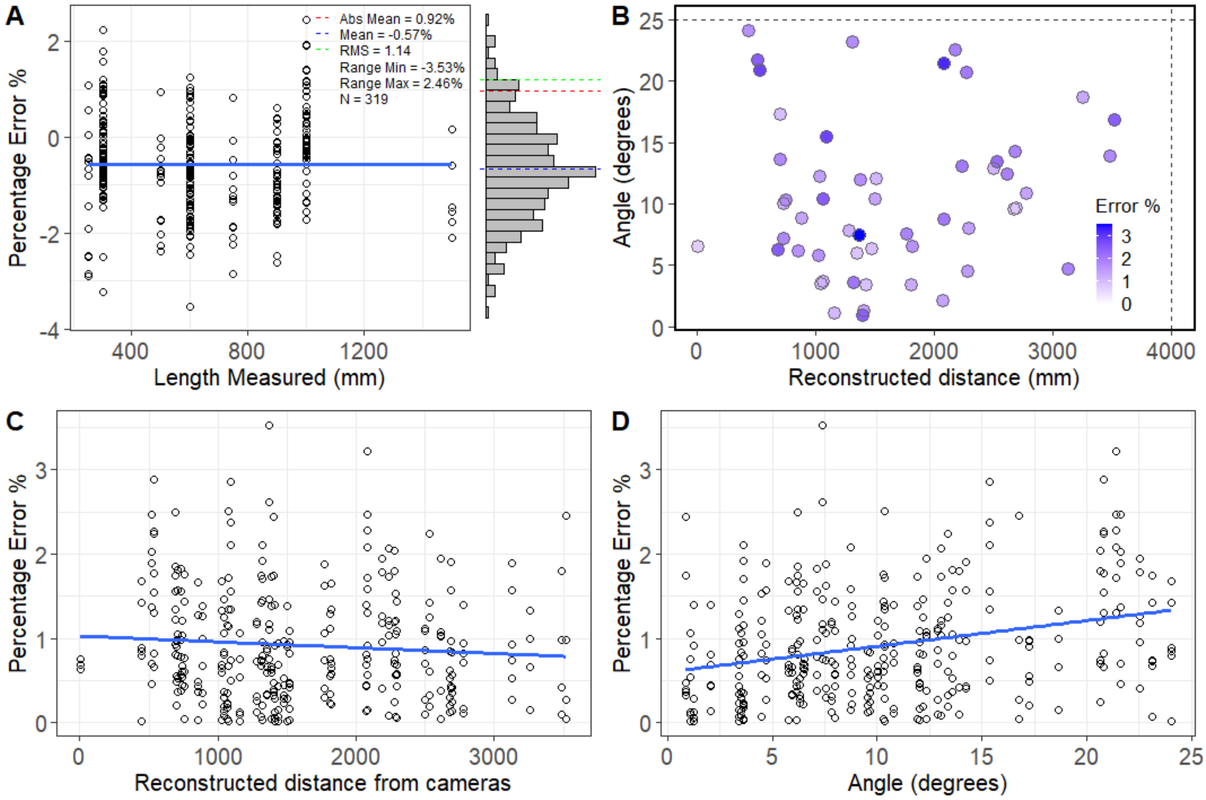


Figure 3.4 (a) absolute proportional percentage error (= measured length * 100 / ground truth length) plotted against known target length measurement, (b) the interactive effect of angle and distance on the absolute proportional percentage error, (c) the effect of distance from the target and (d) angle to the frame on the absolute proportional percentage error for the data remaining after removing all measurements at angles >25^{o} and distances >5m.

3.3.5 Blue shark measurements (objective 5)

Study area and population

All blue shark surveys were conducted between June and October 2023 off the southwest coast of the UK. Two study sites were selected: one in the English Channel approximately 20-30km off the south coast of Penzance, Cornwall, and the other in the Celtic Sea approximately 30-50km off Dale, Pembrokeshire. Surveys were conducted in collaboration with blue shark swim-with tourism operators (Blue Shark Snorkel, Cornwall; Celtic Deep, Pembrokeshire), who chose the specific study sites. To attract sharks and maximize encounter rates, the operators used their own chum mixes, consisting of waste fish, oils, and bran. Snorkel surveys were conducted at the surface in a pelagic environment with depths ranging between approximately 80-100 m.

Protocol

Snorkel surveys were conducted opportunistically when sharks were present. When encountered, the snorkeler attempted to film sharks with the central camera positioned perpendicular to the sagittal or dorsal plane, providing either a lateral or dorsal view of each animal. This allowed the estimation of pre-caudal length (PCL), fork length (FL) and total length (TL). Lasers were aimed at the skin of the sharks, below and either side of the dorsal fin. Metadata were recorded for each trial, including the deployment number, latitude, longitude, date, time, observer, SD card and camera identification numbers. This study was approved by the Newcastle University Animal Welfare Ethical Review Body (AWERB, Project ID No: ID 949).

Length measurements of blue sharks

Results from the pool and field checks demonstrated that stereo-video rig_1 (mean absolute percentage error = 0.92% ± 0.67% SD, range: 0.02-3.53%) outperformed both stereo-video rig_2 and the paired-laser photogrammetry systems. Consequently, stereo-video rig_1 was used to obtain length measurements for sharks. Using Shotcut software version 24.02.29, clips of ten video frames were identified where sharks were oriented approximately perpendicular to the sagittal or dorsal plane, and as close to straight as possible from the rostrum to the pre-caudal peduncle, tail fork and superior caudal fin tip.

Relevant markers from both camera views were digitised using the *digitizeImages* function in the Stereomorph package (Olsen & Westneat, 2015; RStudio Team, 2023). The four markers included (i) caudal fin superior tip, (ii) caudal fin fork, (iii) pre-caudal peduncle, (iv) rostrum anterior tip (Figure 3.5). The digitized markers were then reconstructed into 3D using the *reconstructStereoSets* function and lengths calculated by measuring the distance between the resulting 3D marker positions. This process resulted in measurements in millimetres for PCL, TL and fork length FL. The angle of occurrence was calculated using 3D positions by taking the mean the angles between the tip of the rostrum and the precaudal peduncle, and the tip of the rostrum and the caudal fin fork. Distance to the shark was determined by taking the mean of distances to each point along the z-axis of the reconstructed 3D stereo images.

Figure 3.5 Labelling landmarks for stereo-video digitizeImages function in R shown on a blue shark in field trials. Clip taken from CL271, left video, frame 0/9. A: superior tip of the caudal fin; B: caudal fin fork; C: precaudal peduncle; D: tip of the rostrum.

Measurement of blue sharks by size class

Individual identification of each shark was challenging, due to their relatively uniform colouration and appearance. Therefore, sharks were categorised into size classes. Multiple clips were extracted for each occurrence where sharks were favourably positioned for more than twenty frames, ensuring that clips did not overlap. Consequently, each occurrence was associated with one to five clips, each representing a different view or angle of the same shark. An occurrence was defined as a continuous on-screen presence of the same shark, with a new occurrence recorded every time a shark entered and exited the screen in a favourable orientation. An individual shark was considered unique if there was a difference of greater than 5% between size estimates. For measurements within 5% of each other, the measurement for the lowest angle of incidence was chosen for that individual. This method was chosen because the maximum measurement error was 3.53% and errors were lower at shallower angles, so 5% was deemed to be a conservative estimate for identifying individuals by size class. The approach assumed that there were no re-sightings of individual sharks between different study days. The sex of sharks was determined by the presence (male) or absence (female) of claspers. However, matching the shark sex to the length estimations was not possible for the individuals measured by size class, as the frames did not show the ventral side of the shark on any image.

Demographic estimations

In-water measurements were used to estimate maturity status. Maturity for males was estimated at a TL between 183–218 cm, and for females between 183–221 cm (Pratt, 1979; Nakano, 1994; Carrera-Fernandez et al., 2010). TL was calculated from FL using the equation from Kohler et al. (1996):

$$TL = \frac{PCL}{0.746} \qquad \text{eqn 3}$$

While TL measurements could be taken directly from the labelled data, the superior tip of the caudal fin was often not completely straight, whereas the pre-caudal peduncle was more frequently oriented in line with the shark's body. The total length of individual sharks was plotted on a growth curve (Figure 3.6) to estimate age and maturity status, using the growth function from vertebral rings in Stevens (1975):

$$l_t = 4230(1 - e^{-0.110(t+1.035)} \qquad \text{eqn 4}$$

Where l_t is the length of the shark in mm at age t. This approach allows for an estimation of age and developmental stage, contributing to the broader understanding of the demographics for the transient UK population.

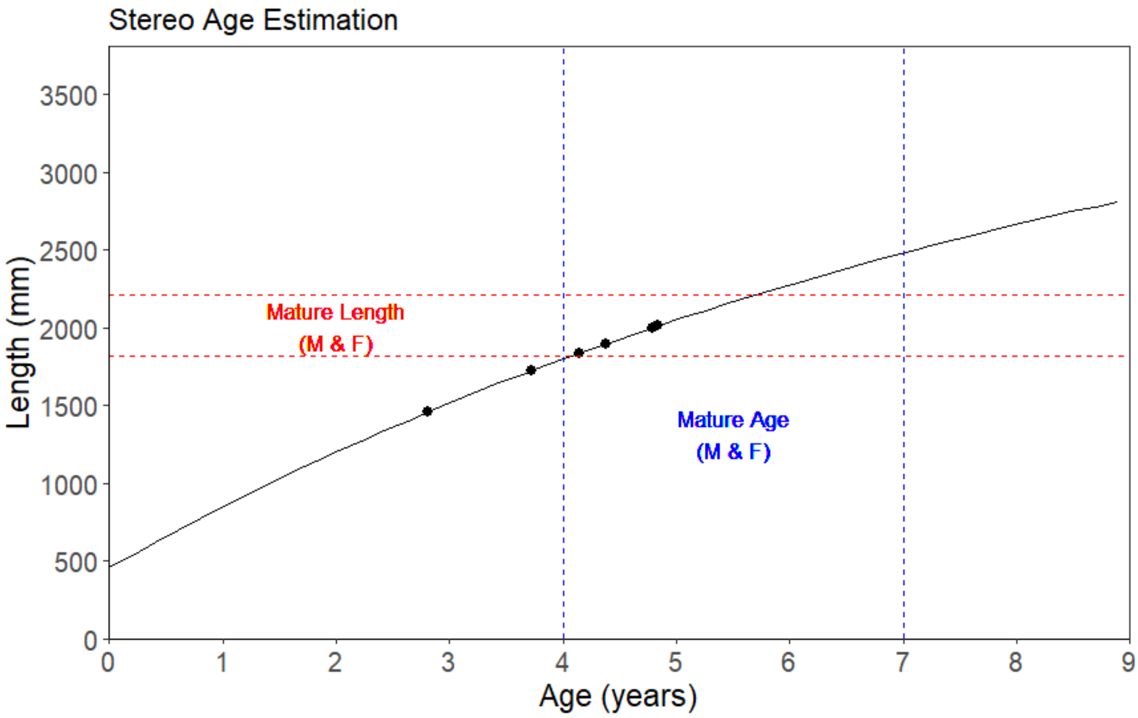


Figure 3.6 The six sharks grouped by size classes were plotted on a growth curve for blue sharks from empirical data. Two sharks were juvenile and four fell into the sub-adult length

range. Maturity for males was estimated at a TL between 183–218 cm, and for females between 183–221 cm (Pratt, 1979; Nakano, 1994; Carrera-Fernandez et al., 2010). TL was calculated from FL using the relationship in Kohler et al. (1996) (eqn 3). The growth function in Stevens (1975) was used to estimate age at length (eqn 4).

3.3.6 Designs of the stereo-video system (objective 6)

Stereo-video was more accurate than laser photogrammetry, so the designs of the stereo-video system were made available on a public repository, including drawings and a component list required to convert the handheld setup to a pelagic-BRUVS with simple modifications (available on Figshare: https://doi.org/10.6084/m9.figshare.27130239). Table 3.2 lists the equipment used and approximate prices in GBP.

Table 3.2 Component list and costs used to build the stereo-video and laser photogrammetry system. Details of equipment needed for the BRUVS conversion also listed. Costs correct as of July 2023.

	Component	**Cost (£ GBP)**
Cameras & Accessories		**£879**
	GoPro Hero9 camera	£500 for two
	GoPro protective housing	£100 for two
	GoPro battery charger	£55
	GoPro Dual Battery Charger with Batteries	£110 for two
	GoPro Battery (spares)	£50 for two
	SD cards (Sandisk 128Gb)	£59 for three
	Antifog inserts	£5
Rig		**£234**
	Aluminium square tube (40x40x3mm)	£17
	1000mm length	£7
	Foam noodle (attached for buoyancy)	£7
	Duct tape	£10
	Cable ties (assorted)	£5
	Camera strap	£20 (pack of 8)
	M12 countersunk rivnuts 24mm	£30 for two
	M12 threaded handle	£4 (pack of four)
	40x40mm plastic end caps	£24 (pack of 40)
	M5 countersunk rivnuts 11.5mm	£35 (pack of 50)
	M5 socket cap bolt 50mm	£20 (pack of 50)
	M5 socket cap bolt 25mm	£7 (pack of 20)
	M5 rubber washers	£9 (pack of 100)
	M5 self-locking nuts	£39

	Prusament PETG plastic and printing for 3D GoPro mounts	
Calibration		**£48**
	A2 Perspex sheet	£13
	~571 × ~317 mm 9x5 checkerboard in waterproof banner material	£35
Total	Stereo-video full setup (snorkeller- or diver-operated, with cameras)	**£1,161**

3.4 Discussion

3.4.1 Stereo-video was more accurate than laser photogrammetry

This study presents the design of an accurate low-cost non-invasive system for measuring marine megafauna. Stereo-video systems showed higher accuracy than laser photogrammetry. Specifically, the stereo-video system (rig_1) measured lower absolute proportional mean error (0.78% in pool trials and 0.67% in the field) and lower maximum proportional error (2.62% in pool trials and 1.63% in the field) compared to laser photogrammetry (mean = 1.73%, max = 4.48% in the pool; mean = 2.78%, max = 8.77% in the field) for angles up to 20^{o}.

We used a stereo-video design (800mm base bar separation and 8^{o} convergence angle) similar to other studies (Boutros et al., 2015; Letessier et al., 2015; Delacy et al., 2017), using bespoke 3D printed GoPro mounts, standard GoPro housings and ~571 × ~317 mm calibration checkerboard. The measurement accuracy of our low-cost stereo-video system (rig_1) and StereoMorph software, was comparable to results in previous studies. The absolute proportional mean error (0.92%) and maximum error (3.53%) for the pole of known length in our study (up to 25^{o} and distances up to ~5m) were similar to previous results using the same method to measure oceanic whitetip sharks (*Carcharhinus longimanus*; absolute proportional mean error = 0.33%, maximum = 3.07%) at angles up to 20^{o} and distances up to 5m (Delacy et al., 2017). Furthermore, these results are comparable with a 3D calibration cube and Sony HDR-CX700 cameras, which obtained mean proportional errors of between 0.1 and 0.5% from 2 to 5m (range not reported; Boutros et al., 2015). Likewise, the results from StereoMorph compared to mean proportional error of measurements using SeaGIS (error = 0.22%) and VidSync (error = 0.63%) software, showed that open-source packages can perform accurate measurements (López-Macías et al., 2023). While 3D calibration methods and paid software generally offer slightly higher performance, results of lower-cost methods demonstrate comparable accuracy.

Interestingly, stereo-video rig_2 demonstrated higher errors (absolute proportional error mean = 3.75% and max = 8.80% in pool trials) that were similar to ranges reported by Letessier et al. (2015) and Garner et al. (2021). Letessier et al. (2015) used a 3D calibration cube, GoPro cameras and EventMeasure software to record mean proportional errors between 1 and 6% between 1 and 5m distance. Garner et al. (2021), reported mean proportional errors of <5% in pool trials for distances up to 5m and angles up to 10^o using a remotely operated vehicle (ROV) with four different camera separation distances using GoPro Hero 5 cameras. The measurements in Garner et al. (2021) were most accurate at the widest base bar separation (762mm), comparable with our study (800mm), where mean proportional error was <5% for distances up to 5m and angles up to 30^o, measuring targets (288, 552 and 890mm) of similar size to this study (250-1500mm). It is not clear why the calibration and performance of rig_2 did not match rig_1. Despite having optional settings such as stabilisation turned off, it is possible that individual differences between each camera have caused the conflicting results between rig_1 and rig_2, although previous research has shown no effect of these differences (Letessier et al., 2013) and all optional settings (such as image stabilisation) were disabled on GoPros used in this study. Therefore, the most likely explanation is that the cameras were unintentionally misaligned either on the boat, or in transit between the manufacture site and the field site. Off-the-shelf systems continue to offer excellent accuracy, but our results show that the low-cost stereo-video system designs presented here are able to provide comparable measurement accuracy (using rig_1).

3.4.2 Recommendations for deployment

Researchers must consider the limitations and calibration performance of measurement methods, whether using off-the-shelf or self-designed produced systems. Paired-laser photogrammetry can achieve high accuracy when laser projections are perpendicular to the target surface as shown by Deakos (2010) (mean error = 0.39%, max error = 1.43%, after accounting for image distortion) and Rohner et al. (2015) (mean error = 1.2%). However, when targets were angled away from the perpendicular axis, mean error increased to >5% for angles $>20^o$ (Deakos, 2010; Rohner et al., 2015). Paired-lasers may be suitable for measuring slow moving, slow turning or rigid-bodied animals, where parallax error can be minimised (Deakos, 2010; Rohner et al., 2011, 2015; Araujo et al., 2016, 2019). However, they are less effective for measuring fast turning and flexible-bodied animals like sharks, where body curvature, added to the relative angle of the researcher, makes it challenging to obtain photographs of the animal perpendicular to the camera and straight from rostrum to pre-caudal peduncle, leading to poor accuracy (Leurs et al., 2015).

In addition to parallax errors, slight movement of lasers would cause errors due to convergence or divergence of the laser beams at larger distances as indicated in our study results. Although they were fixed in place by a clamp and stored in a padded fishing bag, the movement of lasers mounts was possible between calibration and use in the field. Similarly, despite the bespoke mounts, the movement of cameras could occur between calibration and use in the field for the stereo-video systems. Therefore, it is critical to the success of either method to obtain accurate calibration, minimise movement of the system between uses, re-calibrate regularly between uses and confirm consistent accuracy by measuring objects of known length in controlled environments and in the field.

