Understanding and quantifying shark depredation in a recreational fishery in the Ningaloo region of Western Australia

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This thesis is presented for the degree of Doctor of Philosophy in Biological Sciences at The University of Western Australia

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Thesis declaration

I, Jonathan David Mitchell, certify that:

This thesis has been substantially accomplished during enrolment in the degree.

This thesis does not contain material which has been submitted for the award of any other degree or diploma in my name, in any university or other tertiary institution.

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The research involving human data reported in this thesis was assessed and approved by The University of Western Australia Human Research Ethics Committee. Approval # RA/4/1/7462.

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Abstract

Shark depredation, where a shark consumes an animal caught by fishing gear before it can be retrieved to the fishing vessel, occurs in commercial and recreational fisheries worldwide, leading to higher mortality for target species, injury to sharks and costly loss of catch and fishing gear. Despite this, depredation remains relatively understudied compared to other fisheries issues such as bycatch and post-release mortality. This thesis presents a multi-disciplinary investigation of shark depredation, which brings together aspects of biology, behaviour and socio-economics, as well as providing information that addresses key management questions related to depredation. The first goal of this research was to conduct a detailed global review of the shark depredation literature, to collate all existing information on this topic, compare rates of depredation in diverse commercial and recreational fisheries around the world, and identify shark species potentially responsible for depredation. The review was also designed to highlight key research gaps relating to this topic that need to be addressed. Building on this, the research sought to quantify shark depredation rates in a popular recreational fishery in the Ningaloo region of Western Australia, where depredation has been reported to be a management issue. Alongside this, assessing the socio-economic impact of shark depredation was another objective of the research, as well as predicting the potential efficacy of fisheries closures as a management measure to reduce depredation rates. Lastly, this study sought to identify the shark species responsible for depredation in the Ningaloo region, to determine whether protected species or those subject to management measures were involved, and to investigate the dynamics of shark behavioural interactions with fishing gear.

The global review of shark depredation identified 61 published studies between 1955 and 2018, with reported rates of depredation ranging from 0.9% to 26% in commercial and recreational fisheries and during research fishing. Additionally, 27 shark species from seven families have been recorded to be responsible for depredation in these fisheries. Multiple options for mitigation are discussed, including the adoption of changes to fishing methods and the development and use of shark deterrent devices. In the Ningaloo region, data collected through boat ramp surveys recorded shark depredation rates for the first time in a recreational fishery in Australia, as well as assessing spatial variation. Generalised Additive Mixed Models (GAMMs) quantified the influence of environmental variables and fishing methods on depredation rate, indicating that depth, the density of fishing vessels, season, latitude and fishing pressure all affected depredation rates. Results suggest that sharks may have learnt to associate the presence of fishing vessels with the availability of hooked fish to feed on in areas that are regularly fished. Data collected through surveys were also used to assess the socio-economic impacts of shark depredation in the Ningaloo region, using Random Utility Models (RUMs). The RUMs revealed that travel cost had a

significant negative impact on recreational fishers in this region, leading to them choosing sites close to boat ramps. Unexpectedly, shark depredation and catch rate did not significantly influence fisher site choice, perhaps because fishers lacked the detailed spatial knowledge of fishing locations necessary to avoid depredation or maximise catch rates. The use of line-mounted cameras confirmed that sharks were responsible for depredation, and identified the involvement of four key shark species, as well as ground-truthing the depredation rate previously reported from boat ramp surveys. An extensive range of behavioural interactions with fishing gear were also recorded, along with observations of sharks with retained fishing gear from previous interactions.

The inter-disciplinary approach used in this study generated valuable information that will benefit a diverse range of fields, including fisheries and marine park management, knowledge of shark behavioural ecology, and the application of statistical modelling techniques to depredation data. The unique approach used by this thesis therefore provides managers with a well-rounded and balanced assessment of shark depredation. In particular, this study has highlighted that further research into designing and implementing effective non-lethal mitigation strategies is critically needed, which will benefit target fish populations, shark health and survival rates, and both commercial and recreational fishers.

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Chapter two

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Mr. Mitchell conducted all the literature reviewing for this publication, as well as the creation of figures and tables. All sections of the manuscript were written by Mr. Mitchell, with editing and additions made to the main text by the other co-authors.

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Chapter 1: General introduction

1.1. Shark depredation

Sharks are also known to depredate hooked fish in line- and net-based fisheries, although shark depredation remains understudied compared to cetacean depredation (Gilman et al. 2006, Dalla Rosa & Secchi 2007, Romanov et al. 2007, Hamer et al. 2012). This is particularly the case in recreational fisheries around the world (Mitchell et al. 2018a, 2018b). In Australia, there has been an increase in anecdotal reports of depredation in recreational fisheries in the northern regions, particularly in north-west Western Australia (Mercer 2015, Kagi 2016) and northern Queensland (Fraser Coast Chronicle 2012, ABC 2018, Daily Mercury 2018). In the former, the numbers of people visiting the Ningaloo region to fish recreationally has increased in recent decades (Shaw 2000, Wood & Dowling 2002, Westera et al. 2003, CALM & MPRA 2005, Jones et al. 2009), and public awareness and media coverage of shark depredation has spread (Mercer 2015, Kagi 2016). This is set in the context of the wider polarising issue of shark management in Western Australia, which has become a highly emotive issue due to concerns about both public safety and the need to conserve large predatory sharks (Neff 2015). Shark depredation has led to a generally negative attitude towards sharks amongst many recreational fishers, especially in the north-west region. This can, in-turn, lead to impacts on sharks if fishers decide to capture and kill them in order to reduce the likelihood of depredation. The biological and socio-economic impacts of shark depredation also have extra significance in this region, because it occurs in the Ningaloo Marine Park, which seeks to manage biodiversity conservation, whilst also providing recreational fishing opportunities (CALM & MPRA 2005, Beckley et al. 2010). To prevent repetition, background information on shark depredation has been kept to a minimum in this general introduction chapter, because it will be covered in detail in the published review presented in chapter two.

1.2. Rationale for shark depredation research in the Ningaloo region

Despite the socio-economic and biological impacts of shark depredation globally, more research needs to be conducted to address a range of research gaps. Firstly, the existing literature on shark depredation has not been extensively reviewed or collated, which is required to identify global patterns in depredation rates and the potential shark species involved, as well as to quantify impacts. A review would therefore be of great value in bringing together information from a diverse range of fisheries, which is currently presented in journal articles, fisheries reports, research theses and other forms of grey literature. A review would also help to stimulate future research on this topic by identifying new research questions. Additionally, very little quantitative data on shark depredation rates in recreational fisheries is available globally, so it is necessary to investigate this further to better understand the extent and potential impacts of this issue. The

Ningaloo region offers an ideal case study location, because it is a popular recreational fishery, with up to 55,000 fishing trips occurring per year (Ryan et al. 2013, 2017), where shark depredation has been anecdotally reported for many years (P. Barnes, pers. comm.). This area also has added significance because tourism linked to recreational fishing brings important revenue to the local economy (CALM & MPRA 2005, GDC 2006, Jones et al. 2009, Beckley et al. 2010).

The collection of reliable baseline data on the frequency and spatial occurrence of shark depredation is needed in this fishery in particular, because the many anecdotal reports do not offer a reliable or consistent assessment of the magnitude of the issue for managers. Specifically, robust quantitative data on depredation rates are required to evaluate the potential impact on populations of target fish species, due to the extra mortality caused by depredation. This extra mortality occurs because recreational fishers often aim to catch a certain number of fish per day based on the allowed quota, which is five mixed demersal fish per person in the Ningaloo region (DPIRD 2017), but in the process they may lose extra fish to depredation, resulting in a higher overall mortality compared to if shark depredation did not occur. It is also necessary to investigate the potential socio-economic impacts of depredation, including the monetary cost of depredation for fishers and how this may influence the way in which they choose fishing locations. This can inform potential management options for mitigating depredation, such as information campaigns and identification of areas where high rates of shark depredation occur, so that they can be avoided by fishers.

It is important to confirm that sharks are indeed the main predatory taxa responsible for depredation in this fishery, because in many cases the predator responsible is not seen by the fisher, so its identity is unknown. Establishing whether there is a single species of shark responsible for depredation in this region, or a range of different species, has substantial importance to management, as some species are protected or subject to specific management measures, such as grey nurse *Carcharias taurus,* dusky *Carcharhinus obscurus* and sandbar *Carcharhinus plumbeus* sharks (Pollard et al. 1990, Simpfendorfer & Donohue 1998, Simpfendorfer et al. 1999, McAuley et al. 2005, Hoschke & Whisson 2016). It is, therefore, also important to investigate the potential impacts of depredation on sharks, such as how frequently they are hooked and injured in the process of depredating hooked fish, and how commonly they retain fishing gear in their jaw or digestive system after such interactions. Furthermore, to develop future mitigation strategies for reducing depredation, it is necessary to improve our understanding of the way in which sharks interact with fishing vessels and fishing gear, and the behavioural dynamics driving these interactions.

1.3. Thesis aims and structure

These key research questions are the driving force behind the research presented in this thesis, which aims to use a multidisciplinary approach to generate an holistic assessment of shark depredation in the Ningaloo Marine Park and Exmouth Gulf in Western Australia. The second chapter introduces the topic of shark depredation and presents a detailed review of the global literature. This brings together fundamental concepts and issues related to shark depredation, such as the quantification of depredation rates in different fisheries (predominantly commercial) around the world, the identity of the shark species involved, and what biological and socio-economic impacts result from shark depredation. This review is the first of its kind on this topic, and serves as a baseline for future research in other regions. It also identifies key research gaps and approaches for addressing them. Chapter three aims to address one of these vital research gaps, which is to provide the first quantitative assessment of shark depredation in a recreational fishery worldwide. This involves calculating shark depredation rates, as well as identifying the spatial variation in these rates and how environmental and fishing-dependent variables affect its occurrence.

Chapter four uses Random Utility Models (RUMs) to understand the socio-economic context and impact of shark depredation on recreational fisher site choice, which is intended to complement the information on biological impacts presented in the previous chapters. This modelling approach explores the potential costs and benefits of introducing a spatial closure to redistribute fishing effort away from a shark depredation hotpot, aimed at reducing overall depredation rates. Chapter five then develops a novel application of line-mounted underwater video cameras to confirm that sharks are responsible for depredation, and identify which shark species are involved, which is an essential research gap that needs addressing in the Ningaloo region. This study also offers an opportunity to ground-truth the shark depredation rate calculated in chapter three, as well as investigating the behavioural interactions of sharks with fishing gear. In addition, chapter five generates other insights, such as the identity of the teleost species being depredated by sharks, and the occurrence of retained fishing gear in sharks. Lastly, the general discussion provides synthesis and critical analysis of the research findings as a whole, identifying which research questions were addressed, and which remain to be investigated in both Western Australia, and globally.

Chapter 2: Shark depredation in commercial and recreational fisheries

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2.1. Abstract

Shark depredation, where a shark partially or completely consumes an animal caught by fishing gear before it can be retrieved to the fishing vessel, occurs in commercial and recreational fisheries worldwide, causing a range of negative biological and economic impacts. Despite this, it remains relatively understudied compared to other fisheries issues. This is the first review of the literature relating to shark depredation, which also includes an overview of the potential mechanisms underlying its occurrence and options for mitigation. Furthermore, this review highlights key research gaps that remain to be investigated, thereby providing impetus for future research. In total, 61 studies have been published between 1955 and 2018, which include information on shark depredation. These studies recorded quantitative rates of depredation between 0.9% and 26% in commercial and recreational fisheries and during research fishing, identified 27 shark species from seven families that were responsible for depredation and discussed potential factors influencing its occurrence. Information from research into bycatch mitigation and the testing of shark deterrent approaches and technologies is also presented, in the context of applying these approaches to the reduction of shark depredation. This review presents an holistic overview of shark depredation in fisheries globally and, in doing so, provides a central

resource for fisheries researchers and managers focusing on this topic to stimulate further collaborative research on this important fisheries issue.

2.2. Introduction

Depredation of fisheries catch is where a predator partially or completely consumes an animal caught by fishing gear before it can be retrieved to the fishing vessel (IOTC 2007, Gilman et al. 2008, MacNeil et al. 2009), and it is a source of mortality which occurs widely in commercial (Bullis 1955, Hirayama 1976, Gilman et al. 2007, Mandelman et al. 2008, Romanov et al. 2013, Muñoz-Lechuga et al. 2016) and recreational fisheries (Sumner et al. 2002, Labinjoh 2014, Mitchell et al. 2018a) around the world. Depredating taxa can include sharks, cetaceans, pinnipeds, large teleosts, squid, crabs, octopus and seabirds (Meyer et al. 1992, Donoghue et al. 2003, Brock et al. 2006, IOTC 2007, Gilman et al. 2008, Hamer et al. 2012, Remeslo et al. 2015, Shideler et al. 2015), which may consume teleost and elasmobranch fishes, cetaceans, crabs, squid, and marine turtles caught by fishing gear (Dudley & Cliff 1993, Noke & Odell 2002, Gilman et al. 2007, Romanov et al. 2007, Clua et al. 2014, Cruz et al. 2014). Depredation can occur in hook and line (Fig. 2-1a,b), net and trap fisheries (Cliff et al. 1989, Ebert 1991, Noke & Odell 2002, Brock et al. 2006, Gilman et al. 2007, IOTC 2007, Rafferty et al. 2012, Uhlmann & Broadhurst 2015). However, this review will focus only on depredation of fishes caught by commercial and recreational hook and line fisheries. In relation to the terminology used, it must be noted that some past studies refer to the process of hooked fish being consumed as predation (Russo 2015), or scavenging (Ebert 1991). The process of sharks consuming bait directly may also be referred to as depredation (Robbins et al. 2013). Lastly, this review does not cover studies where fish are consumed by sharks after being released, which is known as post-release predation or facilitated predation (Kaiser & Spencer 1994, Gilman et al. 2013, Raby et al. 2014).

Fig. 2-1: Bite-mark patterns resulting from shark depredation on **a)** a yellowfin tuna *Thunnus albacares* in a commercial pelagic longline fishery (image reproduced from Varghese et al. (2008), (2015) with permission from Sijo P. Varghese) and **b)** a golden trevally *Gnathanodon speciosus* in a recreational fishery.

Shark depredation leads to costly losses of commercially valuable fish and fishing gear and has important biological impacts such as increasing the mortality of target fish species and causing injury and mortality to the depredating sharks (Gilman et al. 2007). Despite this, shark depredation has received relatively little research beyond simply quantifying its occurrence in some pelagic longline fisheries. As a result, there is a vital need to collate the available information on shark depredation and identify critical research gaps that need to be addressed in order to reduce the significant impacts it can have on fisheries. For example, in some fisheries it is unknown which shark species are responsible for depredation, which is important from a management perspective for issues such as bycatch, because some sharks can end up becoming hooked after depredating hooked fish, leading to their capture and mortality. Shark depredation also occurs in recreational fisheries, however information on depredation in these fisheries is sparse, and is needed because of the growth in recreational fishing worldwide (Coleman et al. 2004, Cooke & Cowx 2004, Arlinghaus & Cooke 2009), and the potential for human-wildlife conflicts due to shark depredation.

To date, there has been a number of published studies covering the topic of shark depredation in fisheries (Gilman et al. 2007, IOTC 2007, Romanov et al. 2007, Mandelman et al. 2008, MacNeil et al. 2009, Muñoz-Lechuga et al. 2016, Mitchell et al. 2018a), and detailed global reviews of cetacean depredation have been produced by Gilman et al. (2006), Kock et al. (2006) and Hamer et al. (2012). However, there has been no review of existing shark depredation literature or identification of critical knowledge gaps. This review has the following aims; (1) to identify how and why depredation occurs in commercial and recreational fisheries and during research fishing (2) to discuss its prevalence in commercial and recreational fisheries worldwide and summarise the existing literature that quantifies this occurrence, (3) to highlight the biological and economic impacts of shark depredation in fisheries, (4) to explore existing research that has tested methods of reducing shark depredation and (5) to identify current research gaps and suggest remedial approaches.

2.3. Methodological approach

Electronic search engines and databases including Google Scholar, Web of Science, CiteSeer and ResearchGate were employed using different combinations of the keywords: depredation, bite-off, predation of hooked fish, scavenging, fishery, fisheries interaction and shark. The search covered articles published in peer-reviewed scientific journals as well as ‘grey’ literature, such as technical reports by fisheries agencies and research theses.

2.4. Outcome of literature search

In total, 61 sources with information or data on shark depredation were identified, between 1955 and 2018 (Table 2-1). Despite this large temporal spread, the majority (~82%) of these studies have been published since 2000 (Fig. 2-2), highlighting the growing importance of this fisheries issue and the need for further research. The literature generated by the search predominantly focused on reporting shark depredation rates in commercial longline fisheries (Table 2-2), along with how spatial, environmental and fishing method factors influenced depredation rates, with relatively few studies covering the impacts of depredation or the behavioural mechanisms occurring. This review summarises this key literature on shark depredation, discusses its impacts and presents potential strategies for reducing its occurrence.

Table 2-1: Chronological list of studies that include any form of information or data on shark depredation, as identified from an extensive literature search, including the author(s) and year, period of study, location and fishing sector and gear type. Rows highlighted in grey indicate 'grey' literature in the form of fisheries technical reports or theses, all other rows contain studies published in peer-reviewed scientific journals. CDL = Commercial Demersal Longline, CPL = Commercial Pelagic Longline, RD = Research Drumline, ResRL = Research Rod-and-Line, RPL = Research Pelagic Longline, RDL = Research Demersal Longline, RRL = Recreational Rod-and-Line

Author(s) and year	Period of study	Location	Fishing sector and gear type
Bullis (1955)	1954 - 1955	Gulf of Mexico and Caribbean Sea	RPL
Backus et al. (1956)	1953 - 1955	Northwest Atlantic Ocean, Gulf of Mexico and Caribbean Sea	RPL
Wathne (1959)	1954 – 1957	Gulf of Mexico and Caribbean Sea	RPL
Sivasubramaniam (1963)	1955 - 1963	Indian, Atlantic and Pacific Oceans	CPL
Sivasubramaniam (1964)	1955 - 1963	Indian Ocean	CPL
Hirayama (1976)	1954 - 1969	Central and western Pacific Ocean	CPL
Kobayashi & Yamaguchi (1978)	1956 - 1959	Pacific Ocean	CPL
Ebert (1991)	1982 - 1989	San Francisco Bay, USA, South Africa and Namibia	RDL, ResRL
Dudley et al. (1998)	1994 - 1995	KwaZulu-Natal, South Africa	RD
Secchi & Vaske (1998)	1987 – 1991	South Atlantic Ocean	CPL
Hoey & Moore (1999)	1990 - 1997	Atlantic Ocean	CPL
IOTC (2000)		Indian Ocean	CPL

Author(s) and year	**Period of study**	**Location**	**Fishing sector and gear type**
IOTC (2001)		Indian Ocean	CPL
Lawson (2001)	1995 - 2000	Central and western Pacific Ocean	CPL
Beerkircher et al. (2002)	1992 - 2000	Northwest Atlantic Ocean and Gulf of Mexico	CPL
Sumner et al. (2002)	1998-1999	Gascoyne region, Western Australia	RRL
Nishida & Shiba (2004)	2000 - 2002	Indian Ocean	CPL
Ward et al. (2004)	1990 – 2002	Pacific Ocean	CPL
Celona et al. (2005)	2000 - 2003	Sicily, Mediterranean Sea	CPL
Gilman et al. (2006)	1984 - 2006	Worldwide	CPL
Williamson et al. (2006)	1999 - 2000	Pilbara region, Western Australia	RRL
Ariz et al. (2007)	2004 - 2005	South-western Indian Ocean	CPL
Clark et al. (2007)	1997 - 2004	British Indian Ocean Territory (BIOT), Indian Ocean	CPL
Dai et al. (2007)	2003	Tropical Pacific Ocean	CPL
Dalla Rosa & Secchi (2007)	1993 - 1995	South Atlantic Ocean	CPL
Gilman et al. (2007)	1998 - 2006	Worldwide	CPL
IOTC (2007)	1961 - 2007	Indian Ocean	CPL
Ndegwa & Makogola (2007)	2005 - 2007	Kenya, Indian Ocean	CPL, RRL
Poisson et al. (2007)	1997 – 2000	Reunion Island, Indian Ocean	CPL
Rabearisoa et al. (2007)	1995 - 2006	Seychelles, Indian Ocean	CPL
Romanov et al. (2007)	1961 - 1989	Indian Ocean	RPL
Varghese et al. (2007)	2001 - 2005	Arabian Sea, Andaman and Nicobar waters	RPL
Ward (2007)	1950 - 1954, 1995 - 1999	Central Pacific Ocean	CPL
Gilman et al. (2008)	1998 - 2006	Worldwide	CPL
Hernandez-Milian et al. (2008)	2006 – 2007	Atlantic Ocean	CPL
Mandelman et al. (2008)	1992 - 2005	Atlantic Ocean	CPL
Moreno et al. (2008)	2006	Southeast Pacific Ocean	CDL
Varghese et al. (2008)	2000 - 2006	Arabian Sea, Bay of Bengal, Andaman and Nicobar waters	RPL
MacNeil et al. (2009)	1992 - 2006	Northwest Atlantic Ocean	CPL