3.4.3 Potential applications

The low-cost stereo-video system was used to estimate body length and maturity status of blue sharks in field trials. Further data collection could provide a description of the size structure of the migratory population of blue sharks around the UK, as well as use in other areas on different species and populations (e.g. Meekan et al., 2006; Lewis et al., 2023; Letessier et al., 2024). This approach could be extended to other methods including BRUVS, remotely operated vehicles (Garner et al., 2021) or drones (Piacenza et al., 2022). Moreover, individual identification using markings and scarring from photo-ID (Brooks et al., 2010; Gore et al., 2016; Hughes & Burghardt, 2017) would facilitate the measurement of more sharks from existing data (rather than using size classes, as it is likely that there were multiple sharks present of similar size), measurement of biomass (Kohler et al., 1996) and individual growth rates (Harasti et al., 2019). Matching these data to maturity status from sexed individuals could be applied in demographic models, which rely on length measurements, growth rates and maturity status to provide predictions of population growth rates and responses to change (Smallegange & Lucas, 2024; Lucas et al., 2024).

Designs of the handheld systems presented here offer convenient methods for collecting data on marine species with networks of volunteers and tourism operators. Although data analysis requires use of some specialist software, data collection is simple and does not require specialised equipment. This offers a means for data collection in previously untapped areas, or for opportunistic data collection where seasonal or unreliable presence of animals makes it impractical to resource full scientific investigations. Indeed, the stereo-video designs presented in this study are currently being used by tourism operators in field sites in the Maldives and Indonesia as a convenient method to survey resident shark populations (G. Araujo, pers. comm). This study complements the recent publication of a low-cost stereo-video system designed for tracking movements of aquatic species (Dunkley et al., 2023). The cost of each system is similar, although it is likely that tourism operators may have GoPros already available to them, rather than the Raspberry Pi camera system used in Dunkley et al. (2023), and accuracy of length measurements with the system was not tested. Yet, movement data could be useful to tourist operators, by investigating the behavioural responses of marine megafauna to people (Smith et al., 2016). Off-the-shelf systems may continue to provide accurate and precise length measurements, but open-design of future non-invasive measurement systems (as well as improvement to the system presented here) is encouraged, to promote the continuous improvement and accessibility of these low-cost technologies to researchers with limited resources (Raasch et al., 2009; Boisseau et al., 2018).

3.4.4 Monitoring population size structure and genetic connectivity of blue sharks

Chapter 3 developed a low-cost, non-invasive stereo-video system to accurately measure the body size of free-swimming blue sharks in the wild. While the stereo-video system provides a scalable tool for long-term monitoring of size-based population changes, which can be applied to the demographic models in Chapter 2, effective management of blue sharks requires an understanding of genetic structure across the species' global distribution. Therefore, in Chapter 4, I investigate blue shark global genetic structure using powerful genome scans to delineate potential management units.

3.4.5 Conclusions

The design of low-cost stereo-measurement systems presented in this study offer an alternative to commercial off-the-shelf systems to collect measurement data with high accuracy. The comparable SeaGIS stereo diver system, CAL software, EventMeasure software and 3D calibration cube cost a minimum of ~£4,000 GBP (converted from $8,050 AUD for comparison), whereas the equivalent components of our system (rig, calibration equipment and housings) costs £382. The simple, affordable system presented here could broaden the scope for data collection for researchers with limited resources, by providing recreational users or tourist operations the opportunity to collect data to contribute to scientific studies. In addition, the highest equipment costs for the system presented here are for the GoPro Hero9 cameras, so further research could investigate using cheaper action cameras, further reducing costs. Continued development and release of open-source calibration software, design improvements for low-cost systems and high-resolution action cameras will likely improve the accuracy of low-cost, non-invasive measurement systems in future. These data are vital in contributing to inform conservation and management to ensure future viable populations and to prevent species extirpation and extinction.

Chapter 4. Global panmixia or regional substructure in blue sharks (*Prionace glauca*): insights from full genome scans

4.1 Abstract

The blue shark (*Prionace glauca*) faces high levels of anthropogenic mortality, as target and bycatch species in fisheries throughout its global distribution. Despite evidence for genetic population structure in some regions and individual movements by satellite-tagged sharks between ocean basins, most research supports one single global population. Recent advancements in full genome scans have enabled the re-assessment of blue shark genetic structure across thousands of Single Nucleotide Polymorphisms (SNPs). In this study, blue sharks sampled from fisheries catch were genotyped using DArTseq methods. SNP filtering resulted in 6,157 loci recovered for 307 individuals. Although no clear unanimous population structure emerged when three clustering techniques were compared, two methods suggested population substructure in the eastern and southeastern Pacific, adding to research reporting substructure between the Mediterranean and the North Atlantic. Caution is recommended for researchers when interpreting population substructure using proprietary sequencing techniques. Future studies should prioritise combining datasets of genomic markers to investigate blue shark population substructure using samples from all regions across the blue shark's global distribution range. A global study with these samples is required before specific management recommendation can be made for this species.

4.2 Introduction

The blue shark (*Prionace glauca*) is an apex predator with a cosmopolitan distribution, found in all but the Southern Ocean, following productivity fronts in oligotrophic and mesotrophic pelagic environments (Druon et al., 2022). Blue sharks are predominantly caught in longline fishing gear and are the most common species found in the shark meat and fin trade (Cardeñosa et al., 2020, 2022; Pincinato et al., 2022; Poseidon, 2022; Collins et al., 2023). The listing of blue sharks on CITES Appendix II was implemented to better control trade, along with other threatened requiem sharks (Sherman et al., 2023a), although catch levels remain high. Global mortality is estimated to be 7-10 million individuals per year (Poseidon, 2022), with the global population declining by approximately ~29% between 1970 and 2020 (Pacoureau et al., 2021), with particularly steep declines in the Mediterranean (Ferretti et al., 2008). However, blue sharks are highly productive (e.g. Aires-Da-Silva & Gallucci, 2007) and their resilient life history strategies have led to a global assessment of Near Threatened (Rigby et al., 2019a) by the IUCN, although they are Critically Endangered in the Mediterranean (Sims et al., 2016). Catch levels fluctuate in different regions based on fishing effort, changes in legislation and the presence of alternative target catch species (ICCAT, 2023a; Worm et al., 2024). Indeed, blue sharks are positioned between target catch and bycatch in some areas, where some individuals are retained and others discarded at sea (usually based on storage limitations on boats) (ICCAT, 2023a). Fisheries observer programmes are used to characterise blue shark catch, but inconsistent coverage of observers and self-reporting of catch from fishers leads to uncertainty in catch report data, resulting stock assessments and resilience predictions (Aires-da-Silva et al., 2009; ICCAT, 2023a). Given the fluctuation of regional fisheries catch, gaps in observer coverage and uncertainty in predictive models on population health, there is a need to investigate blue shark global population structure to inform regional management plans.

Blue sharks are highly migratory, but satellite tagging and mark recapture studies have revealed that there is little movement between the global north and south (Queiroz et al., 2005; Sippel et al., 2011; Wögerbauer et al., 2016; Fujinami et al., 2021; Elliott et al., 2022), leading to the suggestion of one population across the entire Southern hemisphere (da Silva et al., 2010). Movements between hemispheres have been recorded in the Atlantic (Vandeperre et al., 2014a; Kohler & Turner, 2019; Mas et al., 2022), but mixing and mating between individuals from different hemispheres is poorly understood and there are suggestions that these stocks operate on different reproductive cycles (Nakano & Stevens, 2008). For example, blue sharks in the SW Atlantic can undergo their entire reproductive cycle within this region, leading to the suggestion that this area should be treated as a distinct management unit (Mas et al., 2023). Elsewhere, stable isotope and tagging analyses revealed limited movement between individuals from the NW and NE Pacific (Madigan et al., 2021). Further, satellite tagging and mark recapture research has shown no movement between the Mediterranean and N Atlantic (Poisson et al., 2024), or very little movement between the two, with Kohler & Turner (2008) reporting three of 3941 individuals caught and recaptured between 1962 and 2000 crossing the Strait of Gibraltar in either direction. Limitations for movement research include coverage, sampling area biases and shedding rates (Mas et al., 2022). Non-biological markers contribute to understanding population dynamics, but genetic analyses are required to delineate biological substructure.

Understanding genetic population structure is critical to conservation and management of threatened species (Jensen et al., 2020; Pearce et al., 2021; Hohenlohe et al., 2021; Bertola et al., 2023). There is conflicting information on whether blue sharks display panmixia or substructure in studies using traditional mitochondrial and microsatellite markers (Table 4.1). Evidence for one panmictic population (e.g. King et al., 2015; Taguchi et al., 2015; Bailleul et al., 2018) implies that fisheries would not require regional management, as highly fished stocks could be replenished by individuals moving in from other areas to reproduce. However, powerful genetic studies are revealing population structure when previously none was observed, where individuals would not be replenished by immigration from elsewhere (Hauser & Carvalho, 2008). Recent research suggests that Regional Fisheries Management Organisations (RFMOs) should treat localities as independent management units. For example, weak structuring was found in the SE Pacific from spatial genetic analyses using mitochondrial markers (González et al., 2023). Moreover, recent studies employing full genome scans across thousands of single nucleotide polymorphisms (SNPs) found substructure in the Mediterranean (Leone et al., 2017, 2024) (and North Atlantic; Nikolic et al., 2023). There is a need to investigate genetic population structure of blue sharks on a global scale to better inform evidence-backed fisheries management.

Movement (satellite tagging and mark recapture) and genetic studies have traditionally been confined to regional analyses (e.g. Aires-Da-Silva et al., 2009; Fujinami et al., 2021; Elliott et al., 2022; Poisson et al., 2024; Table 4.1) and international genetic studies lack truly global coverage. Weak genetic differentiation in global studies has been attributed to the ‘population grey zone’, where historic split of common ancestors could result in multiple distinct populations, but there is a time-lag between the split and the presence of sufficient molecular markers for differentiation (Bailleul et al., 2018; Nikolic et al., 2023). Both González et al. (2023) and Bailleul et al. (2018) recommended investigation of population structure using genomic sequencing techniques with denser marker coverage [e.g. DArTseq;DArT Pty Ltd: Sansaloni et al. 2011) or RADseq: Davey & Blaxter, 2010], to enable the detection of distinct populations that could be subject to the population grey zone (Foster et al., 2021). These techniques have been used on other wide-ranging pelagic megafauna species to identify population structure, where previously little or weak differentiation was found (e.g. Pecoraro et al., 2018; Green et al., 2022; Wagner et al., 2024).

Table 4.1 Summary of evidence from blue shark genetic studies, including methods (MtDNA: mitochondrial DNA, 'µsat’: microsatellite markers), sampling locations by region, sample size (n, with sampling method in brackets, ‘CR’: control region, ‘Cytb’: *mitochondrial cytochrome b*) and a brief description of results, with support for either panmixia or population structure.

Reference	**Method**	**Sampling Location**	**n**	**Evidence of population structure?**	
Bailleul et al. (2018)	MtDNA µsat	Med NE Atlantic N Atlantic N Pacific SW Pacific	201 (Cytb) 229 (µsat)	No	Supportive of panmixia across 9 microsatellite markers and 22 unique haplotypes, as well as a STRUCTURE analysis, but could indicate blue sharks fall into ‘population grey zone’.
Bitencourt et al. (2019)	MtDNA	Unspecified	270 (CR)	No	Haplotypic differences, but high gene flow between regions suggesting panmixia.
González et al. (2023)	MtDNA	SE Pacific	79 (CR) 72 (Cytb)	Yes (weak)	Spatial structure analysis of mtDNA markers revealed two clusters in the SE Pacific.
		Med NE Atlantic NW Atlantic SW Atlantic Indian N Pacific NE Pacific SE Pacific NW Pacific SW Pacific	554 (CR) 688 (Cytb)	Yes (weak)	Significant F_{ST} pairwise comparisons suggest Mediterranean and NE Atlantic differ from other regions (max $F_{ST} = 0.28$ between NE Atlantic and NE Pacific). However, there was high genetic connectivity between regions.
(King et al. (2015)	µsat	N Pacific NW Pacific NE Pacific	786	No	Single population of blue sharks from analysis of 14 microsatellite loci.
Leone et al. (2017)	MtDNA	Med NE Atlantic	170 (CR) 207 (Cytb)	Yes (weak)	Weak but significant structure between the Mediterranean and NE Atlantic in pairwise F_{ST} tests, but no apparent structure from haplotype networks.
Leone et al. (2024)	Genomics (ddRAD)	Med NE Atlantic	203 (14,713 SNPs)	Yes (weak)	Subtle differentiation in F_{ST} pairwise comparisons between the E and W Mediterranean, and limited connectivity between the Mediterranean and NE Atlantic. Inconsistent structuring observed in cluster analyses.

Li et al. (2017)	MtDNA	C Pacific	78 (Cytb)	No	Supportive of panmixia across 4 haplotypes.
Nikolic et al. (2023)	Genomics (DArT)	Med NE Atlantic N Atlantic South Africa W Indian N Indian E Indian N Pacific SW Pacific	312 (37,655 SNPs)	Yes (weak)	Mediterranean and N Atlantic samples differ from Indo-west Pacific samples in pairwise F_{ST} tests. Inconsistent structuring observed in cluster analyses. The main cluster may fall into the blue shark population grey zone.
Ovenden et al. (2009)	MtDNA µsat	SE Indian N Pacific SW Pacific	60 (CR)	No	Supportive of panmixia across 5 microsatellite loci and 16 mtDNA haplotypes.
Taguchi et al. (2015)	MtDNA	SE Indian N Pacific NE Pacific SE Pacific NW Pacific SW Pacific	404 (Cytb)	No	Supportive of panmixia across 64 haplotypes.
Veríssimo et al. (2017)	MtDNA µsat	N Atlantic NE Atlantic South Africa SW Atlantic	237 (CR) 302 (µsat)	No	Supportive of panmixia across 12 microsatellite loci, 52 mtDNA haplotypes and in clustering analyses.
		SE Indian N Pacific SW Pacific	60 (CR)	No	Combination of mtDNA sequences with those from Ovenden et al., (2009) study resulting in 41 haplotypes, showing high genetic connectivity between regions

Nikolic et al. (2023) used Diversity Arrays Technology sequencing methods (Wenzl et al., 2004; Kilian et al., 2012) to investigate blue shark population structure in the Western Mediterranean and the Atlantic, Indian and Pacific Oceans. Since the publication of this study, the blue shark genome was successfully sequenced (Li, 2024), allowing for even more accurate filtering and clustering of results into potential management units (Pearce et al., 2021). In the present study, we apply the same powerful genome scan analysis implemented by Nikolic et al. (2023) to blue shark samples collected from eight sampling regions. The aim of this study is to investigate if there is a single panmictic population of blue sharks, or if there are regional subpopulations requiring distinct management. The objectives are to (i) map raw sequenced data to the blue shark genome and filter loci for eight regions sequenced using DArT methods, (ii) test genetic differentiation and heterozygosity between regions (iii) determine population substructure by comparing three separate clustering methods, (iv) identify isolation-by-distance in the largest cluster.

4.3 Methods

4.3.1 Sample collection

349 blue shark samples were sourced (collected between 2013-2023) from a range of locations (Figure 4.1), and 329 were successfully genotyped. The target was to have a minimum of 30 samples per region. Small fin clippings, skin samples or muscle biopsies were collected from individuals caught in fisheries. Where available, individual length (cm), sex (based on presence or absence of claspers) and location (latitude and longitude) were recorded. Samples were preserved in minimum 70% ethanol, RNAlater solution (Qiagen) or dimethyl sulfoxide (DSMO) buffer and shipped to the Diversity Arrays Technology (DArT) laboratory, Canberra, Australia in minimum 70% ethanol solution for analysis. All sample shipments adhered to the Nagoya protocol and were completed before the listing of blue sharks on CITES Appendix II (25th November 2023). This study was approved by the Newcastle University Animal Welfare Ethical Review Body (AWERB, Project ID No: ID 1038).

4.3.2 DArT library preparation and sequencing

Library preparation, sequencing and single nucleotide polymorphism (SNP) genotyping followed the same methods as outlined in Nikolic et al. (2023). Briefly, genomic DNA was extracted from 15 mg of muscle tissue using a modification of the QIAamp 96 DNA QIAcube HT Kit (Qiagen) with a lysis step in the presence of proteinase K followed by bind-wash-elute Qiagen processing. Low-quality or degraded samples were extracted using the modified CTAB method of Grewe et al. (1993). Genomic DNA was processed into reduced representation libraries by DArT using their proprietary technique. *PstI* and *SphI* methylation-sensitive restriction enzymes were used in digestion and ligation reactions to create DNA sample libraries. The *PstI* site was compatible with a forward adapter that included flow cell (Illumina) attachment and sequencing primer sequences, incorporating a staggered barcode region of varying length. In the *SphI* digestion, the resulting overhang sequence was ligated to a reverse adapter, containing a flow cell attachment region and a reverse-priming sequence. Mixed *PstI*–*SphI* restriction fragments were amplified by PCR (polymerase chain reaction), consisting of an initial denaturation at 94°C for 1 min, followed by 30 cycles of 94°C for 20 s, 58°C for 30 s and 72°C for 45 s, with a final extension at 72°C for 7 min. After PCR, equimolar amounts of amplification products from each sample in the 96-well microtitre plate were bulked and subjected to cBot bridge PCR (Illumina), followed by sequencing on an Illumina NovaSeqX automated sequencing system. Single-end sequencing ran for 77 cycles and selected DNA fragments were ~ 75 bp long. For further details on these sequencing methods, see Sansaloni et al. (2011), Kilian et al. (2012 and Georges et al. (2018).

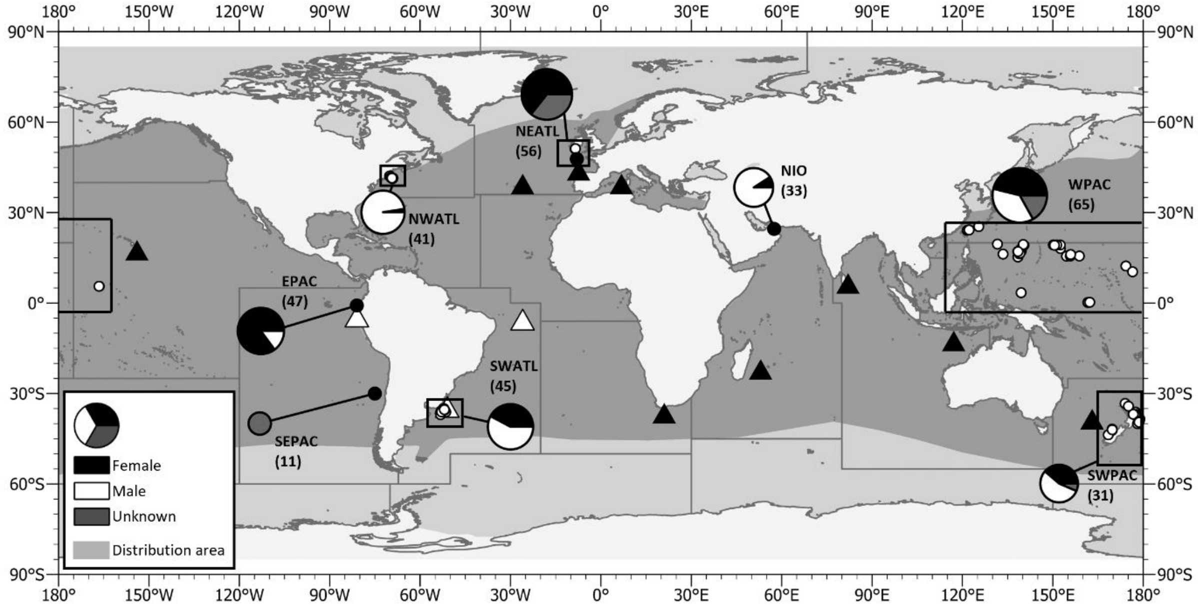


Figure 4.1 Sampling effort for the 329 successfully genotyped blue sharks across the shaded distribution range (downloaded from the IUCN red list: https://www.iucnredlist.org/species/39381/2915850; accessed 3rd August 2024). Region and sample size shown in the format A(B), where A is the sampling region and B is the number of samples that were successfully genotyped in this study. Regions are shown in pie charts proportional to the sample size, where slice colour indicates sex of sampled individuals. Individuals sampled with locational metadata are shown as white circular points at their sampling location. Where locational metadata were not provided, sampling region is labelled as a solid black circle. Black triangles indicate the sampling coverage by (Nikolic et al., 2023) and white triangles indicate sampling by the authors of that study, but where samples were genotyped later, so they were not included in their analyses. Locations were matched to FAO fishing areas, using a shapefile downloaded from the FAO website (https://www.fao.org/fishery/en/area/search). However, the samples collected in Ecuador were labelled as E Pacific rather than SE Pacific, as the sample locations

were not provided, so samples could have been collected in the E or SE Pacific. Geographical regions are northwest Atlantic (NWATL), northeast Atlantic (NEATL), southwest Atlantic (SWATL), northern Indian (NIO), western Pacific (WPAC), southwest Pacific (SWPAC), eastern Pacific (EPAC) and southeastern Pacific (SEPAC).

4.3.3 Reference assembly and SNP filtering (objective i)

The raw FASTQ data were demultiplexed and trimmed using the *process_radtags* module from Stacks v2.59 (Catchen et al., 2013). Reads with low-quality scores were filtered and uncalled bases were removed. Trimmed reads underwent further quality filtering with Trim Galore v0.6.10 (Krueger, 2015). Trim Galore was run with a minimum read length of 60 bp and a Phred quality threshold of 33. Quality checks on both raw and trimmed reads were performed using FastQC v0.11.9 (Andrews, 2010).

Trimmed reads from each sample were then aligned to the reference genome (Li, 2024; NCBI accession number: JBBMRE000000000) using Bowtie2 v2.4.4 (Langmead & Salzberg, 2012) with the “very-sensitive” preset for end-to-end global mapping. Alignments were first converted from SAM to BAM format, followed by sorting and indexing using SAMtools v1.16.1 (Li et al., 2009), retaining only reads with a minimum mapping quality score of 20. Unmapped reads and low-quality alignments were discarded.

For SNP calling the *ref_map.pl* pipeline was employed from the Stacks v2.59 suite with loci required to be present in 1 population and in at least 10% of individuals in a population and present in at least 10% of individuals across the dataset. Further filtering of the resulting Variant Call Format (VCF) file was completed in two phases (Table 4.2) using VCFtools v0.1.16 (Danecek et al., 2011). In the first phase, a minimum read depth of x6 was required. Loci were removed if they were not present in at least 70% of the individuals, had a minor allele frequency of less than 5%, or were not biallelic. Missing data were investigated for each individual, and those with >50% missing were removed. With the remaining individuals, the process was re-started with all loci included. These SNPs were then filtered out if they were not present in 70% of individuals, had a minor allele frequency less than 5%, had a mean depth coverage of less than two standard deviations above the mean depth, or were found in repetitive areas of the genome. Loci were then thinned to retain one site per 10,000 base pairs along the reference genome. Finally, those with >50% missing data were removed.

Table 4.2 Filtering steps taken on the VCF file in VCF tools. The original dataset contained technical replicates, which were removed prior to filtering. The final dataset contained 307 individuals and 6,517 Single Nucleotide Polymorphisms (SNPs).

Filtering step	**Number of loci retained**	**Number of individuals retained**
Original genotyped dataset	939,929	400
Removal of technical replicates	939,929	329
Filtering phase 1		
Minimum read depth: 6x	939,929	
Remove loci missing from >30% of individuals	93,726	
Minor allele frequency <5%	12,181	
Biallelic loci only	12,181	
Remove individuals with >50% missing data and re-start filtering	939,929	310
Filtering phase 2		
Remove loci missing from >30% of individuals	106,244	
Minor allele frequency <5%	13,721	
Maximum mean depth: 20.6x	13,160	
Mask repetitive areas of the genome	9,188	
Thinning: retain one site per 10,000 base pairs	6,157	
Remove individuals with >50% missing data	6,157	307

4.3.4 Population genomic analysis

The filtered VCF file was imported as a genlight object using the *gl.read.vcf* function in the *dartR* (Gruber et al., 2018) package in R version 4.4.1 (R Core Team, 2023). Standard measures of genetic diversity, including observed (H_O) and expected (H_E) heterozygosity and inbreeding coefficient (F_{IS}) were calculated for all samples using the *gl.report.heterozygosity* function in the *dartR* package in R. Pairwise heterozygosity and fixation index, F_{ST}, were tested between sampling regions using the *gl.test.heterozygosity* and *gl.fst.pop* functions in *dartR*, respectively. The pairwise F_{ST} test (Weir & Cockerham, 1984) employed bootstrap resampling for 10,000 replicates to estimate significance level. Principal Components Analysis (PCA) was run to assess data quality (Appendix C: Figure S4.1-S4.2) and Discriminant Analysis of Principal Components (DAPC; (Jombart, 2015) was run to provide initial de novo clustering of the data using the *ADEGENET* (Jombart, 2008) package in R. Two principal components were retained and the appropriate number of clusters (K value) in the DAPC was assessed using the *find.clusters* function and Bayesian Information Criterion (BIC) for values of K between 2 and 6 (Appendix C: Figure S4.3). Group assignment was visually assessed on the inferred clusters, using the minimum value of K in the BIC plot.

Population structure was further tested using STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003) and ADMIXTURE v1.3.0 (Alexander et al., 2009) to compare to DAPC clustering. The VCF file was converted to a STRUCTURE file format using PLINK v1.90b7.3 (Purcell et al., 2007). The best value of K was investigated from 1 to 5, with ten iterations for each K, a run length of 300,000 Markov chain Monte Carlo replicates after a burn-in period of 100,000 and correlated allele frequencies under an admixture model with alpha set to 1.0. The log probability of the data were plotted (ln Pr(X|K) across the range of K values, selecting a likely value of K where the log probability plateaued, as described in the STRUCTURE manual (Pritchard et al., 2009), and by calculating the deltaK statistic (Evanno et al., 2005) in CLUMPAK (Kopelman et al., 2015). The VCF file was converted to a bed file format using PLINK v2.00a6 (Chang et al., 2015) for implementation in ADMIXTURE. Default values were used in ten runs of K from 1 to 8 clusters. Optimal value of K was selected based on the minimum cross-validation error between runs. The results from the ten STRUCTURE and ADMIXTURE runs were aggregated and compared using CLUMPAK.

To investigate patterns of isolation-by-distance, individual level pairwise euclidean genetic distance was calculated between vectors of latitude and longitude points using the *dist* function using *ADEGENET* with the strength of the relationship explored using a Mantel test in the *ade4* package (Dray & Dufour, 2007).

4.4 Results

4.4.1 Genetic differentiation between sampling regions (objective ii)

The filtered dataset (307 individuals, 6,157 SNPs) had an average depth of 13.1x and the average missing data within individuals was 15%. Pairwise tests on expected heterozygosity revealed significant differences between regions, however, the expected heterozygosity values for each sampling region were consistent, each returning H_E=0.27. Observed heterozygosity ranged between 0.25 to 0.28, F_{IS} varied from -0.01 to 0.07 (Table 4.2). Pairwise F_{ST} was low between regions, ranging from <0.001 to 0.026 (Table 4.3).

Table 4.3 Diversity metrics of each of the blue shark sampling regions based on 307 individuals and 6,157 single nucleotide polymorphism loci from the genotyped and filtered dataset. Sampling region, country where samples were collated, number of individual samples (n), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), range of years sampled, sample sex if known (Female / Male / Unknown).

Region	**Country Source**	**n**	**H_O**	**H_E**	**F_{IS}**	**Years**	**Sex**
N Indian	Oman	24	0.28	0.27	-0.01	NA	2 /22 /0
NE Atlantic	Ireland	35	0.27	0.27	0.03	2023	35 /0 /0
	UK	21				2023	1 /0 /20
NW Atlantic	USA	39	0.27	0.27	0.03	2021-2022	1 /38 /0
SW Atlantic	Argentina / Uruguay	43	0.26	0.27	0.06	2013 - 2019	17 /26 /0
W Pacific	Taiwan (RoC)	63	0.26	0.27	0.04	2014 - 2023	29 /23 /11
SE Pacific	Chile	11	0.28	0.27	0.02	2023	0 /0 /11
E Pacific	Ecuador	43	0.27	0.27	0.03	2023	36 /7 /0
SW Pacific	New Zealand	28	0.25	0.27	0.07	2017-2019	10 /16 /2
	Total	307	0.27		0.04	2013-2023	131 /132 /44

Table 4.4 Pairwise fixation index, F_{ST}, tests between sampling regions. Significance levels were calculated based on 100 bootstrap estimates using the *gl.fst.pop* function in the *dartR* package in R. All pairwise comparisons, except Indian N-Pacific SW (p=0.113, were statistically significant, *p<0.05 **p<0.01 ***p<0.001.

	Atlantic NE	Atlantic NW	Atlantic SW	Indian N	Pacific E	Pacific W	Pacific SE
Atlantic NE							
Atlantic NW	**<0.001***						
Atlantic SW	**0.002*****	**0.001****					
Indian N	**0.003*****	**0.004*****	**0.001***				
Pacific E	**0.024*****	**0.023*****	**0.024*****	**0.026*****			
Pacific W	**0.004*****	**0.004*****	**0.001*****	**0.001*****	**0.026*****		

Pacific SE	**0.009*****	**0.008*****	**0.007*****	**0.009*****	**0.005*****	**0.010*****	
Pacific SW	**0.003*****	**0.002*****	<0.001	**0.001***	**0.025*****	**0.001*****	**0.007*****

4.4.2 Comparison of clustering analyses (objective iii)

In the DAPC analysis, the first four principal components explained approximately 3.53% of the variance and the lowest BIC score was for *K=3,* followed by the *K=2* cluster (Appendix C: Figure S4.3-S4.5). The suggested *K=2* clusters contained one cluster for individuals in the east (n=40, 34 female, 6 male) and southeast (n=7, unknown sex) Pacific, and all other individuals (n=260, 97 female, 126 male, 37 unknown sex) allocated to the second cluster (Figure 4.2A). The *K=3* clusters were the same as those for *K=2*, except three individuals (all sourced in Taiwan, western Pacific), which made up a third cluster. In the ADMIXTURE analysis, the cross-validation error was lowest for *K=2* (CV Error = 0.509), followed by *K*=1 (CV Error = 0.511). The *K=2* clustering was similar to that of the DAPC, one cluster for individuals in the east (n=33, 27 female, 6 male) and southeast (n=3, unknown sex) Pacific, and all other regions (n=271, 104 female, 126 male, 41 unsexed) allocated to the second cluster (Figure 4.2B). Of those in the southern and southeastern Pacific cluster, 19 individuals showed strong clustering assignment (Q-value > 0.7), whereas 260 individuals showed strong alignment to the second cluster. For STRUCTURE, the highest level of deltaK was at K=2 (deltaK = 4751.2), but the ln Pr(*X*|*K*) plateaued at K=5. For K=2, admixture was present in samples from all regions. 23 individuals were grouped in the first cluster, but only two showed a Q-value membership >0.7 (Figure 4.2C). All the remaining 284 individuals were grouped into the second cluster, with 226 showing a strong assignment to the cluster. Further pairwise F_{ST} tests showed low, but significant, genetic differentiation between aggregated eastern and southeastern Pacific individuals and all other individuals (F_{ST} = 0.020, p<0.001). Overall, the clustering analyses provided evidence for some substructure in the eastern and southeastern Pacific. However, there was poor agreement with the STRUCURE clustering, as well as low F_{ST} between regions, which suggests panmixia or high levels of geneflow among the regions tested in this study.

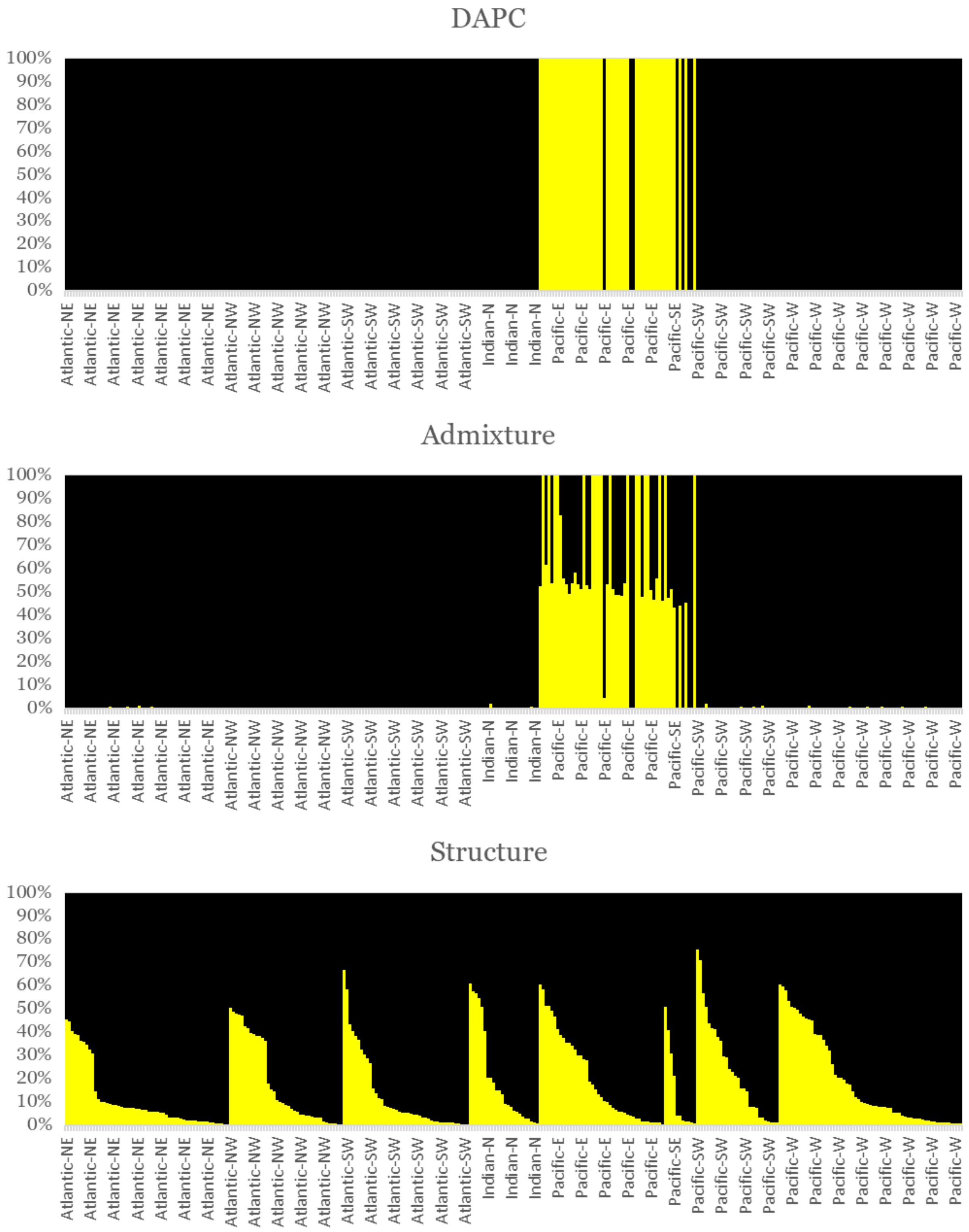


Figure 4.2 Genetic cluster assignment for K=2 populations using (A) discriminant analysis of principal components (DAPC) density plot, (B) ADMIXTURE bar plot and (C) STRUCTURE bar plot. Individuals are represented by each bar in the bar plot but aggregated in the density plot across their sampling regions. The proportion of each bar colour represents their assignment to genetic clusters.

4.4.3 Isolation-By-Distance (objective iv)

Of the 307 individuals in the filtered SNP dataset, 184 had specific sampling location information available (latitude and longitude); these samples were sourced in Ireland (NE Atlantic, n=35), USA (NW Atlantic, n=39), Uruguay and Argentina (SW Atlantic, n=43), Taiwan (W Pacific, n=39) and New Zealand (SW Pacific, n=28). The Isolation-By-Distance (IBD) analysis revealed a significant, but very low positive correlation between geographic and genetic distance (correlation = 0.07, p=0.002) for the 184 individuals in the spatial dataset (Figure 4.3).