Author(s) and year	**Period of study**	**Location**	**Fishing sector and gear type**
McCord & Lamberth (2009)	2009	Breede River, South Africa	RRL
Romanov & Bach (2009)	2009	Indian Ocean	CPL
Figueira & Hunt (2012)		Lord Howe Island, Australia	RRL
Hamer et al. (2012)	1963 – 2011	Worldwide	CPL
Rabearisoa et al. (2012)	2007 - 2008	Seychelles, Indian Ocean	CPL
Gilman et al. (2013)	1959 - 2013	Worldwide	Commercial fisheries, all gear types
Romanov et al. (2013)	2011 - 2013	Southwest Indian Ocean	CPL
Clua et al. (2014)	1998 and 2010	Seychelles, Indian Ocean and New Caledonia, Pacific Ocean	RD
Labinjoh (2014)	2013 - 2014	KwaZulu-Natal, South Africa	RRL
Schifiliti (2014)	2013 - 2014	Ningaloo Marine Park, Gascoyne region, Western Australia	Other (baited camera system)
Hamer et al. (2015)	2010 – 2013	Western Pacific Ocean	CPL
Madigan et al. (2015)	2011 - 2014	The Bahamas, Atlantic Ocean	RRL
O'Shea et al. (2015)	2012	The Bahamas, Atlantic Ocean	RPL
Russo (2015)	1970 - 2001	San Francisco Bay, USA	RDL, ResRL
Varghese et al. (2015)	2004 – 2010	Arabian Sea, Bay of Bengal, Andaman and Nicobar waters	RPL
Kumar et al. (2016)	1955 - 2016	Worldwide	CPL
Muñoz-Lechuga et al. (2016)	2011 - 2015	Indian Ocean	CPL
Mitchell et al. (2018a)	2015 – 2016	Ningaloo Marine Park and Exmouth Gulf, Western Australia	RRL
Niella et al. (2018)	2017	Southwest Atlantic Ocean	ResRL
Rees et al. (2018)		Lord Howe Island, Australia	RRL
Streich et al. (2018)	2012 - 2015	Western Gulf of Mexico	RPL
Grant et al. (in review)	2011 - 2013	Cumberland Sound, Canada	RDL

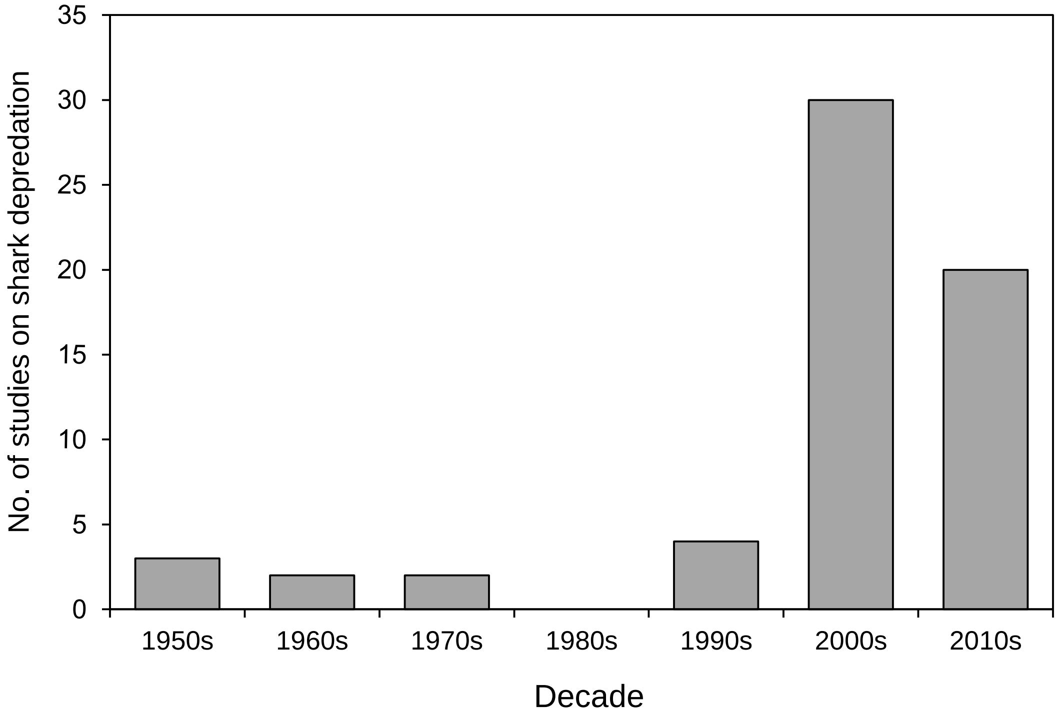

Fig. 2-2: Summary of the number of published studies on shark depredation by decade

2.5. Processes underlying depredation

2.5.1. Feeding behaviour and energetics

Many shark species have varied, flexible diets (Cortés 1999, Heithaus 2001), and display opportunistic feeding behaviour, including where they selectively prey on weak and injured individuals (Wetherbee et al. 1990, Lowe et al. 1996, Motta & Wilga 2001, Lucifora et al. 2009, Roff et al. 2016). Depredation is similar to natural feeding behaviour where sharks opportunistically prey on injured or unhealthy fish, because a hooked fish is also restricted in its ability to escape and will be injured (or already dead in the case of some pelagic longline fisheries with long soak times). Depredating a hooked fish is beneficial to sharks because it is more energy efficient compared to locating, capturing and consuming healthy, free-swimming prey. This is due to the fact that predators have to balance the energetic trade-off between the energy gained from feeding versus the energy expended in capturing and consuming a prey item, according to the Optimal Foraging Theory (OFT) (Charnov 1976, Pyke 1984). For example, it has been theorised that by depredating hooked tuna and billfish in a sport fishery in The Bahamas, oceanic whitetip sharks *Carcharhinus longimanus* have a higher energetic gain compared to their natural feeding pattern, which includes energetically costly deep diving to catch squid at depths of >1000 m (Madigan et al. 2015). Depredation may be also beneficial because it enables sharks to feed on fish species that may otherwise be too large or fast to capture in their natural environment.

2.5.2. Biophysical and environmental cues

2.5.2.1. Auditory cues

When locating and depredating hooked fish, it is likely that the highly evolved sensory systems of sharks respond to a number of biophysical and/or environmental cues. For example, a shark may detect the auditory cues of a boat engine, echosounder or anchor chain first, since sound travels over long distances underwater (Kalmijn 1988, Rogers & Cox 1988). Indeed, silky sharks *Carcharhinus falciformis* have been found to respond to sounds from up to 400 m away (Myrberg et al. 1972), and carcharhinid sharks are able to localise the directionality of sounds from a distance of at least 250 m (Corwin 1989). Audiograms collected for a range of shark species indicate an auditory range between 0.04 kHz and 1.5 kHz, with peak sensitivity from 0.2 kHz to 0.4 kHz (Kritzler & Wood 1961, Nelson 1967, Kelly & Nelson 1975, Corwin 1981, Myrberg 2001, Casper & Mann 2006, 2007, 2009, Chapuis 2017). Sharks will therefore be able to detect the sound generated by boat engines, which is generally in the range of 0.1 kHz to 10 kHz (Scholik & Yan 2002, Buckstaff 2004). Additionally, a number of studies have shown that sharks from different habitats are attracted to pulsed sounds below 0.8 kHz (Nelson & Gruber 1963, Nelson 1967, Myrberg et al. 1969, Nelson & Johnson 1972, Corwin 1981, Myrberg 2001, Chapuis 2017), and that the attraction increases if the frequency is lower and the pulses are irregular (Myrberg 1978, Chapuis 2017). Fish that are injured and moving erratically will likely produce such low frequency, irregular pulsed sounds, hence it is expected that predatory sharks would be attracted to such auditory cues (Banner 1972, Myrberg 1978, Chapuis 2017). Indeed, research has shown that lemon sharks *Negaprion brevirostris* were attracted to the sound of wounded mullet *Mugil sp.*, which are one of their key prey species (Banner 1972). Likewise, the sound of fish struggling after being speared has been shown to attract *C. falciformis* (Evans & Gilbert 1971) and whitetip reef sharks *Triaenodon obesus* (Nelson & Johnson 1970), and the sound of hooked fish was found to be attractive to thresher *Alopias sp.*, blue *Prionace glauca* and shortfin mako *Isurus oxyrinchus* sharks (Nelson and Johnson, unpubl. data). The results of these previous studies, therefore, support the theory that sound is an important sensory cue used by sharks to locate and depredate hooked fish.

2.5.2.2. Chemical cues

Chemical cues produced during fishing activity, particularly organic compounds including amino acids and nucleotides from injured fish, will also attract sharks, as they can detect these chemical compounds hundreds of metres from the source (Collin & Marshall 2003). The large odour plume created by bait and injured fish caught on longlines, as well as any unwanted fish and offal that are discarded from fishing vessels, may therefore attract sharks over a large area. Filmalter et al. (2015) reported an instance where a tagged *C. falciformis* appeared to be able to detect the location of a drifting Fish Aggregating Device (FAD) approximately 1.2 km away, and then navigate towards it. It was suggested that the presence of other fish close to the FAD may have enabled the shark to do this (Filmalter et al. 2015), perhaps because it was able to detect chemical or auditory signals produced by these fish. Certain shark species have been shown to be highly sensitive to amino acids such as alanine, cysteine and methionine, with Electro-Olfactogram (EOG) response thresholds in the micromolar and sub-nanomolar range for *N. brevirostris* and scalloped hammerhead sharks *Sphyrna lewini*, respectively (Zeiske et al. 1986, Tricas et al. 2009). Meredith & Kajiura (2010) also reported similar EOG response thresholds for a wide range of amino acids, with phenylalanine, tyrosine and alanine being the most stimulatory in *N. brevirostris* and bonnethead sharks *Sphyrna tiburo*. Future testing of the sensitivity of other species may indicate similar sensitivity levels. Furthermore, chemical excretions from hooked fish (e.g. ammonia and lactate) may act as “distress signals”, attracting nearby sharks that are sensitive to these chemicals (Collin & Marshall 2003, Jenkins et al. 2004, Dallas et al. 2010).

2.5.2.3. Visual and electrical cues

At closer range, and depending on water clarity and light levels, sharks may use vision from up to 100 m away (Collin 2012). Other cues such as hydrodynamic disturbances from a struggling fish on a hook, are detected up to a distance of 1-2 body lengths from the shark by the lateral line sensory organs (Collin 2012), while the weak bioelectric fields produced by potential prey can be detected by the well-developed electrosensory system of sharks, within approximately 30-50 cm (Kalmijn 1972, Haine et al. 2001, Collin et al. 2015, Collin 2017). Whilst the timeframe for sharks to detect and respond to these sensory cues and depredate hooked fish is relatively short in recreational rod-and-line fishing (usually < 5 minutes between the fish being hooked and retrieved to the boat), it is much longer for commercial pelagic longline fisheries (where lines with thousands of hooks may be deployed for hours at a time), resulting in a much higher potential for depredation. The sensory and behavioural processes underlying depredation in these two types of fishery are therefore likely to be markedly different, with sound and olfactory cues likely attracting sharks to a large scale longline over a wide area, compared to the short term disturbance created by a fish struggling on a recreational fisher’s line, which would more likely attract sharks using visual and mechanosensory cues.

2.5.2.4. Habituation and associative learning

It is possible that depredation may involve a distinct learning component. Firstly, habituation, defined as a reduction in a response to a stimulus over time caused by its repeated occurrence

(Lieberman 1990), could occur as sharks become used to, and are no longer wary of, the presence of fishing boats and the noise they generate. Indeed, the intensity of the escape response of sharks to sound was observed to rapidly decrease after repeated approaches to underwater speakers in an early study by Nelson & Johnson (1972). Additionally, habituation has been reported to occur during depredation of hooked fish by other taxa, including cetaceans (Gilman et al. 2006, Hamer et al. 2012, Tixier et al. 2014, Rabearisoa et al. 2015) and octopus (Briceño et al. 2015), although the sensory biology and behaviour of sharks are markedly different to these other depredating taxa. It is also possible that sharks may form an association between fishing boats and the presence of food in the form of hooked fish, via classical conditioning, which involves the temporal and spatial overlap of a neutral stimulus (e.g. boat engine noise) with a beneficial stimulus (e.g. presence of hooked fish to feed on) (Lieberman 1990). For positive associations to form in this way, the food reward also has to be predictable and regularly occurring (Lieberman 1990). Early research recorded successful conditioning of *N. brevirostris* and nurse sharks *Ginglymostoma cirratum* to the noise of a bell in a captive setting (Clark 1959), while Port Jackson sharks *Heterodontus portusjacksoni* showed a significant decrease in time of arrival and abundance as a result of conditioning when a light or bubble stream was associated with a food reward (Guttridge & Brown 2014). More recent research on *H. portusjacksoni* has shown that some individuals could be conditioned to associate jazz music with the provision of food, although marked differences in behaviour were observed between individuals (Vila Pouca & Brown 2018).

Wild studies of elasmobranch interactions with ecotourism activities have also indicated possible associative learning in sharks, for example, where white sharks *Carcharodon carcharias* displayed decreasing arrival times with increasing experience of food provision in South Africa (Johnson & Kock 2006), and an increase in site-fidelity and changes in diel habitat use as a result of being attracted by berley/chum and tethered baits used by cage-diving vessels in South Australia (Bruce & Bradford 2013). Similarly, *T. obesus* in the Coral Sea showed altered vertical and diel activity patterns in response to boat activity in an area where feeding occurs (Fitzpatrick et al. 2011). However, other research has shown no long-term impact of ecotourism on shark behaviour or movements (Laroche et al. 2007, Hammerschlag et al. 2012a). Further discussion on shark provisioning and its potential behavioural and ecological impacts, can be found in a recent review by Brena et al. (2015).

In recreational fisheries in South Africa and Western Australia, widespread anecdotal reports suggest that sharks associate the sound of engine and echosounder noise with the availability of easy prey in the form of hooked fish, as well as fish that are injured after being released (Exmouth Game Fishing Club, pers. comm., Labinjoh 2014). A preliminary study in the Ningaloo Marine Park in north-west Western Australia also recorded progressively faster arrival times of sicklefin lemon sharks *Negaprion acutidens*, to a baited camera system deployed over six consecutive days in an area that received regular fishing pressure, whereas in no-take sanctuary zones, very few sharks were attracted (Schifiliti 2014). Furthermore, tracking data from a large bull shark *Carcharhinus leucas* in the Breede Estuary in South Africa showed the predator remaining underneath the hull of up to ten different recreational fishing vessels for short periods of time, as well as moving towards and following a vessel that hauled its anchor and began trolling (McCord & Lamberth 2009). Whilst conditioning may be an important factor in some shark depredation, it may only be the case for localised populations of sharks in areas where fishing is predictable in time and space, as has been suggested in South Africa (Labinjoh 2014). Other instances of depredation may be purely opportunistic. Further research is needed to verify whether conditioning does happen in the case of depredation, and if so, how prevalent it is in fisheries worldwide.

2.6. Shark depredation in commercial fisheries

2.6.1. Impact of shark depredation vs cetacean depredation

Sharks and cetaceans are responsible for the majority of depredation in commercial pelagic longline fisheries, however much of the existing depredation literature is focused on cetaceans (e.g. Gilman et al. (2006), Hamer et al. (2012) and Söffker et al. (2015)), with shark depredation remaining comparatively understudied. This is surprising given that research has recorded higher levels of depredation by sharks than by cetaceans. For instance, Nishida & Shiba (2004) reported that 62% of depredation in Indian Ocean pelagic longline fisheries was caused by sharks compared to 35% by killer whales *Orcinus orca* and false killer whales *Pseudorca crassidens* and 3% by other predators. Hernandez-Milian et al. (2008) found that shark depredation occurred on four times more longline sets than cetacean depredation. This distinction between shark and cetacean depredation is possible due to different bite mark patterns on the remains of depredated fish, because sharks remove chunks of flesh with clean cuts, leaving semicircular bite-patterns (see Fig. 2-1a,b), whereas cetaceans cause tears and lacerations in the flesh or remove the whole body of the fish, leaving just the head and gill plates (Secchi & Vaske 1998, Gilman et al. 2006, Dalla Rosa & Secchi 2007, Romanov et al. 2007, Hamer et al. 2012).

Although more pelagic longline sets may be affected by sharks overall, cetaceans often depredate more fish per individual set than sharks, for example 56% versus 13%, respectively, during longline sampling in the Indian Ocean (Romanov et al. 2007). Likewise, Dalla Rosa & Secchi (2007) found that the depredation rate per set caused by *O. orca* (45.28%), was significantly higher than that caused by sharks (20.74%). In some cases, *O. orca* have even been reported to remove the entire catch from the longline (Sivasubramaniam 1964, Secchi & Vaske 1998). Additionally, the extent of the damage to fish from shark depredation is generally less compared to when cetaceans depredate hooked fish, and therefore shark damaged catch can sometimes still be marketed (Romanov et al. 2007). Thus, overall, cetacean depredation may cause greater economic losses (Rabearisoa et al. 2012, Romanov et al. 2013), explaining the greater focus on this group in the depredation literature.

The difference in cetacean and shark depredation rates is likely due to the fact that the cetaceans involved in depredation are larger than the sharks and they locate fishing vessels and depredate fish hooked on longlines in cooperative social groups, especially in the case of *O. orca* and *P. crassidens* (Secchi & Vaske 1998, Dalla Rosa & Secchi 2007, Tixier et al. 2010, Peterson et al. 2013, Tixier et al. 2015). Additionally, the highly sensitive auditory system of these cetaceans enables them to detect and locate fishing vessels over larger distances (Thode et al. 2007, Hamer et al. 2012, Wild et al. 2017), and they have learnt to remove only the body of the hooked fish, so that they do not become hooked themselves (Secchi & Vaske 1998, Visser 2000, Gilman et al. 2006, Hamer et al. 2012).

2.6.2. Shark depredation rates

Despite the greater focus on cetacean depredation, a number of studies have quantified shark depredation rates in commercial pelagic longline fisheries, dating back to the 1950s (Table 2-2). These shark depredation rates are commonly reported in two forms, firstly, the percentage of the total number of longline sets which experienced one or more depredation events and secondly, the percentage of the total number of fish hooked that were depredated. This review will focus on the latter metric, as it is more robust indicator of the total impact of depredation on the overall catch. In the Indian Ocean, the mean shark depredation rate was approximately 11% between 1952 and 1963 (Sivasubramaniam 1964), which is similar to values of 10.16% and 10.45% reported for central and western tropical Pacific fisheries, respectively, between 1954 and 1969 (Hirayama 1976). However, these rates are higher than those recorded in more recent studies, for example 2.1% by Lawson (2001) in the Pacific Ocean and 6% by Rabearisoa et al. (2012) in the Indian Ocean. Gilman et al. (2008) conducted a large-scale study of depredation in 12 commercial pelagic longline fisheries from eight countries worldwide, with the highest rate of shark depredation (20%) recorded in the Australian fishery. Across the Indian Ocean, data on depredation was collected from the fishing fleets of multiple countries, following concern about levels of cetacean and shark depredation and recommendations for coordinated data collection expressed at the 1999 meeting of the Indian Ocean Tuna Commission (IOTC) (IOTC 2000). The results from this large-scale data collection program were presented and discussed at a dedicated workshop run by the IOTC in 2007 (IOTC 2007). Shark depredation rates reported from these fisheries were 3.2% in the Reunion Island fishery (Poisson et al. 2007), 9.1% in the Seychelles fishery (Rabearisoa et al. 2007), and 6.0% for longline sampling by former Soviet Union research vessels (Romanov et al. 2007). To improve future data collection on depredation, a resolution was adopted by the IOTC to implement more effective logbook recording, including accurate reporting of the numbers of damaged fish per set and the identity of depredating taxa (Romanov & Bach 2009). A more recent large-scale study in the Indian Ocean recorded similar levels of depredation, with approximately 3% of the catch depredated in the Portuguese pelagic longline fishery (Muñoz-Lechuga et al. 2016).

In the Northwest Atlantic Ocean, MacNeil et al. (2009) reported that 53% of all longline sets experienced depredation over a 14 year period (1992 – 2006), with 3.9% of hooked fish depredated across all sets. However, it must be noted that shark depredation rates may be overestimated in some cases if depredation by cetaceans or other taxa is wrongly classified as shark depredation. For example, MacNeil et al. (2009) assumed that all depredation was caused by sharks, because cetacean depredation was reported to account for <15% of the total depredation in this fishery. Likewise, Romanov et al. (2007) assumed that depredation caused by unidentified predators, which accounted for 44.6% of the total depredation, was likely to be sharks, because if the depredation was caused by cetaceans they would have been seen surfacing near the fishing vessel. Conversely, depredation rates may be underestimated due to fish being completely consumed from the hook, leaving the fishing gear intact but no remains of the fish (Ward et al. 2004). Furthermore, it is important to recognise that the indices and metrics used to quantify depredation in these studies are not really comparable, due to marked differences in data collection standards and protocols, as well as variation between each of the fisheries in question, such as the vessel sizes, longline gear configurations used and the scale of the fishing operations.