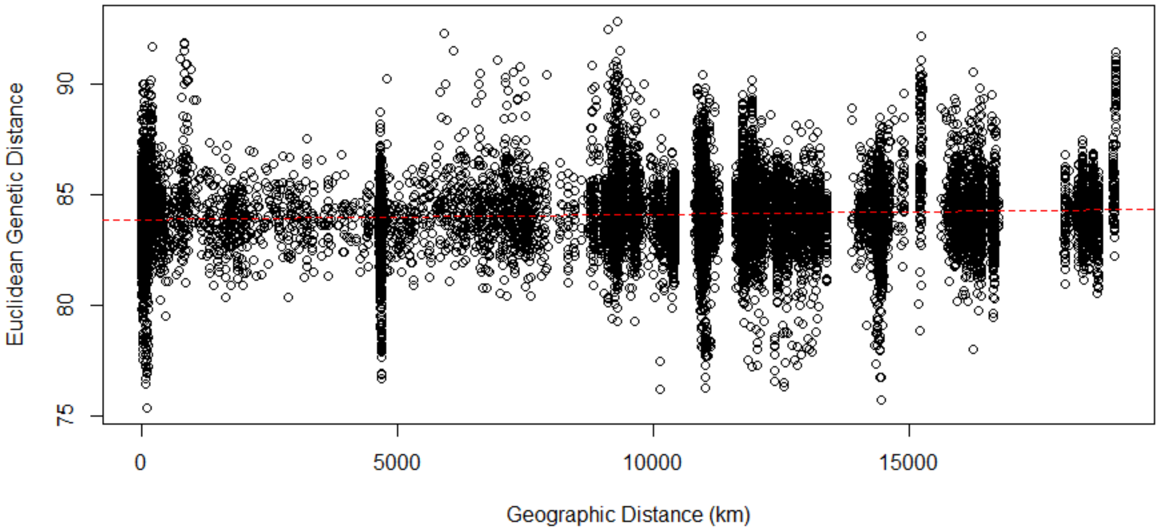


Figure 4.3 Pairwise isolation-by-distance plot for the 184 individuals with location information (latitude and longitude). Geographic distance is the distance in kilometres measured between the latitude and longitude for pairs of individuals and genetic distance is the Euclidean distance between allele frequencies for each pair of individuals. Pairs that were outside 5 standard deviations from the mean Euclidean genetic distance were excluded from the plot (n=9 removed, n=16,827 remaining), with the line of best fit (red dashed line) calculated for the remaining points.

4.5 Discussion

This study tested population structure of blue sharks across 6,157 genome-wide SNP markers and 307 individuals from eight sampling regions. The results broadly align with previous research on blue sharks investigating mitochondrial DNA and microsatellite markers (Table 4.1), with weak genetic differentiation between regions (Table 4.3, Table 4.4). There is evidence for a cluster in the eastern and southeastern Pacific, although the subtle genetic differentiation between regions needs to be further investigated before drawing conclusions on substructure. Previous research investigating samples from different regions, using different methods, highlight the complexity in delineating blue shark population structure using genetic markers.

Tests on genetic differentiation of blue sharks between regions using nuclear DNA have reported significant pairwise F_{ST} values up to 0.0051 (Nikolic et al., 2023), 0.0053 (Bailleul et al., 2018) and 0.0017 (Leone et al., 2024). Similarly, substructure in other large pelagic fish species has been observed with low, but significant fixation index between regions, including in white shark (*Carcharodon carcharias*, F_{ST} = 0.0156-0.0529; Wagner et al., 2024), scalloped hammerhead (*Sphyrna lewini*, F_{ST} = 0.009-0.072; Green et al., 2022), striped marlin (*Kajikia audax*, F_{ST} = 0.0137–0.0819; Mamoozadeh et al., 2020), yellowfin tuna (*Thunnus albacares*, F_{ST} = 0.04 - 0.13; Pecoraro et al., 2018) and bluefin tuna (*Thunnus thynnus*, F_{ST} = 0.0007 – 0.012; Puncher et al., 2018; Rodríguez-Ezpeleta et al., 2019; Díaz-Arce et al., 2024). Therefore, low but significant, F_{ST} values, like the differentiation observed between the eastern and southeastern blue sharks and all other individuals in this study (F_{ST} = 0.020, $p<0.001$) could represent evidence for population structure in widely distribute large pelagic taxa. Observed and expected heterozygosity differed between our results and previous studies (King et al., 2015; Veríssimo et al., 2017; Bailleul et al., 2018; Nikolic et al., 2023), although this is likely due to differences in sampling locations, filtering (Nikolic et al., 2023) and between genome-wide (this study) and locus-specific (King et al., 2015; Veríssimo et al., 2017; Bailleul et al., 2018) methods. The significant, but small differences in genetic diversity, genetic differentiation and isolation-by-distance reported here could represent substructure in blue sharks. However, it is not immediately clear whether statistical significance in these tests, and those in previous studies where weak structure is suggested could be caused by large sample sizes, leading to inflated power in statistical tests, rather than genuine biological differences among regions.

Similarly, the clustering analyses (DAPC, Admixture, STRUCTURE) revealed inconsistent results, but provided some evidence to support population substructure. The DAPC and Admixture results similarly assign substructure to individuals sourced from the eastern and southeastern Pacific regions, as also suggested by González et al. (2023), indicating that this region may harbour a unique sub-population. However, differing likely values of *K* between each analysis, in addition to weak assignment to clusters (using STRUCTURE) and inconsistent assignment of individuals to clusters between analysis techniques lead to results which could be consistent with large scale panmixia. In clustering analyses it is challenging to conclusively provide evidence support for $K=1$ instead of $K=2$, where methods for evaluating values of K either cannot (deltaK method), or are unlikely to deduce $K=1$ in large genomic datasets with inflated statistical power (Janes et al., 2017; Cullingham et al., 2020). The gradient of assignment between the two clusters observed in our STRUCTURE analysis is similar to that found in San Cristobal Island Galapagos giant tortoises (*Chelonoidis chathamensis*), where there was insufficient biological evidence for K>1 using genomic markers (Jensen et al., 2022). Nikolic et al. (2023) described two population clusters, one in the North Atlantic and Mediterranean and one in the Indo-west Pacific across 37,655 SNPs and 312 genotyped individuals. However, similar to our study, the clustering assignment was inconsistent between ADMIXTURE and STOCKR. Further, the full blue shark genome was published after the Nikolic et al. (2023) study, so the authors were not able to map their dataset to the genome and mask repetitive regions. Leone et al. (2024) identified differentiation between the Mediterranean and NE Atlantic in pairwise F_{ST} tests and in a DAPC. However, the statistically significant genetic differentiation results were reported for very low values of F_{ST} (maximum significant $F_{ST} = 0.0017$) and the STRUCTURE analysis did not reveal clear geographical patterns in the data (Leone et al., 2024). Therefore, the suggestion of multiple populations requires further investigation and we emphasise the importance of employing and comparing multiple clustering algorithms when assessing blue shark population structure.

The highest priority for future research should be to investigate a truly global dataset of blue shark population structure, by combining samples between this study and those genotyped by Nikolic et al. (2023), along with samples collected in the interim. Additional samples should be sourced and sequenced from the southeast Pacific region, where a population cluster may exist (e.g. this study and González et al., 2023), to reach a minimum of 30 samples to more accurately estimate the local allele frequencies (Nazareno et al., 2017). Further sampling effort should be undertaken to fill gaps in the blue shark distribution, such as samples from West Africa. Care should be taken to ensure sampling is completed using identical methods and samples run at the same time where possible, to avoid potential ‘batch effects’, where samples sequenced at different times or under different conditions may bias clustering results (Goh et al., 2017; Lou & Therkildsen, 2022). Researchers should also exercise caution using proprietary techniques. Following open science practices (Vicente-Saez & Martinez-Fuentes, 2018) is encouraged, by uploading raw genomic data to public repositories and reporting details of methods for replication. Before further management recommendations can be made using genetic information, a comprehensive global genomic study, integrating samples from different regions and ensuring methodological consistency, is essential for accurately estimating blue shark population structure.

The rapid developed of analysis techniques and availability of full genome datasets could be crucial for delineating population differences in other cosmopolitan species, where previously only mitochondrial DNA analyses were present. For example, the recent publication of the whale shark *(Rhincodon* typus) genome (Weber et al., 2020) could be applied in a similar manner to this study to further investigate the weak structure identified by mitochondrial and microsatellite markers (Castro et al., 2007; Schmidt et al., 2009; Yagishita et al., 2020), taking advantage of the higher power offered by genome scans. Publication of further full genome assemblies for highly fished pelagic shark species, such as the silky shark (*Carcharhinus falciformis*; Cardeñosa et al., 2020), should be a priority, to further informing management efforts for threatened and poorly understood species (Pearce et al., 2021). Comprehensive global studies, leveraging advancements in full genome sequencing techniques and incorporating samples from regions throughout the range of pelagic species, is essential for the management of threatened migratory sharks.

4.5.1 Fisheries managers should exercise a precautionary approach to blue shark population structure

Chapter 4 highlighted the challenge for assessing population substructure in an abundant, highly migratory and globally distributed species. Understanding population connectivity is essential to ensure that fisheries management strategies are aligned with biological population boundaries. While the genetic structure of blue sharks remains undetermined, fisheries management should seek to avoid regional reductions in abundance due to high fishing pressure, which could result in long-term consequences. In Chapter 5, I return to the challenge of reducing blue shark mortality, this time by testing a sensory deterrent (ferrite magnets) on blue shark behaviour.

4.5.2 Conclusions

Management of blue sharks in fisheries is currently based on evidence of one global population, replenishing fished stocks across ocean basins. In this study, powerful full genome scans were employed to detect thousands of SNP markers from 307 individuals and grouped into candidate populations using three clustering algorithms. Some evidence of genetic structuring is presented, with a potential cluster in the eastern and southeastern Pacific, although further evidence is required to reject the assumption of one panmictic blue shark population. Caution should be taken when interpreting analyses utilising powerful full genome scans, where statistical significance may not provide evidence of true population substructure. However, given blue sharks show little migration between ocean basins (e.g. Kohler & Turner, 2008; Sippel et al., 2011), further research on genetic connectivity and movement of blue sharks is required to assess whether this species inhabits a population grey zone (Bailleul et al., 2018) with distinct regions, which would require management of geographically independent units (Carvalho & Hauser, 1994; Waples et al., 2008; Domingues et al., 2018). This study highlights the complexity in interpreting population structure of a cosmopolitan shark species using genomic markers. Managing fisheries by accurately delineating population structure is critical to curbing the anthropogenic mortality faced by declining numbers of threatened pelagic sharks.

Chapter 5. Ferrite magnets do not deter blue sharks (*Prionace glauca*) from bait strikes in behavioural trials

5.1 Abstract

Blue sharks (*Prionace glauca*) are heavily fished, with decreasing populations worldwide. Sensory deterrents, inducing weak electromagnetic fields, have been used to deter sharks from fishing gear, while maintaining target catch quality and quantity. Here, we conducted trials on the efficacy of ferrite magnets as a deterrent on blue shark swim-with tourism trips off the southwest coast of the UK. We tested behavioural responses of blue sharks to ferrite magnets in a field experiment comparing simulated fishing lines (hooks removed) with and without magnets. There was no statistically significant difference in bait choices between the control (n=14) and magnet (n=12) lines. Time to strike, number of prior interactions, number of sharks present or number of people in the water did not influence bait choice in the trials. The study adds to conflicting findings on electrosensory deterrents' effectiveness on shark species. Electrosensory deterrents are currently not suitable for widespread implementation in fisheries and alternative strategies should be explored to reduce shark mortality.

5.2 Introduction

Many shark (Selachimorpha) species are meso- or apex predators, essential for the health of marine ecosystems (Heithaus et al., 2008; Roff et al., 2016; Hammerschlag et al., 2019; Heithaus et al., 2022) and the fisheries that depend on the oceans for food and income. However, overfishing is the main threat to shark populations through targeted and/or incidental catch (Davidson et al., 2016; Dulvy et al., 2021; Worm et al., 2024). Pelagic sharks have experienced steep declines, with populations decreasing by an average of 71% since the 1970s, following an 18-fold increase in relative fishing pressure globally (Pacoureau et al., 2021). The blue shark (*Prionace glauca*) is an intensely fished pelagic shark species, commonly found in the shark meat and fin trade (Davidson et al., 2016; Fields et al., 2018; Poseidon, 2022; Cardeñosa et al., 2022). They are caught mainly in oceanic longlines as target catch or bycatch in fisheries targeting billfishes (e.g. tuna and swordfish) (Simpfendorfer & Dulvy, 2017; Poseidon, 2022). Blue sharks are resilient to fishing pressures, with relatively fast life history strategies and high reproductive output compared to other elasmobranch species (Cortes, 2008; Nakano & Stevens, 2008). However, in spite of their resilient life history strategies, their global population has been classified as Near Threatened by the International Union for the Conservation of Nature (IUCN) red list assessment (Rigby et al., 2019a). Although there are further concerns over some regional stocks, with the Mediterranean population classed as Critically Endangered (Sims et al., 2016) and declines of up to 50% over three generations in the North Atlantic (Rigby et al., 2019b).

Attempts to alleviate fishing pressure on elasmobranch bycatch include time-area closures, gear changes and catch limits (Dunn et al., 2011; Carruthers et al., 2014; Shiffman & Hammerschlag, 2016). When these options are not possible, sensory deterrents offer potential solutions to mitigate the bycatch of shark species, whilst maintaining target catch quantity and quality (Lucas & Berggren, 2023). Elasmobranchs (sharks, skates and rays) have specialised electrosensory organs, the ampullae of Lorenzini, enabling them to detect electrical and magnet fields (Kalmijn, 1982). Electrosensory technologies may deter elasmobranch (shark, skate and ray) species from longline fishing gear, whilst still catching target species. The arrangement and composition of electrosensory deterrents varies, but broadly include magnets, electropositive metals and pulsed electromagnetic fields (Cliff & Dudley, 1992; Jordan et al., 2013; O’Connell et al., 2014g; Favaro & Côté, 2015; Hart & Collin, 2015; Lucas & Berggren, 2023). Results vary depending on the species assessed (Brill et al., 2009; O’Connell et al., 2011b; Hutchinson et al., 2012), the presence of conspecifics (Jordan et al., 2011; Robbins et al., 2011; O’Connell et al., 2014g), the type and characteristics of the electrosensory technology used (Favaro & Côté, 2015; Riley et al., 2022; O’Connell et al., 2022; Lucas & Berggren, 2023), as well as other variables including environmental characteristics and prior satiation of individual animals (O’Connell et al., 2014g).

Tests of two different types of rare earth magnet have not reduced blue shark catch per unit effort (CPUE, measured per hooks per hour, or per 1000 hooks per hour) in trials (Hutchinson et al., 2012; Godin et al., 2013; Porsmoguer et al., 2015), however a recent study on the SharkGuard (a pulsed electromagnetic field) showed that electrosensory deterrents can reduce bycatch of blue sharks in longline gear (Doherty et al., 2022). In addition, ferrite magnets have shown promise as deterrents in multiple species (e.g. *Sphyrna lewini, Carcharhinus perezi, Carcharodon carcharias* & *Carcharhinus leucas*) (Rigg et al., 2009; O’Connell & He, 2014). When testing bycatch reduction technologies, it is crucial that researchers employ pilot studies with power analyses to ensure appropriate implementation of technologies and interpretations of results (Dawson et al., 1998). Here we aimed to complete a proof-of-concept study, examining the behaviour of blue sharks around ferrite magnet deterrents, similar to studies on other species (Robbins et al., 2011), to evaluate the suitability of taking ferrite magnets to a full fishing trial. We designed paired trials to be undertaken on tourist trips, where the presence of people in the water may influence the behaviour of the sharks (Zemah Shamir et al., 2019; Gayford et al., 2023). Therefore, the objectives were to (i) test the suitability of ferrite magnet deterrents compared to controls without magnets in a simple binary choice trial on simulated fishing lines, to assess whether they would be suitable for a full-scale fisheries study; (ii) test whether the choices were affected by the number of prior interactions (bumps and bites), time taken to strike the bait, the presence of conspecifics, or the presence of people in the water; (iii) calculate the necessary power to detect an effect at a full-scale fishery trial.

5.3 Methods

5.3.1 Study area and population

The study was conducted with a blue shark swim-with tourism operator in the English Channel approximately 20-30km south of Penzance, Cornwall (Figure 5.1). The operator chose the study sites, due to the high seasonal density of blue sharks between July-October, and used their own chum mix (waste fish, oils and bran) to attract sharks and maximise encounter rates. Trials took place over five days in October 2023 and September 2024.

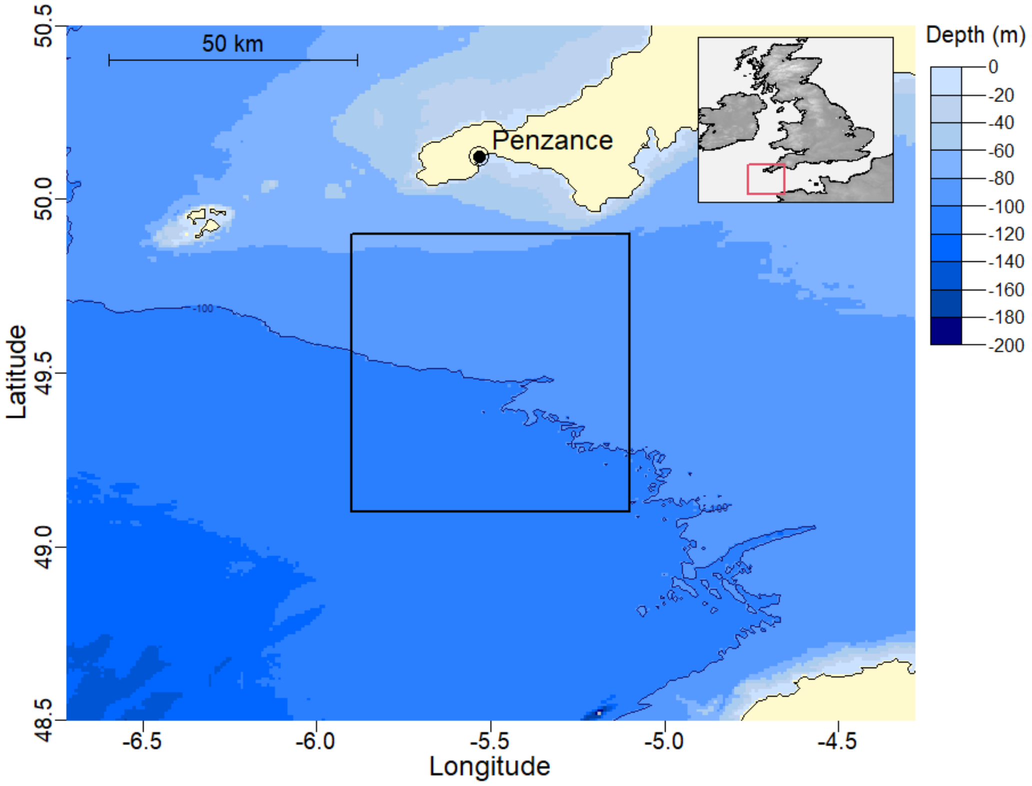


Figure 5.1 The study site was within the black bounding box on the main map, delimiting the areas used in the five trial days investigating blue shark behavioural responses to ferrite magnet deterrents. Depth contour only shown for 100m close to the study site, with depth legend on

the right-hand side. Location near the UK coastline shown in the red bounding box on the map inset, with trips going from Penzance each day. The map was designed in RStudio (RStudio Team, 2023).

5.3.2 Equipment

Shark interactions with baits were filmed with GoPro Hero 4^{TM} and GoPro Hero 5^{TM} cameras in standard underwater housings, tied to simulated fishing lines (no hooks on the line) positioned looking down on the bait (Figure 5.2). For the first day trials (up to the 7th deployment), the cameras were approximately 1.5 metres above the bait. For later deployments (8th and onwards), cameras were moved further up to approximately 2.5m from the bait to increase the field of view.

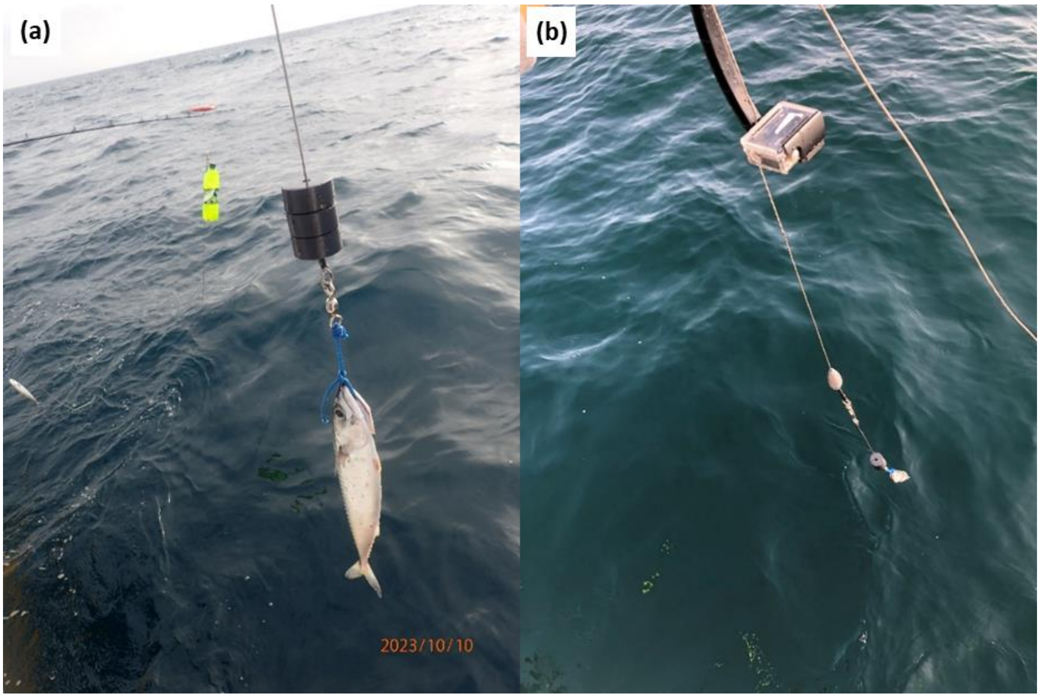


Figure 5.2 Deployment of the baited lines with mackerel bait. (a) Ferrite magnet stack of three rings held in place on a wire trace, with a single mackerel tied on below. The field strength from the bottom of the magnet to the bottom of the mackerel was within the range of 1-2229 Gauss. The control rod, with green float, is shown in the background (Photo credit: Fred Buckingham, Blue Shark Snorkel, 2023)); (b) The positioning of the GoPro camera on the bike mount, looking down on the bait setup and lead sinker.

For the magnetic treatment, the magnets were held in place by a wire trace, and a lead sinker was placed on each line. Ferrite magnet deterrents were configured as a stack of three centre pole ferrite ring magnets (RS Components Ltd, Corby, UK). Three magnets were used in order to maximise the field strength of the deterrent. Field strengths were measured using a Hirst GM04 Gauss meter in a laboratory, rather than in the field, as the Gauss meter was not waterproof. The field strength of the magnet stack was 1.31-2229 Gauss from 0-25cm, with the peak strength at 0cm and weakest strength at 25cm (compared to a strength of 0.8-2153 Gauss for a two-magnet stack and 0-1882 Gauss for a single magnet). The entire mackerel baits were within 25cm of the magnet stack during the trials. Bait consisted of one whole Atlantic mackerel (*Scomber scombrus*) tied onto the end of each line on blue string. Cameras were set at the linear (94^o) field of view (FOV) setting, filming at 1080p video resolution and 60 frames per second (fps).

5.3.3 Procedure

Baits were presented simultaneously on one control and one magnetic treatment line in paired trials. Lines were operated with a hand-held rod, which were placed in rod holders on the boat during the trials after the bait was deployed. Lines were deployed to approximately 5m depth, separated by approximately 2m, with each line approximately 5m away from a chum basket (Figure 5.3). The distance between each line and between the chum sources and the lines would vary throughout the trial due to the action of the waves on the surface. Each line had a bright green float on top, so the researcher could tell when the line was taken by a shark. Cameras were turned on and each filmed a dive slate with the deployment metadata before the start of the trial. Trials were synchronised by counting down from three seconds, at which point both lines were deployed into the water and a stopwatch was used to time the trial duration. As soon as the bait was taken completely off the line by a shark, the stopwatch was stopped, the trial ended and the lines were hauled to replace the bait for the next trial. This study was approved by the Newcastle University Animal Welfare Ethical Review Body (AWERB, Project ID No: ID 1045).

Whether the control or treatment was on the left or right was randomised. Initially the lines were assigned to either Left or Right. After the first trial, the lines were swapped over, then they were swapped every two trials until the 20th deployment. On the 21st deployment we switched to a pseudo-random deployment method to mitigate potential priming effects (Schacter & Buckner, 1998), by flipping a coin to assign Left or Right side, up to a maximum of three deployments on either side (if either condition was assigned to one side for three consecutive trials, we did not flip a coin on the fourth, and automatically changed the sides). We tested whether the baits were presented in a random order of left or right overall, as well as for the final dataset (with 18 excluded trials due to early hauls, bait falling off, no bait being taken during the trial or it was not clear which bait was taken first), with a post-hoc runs test (Swed & Eisenhart, 1943; Bujang & Sapri, 2018) using the *DescTools* package (Signorell, 2023). The runs test concluded that the presentation of the control and treatment were random for both the overall dataset ($p = 0.668$) and for the final dataset with excluded trials removed ($p = 0.099$).

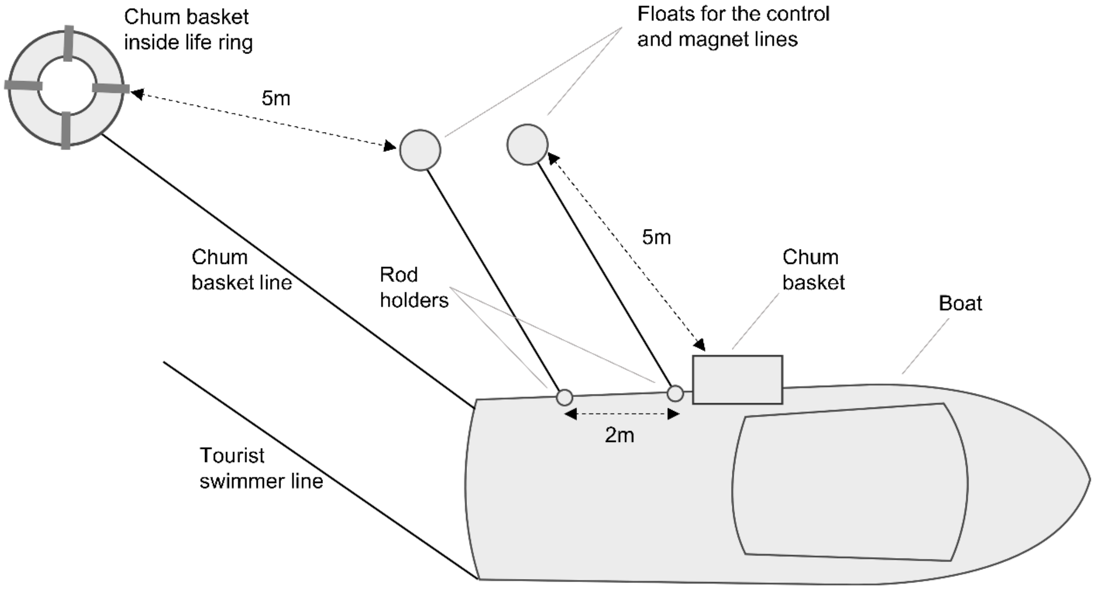


Figure 5.3 The setup of the lines deployed from the boat used in trials investigating blue shark behavioural responses to ferrite magnet deterrents. Lines were positioned approximately 2m apart and secured on rod holders on the boat, with one person allocated to attend to each rod. Each line was separated by approximately 5m from a chum basket, one on the side of the boat and one in a basket in the middle of a life ring, attached by a line to the stern of the boat. The line for swimmers ran parallel to the chum basket line. The drawing is not to scale.

5.3.4 Data analysis

A binary choice (Y_i) was recorded, whether the bait on the control line or on the magnetic treatment line was struck first in the trial. A successful bait choice was recorded when a shark removed the bait from the line with its mouth. The latency to strike (T_s, seconds) was recorded from the footage of the trial. Where the footage did not film the bait being taken (e.g. where the camera may have pointed away from the bait on impact with the water) then the time from the stopwatch was recorded. The latency to strike the bait was calculated from the time each bait settled in the water, which was between 5-10 seconds from the deployment. The settling time for the control and magnetic treatment were synchronised within each trial, but varied between trials.

The number of bumps (direct contact with any part of the sharks' body on the bait) and bites (either actually biting and holding the fish bait, or attempting to bite it and in doing so touching the bait with any part of the mouth) were recorded. The bumps and bites were summed to give the number of prior interactions (F_i) before a strike. Bumps and bites had to be separated by at least 5 seconds to be classed as independent events. The maximum number of sharks ($MaxN_{Shark}$) were recorded for each trial, from the point when the bait settled, until the bait was successfully taken. The maximum $MaxN_{Shark}$ across both videos for each trial was used in the subsequent analysis. The maximum number of people in the water during the trials, $MaxN_{People}$ was also recorded. For examples of bumps, bites, bait choices and $MaxN_{Shark}$, see Figure 5.4. These data were not recorded for three videos on the magnet lines and four on the control lines, when cameras were not facing the bait.

Figure 5.4 Example images of events during paired trials investigating blue shark behavioural responses to ferrite magnet deterrents: (a) Mackerel bait left to settle at the start of the trial; (b) a bump, where the shark makes physical contact with the mackerel bait; (c) three sharks on screen at one time, so $\text{MaxN}_{\text{Shark}}$ = 3; (d-f) an example of a bite: (d) the shark bites onto the bait; (e) the shark swims with the bait in its mouth; (f) the shark releases the line, with the bait still on the line; (g-i) an example of a bait choice; (g) the shark bites onto the bait; (h) the shark swims with the bait in its mouth; (i) the shark consumes the bait, taking it off the line.

Trials were excluded if the bait was hauled after the shark bit on the bait, but before the shark had removed the bait from the line, or if the bait was hauled mistakenly out of the water, or if it was not clear which condition was taken first and footage from the trials was not available to verify the result. If the bait started to be hauled, but the bait remained in the water the whole time, the trial was not excluded.

Finally, we conducted a prior power analysis using a one-proportion z-test in the *pwrss* R package (Bulus, 2023). We set an acceptable bycatch reduction rate of 2/3, requiring 24 paired trials to attain 80% statistical power (Figure 5.5).

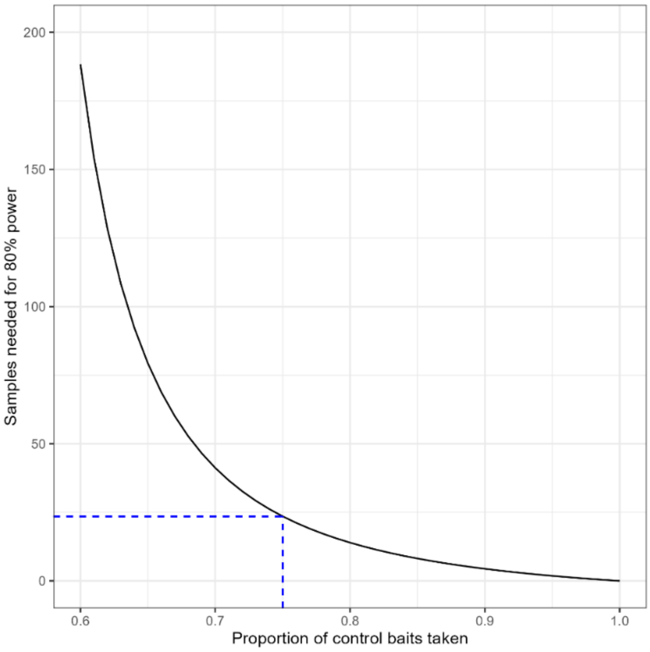


Figure 5.5 A 2/3 bycatch reduction corresponds to the control bait being taken a proportion of 0.75 times compared to 0.25 for the magnet treatment. This requires 24 trials to attain 80% power.

5.3.5 Statistics

We conducted a binomial test to assess whether the baits on the control or the magnetic treatment were taken significantly more than by chance (objective 1). We used a logistic regression to test if the number of prior interactions, time taken to strike, or the presence of conspecific sharks predicted the choice of bait attached to either the control or magnetic treatment (objective 2). The estimation of which side was taken first was estimated with the model (adapted from (Robbins et al., 2011):

$$logit(Y_i) = T_{s_i} + F_{i_i} + MaxN_{Shark_i} + \ MaxN_{People_i}$$

The assumptions for logistic regression models were checked in R. Collinearity was assessed using the *car* package, where all variables were deemed acceptable, with variance inflation factor (VIF) values under a cutoff of VIF<5 (James et al., 2013). There were no outliers above or below three standard deviations from the mean and linear relationships were confirmed by visual inspections of plots between predictor value and the logit of the trial outcome.

5.3.6 Post-hoc power analysis

A post-hoc power analysis was conducted to determine the number of trials required to detect an effect at a full-scale fishery trial with 80% power given the observed effect size in the experiment (objective 4).

All analyses were conducted using R version 4.3.2 in R Studio version 2023.06.0+421 (RStudio Team, 2023; R Core Team, 2023). The *tidyverse* package was used for data manipulation (Wickham et al., 2019). All times were converted to seconds using the *lubridate* package (Grolemund & Wickham, 2011). For each GLM, the model assumptions of Gaussian errors and homoscedacity were confirmed by inspecting the probability plots and error structures using the *check_model* function in the *Performance* package (Lüdecke et al., 2021). The *ggplot2* package was used for all plots (Wickham, 2016).

5.4 Results

5.4.1 Ferrite magnets did not deter blue sharks

During the field trials, 44 replicates were recorded, although 18 were excluded due to early hauls, bait falling off, no bait being taken during the trial or it was not clear which bait was taken first. The final sample size (n=26) exceeded the minimum number of trials identified in the prior power analysis (n>24). Control baits were taken in 14 trials and magnet baits taken in 12 trials (Figure 5.6A). In the binomial test, the frequency of takes from the control side was not significantly different from the frequency of takes from the magnet side (n=26, z=0.54, p=0.845).

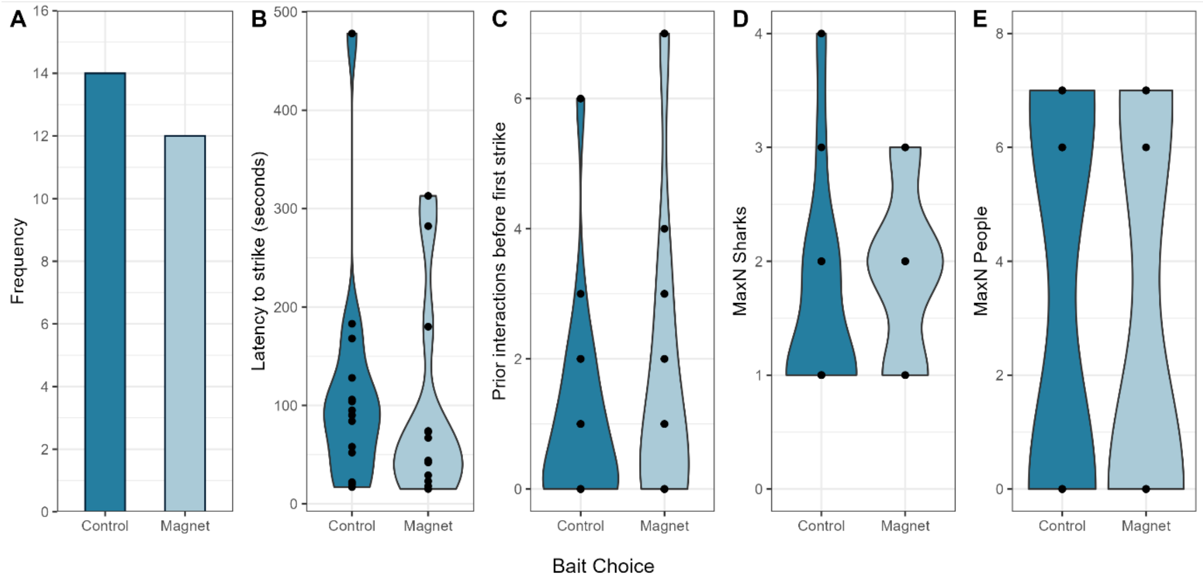


Figure 5.6 (A) the number of trials in which the control or magnet bait was taken first, by a shark removing the fish bait completely off the line in paired trials. (B) The latency to strike the bait in the trials where the control or magnet bait were taken first. (C) The number of prior interactions (bumps and bites) across all trials. (D) The maximum number of sharks present across trials. (E) The maximum number of people in the water across trials.