While most of these studies grouped together a wide range of different teleost and elasmobranch species that were depredated, to calculate an overall rate of depredation, some studies have recorded depredation rates specifically for key target species, which is possible when partially depredated fish can be identified. For example, 4.7% of swordfish *Xiphias gladius* and 9.3% of bigeye tuna *Thunnus obesus* were damaged by sharks between 1992 and 2000 in the Northwest Atlantic Ocean (Beerkircher et al. 2002). Kobayashi & Yamaguchi (1978) reported losses of up to 15% for Atlantic blue marlin *Makaira nigricans*, and 14.5% and 21% for yellowfin tuna *Thunnus albacares* and *T. obesus*, respectively, in the tropical Pacific in the late 1950s. Furthermore, Hoey & Moore (1999) noted that 68% of the total fish depredated in US pelagic longline fisheries between 1990 and 1997, were either *X. gladius*, *T. obesus* or *T. albacares*. Data on the spatial and seasonal breakdown of depredation rates for key target species have also been collected and reported for Indian Ocean pelagic longline fisheries (Lawson 2001, Nishida & Shiba 2004, Varghese et al. 2008, Muñoz-Lechuga et al. 2016). Some studies have also recorded the percentage of hooked sharks that were depredated by sharks, for example Lawson (2001) reported a value of 0.2%, and Romanov et al. (2007) recorded shark depredation rates for 14 species of shark, which ranged from 0.05% to 0.98%. Higher rates were recorded by MacNeil et al. (2009) for some species, such as 6.4% for the Atlantic sharpnose shark *Rhizoprionodon terraenovae* and 2.4% for the night shark *Carcharhinus signatus*, although a number of other species had depredation rates <1%. In total, Romanov et al. (2007) identified 62 different species of elasmobranch and teleost fish were depredated by sharks during longline operations, out of 150 species caught.

Table 2-2: Shark depredation rates (percentage of hooked fish depredated by sharks) reported in the literature for commercial and recreational fisheries and research fishing, in chronological order. Rows highlighted in grey indicate 'grey' literature in the form of fisheries technical reports or theses, all other rows contain studies published in peer-reviewed scientific journals. CPL = Commercial Pelagic Longline, RPL = Research Pelagic Longline, RD = Research Drumline, RRL = Recreational Rod-and-Line

Mean depredation rate (% hooked fish depredated by sharks)	**Time period**	**Location**	**Fishing sector and gear type**	**Author(s) and year**
11	1955 - 1963	Indian Ocean	CPL	Sivasubramaniam (1964)
10.16 10.45	1954 - 1969	Central Pacific Ocean Western Pacific Ocean	CPL	Hirayama (1976)
15 (*M. nigricans*) 14.5 (*T. obesus*) 21 (*T. albacares*)	1956 - 1959	Pacific Ocean	CPL	Kobayashi & Yamaguchi (1978)
26	1994 - 1995	KwaZulu-Natal, South Africa	RD	Dudley et al. (1998)
4	1990 - 1997	Atlantic Ocean	CPL	Hoey & Moore (1999)
2.1	1995 - 2000	Central and western Pacific Ocean	CPL	Lawson (2001)
4.7 (*X. gladius*) 9.3 (*T. albacares*)	1992 - 2000	Northwest Atlantic Ocean and Gulf of Mexico	CPL	Beerkircher et al. (2002)
6.08 (*Scomberomorus commerson*) 4.7 (*Lethrinus nebulosus*)	1998-1999	Gascoyne region, Western Australia	RRL	Sumner et al. (2002)
13.3 (*S. commerson*) 4.6 (*Plectropomus spp.*)	1999 - 2000	Pilbara region, Western Australia	RRL	Williamson et al. (2006)

Mean depredation rate (% hooked fish depredated by sharks)	**Time period**	**Location**	**Fishing sector and gear type**	**Author(s) and year**
4.4 (*T. albacares*)	1997 - 1999	British Indian Ocean Territory (BIOT), Indian Ocean	CPL	Clark et al. (2007)
20.74	1993 - 1995	South Atlantic Ocean	CPL	Dalla Rosa & Secchi (2007)
20 (Australian fishery) 0.9 – 4.2 (Fijian fishery)	1998 - 2006	Western Pacific Ocean	CPL	Gilman et al. (2007) Gilman et al. (2008)
3.2 (*X. gladius*)	1997 - 2000	Reunion Island, Indian Ocean	CPL	Poisson et al. (2007)
9.1	1995 - 2006	Seychelles, Indian Ocean	CPL	Rabearisoa et al. (2007)
6.0	1961 - 1989	Indian Ocean	RPL	Romanov et al. (2007)
2.15	2001 - 2005	Arabian Sea, Andaman and Nicobar waters	RPL	Varghese et al. (2007)
20 9	1950 - 1954 1995 - 1999	Central Pacific Ocean	CPL	Ward (2007)
3.9	1992 - 2006	Northwest Atlantic Ocean	CPL	MacNeil et al. (2009)
6 (without depredation mitigation devices deployed) 3 (with depredation mitigation devices deployed)	2007 - 2008	Seychelles, Indian Ocean	CPL	Rabearisoa et al. (2012)
3 7 9	2011 2012 2013	Southwest Indian Ocean	CPL	Romanov et al. (2013)
8.4	2013 – 2014	KwaZulu-Natal, South Africa	RRL	Labinjoh (2014)
10.21 (caused by cookie-cutter sharks *Isistius brasiliensis*) 1.49 (caused by large pelagic sharks, e.g. *P. glauca*, *C. longimanus* and *Sphyrna spp.*)	2010 – 2013	Western Pacific Ocean	CPL	Hamer et al. (2015)
3	2011 - 2015	Indian Ocean	CPL	Muñoz-Lechuga et al. (2016)

Mean depredation rate (% hooked fish depredated by sharks)	Time period	Location	Fishing sector and gear type	Author(s) and year
13.7 (demersal fishing from west coast boat ramps) 11.8 (trolling from west coast boat ramps) 11.5 (demersal fishing from Exmouth Gulf boat ramps) 7.2 (trolling from Exmouth Gulf boat ramps)	2015 – 2016	Ningaloo Marine Park and Exmouth Gulf, Western Australia	RRL	Mitchell et al. (2018a)

2.6.3. Variables influencing shark depredation

A range of spatial, temporal, environmental and fishing method variables have been reported to influence depredation in commercial fisheries. For example, in the Northwest Atlantic, the occurrence of depredation was mostly influenced by season and geographic region, and the number of depredation events per set was affected by water temperature and the composition of the catch (MacNeil et al. 2009). In particular, the probability of depredation occurring was higher at colder temperatures, especially when *P. glauca* were more abundant (MacNeil et al. 2009). It would be expected that water temperature affects depredation rates, because of the influence it has on the activity patterns, movements and behaviour of sharks (Carey et al. 1990, Sims et al. 2006, Cartamil et al. 2010, Stevens et al. 2010, DiGirolamo et al. 2012, Schlaff et al. 2014), which is caused by the impact temperature has on their metabolism and energy budget (Fry 1971, Bernal et al. 2012). Sets with longer soak times and at shallower depths also experienced more depredation events (MacNeil et al. 2009). Earlier research by Wathne (1959) recorded higher depredation rates when soak times were longer, and this is likely due to the fact that longer soak times give sharks a greater opportunity to detect and locate the longline, using the odour plume created by bait and injured hooked fish, as well as auditory cues from the fishing vessel. Detailed analysis by Romanov et al. (2007) found that key variables influencing the rate of depredation of tuna by sharks were the start time of the longline set, latitude, number of hooks, gear configuration, year, abundance and ecoregion type. In particular, the number of hooks had a positive effect on the depredation rate of tuna, as did the total abundance and Catch-Per-Unit-Effort (CPUE) of tuna, whereas the gear configuration had a negative effect (Romanov et al. 2007). In the Seychelles longline fishery, the length of the longline had a negative effect on shark depredation rates, and the highest depredation rates occurred in areas which had the highest swordfish CPUE, indicating that sharks aggregate in areas of higher swordfish abundance

(Rabearisoa et al. 2007). Lastly, another factor which could influence depredation rates is the extent to which unwanted fish and offal from processed fish are discarded from the vessel during fishing operations, as this could create a larger odour plume and therefore increase the chances of attracting sharks close to the vessel.

2.6.4. Spatial variation in shark depredation rates

The availability of data on shark depredation rates across broad spatial scales enables comparison between areas and ecosystem types. In particular, research has found a common pattern of higher depredation in tropical latitudes compared to subtropical and temperate waters (Sivasubramaniam 1964, IOTC 2007, Romanov et al. 2007). In the Seychelles fishery, shark depredation rates were found to increase from North to South (Rabearisoa et al. 2007), and Muñoz-Lechuga et al. (2016) reported higher depredation rates in the western portion of the Indian Ocean, compared to in the east. Furthermore, distinct hotspots of depredation have been identified by Romanov et al. (2007) in the Indian Ocean, including the Gulf of Aden, Mozambique Channel, Somali Current and South Equatorial Counter-Current areas. In the Pacific Ocean, Hirayama (1976) reported substantial spatial variation in depredation rates, from the highest rate of 14.45% in the eastern tropical Pacific, to 4.77% in the Coral Sea. Depredation rates in the Western Pacific Ocean varied between 0% and 8.8% in the Exclusive Economic Zones (EEZs) of different island nations, although this may have been partly due to differences in data reporting standards (Lawson 2001). Romanov et al. (2007) analysed variation in shark depredation rates in different 'ecoregions', finding that depredation was highest close to seamounts, and lowest in 'mid-oceanic' waters. Additionally, depredation of hooked fish was reported to be four times higher on longline sets near seamounts compared to in high seas areas (Romanov et al. 2007). The higher depredation rates at these seamounts likely occur because these features create upwelling in open ocean areas, leading to an increase in productivity which in turn supports aggregations of predators, including sharks (Boehlert & Genin 1987, Litvinov 2008, Morato et al. 2010, Barnett et al. 2012). The presence of oceanographic features such as frontal systems and convergence zones may also explain patterns of higher depredation in some areas, because these features also generate higher productivity and support higher concentrations of sharks (Lutjeharms et al. 1985, Queiroz et al. 2012).

2.6.5. Temporal variation in shark depredation rates

Across the studies that have quantified shark depredation rates in commercial fisheries, there is a large degree of inter-annual variation. For example, in a recent study in the Portuguese Indian Ocean longline fishery, depredation rates were found to be significantly different between years, increasing by 0.85% per year from 1.5% in 2011 to 4.9% in 2015 (Muñoz-Lechuga et al. 2016). Similarly, Romanov et al. (2013) recorded an increasing trend in depredation rates, from 3% in 2011, to 7% in 2012 and 9% in 2013. However, in the Northwest Atlantic, there was no increasing or decreasing trend in depredation rates between 1992 and 2006 (MacNeil et al. 2009). Seasonal variation in depredation rates has also been reported in a number of fisheries, such as the artisanal fishery in Kenya, where shark depredation was reported to be highest in February and March, when the catch rate of sharks also reached its peak (Ndegwa & Makogola 2007). MacNeil et al. (2009) recorded markedly higher depredation rates in summer (May – September), compared to in winter. However, Dalla Rosa & Secchi (2007) found that whilst *O. orca* depredation occurred predominantly between June and October, shark depredation occurred all year round. Seasonal and inter-annual changes in depredation rates in open ocean areas may be affected by large scale phenomena such as the Indian Ocean monsoon and the El Niño-Southern Oscillation, because these events can substantially change the temperature profile and productivity levels in certain areas (Barber & Chavez 1983, Sharp & McLain 1993, Barber et al. 1996, Veldhuis et al. 1997), which can in turn affect the distribution and diet of pelagic sharks (Preti et al. 2004, Ketchum et al. 2014, White et al. 2015). The depth of the thermocline can have an impact on the depth distribution and vertical movements of pelagic sharks (Carey et al. 1990, Holts & Bedford 1993, Stevens et al. 2010, Ketchum et al. 2014), therefore, seasonal change in thermocline depth could influence depredation rates in pelagic longline fisheries, depending on the depth at which longlines are set.

2.6.6. Shark species responsible for depredation

As well as quantifying shark depredation rates, past research has identified an extensive range of shark species responsible for depredation in commercial fisheries (Table 2-3). *C. longimanus* were observed depredating hooked tuna close to the surface as longlines were hauled in within the Gulf of Mexico (Bullis 1955, Backus et al. 1956). Additionally, *I. oxyrinchus* and *C. falciformis* were reported to consume hooked fish, although at greater depths (Bullis 1955, Backus et al. 1956), suggesting that *C. longimanus* were more commonly distributed in the upper portion of the water column in this region, compared to *I. oxyrinchus* and *C. falciformis*. Behavioural variation could also explain this difference in depredation patterns between these species, as *C. longimanus* were reported to be bolder and more likely than the other species to investigate baits and the fishing vessels (Backus et al. 1956). Copper sharks *Carcharhinus brachyurus* and *C. longimanus* were observed by Sivasubramaniam (1963), (1964) to be common depredating species in the Atlantic, Pacific and Indian Oceans, although more recently it has been theorised that *P. glauca* are the main species responsible for depredation in commercial pelagic longline fisheries (MacNeil et al. 2009), due to their high abundance compared to other pelagic species (Nakano & Stevens 2009), and scavenging habits (Ward et al. 2004). Furthermore, MacNeil et al. (2009) recorded that higher catch rates of *P. glauca* in Northwest Atlantic longline fisheries were correlated with higher depredation levels.

In the Mediterranean Sea, bluntnose sixgill sharks *Hexanchus griseus* have been known to depredate *X. gladius* hooked on commercial pelagic longlines, as evidenced by sharks that have been caught in the process of consuming hooked *X. gladius*, as well as those which were found to have *X. gladius* in their stomach contents (Celona et al. 2005). Romanov et al. (2007) also identified possible depredating shark species based on their stomach contents, recording 18 different species from four families (Alopiidae, Carcharhinidae, Lamnidae and Sphyrnidae) with recently consumed tuna in their stomachs. However, it is not certain that the fish present in the stomachs of these sharks was consumed via depredation, as it may also have been obtained through recent natural predation events on free-swimming fish. Lastly, cookie-cutter sharks *Isistius* spp. have been reported depredating hooked fish (Ariz et al. 2007, Gilman et al. 2007, Hamer et al. 2015, Muñoz-Lechuga et al. 2016, Niella et al. 2018), which was distinguished by the distinctive circular bite-mark pattern they create, although the damage from this species was minimal compared to larger shark species.

Table 2-3: Shark species responsible for depredation, as reported in the literature for commercial and recreational fisheries and research fishing, in chronological order. Rows highlighted in grey indicate 'grey' literature in the form of fisheries technical reports or theses, all other rows contain studies published in peer-reviewed scientific journals. CDL = Commercial Demersal Longline, CPL = Commercial Pelagic Longline, RD = Research Drumline, ResRL = Research Rod-and-Line, RPL = Research Pelagic Longline, RDL = Research Demersal Longline, RRL = Recreational Rod-and-Line

Shark species responsible for depredation (confirmed or suspected)	**Time period**	**Location**	**Fishing sector and gear type**	**Author(s) and year**
C. longimanus (confirmed)	1954 - 1955	Gulf of Mexico and Caribbean Sea	RPL	Bullis (1955)
C. longimanus (confirmed), *C. falciformis* (confirmed), *I. oxyrinchus* (confirmed)	1953 – 1955	Northwest Atlantic Ocean, Gulf of Mexico and Caribbean Sea	RPL	Backus et al. (1956)
C. longimanus (suspected), *C. brachyurus* (suspected)	1955 – 1963	Indian, Atlantic and Pacific Oceans	CPL	Sivasubramaniam (1963)
Notorynchus cepedianus (confirmed)	1982 – 1989	San Francisco Bay, USA, South Africa and Namibia	RDL, ResRL	Ebert (1991)
C. leucas (confirmed)	1994 – 1995	KwaZulu-Natal, South Africa	RD	Dudley et al. (1998)

Shark species responsible for depredation (confirmed or suspected)	**Time period**	**Location**	**Fishing sector and gear type**	**Author(s) and year**
P. glauca (confirmed), *I. oxyrinchus* (confirmed)	1987 – 1991	South Atlantic Ocean	CPL	Secchi & Vaske (1998)
P. glauca (suspected)	1990 – 2002	Pacific Ocean	CPL	Ward et al. (2004)
H. griseus (confirmed)	2000 – 2003	Sicily, Mediterranean Sea	CPL	Celona et al. (2005)
Isistius spp. (confirmed)	2005	South-western Indian Ocean	CPL	Ariz et al. (2007)
I. oxyrinchus (suspected), *C. longimanus* (suspected), *I. brasiliensis* (suspected)	1998 - 2006	Worldwide	CPL	Gilman et al. (2007)
Alopias superciliosus (suspected), *Alopias vulpinus* (suspected), *Carcharhinus albimarginatus* (suspected), *Carcharhinus brevipinna* (suspected), *C. falciformis* (suspected), *C. leucas* (suspected), *Carcharhinus limbatus* (suspected), *C. longimanus* (suspected), *Carcharhinus melanopterus* (suspected), *Carcharhinus plumbeus* (suspected), *Carcharhinus sorrah* (suspected), *Galeocerdo cuvier* (suspected), *P. glauca* (suspected), *I. oxyrinchus* (suspected), *Lamna nasus* (suspected), *S. lewini* (suspected), *Sphyrna mokarran* (suspected), *Sphyrna zygaena* (suspected)	1961 - 1989	Indian Ocean	RPL	Romanov et al. (2007)
Somniosus pacificus (confirmed), *L. nasus* (confirmed)	2006	Southeast Pacific Ocean	CDL	Moreno et al. (2008)
P. glauca (suspected), *I. oxyrinchus* (suspected)	1992 – 2006	Northwest Atlantic Ocean	CPL	MacNeil et al. (2009)
C. leucas (suspected)	2009	Breede River, South Africa	RRL	McCord & Lamberth (2009)
Carcharhinus galapagensis (confirmed)		Lord Howe Island, Australia	RRL	Figueira & Hunt (2012)
				Rees et al. (2018)

Shark species responsible for depredation (confirmed or suspected)	**Time period**	**Location**	**Fishing sector and gear type**	**Author(s) and year**
C. leucas (confirmed), *G. cuvier* (confirmed)	1998 and 2010	Seychelles, Indian Ocean and New Caledonia, Pacific Ocean	RD	Clua et al. (2014)
Carcharhinus obscurus (confirmed), *C. limbatus* (confirmed), *C. brevipinna* (confirmed), *S. lewini* (confirmed)	2013 – 2014	KwaZulu-Natal, South Africa	RRL	Labinjoh (2014)
I. brasiliensis (confirmed), *C. longimanus* (suspected), *P. glauca* (suspected)	2010 – 2013	Western Pacific Ocean	CPL	Hamer et al. (2015)
C. longimanus (confirmed)	2011 – 2014	The Bahamas, Atlantic Ocean	RRL	Madigan et al. (2015)
C. leucas (confirmed), *G. cuvier* (confirmed), *S. mokarran* (confirmed), *Carcharhinus perezi* (confirmed)	2012	The Bahamas, Atlantic Ocean	RPL	O'Shea et al. (2015)
N. cepedianus (confirmed)	1970 - 2001	San Francisco Bay, USA	RDL, ResRL	Russo (2015)
P. glauca (confirmed), *I. oxyrinchus* (confirmed), *L. nasus* (confirmed), *I. brasiliensis* (confirmed)	2011 – 2015	Indian Ocean	CPL	Muñoz-Lechuga et al. (2016)
Isistius spp. (confirmed)	2017	Southwest Atlantic Ocean		Niella et al. (2018)
C. plumbeus (confirmed)	2012 - 2015	Western Gulf of Mexico	RPL	Streich et al. (2018)
Somniosus microcephalus (confirmed)	2011 - 2013	Cumberland Sound, Canada	RDL	Grant et al. (in review)

The temporal and spatial variation in the shark species responsible for depredation is likely related to the spatial and temporal overlap of fishing effort with the distribution and abundance of these species. For example, porbeagle sharks *Lamna nasus* have been reported to depredate hooked fish in the Chilean longline fishery that operates in the southeastern Pacific Ocean at latitudes greater than 47˚S (Moreno et al. 2008), but this species would not cause depredation in tropical waters, because its distribution is confined to temperate and subpolar regions (Compagno 1984, Francis et al. 2008). Similarly, *C. longimanus* and *C. falciformis*, which are only distributed in tropical and subtropical waters (Compagno 1984, Bonfil 2008, Bonfil et al. 2008), would not be responsible for depredation in temperate regions. Additionally, some of the key shark species that are reported to be responsible for depredation are highly migratory, pelagic species, such as *P.*

glauca and *C. longimanus*. Therefore, the extent to which fishing activity overlaps with the presence of these species will vary depending on their migratory movement patterns. For example, in the north Atlantic, *P. glauca* undertake a circular, clockwise migration, and move from lower to higher latitudes in the summer months (Stevens 1990, Queiroz et al. 2005, Nakano & Stevens 2009), therefore, depredation by this species may be high at certain times of year and in certain regions, whilst being negligible in others.