5.4.2 Bait strike choices were not affected by prior interactions or potentially confounding variables

Time to strike, number of prior interactions, number of sharks present and number of people in the water did not affect the bait choice in the trials (Table 5.1, Figure 5.6B-E).

Table 5.1 Logistic regression for the bait choice in trials, as a response to the latency to strike the bait (T_s), the number of prior interactions (bumps and bites, F_i), number of sharks ($MaxN_{Sharks}$) and the number of people ($MaxN_{People}$).

Variable	**Framework axes**	**Estimate**	**p**	**Model**	**Deviance**
$\mathrm{Logit}(Y_i) \sim T_s + F_i + \mathrm{MaxN}_{\mathrm{Shark}}$	Intercept	-0.26	0.838	Null model	28.84 (21)
	T_s	-0.007	0.365		
	F_i	0.51	0.326	Residual	27.11 (17)
	$\mathrm{MaxN}_{\mathrm{Shark}}$	0.05	0.937		
	$\mathrm{MaxN}_{\mathrm{People}}$	-0.10	0.521		

5.4.3 Post-hoc power analysis

The proportion of control baits taken was 0.54 (14 control baits and 12 magnet baits taken). 1,319 trials would be required to reach 80% power with this level of deterrence (Figure 5.7).

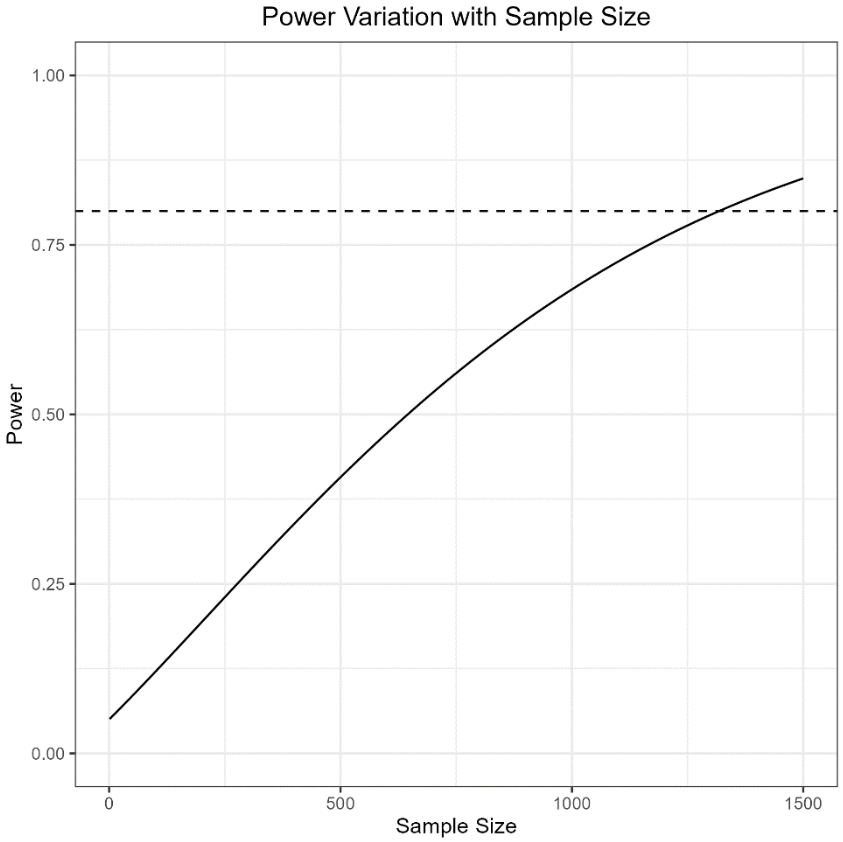


Figure 5.7 Power variation with sample size for the effect size found in the experiment. Horizontal line at 80% power, intersecting with a sample size of 1,319.

5.5 Discussion

The results from paired trials in this study showed that ferrite magnets did not deter blue sharks from longline fishing gear and would not be suitable to test in full fisheries trials. The number of prior interactions, time to strike, number of conspecifics and number of people in the water did not affect bait choice.

Blue sharks show variable responses to electrosensory deterrents. Hooks equipped with neodymium-iron-boron rare earth magnets caught more blue sharks than control hooks in longline trials (mean 0.74 ± 0.15 catch per unit effort, *CPUE*, and mean 0.47 ± 0.17, respectively) (F= 18.29, p< 0.001) (Porsmoguer et al., 2015). Even fewer sharks were caught in areas of longline gear that were separated by a buffer from the experimental lines (mean 0.25 *CPUE*, SD 0.43), suggesting that magnets may even attract blue sharks. Godin et al. (2013) reported no significant difference in bycatch of blue sharks ($CPUE_{Control}$=32.86 per 1000 hooks, $CPUE_{Treatment}$=30.95 per 1000 hooks, p=0.764) using neodymium-praseodymium alloy deterrents, in addition to a reduction in target swordfish (*Xiphias gladius*) catch. Hutchinson et al. (2012) also tested neodymium-praseodymium alloys on blue sharks in two locations. They found no bycatch reduction in either the Southern California Bight ($CPUE_{Control}$= 4.75 x 10^{-3} per hook per hour, $CPUE_{Magnet}$ = 4.18 × 10^{-3} per hook per hour, p=0.36) and the Ecuadorian Eastern Tropical Pacific ($CPUE_{Control}$= 1.78 x 10^{-4} per hook per hour, $CPUE_{Magnet}$ = 6.04 x 10^{-4} per hook per hour, p=0.2). SMART (Selective Magnetic and Repellent-Treated) hooks have been tested in longlines with blue shark catch, although further trials would be needed to assess any effect (n=4 caught on control hooks and n=3 caught on SMART hooks) (O'Connell & He, 2014). Overall, most electrosensory technologies show poor performance as a deterrent, even increasing shark bycatch in some cases, suggesting that they are broadly ineffective as bycatch reduction techniques. However, recent development of the SharkGuard, using a pulsed electrical field, have shown promise for deterring blue sharks from longlines ($CPUE_{Control}$=6.1 ± 1.2 per 1000 hooks, $CPUE_{Treatment}$=0.5 ± 1.6 per 1000 hooks, p=<0.001), although the slight reduction in target bluefin tuna (*Thunnus thynnus*) catch should be investigated further (Doherty et al., 2022). Our study investigated the potential of ferrite magnets as an electrosensory deterrent for blue sharks to address the gaps in current research and to explore alternative strategies that could potentially reduce shark bycatch.

The behavioural responses of elasmobranchs to electrosensory deterrents varies between species (Lucas & Berggren, 2023). Multiple factors affect catch rates (Maunder et al., 2006), indicating that results may not be generalised to other situations and technologies that are effective on one species in one location may not be effective in another context. Therefore, further research should be undertaken to test the SharkGuard (Doherty et al., 2022) in different environments (potentially with a higher density of target and bycatch species), on other species, and with increased number of sets.

Given the lack of results demonstrating reduced catches, at present there is no dependable technology that will reduce the bycatch of blue sharks in longline fisheries. In addition, blue sharks represent target catch rather than bycatch in some areas (Simpfendorfer & Dulvy, 2017), such as the increased consumption seen in South America (López de la Lama et al., 2018; Merten Cruz et al., 2021; Pincinato et al., 2022). Due to the reduction in many billfish populations, blue sharks are now the target in some longline fisheries, exceeding the value of some tuna species (Poseidon, 2022). Given the fishing pressure exerted on blue sharks and the recent declines in some populations (Davidson et al., 2016; Rigby et al., 2019b), alternative conservation measures may be necessary to prevent further population declines and extirpation. In addition, blue sharks may not represent a panmictic population as originally thought (Leone et al., 2024; Nikolic et al., 2023), and research on population structure would be informative for conservation and management plans to ensure their sustained resilience to fishing pressures.

Limitations of this study included a limited understanding of the range and attenuation of the magnetic field and the chum slick in sea water. Given the short range of ferrite magnets (~30cm), it was crucial that the length of the line between the bait and the magnet was minimised. The range and strength of the magnetic field in this experiment were measured on land only. The strength and properties of electromagnetic fields have been controlled (O'Connell et al., 2022; Riley et al., 2022), measured (Thiele et al., 2020) or modelled (Gauthier et al., 2020) in studies on shark responses, although the properties of electromagnetic fields in water remain poorly described (Riley et al., 2022). We encourage the reporting and investigation of electromagnetic field properties in future research, to gain a better understanding of the thresholds required to successfully deter elasmobranch species. This experiment was in collaboration with ecotourism operators. Therefore, there were unavoidable and potentially confounding variables, including the presence of the chum slick. The behaviour and number of sharks present may be influenced by properties of the bait plume, which itself is influenced by the area covered in the experiment and currents while drifting (Priede et al., 1990; Heagney et al., 2007; Westerberg & Westerberg, 2011).

The results from this experiment, combined with other previous studies, indicate that the SharkGuard is currently the only electrosensory deterrent that may be effective for blue sharks (Doherty et al., 2022). We encourage further research in fisheries trials to investigate how catch of blue sharks, other marine megafauna species and target species, may be affected by the SharkGuard. Due to the costs of sensory deterrents, these technologies must provide cross-taxa bycatch reductions for vulnerable populations, whilst maintaining target catch quality and quantity, to be worthwhile for fishers and conservationists alike (Lucas & Berggren, 2023), such as the use of LED lights that have been demonstrated to reduce bycatch across four marine megafauna groups in gillnets (e.g. Bielli et al., 2020). Deterrents must provide sufficient bycatch reductions and statistical power (in addition to statistical significance) to warrant implementation in fisheries (Dawson et al., 1998, 2013). Currently, there are no proven deterrents that provide sufficient and reliable bycatch reductions to warrant the costs of electrosensory technologies in fishing gear (Favaro & Côté, 2015). We encourage the continuation of trialling low-cost technologies and solutions such as gear-changes and alternative livelihoods for small-scale fishers in developing countries, who may be unable to afford existing deterrent technologies.

5.5.1 Towards a holistic understanding of blue shark conservation in the North Atlantic

In Chapter 5, I found no difference in behaviour of blue sharks presented with ferrite magnets against a control line. However, new developments in electrosensory deterrents could provide bycatch reductions of blue sharks. In this thesis, I investigated life history theory (Chapter 2), practical tools for assessing (Chapter 3) and conserving (Chapter 1 and Chapter 5) blue shark populations and their genomic population structure (Chapter 4). Together, these provide a holistic view of blue shark conservation and considerations for management. In Chapter 6, I bring together the findings in this thesis and provide specific recommendations to improve management and monitoring of blue sharks in the North Atlantic.

5.5.2 Conclusions

The efficacy of sensory deterrents are likely context-dependent, varying with species examined, environmental conditions, prior satiation, the presence and behaviour of conspecifics, as well as fisher compliance and adherence to advice on using deterrent devices. Therefore, in their current form, sensory deterrents are unsuitable for many fisheries, and alternative bycatch reduction plans must be urgently investigated to reduce the bycatch of threatened species and populations. Sensory deterrents may form part of the solution, but the pace of their development may not match the pace of decline in many of the species that are threatened by overfishing.

Chapter 6. Thesis Conclusions

6.1 Overview

This thesis investigated sensory deterrents for marine megafauna, life histories of elasmobranch species and genetic population structure of blue sharks (*Prionace glauca*). Further, low-cost field methods were developed and tested to assess shark growth and to reduce bycatch. Marine megafauna are threatened by mortality in fisheries, although the development of sensory deterrent technologies may reduce marine megafauna bycatch whilst maintaining target catch in some situations (Chapter 1). Elasmobranch life history strategies are informed by growth, survival, reproduction and energy budgets, but display plasticity depending on feeding level (Chapter 2). A low-cost stereo-video system to obtain body size measurements was developed (Chapter 3) and blue shark genetic population structure was investigated (Chapter 4) providing evidence for a distinct population in the eastern and southeastern Pacific. Although sensory deterrents may reduce marine megafauna bycatch in some situations (Chapter 1), ferrite magnets did not deter blue sharks from baited lines (Chapter 5). Together, these insights emphasise the importance of multidisciplinary assessment of blue sharks and the results in the thesis have implications for their conservation and management, although further research is needed to delineate genetic population structure and quantify catch levels of blue sharks in the North Atlantic.

Assessment and mitigation of threats to pelagic megafauna are difficult due to their vast distributions (Game et al., 2009), migration patterns (Martin et al., 2007) and high spatial overlap with fisheries (Queiroz et al., 2016). Under-reporting, misreporting and lack of independent observer coverage makes it challenging for researchers and Regional Fisheries Management Organisations (RFMOs) to accurately estimate fisheries catch on the high seas (Hentati-Sundberg et al., 2014; Mucientes et al., 2022). Pelagic elasmobranchs have been impacted by overfishing, with some species, such as the oceanic whitetip (*Carcharhinus longimanus*) and dusky (*Carcharhinus obscurus*) shark experiencing declines in abundance of >70% globally since 1970 (Pacoureau et al., 2021). Blue sharks have faced substantial declines too, but their productivity compared to other pelagic elasmobranchs may have prevented population collapses (Cortés et al., 2010). Simpfendorfer & Dulvy (2017) reported sustainable, but poorly managed, catch levels of blue sharks globally. Yet, declines in the abundance of blue sharks caught in the North Atlantic (Thesis Overview: Figure 0.2B; Rigby et al., 2019b) suggest that blue sharks have recently been overfished (Aires-da-Silva & Gallucci, 2007; Aires-da-Silva et al., 2009; ICCAT, 2023a). Since 2019, blue shark catch has been limited in the North Atlantic (currently 30,000 tonnes per year; ICCAT, 2023b), although quantifying catch levels remains challenging due to incomplete coverage of independent fisheries observers (e.g. Ewell et al., 2020). Therefore, there is still an incomplete understanding of fisheries interactions with blue sharks in the North Atlantic, which must be addressed due to their high catch levels.

Conservation and recovery of shark populations are broadly achieved by measures to avoid interactions between animals and fisheries, implementation of catch limits, live release of individuals, or restriction on trade of shark products (e.g. Shiffman & Hammerschlag, 2016). Trade restrictions have acknowledged the decline of elasmobranch populations, with the recent listing of all requiem sharks on CITES Appendix II (23rd November 2023), making over 140 species protected by CITES legislation (Sherman et al., 2023b) and 38 species listed on the Convention of Migratory Species Memorandum (CMS MoU sharks 2023; https://www.cms.int/sharks/en/document/amendment-annex-1-sharks-mou-1). Despite these restrictions, illegal wildlife trade continues (Cardeñosa et al., 2018, 2020, 2022), making the prevention of overfishing critical for species survival. Research and conservation efforts are promoted by the IUCN SSC Shark Specialist Group (SSG; https://www.iucnssg.org/) and key hotspots for protection are identified by Important Shark and Ray Areas IUCN project (ISRAs; https://sharkrayareas.org/), providing evidence for management decisions. National Plans of Action (NPOA sharks) and shark sanctuaries (Shiffman & Hammerschlag, 2016) have been implemented in global hotspots with the intention of promoting recoveries. Slowing declines in shark abundance, reduced trade and reduced fishing effort have been recorded, although these may not be sufficient for large-scale conservation benefits (Ward-Paige & Worm, 2017), or suitable in low-income and developing nations where sharks are important for food security (Dulvy et al., 2017; Baker-Médard & Faber, 2020). Yet, evidence suggests that commercial high seas fisheries play a small role in supporting food security in regions with low-income (Schiller et al., 2018) and developing nations instead rely on coastal and small-scale fisheries for protein and income (Pauly, 2006; Béné, 2006). Therefore, properly enforced, evidence-based regulations for commercial fisheries, implemented by RFMOs (ICCAT for managing pelagic elasmobranchs in the Atlantic), are key to the recovery of declining oceanic shark populations across large spatial scales (Simpfendorfer & Dulvy, 2017; Pacoureau et al., 2023) and even support coastal fish communities through pelagic-benthic coupling (Griffiths et al., 2017; Morais & Bellwood, 2019).

Life history strategies underpin population responses to harvesting (Chapter 2), used in the creation of evidence-backed policy (Cortés, 2002). Recovery potential for elasmobranch populations have traditionally been informed by the maximum intrinsic rate of population increase, r_{max} (Hutchings et al., 2012). However, Chapter 2 demonstrates that incorporating expected feeding level ($E(Y)$) into mechanistic models of growth, reproduction and survival revealed plasticity in elasmobranch life history strategies. For these strategies, population growth rates and demographic resilience changed in response to a poor ($E(Y) = 0.6$) and high ($E(Y) = 0.9$) quality environment, indicating that traditional metrics like r_{max} should be used with caution in shark species conservation assessments. Besides fisheries, blue sharks face the threat of habitat loss by deoxygenation of marine habitats, which may prevent them from accessing feeding grounds (Vedor et al., 2021). The effects this may have on blue shark population trajectories is not clear, so further investigation of foraging habitat quality and the implications for population performance are needed to inform management plans (Kindsvater et al., 2024). Mechanistic models capable of predicting population performance based on environmental quality, environmental change and fishing mortality could be crucial for accurate assessment of blue shark populations and resulting conservation implications.