The fishing methods used, including the gear type, depth, soak time and the overall scale of the fishing operation, will also influence which species of sharks are responsible for depredation. For example, longlines set in deeper water may lead to a lower proportion of depredation by certain species, due to it being beyond their depth distribution. Additionally, the depredating shark species are likely to be markedly different in demersal vs pelagic longline fisheries, as the former will attract predominantly demersal sharks such as Pacific sleeper sharks *Somniosus pacificus*, whereas the latter will likely be depredated by pelagic sharks like *P. glauca* and *I. oxyrinchus*. Likewise, the soak time of the longline set is likely to be important because shorter soak times would favour more active, faster swimming shark species such as *I. oxyrinchus*, *C. longimanus* and *P. glauca*, because they can cover a greater area in the open ocean searching for prey, and thus would be able to locate a longline quicker than a slower moving species such as *H. griseus*. The sensory capability of different shark species, particularly the auditory and olfactory sensitivity, would also influence the likelihood of them detecting longline fishing operations in the open ocean. In particular, the apparent ability of a *C. falciformis* to detect and navigate towards a FAD which was 1.2 km away (Filmalter et al. 2015), indicates the highly developed sensory abilities of this pelagic species. Lastly, the target species of the fishery will also be important as, for example, *P. glauca* and *C. falciformis* are known to associate with tuna schools (Au 1991, Bromhead et al. 2005, Bonfil 2008), making depredation by these species in fisheries targeting tuna more likely. Overall, it is clear from the existing literature that *P. glauca*, *I. oxyrinchus* and *C. longimanus* are the main species responsible for depredation in a number of commercial fisheries around the world. This is likely due to their broad geographical distribution and relatively high abundance compared to other pelagic shark species (Nakano & Seki 2003, Aires-da-Silva et al. 2008, Bonfil et al. 2008, Stevens 2008, Camhi et al. 2009, Nakano & Stevens 2009), as well as their wide ranging vertical and horizontal movements (Kohler et al. 2002, Camhi et al. 2009, Stevens et al. 2010, Block et al. 2011, Musyl et al. 2011, Howey-Jordan et al. 2013). The widespread occurrence of shark depredation in commercial pelagic longline fisheries worldwide, highlights its importance as a fisheries management issue and the need for extensive monitoring and research.

2.7. Shark depredation in recreational fisheries

Compared to commercial fisheries, very little research has been conducted on shark depredation in recreational fisheries, likely because commercial longline fisheries are much larger in scale, have greater economic importance, and have more established methods for data collection, such as logbooks and fisheries observers. Conversely, recreational fisheries are usually concentrated in relatively smaller areas and there is greater difficulty in collecting data from individual fishers. A study by Madigan et al. (2015) covered anecdotally reported depredation by *C. longimanus* in a recreational fishery in The Bahamas, in the context of how feeding on recreationally caught fish may contribute to their diet. Galapagos sharks *Carcharhinus galapagensis* have also been observed depredating hooked fish in a recreational fishery at Lord Howe Island, Australia (Figueira & Hunt 2012, Rees et al. 2018), although no data exists for the rate of depredation. Shark depredation has also been reported to occur in recreational fisheries in Kenya (Ndegwa & Makogola 2007), however there is also no information on depredation rates in this fishery. In terms of quantitative research, an average shark depredation rate of 8.4% was recorded in a charter fishery operating on the Protea Banks in KwaZulu-Natal, South Africa (Table 2-2) (Labinjoh 2014). When separated into different fishing methods, the depredation rate was recorded to be 18.6% when targeting pelagic species and 1.9% when targeting reef species (Labinjoh 2014). Four shark species were reported to be responsible for depredation, including dusky *Carcharhinus obscurus*, blacktip *Carcharhinus limbatus* and spinner *Carcharhinus brevipinna* sharks, and *S. lewini* (Labinjoh 2014). However, the small spatial and temporal scope of this study, as well as a low sample size, must be noted when considering these results.

In north-west Western Australia, estimated values for the number of fish retained, released and depredated by sharks were collected and separated by species, in two 12-month recreational fishing surveys conducted in the Gascoyne and Pilbara regions, between 1998 and 2000 (Sumner et al. 2002, Williamson et al. 2006). The estimated rates of depredation ranged widely by species, with higher rates occurring for narrow-barred Spanish mackerel *Scomberomorus commerson* (6.08%) and spangled emperor *Lethrinus nebulosus* (4.7%) in the Gascoyne region, and *S. commerson* (13.3%) and coral trout *Plectropomus* spp. (5%) in the Pilbara region (Sumner et al. 2002, Williamson et al. 2006). Whilst these species experienced the highest levels of depredation in these regions, most other species had depredation rates of <1% for the Gascoyne and <2% for the Pilbara (Sumner et al. 2002, Williamson et al. 2006). The higher rates of depredation reported for *S. commerson*, *L. nebulosus* and *Plectropomus spp.* could also reflect the fact that fishers commonly targeted these enigmatic species. Therefore, it would be more memorable and have more of an impact on the fisher if they were depredated, compared to less sought-after species. Additionally, it should be noted that the depredation rates in these two studies were estimated, based on extrapolation, and that there may have been inaccuracies in species identification.

To collect more accurate and reliable data specifically on the frequency and spatial variation of shark depredation in the Gascoyne region, a recent large-scale survey was conducted in the Ningaloo Marine Park and Exmouth Gulf (Mitchell et al. 2018a). This study reported a mean shark depredation rate of 13.7% for demersal fishing and 11.8% for trolling in the Ningaloo Marine Park, compared to 11.5% for demersal fishing and 7.2% for trolling in Exmouth Gulf (Mitchell et al. 2018a). Furthermore, substantial spatial variation in depredation rate occurred, with higher depredation in areas that received greater fishing pressure (Mitchell et al. 2018a). Whilst a small amount of quantitative research has been conducted on shark depredation in Australia and South Africa, it is clear that to broaden our understanding of shark depredation in recreational fisheries globally, and to quantify its impact, a large amount of future research is needed.

2.8. Shark depredation during research fishing

Shark depredation has also been recorded in a number of studies where fishing gear was deployed for research purposes, for example in the Gulf of Mexico, where video cameras mounted on vertical longlines recorded depredation on 19% of deployments, with sandbar sharks *Carcharhinus plumbeus* consuming hooked red snapper *Lutjanus campechanus* (Streich et al. 2018). Additionally, Greenland sharks *Somniosus microcephalus* have been observed depredating hooked Greenland halibut *Reinhardtius hippoglossoides* during experimental demersal longline fishing in Cumberland Sound, Canada (Grant et al. in review). Depredation of hooked sharks by other, larger sharks has also been reported, notably depredation of leopard sharks *Triakis semifasciata* and brown smoothhounds *Mustelus henlei* by broadnose sevengill sharks *Notorynchus cepedianus*, which occurred during demersal longline sampling in San Francisco Bay, USA (Russo 2015). In total, 12.8% of demersal longline sets in this area experienced depredation, with two particular sets recording losses of 88% and 93% of sharks hooked (Russo 2015). Ebert (1991) also observed depredation of sharks and rays caught on demersal longlines in this area, and one instance where a rod-and-line caught *N. cepedianus* was depredated by a conspecific.

During longline sampling off South Eleuthera, in The Bahamas, video footage of four sharks of different species attempting to depredate a hooked Caribbean reef shark *Carcharhinus perezi*, was recorded (O'Shea et al. 2015). Competitive behaviour was observed between the tiger shark *Galeocerdo cuvier*, great hammerhead shark *Sphyrna mokarran*, *C. leucas* and *C. perezi*, and only the *G. cuvier* and *C. leucas* actually fed on the hooked shark, because they were able to control the resource and prevent the other sharks from feeding (O'Shea et al. 2015). Furthermore, Clua et al. (2014), reported not only a single depredation event but a process of 'cumulative' depredation, where a grey reef shark *Carcharhinus amblyrhynchos* was consumed by a *C. leucas*, which was then itself depredated by a larger *G. cuvier*, on drumlines deployed in the Seychelles and New Caledonia. Depredation also occurred on drumlines deployed in KwaZulu-Natal, South Africa, which were tested as part of a shark control program (Dudley et al. 1998). Out of 76 *C. obscurus* caught on these drumlines, 26% (20 individuals) were subsequently depredated (Table 2-2) by other, larger sharks, particularly *C. leucas* (Dudley et al. 1998). Overall, the nature of these depredation events observed during research sampling highlights the opportunistic behaviour of the sharks involved.

2.9. Impacts of shark depredation

2.9.1. Biological impacts

Shark depredation may cause a number of biological impacts in both commercial and recreational fisheries, affecting both target fish species and the sharks causing depredation. The populations of target fish species may be impacted, as the overall mortality will likely be higher in fisheries where depredation occurs. This is because fishers often aim to catch a particular volume of fish based on their allowed quota, daily bag limit or hold size. Therefore in order to reach the quota, more fish will be hooked overall to compensate for those depredated by sharks (Gilman et al. 2006). This extra mortality may not be recorded in commercial fisheries logbooks, or accounted for by measures such as recreational daily bag limits. This is especially the case if the shark consumes the whole fish, leaving no sign of its original presence, which is a form of “pre-catch loss” (Gilman et al. 2013). By not incorporating this extra mortality, fisheries management measures may be less effective. Depredation could also be a substantial problem for catch-and-release recreational fisheries, especially those which tag certain species (e.g. protected species), because fish that would otherwise be caught and released alive are instead depredated by sharks.

In most cases, when sharks depredate hooked fish in commercial longline fisheries, they will consume part of the fish and then swim away, however, sometimes, the shark may itself become hooked or entangled in the line in the process of depredating the hooked fish. This may then lead to the shark being retrieved to the fishing vessel and retained. This could therefore increase the level of shark bycatch in some commercial longline fisheries, which is an important issue because high bycatch has already been reported to cause unsustainable catches and population declines of some shark species (Gilman et al. 2007, Dulvy et al. 2008, Mandelman et al. 2008, Worm et al. 2013, Cortés et al. 2015), which are retained due to the value of their fins and meat (Francis et al. 2001, Clarke et al. 2006). However, even if sharks are released alive, they may still suffer post-release mortality due to the physiological stress and injury caused by being hooked for long periods and hauled on to the fishing vessel (Skomal 2007, Campana et al. 2009, Musyl et al. 2011, Ellis et al. 2017). Further mortality may also occur from deliberate killing or wounding of sharks, to prevent future depredation and the resulting damage to fish and gear (Gilman et al. 2006).

Indeed, human-wildlife conflict already occurs in certain US recreational fisheries due to depredation by goliath grouper *Epinephelus itajara* (Shideler et al. 2015), California sea lions *Zalophus californianus* (Cook et al. 2015) and common bottlenose dolphins *Tursiops truncatus* (Powell & Wells 2011). There is the possibility that similar conflicts could occur in the future due to shark depredation.

In recreational fisheries, rather than being retrieved to the fishing vessel, sharks that get hooked in the process of depredating a hooked fish often snap off or bite through the fishing line, potentially causing hooks and line to be retained in their jaw and digestive system. These retained hooks can lead to a range of sub-lethal effects, such as tissue necrosis and abscesses in the jaw (Bansemer & Bennett 2010), as well as serious internal injuries including perforations to the gastric wall and liver and resulting infections (Borucinska et al. 2001, Borucinska et al. 2002). These impacts may be widespread, for example, Bansemer & Bennett (2010) observed a high prevalence of retained recreational fishing gear in grey nurse sharks *Carcharias taurus* in New South Wales, Australia, with 113 out of 673 sharks (16.79%) having visible hooks present and 3.4% of individuals showing signs of internal hooking, where fishing line was observed to be trailing from the mouth, gills or cloaca. These hook injuries may therefore cause long-term reduction in fitness of sharks through disease, reduced capacity for feeding and reduced reproductive output, eventually leading to death (Borucinska et al. 2001, Borucinska et al. 2002, Bansemer & Bennett 2010, Whitney et al. 2012, Adams et al. 2015).

2.9.2. Behavioural impacts

The availability of hooked fish to depredate may lead to changes in the behaviour and movement patterns of sharks (Gilman et al. 2008), especially in recreational fisheries, where fishing effort can be concentrated over small spatial scales. This may occur in a similar pattern to where sharks are provisioned for ecotourism activities. For example, Clua et al. (2010) observed a reduction in mobility, increased residency and greater levels of aggression in *N. acutidens* over a long-term (44 month) study, as a result of feeding by divers. Likewise, Clarke et al. (2011) recorded *C. falciformis* spending more time close to a reef site where feeding occurred regularly, and research has shown that provisioning can temporarily provide a substantial portion of the energy requirement of *C. leucas* in Fiji (Brunnschweiler et al. 2018), as well as leading to a change in their relative abundance and movement patterns (Brunnschweiler & Baensch 2011, Brunnschweiler & Barnett 2013). The use of accelerometers has identified substantial changes in the activity patterns and vertical movements of individual *C. carcharias* in the vicinity of cage-diving operations in South Australia (Huveneers et al. 2018a). Furthermore, a study on the diet and movement patterns of *C. longimanus* suggests the possibility that the presence of large fish to opportunistically feed on, including those depredated in a recreational fishery and those provided by dive operators, may be influencing recurrent seasonal movements of these sharks to The Bahamas (Madigan et al. 2015). However, it is also possible that depredation may just offer an attractive and occasional supplement to the diet of these mobile predators, as observed by Maljkovic & Cote (2011) for sharks provisioned by divers, which showed different stable isotope signatures compared to non-fed sharks, but little difference in both movement and residency patterns for these two groups. Satellite-tagged *G. cuvier* also showed no changes in space use or site fidelity as a result of provisioning in The Bahamas (Hammerschlag et al. 2012a). The potential impacts of provisioning on sharks are further discussed in detail in a recent review by Patroni et al. (2018).

Another potential behavioural impact of shark depredation could be the occurrence of intra- and inter-specific competition when multiple sharks are attempting to depredate a hooked fish. An example of this was recorded by O'Shea et al. (2015), where four sharks of different species competed to access and feed on a hooked *C. perezi*. The *G. cuvier* and *C. leucas* appeared to outcompete the *S. mokarran* and *C. perezi* by controlling the resource and deterring them from feeding (O'Shea et al. 2015). Similar occurrences of competition could occur in commercial and recreational fisheries, and in these circumstances, it is possible that sharks may bite and injure each other whilst competing to depredate the hooked fish. Overall, it is clear that more research is necessary to understand and determine the extent of short- and long-term biological and behavioural impacts that are occurring as a result of shark depredation in fisheries.

2.9.3. Economic impacts

In both recreational and commercial fisheries, loss of target fish and gear (e.g. hooks, line, sinkers and lures) due to shark depredation can result in substantial financial costs. For example, losses of gear in a charter fishery in KwaZulu-Natal, South Africa, were estimated to be on average US$22 per trip, which represented 8% of daily earnings (Labinjoh 2014). In commercial fisheries, costs can be far higher, reaching hundreds of dollars per pelagic longline set, and even over US$1,000 per set in the Chilean *X. gladius* fishery (Gilman et al. 2007). The majority of this cost is from valuable target species that are lost or damaged, such as large tuna and *X. gladius*, with the cost of lost gear generally less than US$100 per set (Gilman et al. 2007). Fish that have been partially depredated are often not marketable and are therefore discarded (Gilman et al. 2017). In pelagic longline fisheries in the Seychelles, costs of US$419 per 1,000 hooks resulted from depredation, causing a cumulative loss of US$1,232,440 between 1995 and 2006 in this fishery, although it should be noted that this value represented the combined cost of both shark and cetacean depredation (IOTC 2007). In addition, indirect costs occur, such as time spent removing sharks and repairing and resetting pelagic longline gear, and occupation of hooks by sharks preventing capture of target species (Gilman et al. 2008). In recreational fisheries, extra fuel usage resulting from longer trips and frequent movement between fishing spots to avoid sharks, may be another indirect cost.

Globally, the cumulative ecological and economic impacts of shark depredation in both commercial and recreational fisheries, are substantial. Additionally, its occurrence may increase worldwide if fishing effort continues to rise (Anticamara et al. 2011) and natural prey populations decline (Srinivasan et al. 2010, Froese et al. 2012), due to the increased potential for learned behaviour in sharks through repeated interactions with fishing vessels. This pattern has already been recorded for cetacean depredation in both recreational (Powell & Wells 2011) and commercial (Read 2008, Clark & Agnew 2010, Peterson et al. 2013) fisheries. However, there is also a possibility that depredation may decrease in future, due to the continuation of declines already seen in shark populations as a result of overfishing (Ward & Myers 2005, Ferretti et al. 2010). This was theorised by Ward (2007) to explain the decrease from an estimated depredation rate of 20% in Pacific pelagic longline fisheries in the 1950s, to 9% in the 1990s. Regardless of the future trend, further research is needed to monitor changes in commercial and recreational fisheries worldwide, as well as assessing ecological and economic impacts of depredation in these fisheries.

2.10. Measures for reducing shark depredation

2.10.1. Fishing methods

Due to these significant impacts, there is a vital need for effective mitigation measures to reduce shark depredation. Pelagic longline fisheries can employ a range of tactics to minimise depredation, foremost of which being careful selection of fishing sites to avoid known areas of high shark abundance, such as topographic (e.g. seamounts) or oceanographic (e.g. thermal fronts) features (Gilman et al. 2007, IOTC 2007). This is a practice already followed in a number of fisheries, such as the Australian, Fijian and Japanese pelagic longline fisheries (Gilman et al. 2007, 2008). Avoiding temperature ranges where higher catch rates of sharks occur, such as between 16 ˚C and 17 ˚C for *P. glauca* (Bigelow et al. 1999, Carvalho et al. 2011, Mitchell et al. 2014), could also reduce depredation. This strategy has been successfully used to avoid bycatch of sea turtles (Howell et al. 2008), and recent advances in predictive modelling based on satellite telemetry and fisheries data, have enabled the development of near real-time management approaches to reduce interactions between fisheries and protected species (Hazen et al. 2018). This system shows promise for reducing shark bycatch and could also be adopted to mitigate shark depredation. However, it must be considered that pelagic sharks such as *P. glauca, I. oxyrinchus* and *C. falciformis* are often present around tuna schools (Au 1991, Bromhead et al. 2005, Watson et al. 2009), so avoiding areas where these sharks occur may have a negative impact on fishing operations by reducing the overall catch rate of target species.

Modifying fishing methods may also reduce depredation rates (Mandelman et al. 2008, Kumar et al. 2016), i.e. shorter soak times and deeper setting of pelagic longlines led to lower depredation rates in Atlantic fisheries (MacNeil et al. 2009). Likewise, Romanov et al. (2007) reported that increasing longline soak time by one hour led to the occurrence of cetacean depredation on tuna being four times higher, although depredation of billfish by sharks was only 1.09 times higher. Limiting the discarding of unwanted fish and offal generated by fish processing whilst conducting longline fishing, could also help to reduce depredation rates, because it would decrease the chances of attracting sharks to the vessel. Furthermore, conducting fishing operations only during daylight hours may mitigate depredation because some shark species have been recorded to be more active during crepuscular and nocturnal periods (Sundström et al. 2001, Hammerschlag et al. 2017), and fishers in Pacific pelagic longline fisheries anecdotally report higher depredation rates at night (Ward 2007). If operating at night is unavoidable, then not using lightsticks could mitigate losses, because they may be a visual cue attracting sharks to fishing gear. Indeed, pelagic longline fisheries in Australia already avoid the use of lightsticks to reduce catch rates of sharks (Gilman et al. 2008). Commercial line fisheries targeting demersal species could potentially switch to using traps, such as those used in Australia (Whitelaw et al. 1991, Stewart & Ferrell 2003) and the USA (Eklund & Targett 1991, Garrison et al. 2004), to prevent sharks from depredating the catch. This would, however, depend on the species being targeted and the depth and benthic topography of the area being fished.

In recreational fisheries, regular movement between fishing spots may reduce the chance of sharks locating a fishing vessel in the first place, and relocating to another fishing spot after a fish is depredated will minimise losses. The choice of certain fishing gear can also reduce depredation rate, for example using jigs and lures instead of bait, using single instead of multiple hooks on each line to avoid having multiple fish struggling on the line at once, and avoiding the use of burley. In addition, the use of stronger fishing line would allow for faster reeling of fish to the fishing vessel, thus reducing the timeframe for depredation to occur, and electric reels could be used when fishing at depths of >50 m to further reduce the time between hooking and retrieving a fish (Exmouth Game Fishing Club, pers. comm). The adoption of these modified fishing techniques would need to be trialled in relation to the specific conditions of each recreational fishery where they are applied, to ensure that catch rates and fisher satisfaction are high.

2.10.2. Shark deterrents

A range of deterrents have been designed and tested in an attempt to reduce both depredation and bycatch of sharks. Firstly, physical deterrents have been developed, which attach to the branchlines of longline gear and then descend to cover the hooked fish, either due to the fish tugging on the branchline when it takes the bait, or when the longline is being hauled (Moreno et al. 2008, Goetz et al. 2011, Rabearisoa et al. 2012, Hamer et al. 2015). In particular, depredation mitigation devices known as 'spiders' and 'socks' were tested in the Seychelles longline fishery, and led to a reduction in shark depredation from 6% to 3% (Rabearisoa et al. 2012). Likewise, the 'net sleeve' device tested by Moreno et al. (2008) in demersal longline fisheries reduced depredation by *S. pacificus* and *L. nasus*. These devices were designed to work by covering and protecting the hooked fish, so that the shark is physically prevented from accessing it, however they sometimes failed to trigger, caused tangles in the longline, increased hauling time, and were not totally effective in reducing shark depredation (Rabearisoa et al. 2012, Hamer et al. 2015).

Acoustic and chemical deterrents have also been tested on sharks, with some degree of success (Myrberg et al. 1978, Clark & George 1979, Klimley & Myrberg 1979, Clark 1983, Nelson 1983, Nelson & Strong 1996, Stroud et al. 2014, Hart & Collin 2015). However, there are few acoustic deterrents that have been found to be effective in deterring sharks and, at least for longline sets where sounds may be presented over long periods of time, these types of deterrents are likely to be unsuccessful in the long-term due to habituation (Myrberg et al. 1969, 1978). Chemical deterrents, such as 'paradaxin' derived from the moses sole *Pardachirus marmoratus*, sodium lauryl sulphate and semiochemical compounds, have been effective at repelling sharks under certain circumstances (Smith 1991, Sisneros & Nelson 2001, Stroud et al. 2014). However, such compounds may be impractical for fisheries use, due to the potentially harmful effects they may have on target fish and non-target marine organisms, and because of rapid dilution in open water, especially in the presence of currents (Baldridge 1990). A recent study combining the use of visual and auditory stimuli in the form of strobe lights and loud, irregular sounds, recorded a reduction in the number of times that *H. portusjacksoni* and epaulette sharks *Hemiscyllium ocellatum* took bait in a laboratory setting (Ryan et al. 2018). The same combination of deterrents also led to a decrease in the time that *C. carcharias* spent in close proximity to baits, however it was concluded that this configuration would not represent an effective deterrent for reducing *C. carcharias* interactions (Ryan et al. 2018).

The electrosensory system of sharks has been found to be particularly sensitive to electric fields (Murray 1962, Kalmijn 1966, 1971, 1972) and electric deterrent devices (producing strong electric fields) may represent an effective strategy for repelling sharks from fishing gear, because the target teleost species lack an electrosensory system (O'Connell et al. 2014, Collin et al. 2015, Collin 2017). Devices such as the SharkPOD and SharkShield use a battery to generate a strong electric field in seawater, which has been shown to significantly reduce the frequency of *C. carcharias* attacks on bait (Smit & Peddemors 2003, Kempster et al. 2016) and substantially fewer occurrences of breaching and surface investigation of seal decoys (Huveneers et al. 2013). However, the effectiveness of these and other devices can be highly variable depending on the shark species tested (Hart & Collin 2015) and they may not be suitable for use in fisheries due to their high cost, large size and limited battery life. Further research is needed to create small, cost effective and energy efficient devices that could be easily deployed on fishing gear but still protect the target species from shark depredation (Jordan et al. 2013).

Passive deterrents, such as ceramic or rare-earth type magnets, are believed to stimulate the electrosensory system of sharks through electromagnetic induction (Kalmijn 1982, Rigg et al. 2009, O'Connell et al. 2014), creating electrical potentials far stronger than would naturally be experienced by sharks (Hart & Collin 2015). They may therefore have potential as deterrents when mounted close to the hooks of pelagic longline gear (Kaimmer & Stoner 2008, Brill et al. 2009, Tallack & Mandelman 2009, O'Connell et al. 2011, 2014). Indeed, research has recorded reduced catch rates of sharks when magnets were deployed close to hooks, although the effectiveness varied widely depending on the shark species involved (Brill et al. 2009, Tallack & Mandelman 2009, Robbins et al. 2011, O'Connell et al. 2014). Similarly, the use of electropositive lanthanide metals (e.g. cerium, neodymium) as a passive deterrent has had mixed success (Brill et al. 2009, Robbins et al. 2011, Hutchinson et al. 2012, Godin et al. 2013). In addition to this species-specific variation, the effectiveness of electropositive metals and magnets as deterrents may be reduced when multiple sharks are competing for food (Brill et al. 2009, Jordan et al. 2011, Robbins et al. 2011). The cost of lanthanide metals, combined with their fast breakdown in seawater, would also limit their viability as a deterrent in commercial fisheries (McCutcheon & Kajiura 2013, Hart & Collin 2015).

Overall, it is likely that a combination of different mitigation strategies will be needed to effectively reduce depredation by sharks, rather than using either modified fishing strategies or deterrents on their own. For example, fisheries managers could assist longline fisheries in reducing depredation by developing real-time predictive models that identify the probability of shark depredation events occurring based on the known distribution of key depredating shark species and the prevailing environmental conditions, particularly temperature and productivity levels, whilst also providing fishing operators with a suite of deterrents that target multiple sensory systems of sharks and can be deployed at the same time. This adaptive and flexible strategy would therefore increase the likelihood of mitigating depredation because it reduces the chance of encountering sharks and presents them with a multi-sensory deterrent if they do attempt to depredate hooked fish. Such a deterrent system would be less prone to habituation of sharks and would likely be more effective at deterring a wider range of shark species, which have different sensory abilities. Further work is therefore required to design such an integrated strategy, which would benefit fishers, managers, target species and sharks through reduced depredation.

2.11. Current research gaps and approaches for addressing them

2.11.1. Quantifying shark depredation rates and factors influencing its occurrence

To build on the existing shark depredation research reviewed, further investigation is needed to address a variety of questions. Firstly, whilst the spatial coverage of data on shark depredation rates in commercial fisheries is relatively extensive, particularly in the Indian Ocean, there are noticeable gaps where data is sparse, such as the South Atlantic and eastern Pacific. Future work should therefore aim to collect quantitative data in these regions, to support global comparisons of shark depredation rates between ocean basins. Secondly, the collection of quantitative data on shark depredation in recreational fisheries is particularly important, given the distinct lack of existing data and the growth in recreational fisheries landings and participation worldwide (Coleman et al. 2004, Cooke & Cowx 2004, Lewin et al. 2006, Arlinghaus & Cooke 2009). To address this, long-term assessment of shark depredation in recreational fisheries needs to be conducted, to quantify the occurrence of depredation and identify ways to improve fishing practices, especially in regions where there are substantial human-wildlife conflicts. To collect such data, regular surveys of recreational fishers should be employed using a variety of techniques, such as access point surveys (Hayne 1991, Pollock et al. 1994) at boat ramps and marinas, interrogation of fisher logbooks and recording of this data online. For example, a recent study by Mitchell et al. (2018a) highlights the efficacy of using access point surveys to collect data on shark depredation in recreational fisheries. These data collection methods will ultimately provide a greater understanding of the factors driving depredation in these fisheries, particularly through quantitative assessment of how fishing methods and environmental conditions may influence the rate of depredation.

Statistical modelling approaches such as Generalised Additive and Linear Models (GAMs/GLMs), which have been widely used in fisheries research to assess the impacts of environmental factors and fishing methods on catch rates (Bigelow et al. 1999, Walsh & Kleiber 2001, Venables & Dichmont 2004, Damalas et al. 2007, Mitchell et al. 2014), would be an effective way of analysing such relationships. MacNeil et al. (2009) was the first to apply these techniques to modelling depredation data and future research should aim to build on this information, and quantify depredation in other fisheries. Furthermore, meta-analyses could be conducted to provide depredation rates specific to different fishing gear types, along with analysis of factors affecting these gear-specific rates, such as environmental variables, season, region and target species. This approach was used recently to investigate gear-specific bycatch rates of elasmobranchs in longline fisheries (Gilman et al. 2016b). Such meta-analyses provide higher precision and accuracy than individual studies, along with greater statistical power, due to their substantially larger sample size (Borenstein et al. 2011, Musyl et al. 2011). Overall, this would create an improved understanding of the processes underlying depredation, which would be of great benefit for designing more effective mitigation measures.

2.11.2. Identifying depredating shark species

In order to develop future strategies for reducing depredation, it is necessary to identify the shark species responsible for depredation and the behavioural processes involved. Whilst there is some knowledge of the species responsible for depredation in fisheries (Table 2-3), identification is usually difficult because depredation occurs at depth and over long soak periods in commercial fisheries, leaving either no trace or only remains of depredated fish with ambiguous bite marks. As a result, it is often only possible to infer the identity of depredating sharks based on those that are caught (MacNeil et al. 2009). To address these difficulties, and enable reliable collection of species identity data, new techniques are needed. Stomach contents analysis may be used to identify depredating shark species that have recently consumed the target species, which is an approach previously used by Romanov et al. (2007). However, this requires the depredating sharks to be caught, which may often not occur, especially in recreational fisheries. Non-invasive techniques, such as the deployment of underwater video cameras close to the hook on fishing lines, could also enable identification of depredating shark species. Indeed, the potential of this concept has been shown by O'Shea et al. (2015) and Streich et al. (2018), who were able to positively identify depredating shark species from video footage collected by line-mounted cameras. Additionally, in the Gulf of Mexico, pilot research was successful in identifying depredating shark species from DNA traces taken from bite marks on the remains of depredated *L. campechanus* (Drymon et al. 2015). This technique could therefore be used in conjunction with the deployment of video cameras, as a powerful and non-invasive approach for determining the shark species causing depredation in fisheries. Such knowledge will facilitate targeted development and testing of deterrents, where effectiveness can be assessed in conjunction with what is known of the sensory thresholds of individual species (O'Connell et al. 2011, Hutchinson et al. 2012, Collin et al. 2015, Kempster et al. 2016). Likewise, footage collected from line-mounted cameras would provide an opportunity to assess how sharks may be impacted by depredating hooked fish and interacting with fishing gear, for which very little data currently exists. For example, it would allow detection of individuals with fishing hooks in their jaw or other visible injuries resulting from previous depredation events. The use of cameras could also identify whether sharks preferentially depredate certain teleost species when they are hooked, or whether all hooked fish are depredated opportunistically. This would provide interesting insights into whether sharks are consuming teleost species that are not part of their normal diet.

2.11.3. Understanding shark depredation behaviour

Understanding the behaviour of sharks before, during and after depredation events is an important research gap that may also be addressed through the innovative use of underwater video technology. Specifically, observing the sequential process where sharks locate a hooked fish using sensory cues, then approach and investigate, before finally consuming the fish, would increase our understanding of these behavioural interactions. Similar techniques to those used by Robbins et al. (2013), where line-mounted cameras were deployed to investigate *C. taurus* interactions with fishing gear, could be applied. Autonomous camera systems could also be used, as highlighted by recent research which utilised this technology to observe southern elephant seals *Mirounga leonina* depredating fish hooked on demersal longlines in the Southern Ocean (van den Hoff et al. 2017). Additionally, observing the behavioural reaction of sharks to deterrent devices could also be undertaken using line-mounted cameras, similar to work by Robbins et al. (2011), where magnets and electropositive metals were tested as potential deterrents for *C. galapagensis*. Further testing on a wide range of species would provide vital insights into how to design more effective species-specific deterrents and modify fishing gear to make it more difficult for sharks to consume hooked fish.

Future research to investigate the behavioural and sensory aspects of shark depredation should focus on the potential role of conditioning in sharks. For example, reproducible experimental protocols could be designed to identify the behaviour of sharks in response to the repeated presentation of sensory cues, particularly boat engine noise, and the availability of hooked fish to feed on, versus a control where no hooked fish are available. Such testing could be conducted in areas where depredation is anecdotally reported to be influenced by this cue, such as in South Africa (Labinjoh 2014), The Bahamas (Madigan et al. 2015) and Western Australia (Exmouth Game Fishing Club, pers. comm.) Active acoustic tracking, similar to that conducted by McCord & Lamberth (2009) in South Africa on *C. leucas*, would be a tool that could help record the behaviour of individuals in response to boat activity in real-time. Likewise, cameras mounted directly on sharks, such as Crittercam (Marshall 1998, Heithaus et al. 2001, Skomal et al. 2007), could allow observation of depredation from a shark’s perspective. Overall, a range of approaches are required to provide information on how, why and to what extent shark depredation occurs in commercial and recreational fisheries. By focusing on these research gaps, a more holistic understanding of depredation will be achieved, greatly increasing the chances for designing effective mitigation measures. This is a highly significant goal given the potential biological, economic and social impacts of shark depredation worldwide.

2.12. Conclusion

The research reviewed in this study highlights the widespread occurrence of shark depredation in a range of commercial and recreational fisheries spanning different ocean basins, ecosystem types and fishing methods. It is therefore clear that depredation by sharks is a prevalent fisheries issue, with rates of between 0.9% and 26% of hooked fish being lost, as well as large quantities of fishing gear. Furthermore, it has been found to have significant biological ramifications for target species and the sharks responsible for depredation, and we are only just beginning to understand the greater complexity of these impacts. In an age of increasing overexploitation of fisheries resources (Srinivasan et al. 2010, Swartz et al. 2010, Neubauer et al. 2013, Costello et al. 2016) and declining economic viability of fishing operations (Lam et al. 2016, Schuhbauer & Sumaila 2016, Sumaila et al. 2016, Bell et al. 2017), the economic and biological impacts of shark depredation on fisheries are more important than ever. However, shark depredation remains a relatively overlooked issue compared to other fisheries management challenges. The complexity of conducting research on shark depredation has contributed to this lack of research to date, such as the difficulties of identifying the shark species involved and determining the extent of damage and loss to catch. A lack of resources and effective methods for data collection, such as logbook reporting or trained fisheries observers, also likely explains why no data has been collected in many fisheries. Whilst this review has shown that up to 27 different shark species from seven families can cause depredation, there needs to be a much more comprehensive investigation of how and why the depredating species varies, to inform management issues such as shark bycatch. Recent advances in technology and our understanding of shark behaviour and sensory ecology open up vital opportunities for conducting this new research on shark depredation to address these gaps. Such research will be critical for developing more comprehensive and effective strategies for reducing shark depredation, which would, in turn, have wide-ranging benefits for fish stocks, shark conservation and management and the productivity of fishing operations.

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Chapter 3: Quantifying shark depredation in a recreational fishery in the Ningaloo Marine Park and Exmouth Gulf, Western Australia

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3.1. Abstract

Shark depredation, where a shark consumes a hooked fish before it can be retrieved to the fishing vessel, can occur in recreational fisheries. This may cause higher mortality rates in target fish species, injuries to sharks from fishing gear and negatively impact the recreational fishing experience. This study quantified spatial variation and frequency of shark depredation in a recreational fishery in the Ningaloo Marine Park and Exmouth Gulf, Western Australia, by surveying 248 fishing boats at west coast boat ramps and 155 boats at Exmouth Gulf boat ramps from July 2015 to May 2016. Shark depredation occurred on 38.7% of fishing trips from west coast boat ramps and 41.9% of trips from Exmouth Gulf boat ramps. The mean (±95% CI) shark depredation rate per trip was 13.7 ± 3.3% for demersal fishing (n = 185) and 11.8 ± 6.8% for trolling (n = 63) for west coast boat ramps, compared to 11.5 ± 2.8% (n = 128) and 7.2 ± 8.4% (n = 27) for Exmouth Gulf ramps. Depredation rates varied spatially, with higher depredation in areas which received greater fishing pressure. A novel application of Tweedie Generalised Additive Mixed Models indicated that depth, the number of other boats fishing within 5 km and survey period influenced depredation rates for fishing trips from west coast boat ramps. For the Exmouth Gulf ramps, fishing pressure and decreasing latitude positively affected the number of fish depredated. These results highlight the important influence of spatial variation in fishing pressure. The occurrence of higher depredation rates in areas which receive greater fishing pressure may indicate the formation of a behavioural association in the depredating sharks. This study is the first quantitative assessment of shark depredation in an Australian recreational fishery, and provides important insights that can assist recreational fishers and managers in reducing depredation.

3.2. Introduction

Depredation of a fishing catch refers to the partial or complete consumption of a hooked fish by a predator before that fish can be retrieved by the fisher (Gilman et al. 2008, MacNeil et al. 2009, Mitchell et al. 2018b). This occurs in commercial and recreational fisheries worldwide (Sumner et al. 2002, Nishida & Shiba 2004, MacNeil et al. 2009, Labinjoh 2014) and is caused by a diverse range of predators, including sharks, teleosts, cetaceans, pinnipeds, seabirds and squid (Meyer et al. 1992, Donoghue et al. 2003, Gilman et al. 2008, Remeslo et al. 2015, van den Hoff et al. 2017). Depredating hooked fish is likely to be an opportunistic and energy efficient feeding strategy for these animals compared to capturing prey naturally (Madigan et al. 2015). Depredation by sharks is problematic in commercial fisheries worldwide, due to costly losses of target fish and fishing gear, as well as bycatch and mortality of sharks (IOTC 2007, Gilman et al. 2008, MacNeil et al. 2009). As a result of these impacts, past research has quantified shark depredation rates (the percentage of hooked fish partially or completely taken by sharks) in pelagic longline fisheries worldwide, with values ranging from <1 to 26% (Lawson 2001, Gilman et al. 2008, MacNeil et al. 2009, Mitchell et al. 2018b). Shark depredation in recreational fisheries has received far less attention, with very little published research quantifying its occurrence (Sumner et al. 2002, Williamson et al. 2006, Labinjoh 2014), despite anecdotal reports of it regularly occurring in a number of recreational fisheries, including in Australia, mainland USA, Hawaii and South Africa. Depredation in recreational fisheries is an important issue, due to its potential to cause higher mortality in target fish species, hooking injuries or mortalities to the depredating taxa and loss of fishing gear for fishers. Furthermore, mortality of target species caused by depredation is often cryptic, because it can occur at depth and out of sight, compared to more easily quantifiable sources of mortality such as the fish retained by fishers. Depredation as a source of mortality may therefore not be accounted for in fish stock assessments, leading to underestimation of overall target species mortality.

This study investigated and quantified shark depredation in a boat-based recreational rod-and-line fishery in Exmouth Gulf and the Ningaloo Marine Park in north-west Western Australia (see Fig. 3-1), where shark depredation was anecdotally reported to regularly occur (Exmouth Game Fishing Club pers. comm.). This location is regarded as one of the best boat-based rod-and-line recreational fishing areas in Australia, for both pelagic (e.g. Spanish mackerel *Scomberomorus commerson)* and demersal (e.g. spangled emperor *Lethrinus nebulosus)* species (Sumner et al. 2002, CALM & MPRA 2005, Williamson et al. 2006). As a result, this fishery receives a relatively high level of fishing effort; for example, 55000 boat fishing days were recorded across the north-west (Gascoyne) region of Western Australia over a recent 12 mo survey period (2011 to 2012) (Ryan et al. 2013). In this time, an estimated 16884 ± 2270 (SE) individual *L. nebulosus* (equal to 35.3 ± 4.8 tonnes) were caught and retained (Ryan et al. 2013). The Ningaloo Marine Park plays an important role in biodiversity conservation in this region, with a zoning plan that includes areas open to fishing and no-take sanctuary zones where no fishing is permitted, the latter of which comprise 34% of the marine park (CALM & MPRA 2005) (see Fig. 3-1). Targeted recreational fishing for sharks is uncommon in this region (Ryan et al. 2013). Also, there is a commercial ban on shark fishing between Steep Point (26.15° S, 113.16° E) and Broome (17.96° S, 122.22° E) to enable sufficient recruitment of dusky sharks *Carcharhinus obscurus* and sandbar sharks *Carcharhinus plumbeus*, which are targeted as juveniles by commercial fisheries in the central and southern regions of Western Australia (Simpfendorfer et al. 1999, McAuley & Simpfendorfer 2003, McAuley et al. 2005, Braccini et al. 2017). Also, the Ningaloo Marine Park and Exmouth Gulf provide important habitat for adult and juvenile life stages of numerous reef-associated shark species (Speed et al. 2011, Escalle et al. 2015, Oh et al. 2017).

To quantify shark depredation within a recreational fishery, a boat ramp survey was conducted to gather information on depredation rates and locations, in addition to a range of environmental variables and the fishing methods used. It was hypothesised that depredation rates would vary spatially, and that proportionally higher rates would occur in areas that receive consistent fishing pressure, due to the attraction of sharks to chemical and auditory cues created by fishing activity, and the associated availability of hooked fish to feed on. Likewise, depth was expected to be an important factor determining depredation rate, due to its influence on seabed habitat type and the distribution and abundance of sharks (Espinoza et al. 2014, Rizzari et al. 2014a). This study was undertaken to provide quantitative information on shark depredation in a recreational fishery in Western Australia, in order to inform fisheries and marine park management strategies in this area, as well as broadening our understanding of shark depredation.

3.3. Methods

3.3.1. Study location

Data for this study were collected during surveys conducted at Coral Bay (23.16° S, 113.77° E) and Tantabiddi (21.91° S, 113.98° E) boat ramps (hereafter west coast boat ramps), and Bundegi (21.83° S, 114.17° E) and Exmouth marina (21.96° S, 114.14° E) boat ramps (hereafter Exmouth Gulf boat ramps) (see Fig. 3-1). Boat ramps were grouped in this way due to the oceanographic, bathymetric and ecological differences between the west coast and Exmouth Gulf areas of the fishery. The former is characterised by a shallow (<10 m) lagoon close to the coast, followed by an extensive north–south oriented fringing reef which drops away steeply to deep water with increasing distance from the coast (CALM & MPRA 2005). Conversely, the latter is shallow with mostly bare sand substrate, apart from isolated reef and seagrass patches and islands (Kenyon et al. 2003).

3.3.2. Boat ramp survey data

Data on shark depredation were collected directly from fishers, using a boat ramp survey conducted from July 2015 to May 2016. A systematic sampling strategy was used, where each boat ramp was sampled on 10 randomly selected days across three survey trips in July and August (austral winter) 2015, September and October (austral spring) 2015 and April (austral autumn) 2016, producing a total sample size of 40 days. The primary sampling unit (PSU) was each sampling day (Murphy 2008, Jones & Pollock 2012, Levy & Lemeshow 2013). The time of year of the three sampling trips was chosen to provide coverage of the peak fishing season from April to October (Sumner et al. 2002, Ryan et al. 2013). Sampling was also stratified by day type, with each boat ramp sampled using a ratio of two weekdays for each weekend day (Jones & Pollock 2012, Smallwood & Gaughan 2013). All boats were surveyed between 10:00 and 18:00 h as they returned to the boat ramp after fishing.