Informing demographic models that predict population trajectories requires quality life history data for parameterisation (Kindsvater et al., 2018). Low-cost systems for collecting these data (Chapter 3) could provide new insights into demographic differences between different regions, especially where identification of individuals and maturity assessment is possible through video data collection methods (Brooks et al., 2010; Gore et al., 2016; Rogers et al., 2017; Lewis et al., 2023). In addition, evidence of genetic population substructure (Chapter 4) and demographic differences (e.g. da Silva et al., 2021) suggest that blue sharks could exhibit differing population responses between regions, potentially requiring different management strategies (Benton & Grant, 1999).

The market for blue shark meat and fins has led to their global ex-vessel value exceeding that of some tuna species (Poseidon, 2022). However, discards occur in some fisheries, such as longline operations in the Mediterranean, where fishers lack the facilities to store shark meat and only retain individuals caught in the last few hauls when returning to port (ICCAT, 2023a). While post-release survival is possible (e.g. Campana et al., 2016), most sharks die before they reach vessels during hauling operations and trade bans do not stop incidental catches occurring, so preventing wasteful catch should be prioritised (Tolotti et al., 2015). Methods to prevent elasmobranch catch in fisheries include the implementation of electrosensory deterrents

(Chapter 1). Although these have shown promise for some species, most have been ineffective at reducing catch of blue sharks (Chapter 1, Chapter 5), except for the recently developed SharkGuard (Doherty et al., 2022). Affordable measures to reduce bycatch across threatened marine megafauna taxonomic groups (e.g. Bielli et al., 2020; Senko et al., 2022), whilst maintaining target catch quality and quantity, are key to the success of sensory deterrents (Chapter 5). However, the efficacy of the SharkGuard in different environments and for other shark species remains uncertain, and its cost may be prohibitive for longline fishers (Cox et al., 2007; Lent & Squires, 2017), especially if target catch shows even minor reductions (Doherty et al., 2022). Therefore, alternative measures are likely required to ensure blue shark bycatch is minimised in commercial longlines.

6.2 Recommendations for future research and management of blue sharks in the North Atlantic

Beyond the recommendations and avenues for future research presented in the chapters of this thesis, there are additional areas of investigation and recommendations that would benefit from more holistic assessment and management of blue sharks in the North Atlantic.

Current evidence suggests that blue sharks may be overfished in the North Atlantic (B/B_{MSY} = 1.0, 95% confidence interval: 0.75-1.31), but that the current rate of extraction has reduced to sustainable levels (F/F_{MSY} = 0.70, 95% confidence interval: 0.50-0.93) by 2021, falling between the yellow and green quadrant on a Kobe phase plot assessing fishing pressure compared to biomass (Figure 6.1; ICCAT, 2023a). Yet, onboard independent fisheries monitoring may lack sufficient coverage to provide accurate catch estimates (Ewell et al., 2020) and the Kobe phase plot indicates that the North Atlantic blue shark stock was overfished with an unsustainable rate of extraction in the 2000s and 2010s (Figure 6.1; ICCAT, 2023a). Remote monitoring options could improve coverage and reporting accuracy (Bartholomew et al., 2018; Emery et al., 2018), though they may be unpopular with fishers (van Helmond et al., 2020). Efforts to enhance monitoring and reporting should focus on Spanish and Portuguese commercial longline vessels, which are responsible for the highest mortality of blue sharks in the North Atlantic (Thesis Overview: Figure 0.2), as well as in the Mediterranean. Moreover, mapping catch levels to fishing areas is crucial for quantifying impacts on blue sharks in key locations, such as putative nursery areas in central North Atlantic (Vandeperre et al., 2014a, 2014b). Improving IUU and small-scale fishing reporting accuracy will aid assessments (Watson, 2017; Temple et al., 2024), although the true impact of these are challenging to estimate (Béné, 2006) and indirect methods such as satellite surveillance and inspection data from patrols may be required (Agnew et al., 2009; Macfadyen et al., 2016). Improved understanding of catch figures and areas of blue shark mortality on a detailed spatial and temporal level are critical for developing demographic models to determine acceptable catch levels and necessary protections for effective regional management (ICCAT, 2023a).

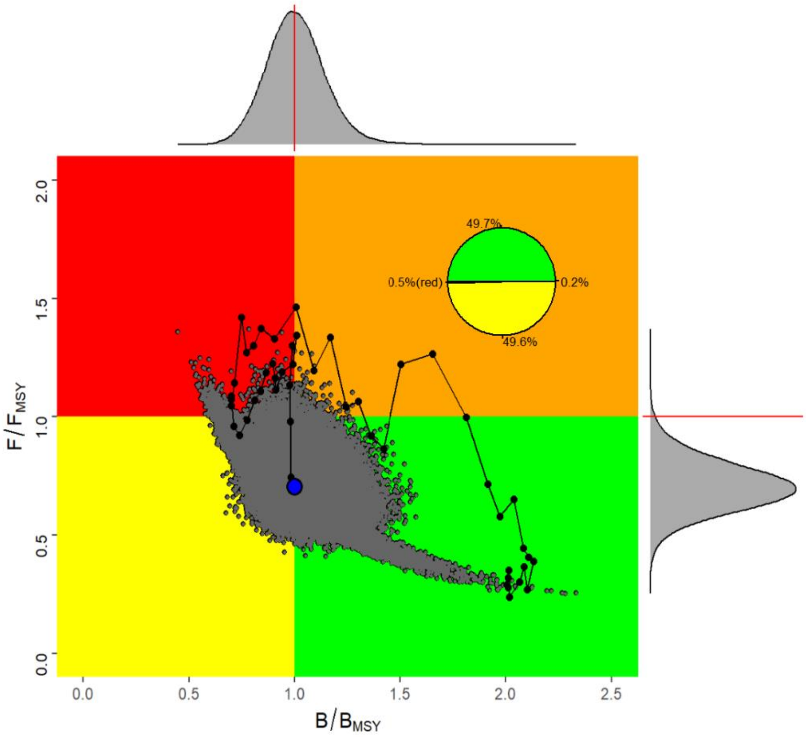


Figure 6.1 Kobe phase plot for the North Atlantic blue shark stock, from ICCAT (2023a). The solid blue dot indicates the final year (2021) with the solid line and connected black dots representing stock status trajectory since 1971. Grey dots indicate interactions between two models used to calculate position of the terminal year on the plot. Marginal distributions are plotted for each axis. The x-axis refers to the stock level (either overfished or not overfished) and y-axis refers to the rate at which the stock is being fished (either overfishing is occurring or not occurring). The colours indicate the following patterns: red: overfished and overfishing currently occurring; orange: not overfished but overfishing currently occurring; yellow: overfished but overfishing not currently occurring; green: not overfished and overfishing not currently occurring.

Further investigation into blue shark genetic population substructure, including synthesis of existing genomic data (combining results from Chapter 4 with those from Nikolic et al., 2023), would greatly aid evidence-based management for RFMOs (Domingues et al., 2018). Different regions could contain populations with distinct demographic traits (e.g. da Silva et al., 2021), as seen in the porbeagle shark (*Lamna nasus*; Francis et al., 2008). It would be informative for management to predict population trajectories (such as those investigated in Chapter 2) specific to the demographics of blue sharks in the North Atlantic, as well as at the species level. Individual identification of blue sharks and assessment of maturity from video footage would allow for non-invasive collection of life history traits for parameterising these models, using long-term datasets which could be collected by tourism operators and fishers across the North Atlantic (Chapter 3). Further research using mechanistic models incorporating individual energy budgets (Chapter 2) could leverage recent estimates of fishing mortality from the North Atlantic (ICCAT, 2023a) to predict population performance under various harvesting and environmental quality scenarios.

Preventing unnecessary mortality of marine megafauna should be a priority for managers to maintain healthy, resilient and productive pelagic ecosystems. Electrosensory deterrents are not currently suitable for implementation in fisheries with elasmobranch bycatch (Chapter 5). In addition, cross-taxonomic bycatch reductions should be the goal to ensure management measures are cost-effective and provide meaningful reductions in bycatch of threatened species (e.g. LED lights, as discussed in Chapter 1; Bielli et al., 2020). While cessation of recreational catch and release fisheries may prevent mortality, stopping recreational fisheries would not have a major impact on the overall survival of blue shark populations (Figure 0.2D) and this industry offers a potentially valuable avenue for research (Scotts et al., 2023). Therefore, the highest priority should be to quantify the impact of longline fisheries on blue sharks to inform evidence-based management plans.

6.3 Conclusions

The research results presented in this thesis have addressed data gaps in elasmobranch life history, blue shark genetic population structure and fisheries management options in a multidisciplinary assessment of blue sharks in the North Atlantic. Solutions to the threats faced by pelagic sharks, whilst protecting the interests of fishers in a rapidly changing world, still seem distant. Yet, this thesis has contributed to the improved understanding of elasmobranch life history strategies and how these strategies predict population performance and conservation status. It has further provided open-source designs for low-cost video methods for collection of body size data of sharks in the wild, opening opportunities for researchers with limited resources. For blue sharks, a truly global view of genetic population structure is within reach, with the potential to synthesise large datasets of blue shark samples from across its distribution using powerful genome scans. Improved understanding of interactions between blue sharks and sensory deterrents has revealed that alternative conservation measures may be required to reduce their wasteful and detrimental bycatch. Although there is no immediate concern for the collapse of blue shark globally, some populations are threatened and the impact of losing this species could be catastrophic for pelagic ecosystems. Declines of pelagic elasmobranchs across the world are likely underestimated given the lack of monitoring in many fisheries. Continued research of population health, prevention of bycatch and improved monitoring in the North Atlantic (and across its distribution) is necessary to ensure the long-term conservation and effective management of the blue shark.

Appendices

Appendix A Chapter 2

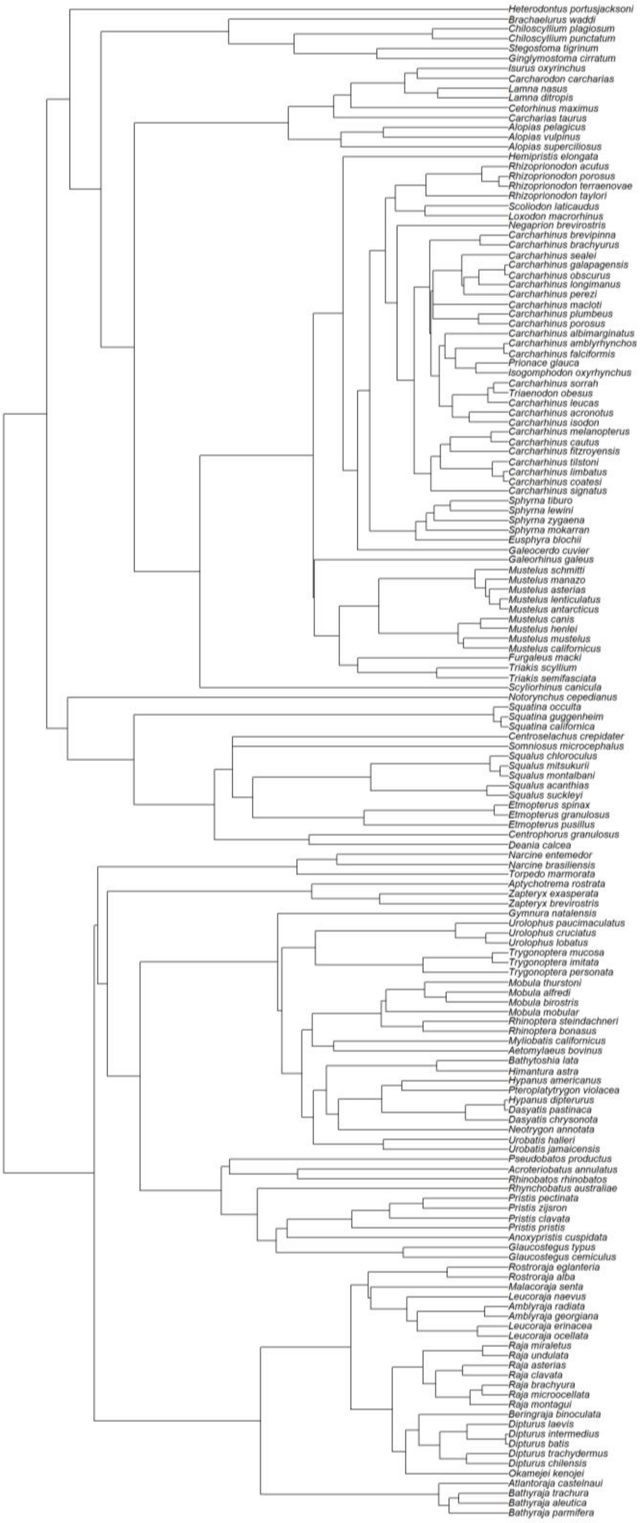


Figure S2.1 Phylogenetic tree for 154 of the 157 species in the database. 3 species were not found from the database: *Squalus hawaiiensis*, *Aetobatus narutobiei* and *Maculabatis ambigua*.

Table S2.1 Loadings and variance explained for the (p)PCAs with and without mass-correction, across each feeding level, with eigenvalues >1. All species available were included in each analysis. Therefore, for mass-corrected models there are 51 species for the 0.6 feeding level and 117 species for the 0.9 feeding level. For models without mass correction there are 63 species for the 0.6 feeding level and 151 species for the 0.9 feeding level. Loading values greater the 0.5 are in bold. Where loadings for a variable are less than 0.5, the highest loading value is in bold. Pagel's $\lambda > 0.25$ for E(Y) = 0.9, so the pPCA was used. Pagel's $\lambda < 0.25$ for E(Y) = 0.6, so the PCA was used. The qualitative check concluded that the loading of variables were on the same axes and in the same direction for both feeding levels, comparing the PCA and mass-corrected PCA for E(Y) = 0.6 and pPCA and mass-corrected pPCA for E(Y) = 0.9.

PCA	**Full Model**			**Mass-corrected**			**Phylogeny**			**Phylogeny Mass-corrected**		
Eigenvalue >1	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cumulative variance	0.432	0.749	0.899	0.453	0.744	0.900	0.432	0.749	0.899	0.453	0.744	0.900
Feeding Level	0.6			0.6			0.6			0.6		
Pagel's lambda	-			-			<0.001			<0.001		
Number of species	63			51			63			51		
T	**-0.532**	-0.215	-0.007	**-0.547**	0.203	-0.002	**0.920**	0.331	-0.071	**0.938**	0.269	-0.074
H	-0.281	0.110	**0.772**	-0.311	-0.148	**-0.705**	0.157	-0.147	**-0.954**	0.294	-0.214	**-0.902**
L_α	-0.274	0.048	**-0.538**	-0.230	-0.030	**0.612**	**0.751**	-0.158	**0.557**	**0.672**	-0.183	**0.672**
γ	**-0.511**	0.006	-0.007	**-0.536**	0.006	-0.045	**0.918**	-0.057	-0.094	**0.941**	-0.076	-0.147
ρ	0.161	**-0.462**	0.042	0.173	**0.434**	-0.033	-0.381	**0.832**	0.040	-0.412	**0.811**	0.049
φ	0.210	**0.521**	0.043	0.198	**-0.535**	-0.074	-0.313	**-0.896**	-0.071	-0.276	**-0.912**	-0.121
S	0.045	**0.451**	0.169	0.061	**-0.477**	-0.103	-0.089	**-0.775**	-0.240	-0.055	**-0.827**	-0.172
R_0	-0.097	**0.474**	-0.287	-0.091	**-0.445**	0.310	0.383	**-0.870**	0.252	0.383	**-0.857**	0.289
L_ω	**-0.469**	0.162	-0.023	**-0.427**	-0.188	0.115	**0.876**	-0.330	-0.087	**0.852**	-0.427	0.033

Eigenvalue >1	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Cumulative variance	0.438	0.732	0.866	0.425	0.726	0.859	0.438	0.748	0.871	0.421	0.739	0.865
Feeding Level		0.9			0.9			0.9			0.9	
Pagel’s lambda		-			-			0.303			0.248	
Number of species		151			117			151			117	
T	**-0.495**	-0.102	-0.030	**-0.502**	-0.105	-0.037	**0.942**	-0.234	0.147	**0.943**	-0.266	-0.093
H	-0.158	-0.168	**0.839**	-0.177	-0.153	**0.834**	0.086	0.083	**0.987**	0.062	0.098	**-0.976**
L_α	**-0.377**	0.286	-0.196	**-0.345**	0.307	-0.235	**0.828**	0.384	-0.228	**0.799**	0.376	0.350
γ	**-0.448**	0.021	0.003	**-0.463**	0.021	0.023	**0.869**	-0.004	0.043	**0.873**	-0.023	-0.059
ρ	0.017	**-0.563**	-0.092	0.019	**-0.550**	-0.113	-0.138	**-0.898**	-0.066	-0.138	**-0.901**	0.064
φ	0.368	**0.384**	0.139	0.368	**0.383**	0.140	**-0.720**	**0.643**	0.092	**-0.688**	**0.681**	-0.092
S	0.117	0.257	**0.452**	0.113	0.263	**0.444**	-0.228	**0.734**	0.059	-0.236	**0.726**	-0.142
R_0	-0.102	**0.576**	-0.079	-0.080	**0.571**	-0.094	0.344	**0.870**	-0.028	0.332	**0.873**	0.136
L_ω	**-0.476**	0.132	0.137	**-0.478**	0.166	0.101	**0.899**	0.264	0.187	**0.909**	0.269	-0.079

Table S2.2 Comparison of the dominant variables and their direction on the principal two axes from our study (using the 0.9 feeding level) compared with previous literature. Positive directions are highlighted in green and negative in red. Grey highlights indicate that the trait was not used in the analysis and blank boxes indicates that the trait was not a dominant variable for that axis. The directions for PC1 in this study have been multiplied by -1 for the 0.6 feeding level only, so all negative values have been changed to positive, and vice-versa, because the directions of the PC axes are arbitrary.