Interviews were conducted by the same researcher, using a pre-set question form and map on the software application ‘Collector for ArcGIS’ (Environmental Systems Research Institute (ESRI) 2015, Redlands, CA), which was downloaded onto a tablet device. Each interview consisted of 20 short-answer questions, including boat level questions and individual fisher questions (see Appendix A for list of survey questions), and lasted 3 - 5 min. Before commencing the actual survey, survey questions were pilot tested at a boat ramp in Perth, Western Australia, to ensure that they were easy to interpret and provided reliable data. In the survey, the identity of depredated fish was rarely available because the sharks mostly consumed hooked fish at depth, with no sighting of the fish or remains retrieved. Fish that were caught undamaged and retained by fishers were also not identified due to time constraints. A depredation event was known to have occurred when fishers either retrieved a partially depredated fish to the boat, or when a fish was hooked and then shortly after, a noticeably stronger pull on the line occurred as the fisher was reeling the fish to the boat, indicating a predator consuming the hooked fish and becoming hooked itself. The latter was then usually followed by the predator snapping off the fishing line. Sharks were likely the main taxa responsible for depredation in this fishery, because fishers commonly reported seeing sharks (predominantly carcharhinids) depredating hooked fish as they were reeled to the boat. Likewise, sharks were also confirmed to be the depredating taxa when they became hooked after depredating a hooked fish, and were then retrieved to the boat. It is possible that other taxa were responsible for depredation in some cases, particularly large teleosts such as cod/grouper *Epinephelus* spp. and barracuda *Sphyraena* spp., or marine mammals such as bottlenose *Tursiops* spp. and Indo-Pacific humpback dolphins *Sousa chinensis*, all of which are known to occur in the Ningaloo Marine Park and Exmouth Gulf (Preen et al. 1997, Farmer & Wilson 2011, Brown et al. 2012). However, depredation by these taxa was rarely reported by fishers in comparison to shark depredation.

The response rate, i.e. the percentage of fishers approached that completed the survey, was 97.14%. This high response rate was achieved because fishers were interested in providing information on depredation due to the impact it has on their catch rate and fishing experience, and also because the interviews were short in duration. The survey used in this study was designed to cover all daytime boat-based recreational fishing from boats launching from the four main access points (boat ramps) serving the west coast and Exmouth Gulf. Boats ranging from 3 - 9 m in length were able to launch from these access points and were thus covered by the survey scope. A broad fisher demographic was also represented in the survey data, including fishers of both sexes ranging from approximately 10 to 80 yr old, local residents as well as visitors from Western Australia and interstate, and a wide range of experience levels, from first-time fishers to professional and ex-professional fishers. Due to time and logistical constraints, some boat-based recreational fishing in the region was, however, outside the scope of the survey used in this study, including boats launching from beaches, private access points or marinas as well as those fishing at night or on multi-day trips (Table 3-1).

Table 3-1: Fishing methods, fisher demographics and boat sizes that were in scope or out of scope for the boat ramp survey conducted in this study

In scope	Out of scope
Boat-based line fishing	Shore-based fishing and spearfishing
Boats returning to boat ramps between 10:00 and 18:00 h	Boats returning to boat ramps before 10:00 or after 18:00 h
Boats <9 m that could be launched and retrieved from a boat ramp	Boats >9 m that were unable to launch from a boat ramp
Single day fishing trips	Multi-day fishing trips
Boats returning to the boat ramp being surveyed that day	Boats returning to other boat ramps in the study area that were not being surveyed that day
Boats fishing in the study area during the July/August 2015, September/October 2015 and April 2016 survey periods	Boats fishing at other times of year outside of the three survey periods
Boats launching from Coral Bay, Tantabiddi, Bundegi and Exmouth marina boat ramps	Boats launching from private moorings in Exmouth marina, beaches or other access points near coastal campsites
Local fishers and those from outside locations	
Male and female fishers ranging from ca. 10 to 80 yr old	
Fishers targeting both demersal and pelagic fish species	
A range of fisher experience levels, from novice first-time fishers to professional fishers	

3.3.3. Sea surface temperature data

Satellite Sea Surface Temperature (SST) data were sourced retrospectively from the US National Oceanic and Atmospheric Administration (NOAA 2016). These data were in the form of high resolution optimum interpolation (OI) SST (see Reynolds et al. (2007) for details), collected by advanced very high resolution radiometer (AVHRR) instruments on polar orbiting satellites (NOAA 2016). The data were daily mean SST values at a spatial resolution of 0.25 × 0.25° grid squares (NOAA 2016). SST values were extracted for the dates on which boat ramp surveys took place, and for the latitude/longitude position closest to each fishing location to allow assessment of the influence of SST on shark depredation rate.

3.3.4. Shark depredation rate

Survey data collected from the west coast boat ramps and the Exmouth Gulf boat ramps were treated separately throughout, due to differences in the depth profile, habitat types and fishing methods used in these two areas. Additionally, to ensure all data points were independent, entries where the same fisher had been interviewed multiple times were removed, so that each fisher/boat was represented by a single data point only (the first time they were interviewed). This was possible through the recording of boat registration numbers, and it was necessary due to the quality and reliability of data declining after multiple interviews due to survey fatigue. Only data from the two main fishing methods — demersal fishing (where the boat was either anchored or drifting and bait was used) and trolling (where lures were towed close to the surface to target pelagic fish, covering distances from 1 to 20 km) — were used, due to small sample sizes (<20 data points) for other methods such as squid jigging or fishing with stationary lures floating on the surface. The sample size for these two fishing methods was 185 demersal fishing trips and 63 trolling trips (248 in total) for the west coast boat ramps and 128 demersal and 27 trolling trips (155 in total) for Exmouth Gulf boat ramps. The 248 boats surveyed for the west coast boat ramps represented an estimated 5.8% of the total fishing trips that occurred from these ramps over a 12 month period, from July 2015 to June 2016, based on boat ramp traffic counter figures of 4248 visits by vehicles towing boat trailers over this period (Department of Biodiversity Conservation and Attractions, Government of Western Australia unpubl. data). This value of 4248 fishing trips represented 70% of the total number of visits for vehicles with boat trailers (6069), because it was estimated that 30% of boats launching from these boat ramps engaged in recreational activities other than fishing, such as diving or whale watching. These values also assume that all vehicles that crossed the traffic counter and entered the boat ramp launched their boat, which does not always occur, for example if the occupants decided to go to another boat ramp due to weather conditions. Calculation of the percentage of total boat launches represented by the survey sample was not possible for the Exmouth Gulf boat ramps, because traffic counter data were not available for both of these ramps.

Shark depredation rate was analysed at the level of each individual fishing trip as opposed to at the PSU level of each sampling day, because there was expected to be a large degree of variation in fishing methods, spatial fishing locations and thus depredation rates between trips. The depredation rate (%) for each fishing trip was calculated by dividing the number of hooked fish partially or completely consumed by sharks by the total number of fish hooked (which included fish caught and retained, fish caught and released and fish depredated). This metric was used because it has been applied by a number of previous studies to quantify shark depredation in both recreational and commercial fisheries (Lawson 2001, Gilman et al. 2008, MacNeil et al. 2009, Labinjoh 2014, Muñoz-Lechuga et al. 2016), and therefore allows direct comparison with these studies. Depredation only included instances where fish were consumed from a fishing hook whilst being retrieved to a boat, not those where fish were consumed after being released, which is known as post-release predation (Raby et al. 2014). Spatial variation in depredation rate was visualised by plotting all approximate latitude/longitude fishing locations in the study area on a map, with a colour scale to indicate depredation rate for each trip.

3.3.5. Generalised Additive Mixed Model analysis

To quantify the influence of spatial, environmental and fishing method variables on the rate of shark depredation, Generalised Additive Mixed Models (GAMMs) (Lin & Zhang 1999) were used. GAMMs are an extension of Generalised Additive Models (GAMs) (Hastie & Tibshirani 1986, Wood 2006) which utilise smoothing techniques to account for noise and non-linearity in the predictor variables (Craven & Wahba 1978, Wood 2008). GAMMs also differ from GAMs in that they include both fixed and random effects, with the fixed effects assessing the impact of each predictor variable on the response at specific levels, and the random effects evaluating the impact of variations between levels for grouped data (Bolker et al. 2009, Zuur et al. 2009). Due to the small sample size for trolling and other fishing methods reported in this study, GAMMs were only fitted to demersal fishing data. Raw count data for the number of fish depredated per trip were used as the response variable, because this form of data was more appropriate for GAMM analysis than a calculated rate of depredation per trip. However, the raw count data had many zeros (54% of data points) and were over-dispersed due to the high number of zeros and low values as well as a large range (0 to 50) in the number of fish depredated per trip. Zero-inflated and over-dispersed response data are common in fisheries datasets (Maunder & Punt 2004, Venables & Dichmont 2004), and different approaches have been used to model this form of data, including delta two-part models (Lo et al. 1992), negative binomial models (Zeileis et al. 2008, MacNeil et al. 2009), zero-inflated mixture models (Minami et al. 2007, Arab et al. 2008, MacNeil et al. 2009, Zuur et al. 2009) and Tweedie models (Tweedie 1984, Candy 2004, Shono 2008, Tascheri et al. 2010, Coelho et al. 2016).

This study applied a full-subsets GAMM approach, which tested all possible combinations of the specified predictor variables to identify the best-fitting, most parsimonious model (Fisher et al. 2018). The predictor variables tested in these GAMMs (Table 3-2) were checked for potential correlation to ensure that collinearity was within acceptable levels, denoted by Pearson's correlation coefficient values <0.28 (Graham 2003). The final dataset used for GAMM analysis had 170 data points for the west coast boat ramps and 123 for the Exmouth Gulf boat ramps. The date of sampling (in Julian day format) was also included as a random factor to account for any unexplained variation at the day level. Total number of fish hooked was used as an offset in the GAMMs, because the number of fish depredated was assumed to be directly dependent on the total number of fish hooked. This offset variable was highly skewed, therefore it was $\log(x + 1)$ transformed to achieve an even distribution for more robust model fitting (Zuur et al. 2009).

Each of the model distributions discussed previously (e.g. negative binomial, zero-inflated mixture models etc.) were tested using this full-subsets GAMM approach. The Tweedie distribution was identified by goodness-of-fit metrics, particularly the distribution of model residuals as visualised in residual plots and the percentage of deviance explained, to be the most appropriate for this dataset. Separate Tweedie GAMMs were run for the west coast and Exmouth Gulf boat ramps. To identify the combination of predictor variables that produced the best-fitting model, all possible combinations were tested and ranked by Akaike's information criterion (AIC) (Akaike 1974) values, with the most parsimonious model being that within two AIC values of the lowest AIC and having the smallest number of predictor variables (Burnham & Anderson 2002). The maximum number of predictor variables allowed in this approach was three (to prevent potential overfitting), and the AIC criteria of being within two units of the lowest AIC was used because models that have less than two units of difference show negligible change in goodness-of-fit (Raftery 1995, Burnham & Anderson 2002). Additionally, AIC weights (wAIC) (Burnham & Anderson 2002) were used to give extra strength to the model selection, applying the averaged wAIC approach set out in Fisher et al. (2018). The robustness and fit of the final models selected by the full-subsets approach was also checked by visualisation of residual plots, which confirmed normal distribution of residuals, independence of data points and goodness-of-fit of the fitted to the observed response values. Plots were then generated for the most parsimonious models to show the effect of each predictor variable on the response across its range of values. Predictor variable importance values, which represented the average wAIC of all models containing that variable, calculated on a scale between zero and one and multiplied by the R^2 value for the most parsimonious model (Fisher et al. 2018), were also generated and plotted to identify the relative importance of all the predictor variables tested in both models.

Table 3-2: Predictor variables considered for Generalised Additive Mixed Model (GAMM) analysis of shark depredation, the metric used to represent that variable and its hypothesised importance to depredation

Predictor variable	Metric used in GAMM	Hypothesised importance to shark depredation
Smoothed continuous predictor variables		
Latitude	Latitude coordinates	Latitude influences shark distribution patterns and defines different fishing grounds accessible from the four different boat ramps. Latitude also acts as a proxy for spatial variability caused by other factors not included in the model, such as habitat type

Predictor variable	**Metric used in GAMM**	**Hypothesised importance to shark depredation**
Depth	Maximum hook depth (m)	Depth governs available shark habitat and influences distribution patterns, thus affecting abundance
Temperature	Sea Surface Temperature (SST; °C)	Temperature influences the activity patterns (including feeding behaviour) of sharks
Time of day	Median time between times lines in and time of lines out	The activity patterns of sharks, especially for feeding, vary throughout diel periods
Fishing effort for that trip	Fishing trip duration (hours from lines in to lines out)	Longer fishing times provide greater opportunity for sharks to locate fishing boats and depredate on hooked fish
Number of other boats fishing within 5 km	Number of other boats fishing within a 5 km radius of the boat in question on the same day, calculated using the minimum linear distance to the recorded lat/long locations of other boats fishing on that day, with the 'RANN' package (version 2.5.1) (Arya et al. 2017) in R. This metric assumed that boats launching from other ramps on the same day would not fish in overlapping areas, due to the relatively large distances between boat ramps	The number of other boats fishing in the surrounding area will influence the likelihood of attracting sharks into that area, due to the increased magnitude of sound and odour cues from fishing boats and the availability of hooked fish
Fishing pressure	Kernel density value for each fishing trip location, based on the density distribution of all 403 fishing locations (see Fig. 3-1a)	Higher fishing pressure in specific areas may act to provide sharks with regular and predictable opportunities to depredate hooked fish. This may lead to sharks remaining in these areas for longer time periods and potential changes in their behaviour, influencing the likelihood of depredation occurring in that location
Categorical factor predictor variable		
Survey period	Month/year of survey	The time of year influences seasonal movement patterns and distribution of shark species, due to changes in environmental factors and through movement linked to reproduction. Additionally, changes in weather patterns and currents occur throughout the year, influencing fishing dynamics

All data analyses were conducted in the R language for statistical computing (R Development Core Team 2015), and GAMMs were run using the 'mgcv' package (version 1.8-17) (Wood & Scheipl 2015).

3.4. Results

3.4.1. Shark depredation rate

From the 248 fishing trips (including both demersal fishing and trolling) recorded at west coast boat ramps, 2420 fish were caught undamaged (including both those retained and those released) and 354 were reported to have been depredated by sharks, whereas in the 155 trips from Exmouth Gulf boat ramps, 2068 fish were caught undamaged and 344 were depredated. Shark depredation occurred on 38.7% of fishing trips from west coast boat ramps and 41.9% of fishing trips from Exmouth Gulf boat ramps. The mean (±95% CI) shark depredation rate per trip (% of the total number of fish hooked that were depredated) was 13.7 ± 3.3% for demersal fishing and 11.8 ± 6.8% for trolling at west coast boat ramps, compared to 11.5 ± 2.8% and 7.2 ± 8.4% at Exmouth Gulf boat ramps.

3.4.2. Spatial variation in shark depredation rate

Shark depredation showed substantial spatial variation across the study area, with values for individual trips ranging between 0 and 100% (Fig. 3-1b). The vast majority of fishing trips were, however, at the lower end of this scale, with values between 0 and 20%, as indicated by the high number and density of low values (Fig. 3-1b). Higher rates of depredation (25 to 50%) were experienced in a number of trips close to the Tantabiddi boat ramp, particularly in the 50 to 100 m depth range (Fig. 3-1b). Additionally, this area included seven individual trips that reported >80% depredation. The area at the northern end of Exmouth Gulf as well as north of Bundegi boat ramp also showed a number of fishing trips where depredation rates were 25 to 50%. However, it must be noted that the fishing locations recorded (Fig. 3-1b) were approximate, especially in the case of trolling trips where boats covered distances ranging from 1 to 20 km.

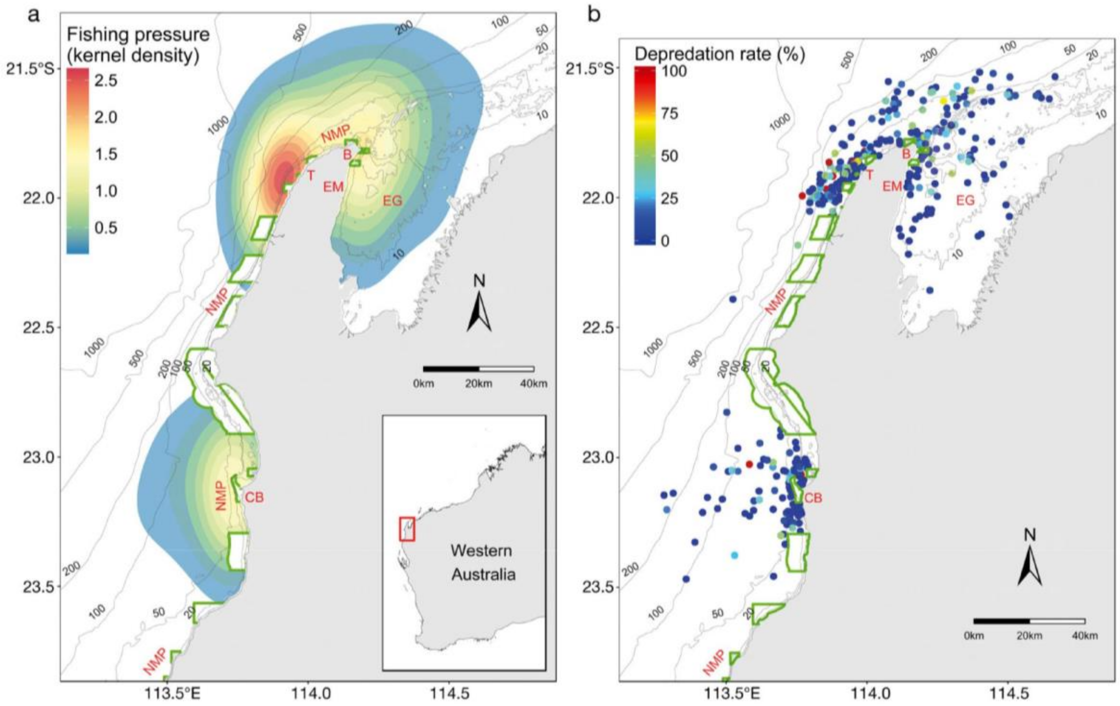

Fig. 3-1: a) Spatial variation in estimated fishing pressure, calculated using kernel density estimation to analyse the density distribution of the 248 and 155 (403 total) boat-based fishing locations (for both demersal fishing and trolling) reported by boats launching from west coast boat ramps (Coral Bay [CB] and Tantabiddi [T]) and Exmouth Gulf (EG) boat ramps (Bundegi [B] and Exmouth marina [EM]), respectively. Red areas: highest estimated fishing pressure; blue: lowest estimated fishing pressure. Labelled contour lines show depth (in m). Solid green lines: Ningaloo Marine Park (NMP) sanctuary zone boundaries. **b)** Spatial variation in the rate of shark depredation (the percentage of hooked fish consumed by sharks) for the 248 fishing trips launched from west coast boat ramps and 155 fishing trips from Exmouth Gulf boat ramps. Colour scale: range of shark depredation rate values for all fishing trips from dark blue for 0% of hooked fish depredated to dark red for 100% depredated.

3.4.3. Influence of spatial, environmental and fishing method variables on shark depredation rate

The most parsimonious GAMM for the west coast boat ramps included the predictor variables maximum hook depth, number of other boats fishing within 5 km and survey period, which explained 36.6% of the deviance in the response variable (number of fish depredated by sharks per trip). Maximum hook depth was an important predictor of the number of fish depredated across all of the west coast models, as indicated by a high relative importance value of 0.38 (Table 3-3). This variable showed a distinctly non-linear relationship with number of fish depredated per trip, with a peak at 60 m (Fig. 3-2a). The number of other boats fishing within 5 km was another important predictor across all of the west coast models, and showed a positive linear relationship of increasing rates of depredation with increasing number of other boats fishing within 5 km (Fig. 3-2b). Survey period showed slightly higher importance than the number of other boats within 5 km, with a strong positive effect on depredation from the lowest value for the April (austral autumn) 2016 survey trip to the highest for the September/ October (austral spring) 2015 survey trip (Fig. 3-2c).

For the Exmouth Gulf boat ramps, the most parsimonious GAMM included the predictor variables fishing pressure and latitude, which explained 54.9% of the deviance in the response. Increasing fishing pressure displayed a broadly positive relationship with increasing number of fish depredated (Fig. 3-2d), and had a relatively high level of importance across all of the Exmouth Gulf GAMMs (Table 3-3). Latitude was a very important variable across all Exmouth Gulf models, with a strong positive linear relationship between decreasing latitude and the number of fish depredated (Fig. 3-2e). The remaining predictor variables tested in the west coast and Exmouth Gulf GAMMs had little effect on the number of fish depredated, with relative importance values <0.1 (Table 3-3).

Table 3-3: Relative importance of the predictor variables tested in Generalised Additive Mixed Models (GAMMs) (see Table 3-2), for predicting the number of fish depredated by sharks per fishing trip for the west coast boat ramps (Coral Bay and Tantabiddi) and the Exmouth Gulf boat ramps (Bundegi and Exmouth marina). Predictor variables which featured in the most parsimonious model for the west coast boat ramps or the Exmouth Gulf boat ramps are labelled with an 'X' in parentheses. Predictor variable relative importance values represent the average Akaike information criterion weights (wAIC) of all models that included that variable, which is then calculated on a scale between zero and one and multiplied by the R^2 value for most parsimonious model. SST = Sea Surface Temperature.

Predictor variables	**West coast boat ramps**	**Exmouth Gulf boat ramps**
Latitude	0.07	0.55 (X)
Max. hook depth	0.38 (X)	<0.01
SST	0.04	0.08
Time of day	0.03	0.08
Fishing effort	<0.01	<0.01
No. boats within 5 km	0.17 (X)	0.07
Fishing pressure	<0.01	0.17 (X)
Survey period	0.18 (X)	0.03

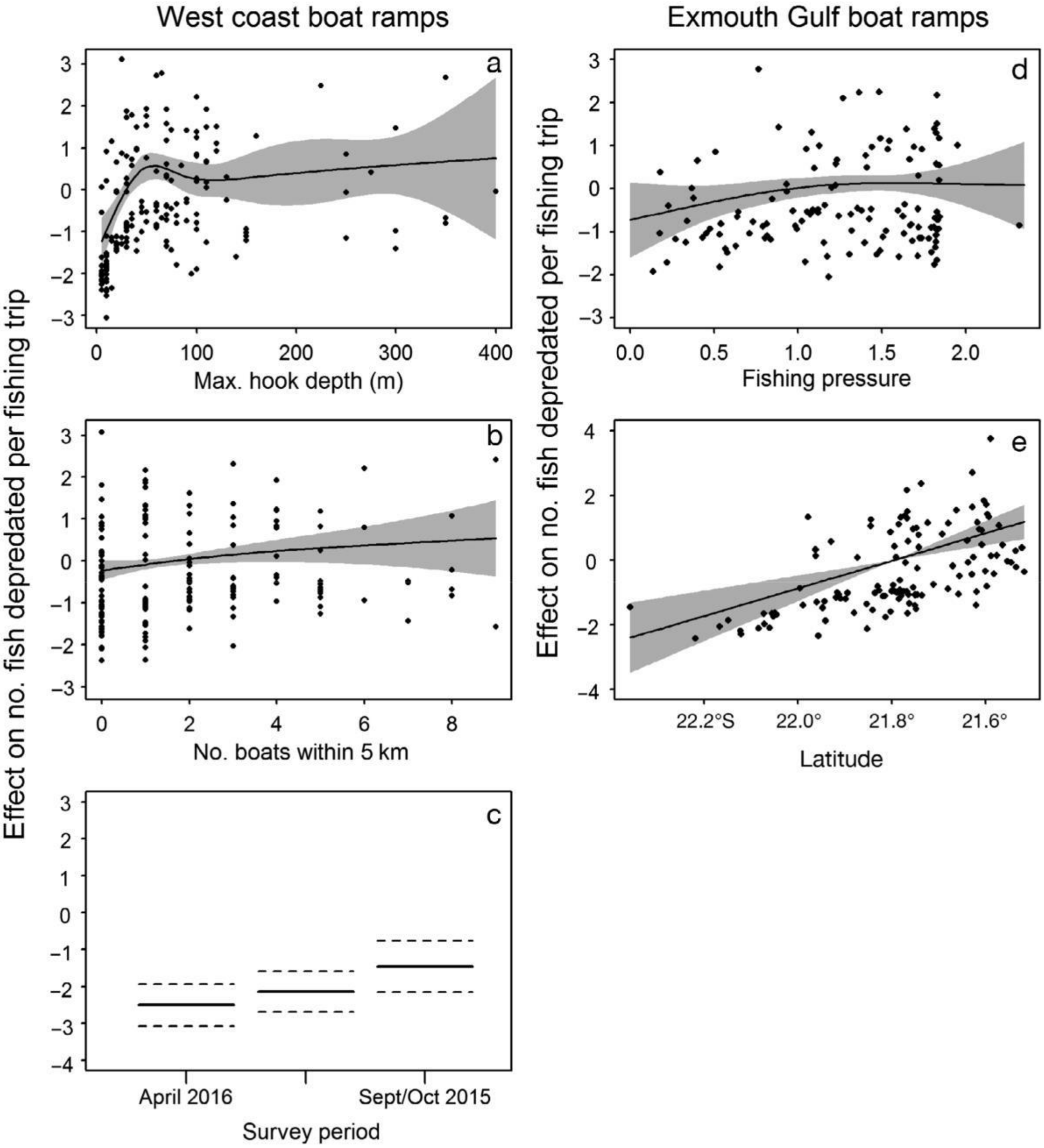

Fig. 3-2: Effect of individual smoothed continuous predictor variables and the factor variable survey period on the number of fish depredated per fishing trip, across their range of values. Shown are the most parsimonious Tweedie Generalised Additive Mixed Models (GAMMs) for **(a–c)** the west coast boat ramps (Coral Bay and Tantabiddi) and **(d,e)** the Exmouth Gulf (EG) boat ramps (Bundegi and Exmouth marina). Solid black lines: fitted GAMM smooth curves; shaded regions (dashed lines in panel c): 95% pointwise confidence intervals (fitted smooth curve ±2 SE). Points represent model residuals.

3.5. Discussion

3.5.1. Shark depredation rate

This study collected important quantitative information on shark depredation rates within the Ningaloo Marine Park and Exmouth Gulf, achieving a high survey response rate and covering the large variation in fishing methods, locations, boat sizes and fisher demographics that occur in this fishery. By quantifying the rate of shark depredation and its spatial variation, as well as identifying how spatial and environmental factors and fishing methods influenced the number of fish depredated in this fishery, this study provides an important addition to the existing global literature on shark depredation. This is highlighted by the fact that very little data exist for depredation in recreational compared to commercial fisheries. Therefore, the results in this study increase our understanding of the full range of impacts and potential underlying factors driving shark depredation.

Previous research conducted recreational fishing surveys in the north-west (Gascoyne) region of Western Australia in 1998 and 1999, with estimated numbers of fish depredated in the Ningaloo Marine Park reported for certain species (Sumner et al. 2002). The reported values varied widely by species, with *L. nebulosus*, the most commonly caught demersal species, having an estimated catch of 22575 individuals retained, 25056 individuals released and 2482 depredated by sharks (Sumner et al. 2002), which represents a 5.2% depredation rate (number of fish depredated/total number of fish hooked). In another area of north-west Western Australia known as the Pilbara region, a similar survey from 1999−2000 recorded estimated depredation rates of 5% for coral trout *Plectropomus* spp. and 1.3% for blackspot tuskfish *Choerodon schoenleinii* (Williamson et al. 2006). However, the estimated depredation rates for the majority of other species were much lower, at <1% for the Gascoyne and <2% for the Pilbara region (Sumner et al. 2002, Williamson et al. 2006). The results of both of these previous surveys should, however, be viewed with caution, because the number of fish depredated was only estimated by multiplying the per hour depredation rate by the estimated total number of fishing hours. Additionally, the species identification for fish consumed by sharks was likely to have been unreliable, because the loss often happened at depth and no remains of the fish were retrieved.

Beyond Western Australia, the majority of data on shark depredation comes from large-scale commercial pelagic longline fisheries. For example, 3.9% of the total number of fish hooked were reported to have been depredated in the US Northwest Atlantic pelagic longline fishery (MacNeil et al. 2009), compared to 2.1 and 6% in Pacific and Indian Ocean fisheries respectively (Lawson 2001, Rabearisoa et al. 2012). However, rates as high as 20% have been recorded in the Australian east coast tuna and billfish longline fishery (Gilman et al. 2008). A small-scale study in a recreational charter fishery operating on the Protea Banks in KwaZulu-Natal, South Africa, recorded an overall mean depredation rate of 8.4% (43 fish depredated out of 512 hooked), with 75% of trips experiencing at least one depredation event (Labinjoh 2014). By fishing method, the depredation rate was 18.6% for pelagic fishing and 1.9% for demersal fishing (Labinjoh 2014). Although the depredation rate per trip in this charter fishery in South Africa was similar to this study, there was a markedly higher prevalence of depredation, i.e. the percentage of trips which experienced depredation (75 versus 38.7% for the west coast boat ramps and 41.9% for the Exmouth Gulf boat ramps). This discrepancy may have been caused by that fishery using larger boats (>6 m) and carrying more fishers (up to 11) (Labinjoh 2014) compared to the present study, with the greater fishing effort more likely to attract sharks. The higher depredation rate for pelagic versus demersal fishing in the KwaZulu-Natal fishery, compared to the opposite result in the present study, is unexpected. This is because sharks would be able to follow and attack fish hooked by boats targeting demersal species more easily (due to them being stationary or slowly drifting) than boats moving through an area at 10 km h^{-1} whilst trolling. This disparity in results may also have occurred because different teleost species were targeted in these fisheries, and different shark species (with dissimilar feeding ecologies and behaviours) may have been responsible for depredation, although this is unknown. Likewise, the dynamics of the two fisheries, including their fisher demographics, methods and equipment used, may have contributed to disparate results. The small temporal scale (3 month period) and low sample size of the study in South Africa, with just 16 trips sampled (compared to 403 in the present study), must be considered when comparing the reported values for shark depredation rate, as there will be a larger degree of variability and uncertainty in the results. Lastly, across these previous studies and this study, shark depredation rates may have been overestimated due to depredation by large predatory teleosts (e.g. *Epinephelus* spp. and *Sphyraena* spp.) or dolphins (e.g. *Tursiops* spp. and *S. chinensis)* being incorrectly attributed to sharks. Indeed, research on red snapper *Lutjanus campechanus* catch rates in the Gulf of Mexico reported only 42% of depredation events to be caused by *C. plumbeus*, as observed by video cameras mounted on fishing lines, with great barracuda *Sphyraena barracuda*, greater amberjack *Seriola dumerili* and Warsaw grouper *Hyporthodus nigritus* responsible for the other 58% (Streich et al. 2018). However, in the recreational fishery covered by this study, such reports of depredation by other taxa were notably rare in comparison to the large number of confirmed records of carcharhinid sharks depredating hooked fish, therefore indicating that sharks were likely to have been the main taxa responsible for depredation.

When considering the results of this study, it is important to note that the sample size represented only a small portion (5.8% of trips from west coast boat ramps) of the total fishing effort that occurred in this fishery over the annual period from July 2015 to June 2016. The results obtained should therefore not be used as an indicator of the entire fishery, due to this proportionately small sample size, incomplete temporal coverage, lack of replication over multiple years and the fact that other forms of fishing were outside the scope of the survey (Table 3-1).

3.5.2. Spatial variation and influence of environmental variables and fishing methods on shark depredation rate

The relative importance of fishing pressure and number of other boats within 5 km in the Exmouth Gulf and west coast GAMMs, respectively, highlights the substantial influence of fishing activity on depredation. Likewise, the overlap between multiple trips which experienced higher depredation rates (>25% fish depredated) and the area of higher fishing pressure close to Tantabiddi boat ramp further indicates this potential relationship between fishing pressure and depredation. It is possible that sharks may be attracted to areas that receive high and consistent levels of fishing pressure by responding to sensory cues created by fishing activity, notably boat engine noise, fish oil and blood and hydrodynamic and electrical disturbances created by struggling hooked fish, all of which sharks can detect (Kalmijn 1972, Corwin 1989, Haine et al. 2001, Collin & Marshall 2003, Dallas et al. 2010, Collin 2012). This may also explain the positive relationship between depredation and the number of other boats fishing within 5 km, because a greater number of boats fishing in a small area would likely generate more boat engine noise and fish oil/blood, thus making it easier for sharks to detect and locate these boats. The co-occurrence of these cues with the availability of hooked fish to depredate, which is an energy-efficient feeding strategy compared to capturing free-swimming prey, may have created a behavioural association for sharks. Past research has recorded evidence of conditioning in sharks in a laboratory setting (Clark 1959, Guttridge & Brown 2014), and there are examples of conditioning occurring in the wild, including in the Ningaloo Marine Park, where sharks showed increasingly faster arrival times to a baited camera deployed over consecutive days in a fished area (Schifiliti 2014).

In the Breede Estuary in South Africa, active acoustic telemetry recorded a bull shark *Carcharhinus leucas* remaining close to fishing boats for extended periods, as well as clear movements towards boats in response to engine noise (McCord & Lamberth 2009), further supporting the possibility that sharks associate these sensory cues with food. Madigan et al. (2015) proposed that the availability of recreationally hooked pelagic fish to depredate may even be influencing the site fidelity and migratory movements of oceanic whitetip sharks *Carcharhinus longimanus*, which return to a localised area in The Bahamas each year. Likewise, changes in movement, feeding patterns and behaviour have been observed in a range of shark species where they are provisioned by ecotourism activities (Johnson & Kock 2006, Fitzpatrick et al. 2011, Maljkovic & Cote 2011, Bruce & Bradford 2013, Brunnschweiler & Barnett 2013, Brena et al. 2015). However, other studies have recorded negligible effects (Laroche et al. 2007, Hammerschlag et al. 2012a), and there is a possibility that depredation is just an opportunistic behaviour that occurs without any behavioural association. Additional work is therefore needed to identify and rigorously test the behavioural processes underpinning shark depredation. Nonetheless, the identification of discrete areas of higher depredation and the influence of fishing pressure is a particularly significant finding of this study, because this information can be used directly by fishers to reduce depredation by avoiding such areas and spreading fishing effort more evenly.

In this study, the number of fish depredated by sharks varied with depth, a relationship also recorded by MacNeil et al. (2009), who reported lower depredation rates on deeper longline sets. The relationship between depth and depredation reported in this study, particularly the peak at 60 m, may have occurred due to the distribution and abundance of sharks. In particular, it is possible that reef-associated shark species, particularly larger, highly mobile carcharhinids, were responsible for the majority of depredation that occurred during demersal fishing. This is because fishers mostly targeted reef areas, where lethrinids and epinephelids were more likely to be caught. Indeed, research by Schifiliti (2014) recorded sicklefin lemon *Negaprion acutidens*, pigeye *Carcharhinus amboinensis*, tiger *Galeocerdo cuvier* and blacktip *Carcharhinus limbatus* sharks and *C. obscurus* during baited camera deployments in fished areas of the Ningaloo Marine Park. A number of other studies have also identified the presence of these reef-associated carcharhinid species, such as grey reef *Carcharhinus amblyrhynchos* and blacktip reef *Carcharhinus melanopterus* sharks and *N. acutidens*, in the Ningaloo Marine Park (Speed et al. 2016, Oh et al. 2017). Past research has reported *C. amblyrhynchos* spending a greater proportion of time, and being present in higher densities, in deeper outer-reef slope zones than in shallower reef flat, back reef and lagoon areas, due to habitat type and the presence of stronger currents (Wetherbee et al. 1997, Field et al. 2011, Rizzari et al. 2014a). The fact that shark depredation peaked at 60 m in this study therefore supports the possibility that these reef-associated species were responsible for the majority of depredation in this fishery. It is also possible that *C. obscurus* and *C. plumbeus*, which have been observed to spend large portions of their adult phase in the Ningaloo Marine Park (Braccini et al. 2017), were responsible for depredating recreational catch in this fishery. However, further research is needed to definitively identify the shark species responsible for depredation in this fishery, which would add important context to the spatial variation in depredation rate recorded in this study.

The importance of latitude and its positive linear relationship with depredation in the Exmouth Gulf GAMM (Table 3-3, Fig. 3-2e) may have been linked to change in habitat type from the central Exmouth Gulf to the northern section. This is because there is a transition from shallow (<20 m) bare sand substrate with isolated patch reefs and seagrass beds in the central and southern region of the Exmouth Gulf (higher latitude), to larger and deeper (>20 m) sections of coral substrate and islands in the northern region (lower latitude) (Kenyon et al. 2003). This greater proportion of reef habitat at the northern end of the Exmouth Gulf may have supported a greater abundance and diversity of sharks, thus leading to higher depredation rates. Indeed, habitat influences the distribution and diversity of reef sharks, with closer proximity to reef habitat, greater coral cover and higher structural complexity all leading to higher species richness (Chin et al. 2012, Espinoza et al. 2014). Latitude also has a significant effect on depredation rate in the Portuguese Indian Ocean longline fishery (Muñoz-Lechuga et al. 2016), although this was at a much larger scale and may have reflected the impact of environmental variables such as sea temperature, rather than habitat. Whilst latitude may act as a proxy for certain spatially heterogeneous variables, future work should focus on directly incorporating small-scale habitat and environmental variation and data on shark distribution and abundance into analyses.

Survey period showed an important influence on depredation in the west coast GAMM, with the highest depredation rates in September/October (austral spring) 2015. Similarly, time of year was an important covariate influencing depredation in the US Atlantic longline fishery, with a higher likelihood of depredation occurring in the boreal summer (MacNeil et al. 2009). Our result may reflect the seasonal movement patterns, and therefore localised abundance of shark species responsible for depredation, which can be driven by environmental factors and reproductive cycles. For example, *C. obscurus* and *C. plumbeus* are thought to move southwards from the northern regions of Western Australia in the austral autumn months to give birth (Simpfendorfer et al. 1996, McAuley & Simpfendorfer 2003, McAuley et al. 2005, Braccini et al. 2017), although it is unknown whether these species are responsible for depredating recreational fish catches in the region. Variability in depredation rates over the survey period may have also been caused by changes in fisher behaviour, because wind and tide patterns may determine the accessibility of certain fishing locations at different times of year, influencing fisher site choice (Tink 2015), and thus depredation rates. However, the limited temporal scope and replication of this study, with sampling conducted at discrete periods throughout a single year rather than continuous coverage over multiple years, restricts the confidence with which inferences can be made about these factors.

Fishing effort per trip, time of day and SST had little effect on the number of fish depredated per trip, as indicated by their low relative importance values (Table 3-3). Higher fishing effort in the form of a longer trip might be expected to increase the chance of depredation occurring due to the greater likelihood of attracting sharks, although this was not reflected in the GAMMs. This may have been due to the spatial distribution and abundance of sharks, because areas with a higher abundance of sharks would likely experience depredation early in the trip, whereas in areas where few sharks were present no depredation would occur, regardless of the trip duration. Also, depredation can only occur if hooked fish are available, therefore the number of fish hooked is a more important determinant of depredation than the trip duration. Time of day/night can variably influence different shark species' activity patterns (Nixon & Gruber 1988, Garla et al. 2006), although this variable had little effect on the number of fish depredated per trip in this study, perhaps because the majority of fishing occurred at similar times, with none happening at night. Lastly, SST might be expected to influence depredation, because it also affects the distribution and movement patterns of sharks (Sims et al. 2006, DiGirolamo et al. 2012). However, this variable also had little effect on depredation in the GAMMs. This result could have occurred because multiple shark species were responsible for depredation, thus the thermal ranges and activity patterns of these species would vary, and be influenced by seasonal changes in sea temperature.

3.5.3. Ecological, socio-economic and fisheries management implications

Over long timescales, shark depredation in this fishery may have a negative impact on target fish populations, due to the cumulative total mortality of fish comprising the cryptic mortality caused by depredation, in addition to the mortality derived from fishers retaining fish. This is particularly the case where fishers aim to catch their permitted daily bag limit of five demersal fish per person in this region (DPIRD 2017), because in the process they may lose, on average, an extra 13.7% of hooked fish to shark depredation for west coast boat ramps or 11.5% for Exmouth Gulf boat ramps. Over the thousands of fishing trips that occur in the Ningaloo Marine Park and Exmouth Gulf each year, this extra mortality may be substantial. Sharks can also be impacted through the retention of fishing gear in their jaws and digestive systems, which may occur after they consume a hooked fish and break off the line. Within the study area, sharks were regularly observed with fishing hooks in their jaws (Mitchell et al. *in review*), which can cause abscesses and tissue necrosis in the jaw (Bansemer & Bennett 2010). However, in some cases, retained hooks may fall out naturally or be dislodged when the shark feeds, reducing the likelihood of long-term injury. If fishing hooks are retained in the digestive system, more serious injuries such as perforations of the gastric wall and liver can occur, along with associated bacterial infections (Borucinska et al. 2002). These injuries can cause reduced fitness due to restricted feeding capacity and disease, possibly leading to eventual death (Borucinska et al. 2002, Bansemer & Bennett 2010, Whitney et al. 2012).

Shark depredation may also lead to a number of biological consequences, such as a change in the behaviour and movement patterns of sharks due to the consistent availability of hooked fish to feed on at specific locations where fishing pressure is high. This could result in greater residency and higher densities of sharks in these areas, potentially impacting the abundance of certain prey species and the overall community structure. This form of broader ecological change could have significant long-term effects, particularly in sensitive areas that are specifically managed to protect unique or threatened habitats and fauna in the Ningaloo Marine Park (see CALM & MPRA (2005)). Additionally, the recreational fishing experience may be negatively impacted by depredation, due to the loss of prized fish and fishing gear. Indeed, this study recorded estimated costs for gear lost on fishing trips where depredation events occurred, which ranged from AUD$10 to AUD$200, with a mean value of AUD$38. As a result, the frequency of depredation in this fishery may lead to increased human−wildlife conflict over time, as has been reported in US recreational fisheries where other predators, such as goliath grouper *Epinephelus itajara* (Shideler et al. 2015), California sea lions *Zalophus californianus* (Cook et al. 2015) and common bottlenose dolphins *Tursiops truncatus* (Powell & Wells 2011) depredate hooked fish. In light of this, it is important that further research on shark depredation is undertaken in this and other recreational fisheries, to increase our knowledge of the factors influencing it and to identify measures for reducing its occurrence.