		This study E(Y)=0.6		This study E(Y)=0.9		Salguero-Gómez et al., 2016		Salguero-Gómez, 2017		Capdevila et al., 2020a		Healy et al., 2019	
Life history trait		PC1 Fast-slow	PC2 Repro	PC1 Fast-slow	PC2 Repro	PC1 Fast-slow	PC2 Repro	PC1 Fast-slow	PC2 Repro	PC1 Fast-slow	PC2 Repro	PC1 Fast-slow	PC2 Repro & mortality
Generation time	T	+		+		+		+		+		+	
Survivorship curve	H					+		+		+			-
Age at maturity	L_a			+		+		+		+		+	
Progressive growth	g	+		+		-		-		-		▨	▨
Retrogressive growth	r		-		-		-		-	▨	▨	▨	▨
Mean recruitment success	φ		+	-	+	-		-		-	-		-
Degree of iteroparity	S		+		+		+		+		+		+
Net reproductive rate	R_0		+		+		+		+	▨	▨	▨	▨
Mature life expectancy	L_w	+		+						▨	▨		

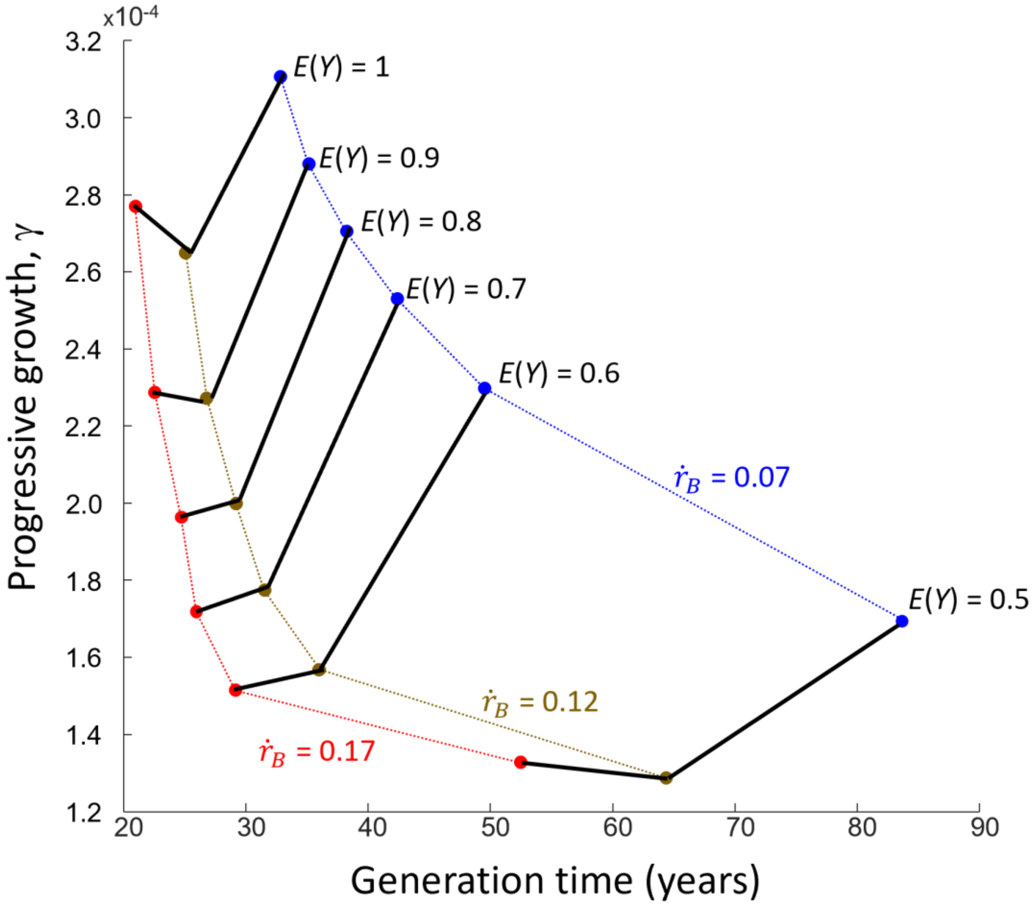


Figure S2.2 The relationship between generation time (years) and progressive growth, g, for the reef manta ray, *Mobula alfredi* in relation to feeding level E(Y) and the von Bertalanffy growth rate, $\dot{r}_B$. At the default value of $\dot{r}_B$=0.07 (Smallegange & Lucas, 2024) (blue dotted line), generation time increases with decreasing feeding level, which is what you would expect from life history theory, and progressive growth, g, decreases. When we increase $\dot{r}_B$ to 0.12 (brown dotted line) and 0.17 (red dotted line) the same pattern exists, and, overall, generation time decreases and so does progressive growth. As a result, at almost each constant feeding level (black solid lines), progressive growth increases with decreasing $\dot{r}_B$, and, at the same time, generation time increases. It thus appears that large variation in $\dot{r}_B$ within or between species and low variation in feeding level can drive a positive correlation between generation time and progressive growth (cf. van Noordwijk & de Jong, 1986). This would explain why we found that the slower a species pace of life, the higher is its progressive growth (Fig. 2) (and the lower its $\dot{r}_B$; see Results).

Figure S3.1 Example image from the stereo-video corner detection in the StereoMorph calibrateCameras function.

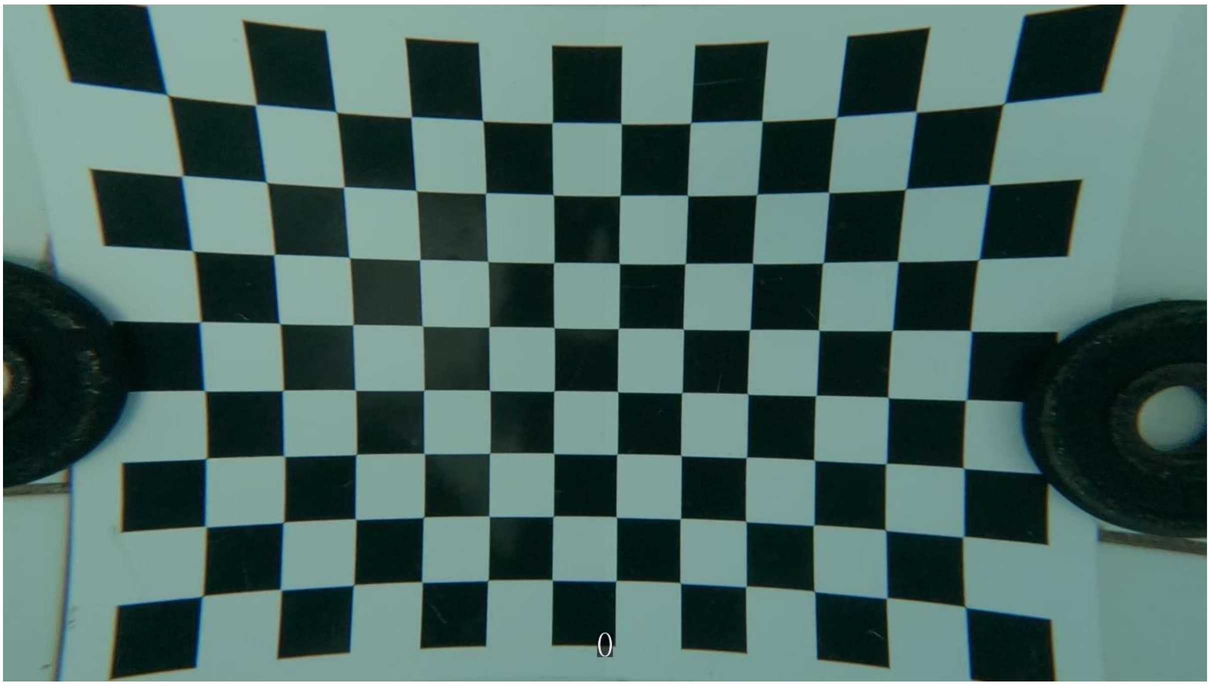


Figure S3.2 Photograph of the small 13x9 checkerboard used in the laser distortion calculation.

Appendix C Chapter 4

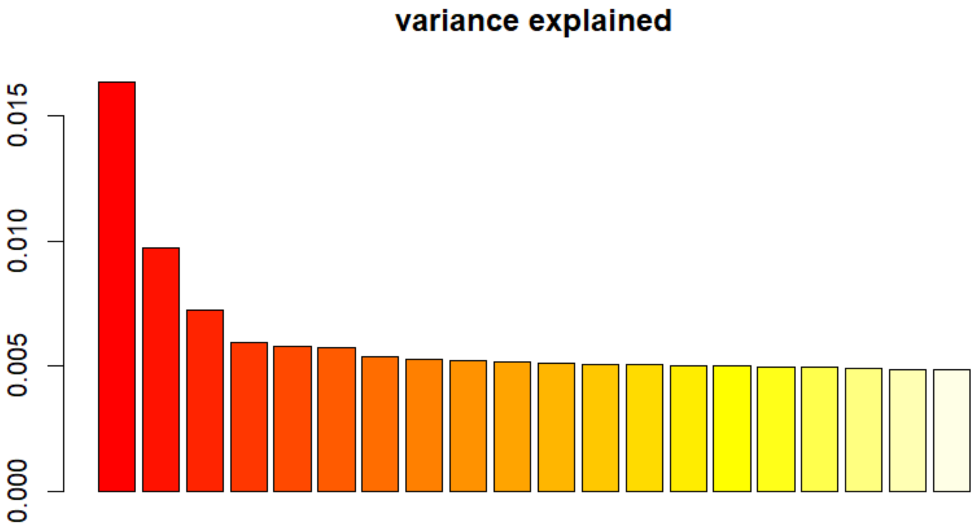


Figure S4.1 Variance explained by the first 20 principal components in the PCA analysis of 307 individual blue sharks across 6,517 Single Nucleotide Polymorphisms. Four principal components were retained, explaining approximately 3.53% of the variance in the data.

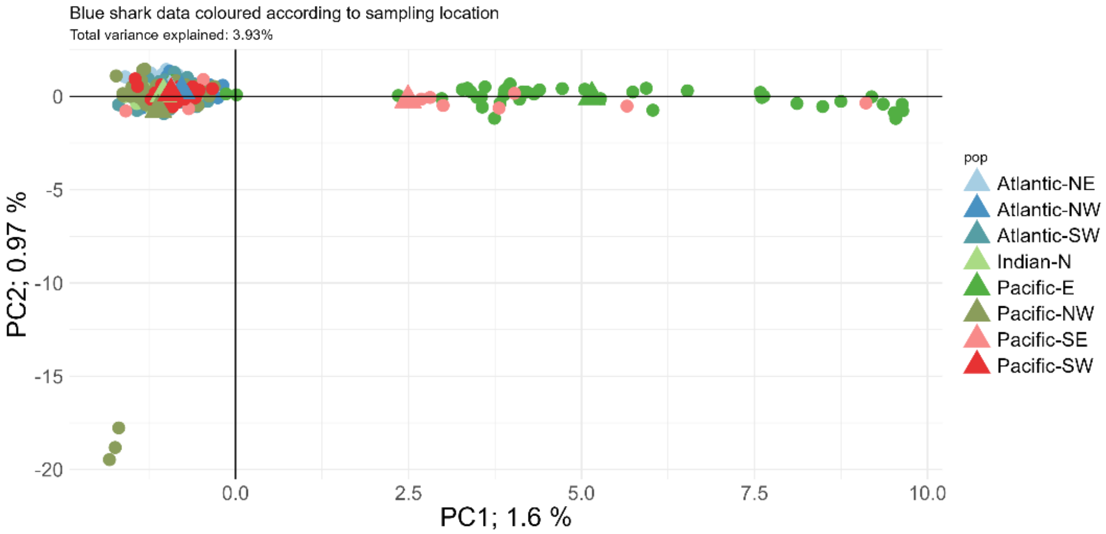


Figure S4.2 Principal component scores for the first two axes plotted for individuals (circles) and populations (triangles) from the filtered blue shark dataset.

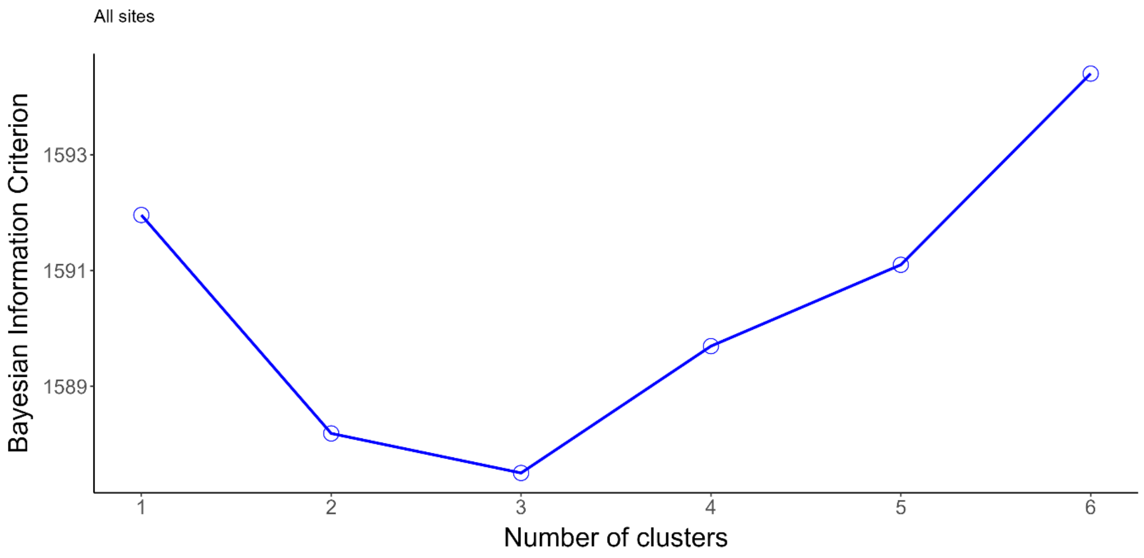


Figure S4.3 Bayesian Information Criterion (BIC) scores for K cluster values between 1 and 6 in the DAPC. K=3 resulted in the lowest BIC score.

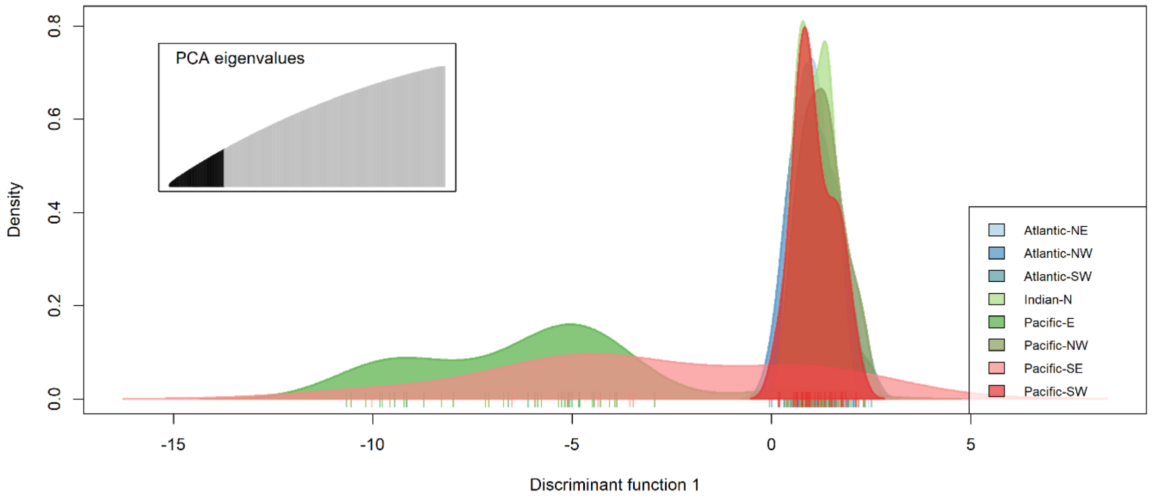


Figure S4.4 DAPC density plot for K=2. Scores are aggregated across individuals in each of the eight sampling regions.

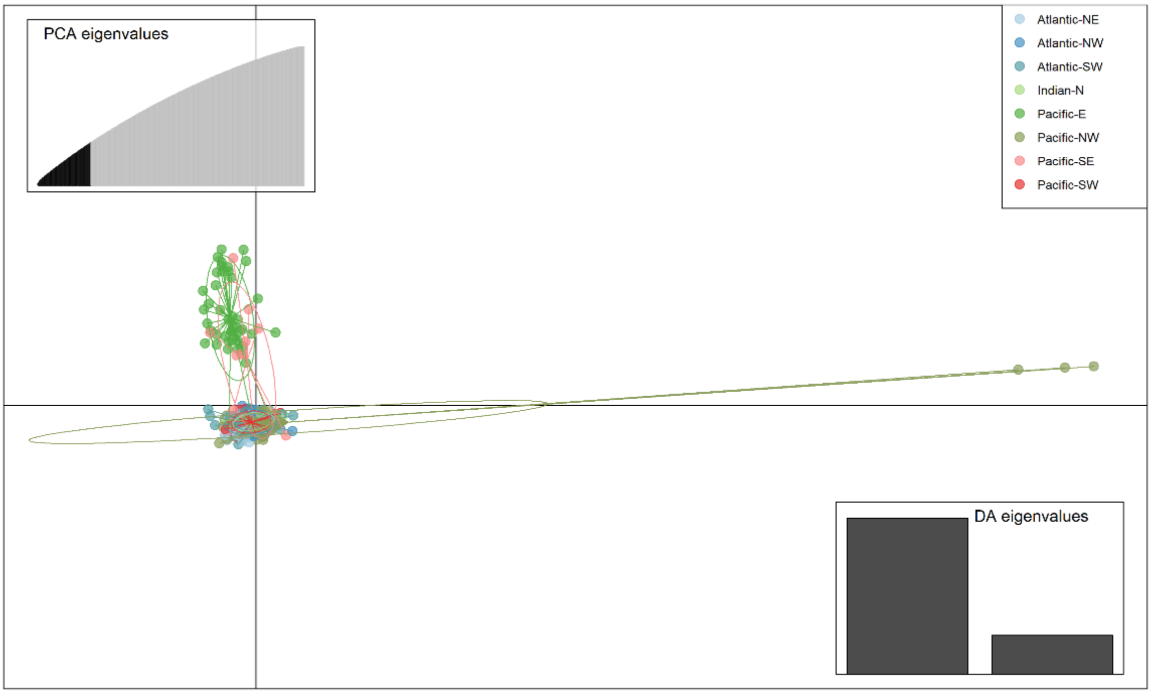


Figure S4.5 DAPC density plot for K=3. Scores are aggregated across individuals in each of the eight sampling regions.

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