3.5.4. Future research

To improve modelling and analytical approaches, future research should focus on the collection of behavioural, habitat and shark species identity data. There is also a need to expand the temporal and spatial scope of data collection, to provide long-term data on trends in depredation across Western Australia. Such information could be collected through further use of well-designed probability-based access point surveys. Quantifying the proportion of released fish that are consumed by sharks is another important avenue for future research, as this may further increase mortality of recreationally caught fish species. The deployment of video cameras underneath fishing boats and deeper in the water column may enable effective collection of this data. Importantly, cameras could be used to identify shark species responsible for depredation, whilst also assessing the proportion of depredation events caused by taxa other than sharks. Finally, future work should aim to assess the efficacy of a wide range of measures for reducing depredation. Modifications to fishing methods may lead to lower depredation rates, for example using electric fishing reels to allow faster retrieval of hooked fish, especially when demersal fishing at depths >50 m, or only fishing with a single hook on each line, to prevent multiple fish being caught simultaneously. The results of this study suggest that altering spatial fishing patterns may reduce depredation, particularly by avoiding areas where higher depredation rates were recorded, i.e. west of Tantabiddi boat ramp and at the northern end of Exmouth Gulf. However, this strategy relies on finding new fishing sites where depredation rates are low and catch rates for target species are high, in order to make it beneficial for fishers. Spending only a small amount of time at each fishing location (e.g. a maximum of 30 min) before moving to another location will further minimise the predictability of fishing effort, allowing sharks less time to locate and move towards fishing boats and depredate hooked fish. When fishing for demersal species, turning the boat engine off may also reduce the chance of attracting sharks, due to the potential behavioural association discussed previously. Education campaigns to disseminate such information could be an important tool for fisheries management agencies and the recreational fishing industry to help mitigate depredation. Lastly, whilst a range of shark deterrents have been tested for the purposes of improving human safety and reducing shark bycatch, further development and testing of deterrents specifically for use against shark depredation should be prioritised.

3.6. Conclusion

This study provided the first quantitative assessment of shark depredation in a recreational fishery in Australia, identifying both the prevalence of depredation in terms of the percentage of trips affected, and the mean percentage of hooked fish lost. As such, this information provides an important basis for assessing this additional source of mortality for recreationally targeted species, and creates a foundation for future studies to build on in this regionally important fishery. Furthermore, the results of this study indicated that depth, the number of boats fishing within 5 km of each other, survey period, fishing pressure and latitude were important factors influencing depredation rate, providing insights into how fishing strategies can be modified to potentially reduce depredation, and the negative consequences depredation can have for target species, sharks and fishers. On a broader level, this study also offers an important perspective for comparison with depredation in other recreational fisheries and large-scale commercial line-based fisheries around the world, both of which may be impacted by shark depredation.

3.7. Ethics statement

The boat ramp survey conducted for this study was carried out with human ethics approval from The University of Western Australia (approval number RA/4/1/7462).

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Chapter 4: The influence of shark depredation, catch rate and travel cost on fisher site choice in a recreational fishery in Western Australia

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4.1. Abstract

Site choice in recreational fisheries can be strongly influenced by the expected catch rate and the travel cost to reach a particular site, as well as environmental factors. In a recreational fishery within the Ningaloo Marine Park (NMP), Western Australia, shark depredation, where a shark consumes an animal caught by fishing gear, has been shown to occur frequently and at a higher rate adjacent to boat ramps or where other fishers are active. Shark depredation within the NMP has been reported to lead to loss of catch and fishing gear, extra mortality to fish populations, injury to sharks and a decrease in the quality of the recreational fishing experience. This study developed a novel application of Random Utility Models (RUMs) to identify how shark depredation, in addition to catch rate and travel cost, influenced fisher site choice behaviour, using

data collected from boat ramp surveys. As expected, travel cost, which is a proxy for time and distance, had a significant negative influence on fisher site choice, with sites close to the boat ramps being chosen more frequently. This reflected the importance of travel time, which is likely to be a limiting factor for recreational fishers. Additionally, interaction terms of travel cost with vessel length and windspeed had significant effects on fisher site choice, reflecting the ability of fishers to travel further offshore when using larger vessels and in favourable weather conditions.

Unexpectedly, catch rate and depredation rate were non-significant, perhaps because some fishers had limited knowledge of spatial variation in target species' abundance and the occurrence of depredation or because non-catch related motivations were more important. This counter-intuitive finding suggests no impact from shark depredation on recreational fishing utlity, relative to travel and time related cost. Whilst predicted depredation did not influence fisher site choice *ex ante*, it would likely have a negative effect *ex post* on the evaluation of the fishing trip, resulting in fishers seeking to avoid depredation in future. To reduce overall depredation rates, we simulated a fisheries closure of a site adjacent to a boat ramp, where visitation and depredation rates were high. Such a closure could be used to redistribute recreational fishing effort and reduce behavioural association reported to occur between sharks and recreational fishing. Whilst this scenario caused a mean loss in utility equivalent to AUD$1.88 per trip due to greater travel cost, we predicted an increase in net catch rate worth AUD$1.51 per trip, due to lower depredation rates. We also predict an improvement in the quality of the recreational fishing experience due to lower depredation rates, however the response of sharks to this redistribution of fishing effort is unknown and may change over time. This study is the first to utilise RUMs to investigate the influence of shark depredation on recreational fisher site choice, and provides a socio-economic assessment of potential depredation mitigation measures designed to reduce shark-fisher interactions. By demonstrating the application of this modelling approach to the issue of shark depredation, this work aimed to stimulate future use of RUMs in other fisheries, to assess the broader economic impacts of depredation worldwide.

4.2. Introduction

Recreational fishers may choose a fishing location based on a number of characteristics, including the perceived catch rate (McConnell et al. 1995, Hunt 2005, Prayaga et al. 2010, Gao & Hailu 2011), the distance or travel cost, in terms of both time and monetary value that they have to incur to get to a location (Parsons 2003, Camp et al. 2018), and the presence and density of other fishers (Schuhmann & Schwabe 2004). The environmental quality of the location may also be influential (Kaoru et al. 1995, Lipton & Hicks 2003, Hunt 2005). Understanding fisher site choice (where a site could be either a discrete point location, a particular feature such as a reef or shipwreck, or a specific cell within a larger grid of many cells) is important because it enables researchers and fishery managers to assess spatial and temporal variation in biological and ecological impacts from fishing (Hunt 2005, Camp et al. 2018), and investigate the welfare implications of management options (Navarro et al. 2018).

In light of the need to understand fisher site choice, statistical approaches have been developed and tested in marine and freshwater recreational fisheries, to provide quantitative assessments of factors influencing site choice. The most widely used is the Travel Cost Model (TCM) (Hotelling 1947, Ward & Loomis 1986, Smith & Kaoru 1990, Parsons 2003), which has been utilised for non-market valuation of a range of recreational activities (Garrod & Willis 1999, Shrestha et al. 2007, Thiene & Scarpa 2008, Riera et al. 2011). Random Utility Models (RUMs) are a form of TCM that was initially derived by McFadden (1974), which can be used to assess discrete site choices from a set of multiple possible sites (Morey et al. 1991, Blamey 2002, Parsons 2003, Train 2003). These models assume that a person will choose the option that gives them the highest expected utility (Parsons 2003, Hunt 2005). Whilst they can be applied to assessing choices such as which form of transport to use (McFadden 1998, Bachmann et al. 2014), or which product to buy (Eom 1994, Cicia et al. 2002), RUMs have also been used to investigate the factors influencing recreational fishers' site choice globally (Bockstael et al. 1989, McConnell et al. 1995, Whitehead & Haab 1999, Schuhmann & Schwabe 2004, Gao & Hailu 2011, Camp et al. 2018), and in Western Australia (Van Bueren 1999, Zhang 2003, Raguragavan et al. 2013).

Depredation, where a predator partially or completely consumes an animal caught by fishing gear (Gilman et al. 2007, IOTC 2007, MacNeil et al. 2009, Mitchell et al. 2018b), occurs in both commercial and recreational fisheries, and has been reported to be caused by sharks, cetaceans, teleost fishes, squid, pinnipeds, seabirds, octopus and crabs (Bullis 1955, Meyer et al. 1992, Dieperink 1995, Lawson 2001, Donoghue et al. 2003, Brock et al. 2006, Gilman et al. 2006, Briceño et al. 2015, Madigan et al. 2015, Remeslo et al. 2015, Shideler et al. 2015, Mitchell et al. 2018a, Rabearisoa et al. 2018). Depredation by sharks in particular has been reported to result in substantial loss of catch in commercial and recreational fisheries (0.9% - 26%) (Hirayama 1976, Donoghue et al. 2003, Gilman et al. 2007, IOTC 2007, Romanov et al. 2007, Mandelman et al. 2008, Varghese et al. 2008, Labinjoh 2014, Muñoz-Lechuga et al. 2016, Mitchell et al. 2018b), and has been implicated in decreasing the quality of the recreational fishing experience in Western Australia (Mercer 2015, Kagi 2016).

A recent study in the Ningaloo Marine Park (NMP) and Exmouth Gulf, Western Australia, found that shark depredation rates were highly variable over small spatial scales, and that sites adjacent to boat ramps or intense fishing activity had higher rates of depredation (Mitchell et al. 2018a). This may indicate that those sharks involved in depredation have developed a behavioural association between the presence of fishing vessels and the availability of hooked fish to feed on

(Mitchell et al. 2018a). The same behavioural mechanism has also been theorised to occur in other recreational fisheries around the world (McCord & Lamberth 2009, Labinjoh 2014, Madigan et al. 2015). However, the higher rates of depredation in certain areas may also be linked to greater shark abundance. By choosing certain fishing locations over others, recreational fishers may therefore be able to reduce losses of target fish and fishing gear due to depredation to maximise the quality of their recreational fishing experience. Despite this, shark depredation has never been investigated as a variable in recreational fisher site choice modelling.

To identify how shark depredation, catch rate and travel cost (a proxy for distance and time) may influence the site choice of recreational fishers in the NMP, this study utilised RUMs. Approximately 33% of the marine park is closed to boat-based recreational fishing, through sanctuary zones distributed throughout the marine park (CALM & MPRA 2005, Beckley et al. 2010) Furthermore, there are only three public boat ramps which provide access to the marine park along its ~300 km coastline, which therefore determines the site choices available to boat-based recreational fishers. Previous research has investigated site choice of recreational fishers in this marine park (Raguragavan et al. 2013), and how the introduction of closures would affect site choice (Gao & Hailu 2011). It was expected that predicted shark depredation rate would have an influence on fisher site choice, due to the negative impacts it can have in terms of loss of fish and fishing gear and the reported negative impact on the quality of the recreational fishing experience. We predicted that fishers would be expected to actively choose sites where depredation rates were low. Sites with higher catch rates and lower travel costs were also expected to be favoured by fishers, because of the desire to maximise the number of fish caught on the trip in the shortest amount of time. Fishers with a greater knowledge and experience of the local area may be more aware of the occurrence and impact of depredation and the spatial patterns in cath rate, so depredation and catch rate were expected to have an even stronger influence on the site choice of these fishers. The positive effect of catch rate and the negative effect of travel cost have been recorded in previous studies which used RUMs in Western Australia (Van Bueren 1999, Zhang 2003, Raguragavan et al. 2013), and other locations (Kaoru et al. 1995, Schuhmann & Schwabe 2004, Prayaga et al. 2010). Weather conditions and vessel size were also expected to influence the site choice of fishers, because they determine the ability of a fisher to access certain sites, especially those further offshore.

There have been calls in Western Australia for mitigation measures to reduce the impact of depredation on target species, sharks and the quality of the recreational fishing experience (Mercer 2015, Kagi 2016). Various shark deterrents hold potential for mitigation and have been more comphrehensivly investigated as personal safety devices for in-water users (Kempster et al. 2016, Huveneers et al. 2018b), but such devices would likely require extensive development before they can be effectively tested for use for depredation mitigation in recreational fishing (Mitchell et al. 2018b). Shark population control measures would be difficult to employ due to the complexity of shark depredation, which involves multiple shark species (Mitchell et al. *in review*), and given the behavioural adaption implicated in shark depredation this may not directly result in reduced rates of depredation (Mitchell et al. 2018a). Here we investigate the use of fisheries closures at depredation hotspots, to counteract the potential behavioural association of sharks with intense recreational fishing activity, and explore the potential of these closure to reduce rates of depredation across the fishery. These closed areas could be temporary and rotated to areas of high depredation rate as necessary. It would be expected that whilst a site closure would have a negative impact in terms of travel cost, this would be offset by the value of lower depredation rates and therefore an increased net catch rate.

4.3. Methods

4.3.1. Study location

Data were collected between July 2015 and May 2016, at Coral Bay (23.16˚S, 113.77˚E) and Tantabiddi (21.91˚S, 113.98˚E) boat ramps, which are located within the Ningaloo Marine Park (NMP), Western Australia. The NMP contains the ~260 km long, north-south oriented Ningaloo Reef, which is a fringing reef system bounded by shallow lagoons close to the coast, and steep drop-offs at the reef edge (CALM & MPRA 2005). Recreational fishing is popular in this region, especially between April and October (Sumner et al. 2002, CALM & MPRA 2005, Williamson et al. 2006).

4.3.2. Boat ramp survey data

Data were collected through a survey of 185 recreational fishers at Tantabiddi (92 fishers) and Coral Bay (93 fishers) boat ramps, following the methodology described by Mitchell et al. (2018a). Here, we only consider those fishers interviewed who targeted mixed demersal fish species, particularly lethrinids and epinephelids, with baited hooks set on or near the seabed. Data collected at Bundegi and Exmouth marina boat ramps during these previous surveys was not used in the current study, due to their smaller sample size.

4.3.3. Random Utility Model

In this study we used RUMs to analyse how site choice is influenced by both individual fisher characteristics (e.g. age, income, employment status, fishing experience) and site characteristics (e.g. depth, distance from access point, benthic habitat type) (Parsons 2003, Hunt 2005, Raguragavan et al. 2013). The benefit of using RUMs with recreational fishing data is that they provide both an indication of whether these factors have a significant positive or negative effect on fisher site choice, as well as a means to provide a monetary value of that effect relative to the travel cost. In the context of recreational fishing data, RUMs are designed to describe a site choice situation where a fisher ***i*** has a set of ***j*** sites that they can choose between (Bockstael et al. 1989, Morey et al. 1991, Lipton & Hicks 2003, Gao & Hailu 2011, Raguragavan et al. 2013). The utility U_{ij} obtained by fisher ***i*** when visiting site ***j*** depends on a vector of site characteristics s_{ij} (such as travel cost and catch rate), and a vector of individual-specific attributes z_i (Bockstael et al. 1989, Lipton & Hicks 2003, Raguragavan et al. 2013). The RUM assumes that fisher ***i*** will choose site ***j*** if it has a higher utility than all of the other possible sites (Lipton & Hicks 2003, Hunt 2005, Gao & Hailu 2011). However, in addition to this observable deterministic component (***V***), the utility of a site also contains an unobservable, random component ε_{ij}, which is unknown to the researcher (Parsons 2003, Raguragavan et al. 2013). The RUM is, therefore, designed to also incorporate this unobservable component alongside the deterministic component (Parsons 2003, Hunt 2005). The utility of a site in a RUM is thus characterised in the following way:

$$U_{ij} = V(s_{ij}, z_i) + \varepsilon_{ij} \tag{1}$$

The most common form of RUM used is the multinomial logit (McFadden 1974, Parsons 2003, Hunt 2005, Raguragavan et al. 2013), which assumes that the random component (ε_{ij}) is independent and has a Type-1 extreme value distribution (Morey et al. 1991, Lipton & Hicks 2003, Gao & Hailu 2011). Using this approach, the probability $prob_{ij}$ that fisher ***i*** selects site ***j*** in the deterministic component (***V***) of equation 1 (i.e. not including the error term), is expressed as:

$$prob_{ij} = \frac{\exp(V_{ij})}{\sum_{j=1}^{J} \exp(V_{ij})} \tag{2}$$

This form was used for the current study due to its straightforward approach for estimating maximum likelihood, compared to other forms such as nested or mixed logit models (Heiss 2002, Parsons 2003, Croissant 2010). The site-specific attributes chosen for inclusion in the RUM in this study were travel cost (***tc***), predicted catch rate (***cr***; total no. fish hooked per hour), predicted depredation rate (***dr***; number of fish depredated per hour) and depth (***de***). Individual-specific metrics, which included local fishing experience (***lf***; categorical from 1 = low (0-20 times) to 5 = high (81-100+ times) for how many times the fisher had fished from that boat ramp before), frequency of fishing (***fr***; categorical from 1 = low (0-20 times) to 5 = high (81-100+ times) for how many times the fisher had fished from a boat in the last 12 months) and vessel length (***vl***), were also analysed in the RUM, by interacting these terms with the site-specific variables. The daily value for deviation from mean windspeed (***dmws***) was interacted with travel cost to allow for the possibility that environmental factors may alter the marginal (dis)utility associated with distance travelled. The deterministic component (V) of the final RUM was therefore computed as:

$$V_{ij} = \beta tc_{ij} + \beta cr_{ij} + \beta dr_{ij} + \beta de_j + \beta cr_{ij}*lf_i + \beta dr_{ij}*lf_i + \beta cr_{ij}*fr_i + \beta dr_{ij}*fr_i + \beta tc_{ij}*vl_i + \beta tc_{ij}*dmws \quad (3)$$

where β = coefficient value for each variable in the RUM. The RUM was run in the R language for statistical computing (R Development Core Team 2015), using the ‘mlogit’ package (version 0.2-4) (Croissant 2010).

4.3.4. Change in welfare under a closure scenario

To assess the change in recreational fisher welfare under a scenario where a site is closed as a management measure to reduce shark depredation, the following equation, which has been applied in other studies using RUMs (Small & Rosen 1981, Lipton & Hicks 2003, Schuhmann & Schwabe 2004, Raguragavan et al. 2013), was used:

$$\mathbf{CV} = -\frac{1}{\beta}\left[\ln\left(\sum_{j=1}^{J-1} \exp V_j(q^1)\right) - \ln\left(\sum_{j=1}^{J} \exp V_j(q^0)\right)\right] \quad (4)$$

where CV = Compensating Variation or change in welfare, calculated as a \$ value, β = the coefficient value for travel cost produced by the RUM, V_j is the utility (deterministic component only) of site j and q^0 and q^1 are the site attributes before and after the closure, respectively. The CV values were calculated based on the most parsimonious RUM, which only included the variables that were significant. A sample average CV value was generated by taking the mean of the CV values for all of the 92 fishers who launched from Tantabiddi boat ramp. The site which was closed under this scenario (located at 21.91˚S, 113.91˚E) had a high visitation rate (chosen by 44 out of the 92 fishers who launched from Tantabiddi) and was close to the boat ramp, therefore having a low travel cost. This site also had high depredation rates, likely because of a behavioural association occurring in sharks in this area, where they associated the regular presence of vessels with the availability of hooked fish to depredate (Mitchell et al. 2018a).

Closing this site would therefore be expected to lead to lower overall depredation rates across the Tantabiddi site choices, and thus an increase in net catch rate. However, this involves a number of key assumptions. Firstly, the closure is based on the theory that behavioural associations in sharks are occurring at this site and are leading to higher depredation, rather than it being driven by a greater abundance of sharks in this area. Once the closure is introducted, we assume that these behavioural associations will not occur in other sharks in different locations outside the closed area, or that the sharks which have formed behavioural associations within the closed area will not simply follow vessels and move outside of it. The latter would depend on the shark species involved and their respective home ranges and movement patterns. The effectiveness of the closure also involves the assumption that other suitable fishing locations are available outside the closed area, which would have high enough catch rates to be of benefit to fishers.

To quantify the value of an increased net catch rate, the site choice probability values produced by the RUM for each of the 27 site choices for each fisher, were used in the following equation:

$$\mathbf{ncv}_{\boldsymbol{ij}} = \left[\left(\boldsymbol{RUMprob^{1}_{ij}}\left(\boldsymbol{cr^{t}_{ij}} - \boldsymbol{dr^{t}_{ij}}\right)\right) - \left(\boldsymbol{RUMprob^{0}_{ij}}\left(\boldsymbol{cr^{t}_{ij}} - \boldsymbol{dr^{t}_{ij}}\right)\right)\right] * \mathbf{9.47} \tag{5}$$

where $\boldsymbol{ncv_{ij}}$ = value of the change in net catch rate after site closure, for each each fisher (***i***) at each site (***j***), $\boldsymbol{RUMprob^{1}}$ = probability value generated by the RUM after the site is closed, $\boldsymbol{RUMprob^{0}}$ = probability value generated by the original RUM before site closure, $\boldsymbol{cr^{t}}$ = total number of fish hooked per trip, $\boldsymbol{dr^{t}}$ = number of fish depredated per trip. The per trip values for ***cr*** and ***dr*** were calculated by multiplying the per hour values by the mean trip duration of 4.77 hours. The value 9.47 represented the dollar value per fish generated by Raguragavan et al. (2013) for reef fish, and was used to convert the value of change in net catch rate before and after the site closure into a monetary value. This dollar value per fish was calculated from the ratio of the RUM coefficients for expected catch rate and travel cost, and thus reflected the trade-off between these two variables (Raguragavan et al. 2013). The value from Raguragavan et al. (2013) was used instead of calculating the equivalent value using the RUM in the current study, because the catch rate term was non-significant and therefore the ratio between catch rate and travel cost would not be meaningful. The mean ***ncv*** value across all sites for all fishers was then taken as the final dollar value of increased net catch, which allowed comparison with the CV value for the site closure. However, this comparison must be viewed with caution due to the differences in the way the CV and *ncv* values were calculated.

4.3.5. Data included in the Random Utility Model

4.3.5.1. Site choice locations

Site choice locations for the RUM were selected based on the distribution of the demersal fishing locations recorded in boat ramp surveys (Fig. 4-1). Demersal fishing was the only fishing method considered, because trolling, which was the other main fishing method in this fishery (Mitchell et al. 2018a), involved vessels covering a large area. Therefore, it was not site-specific and did not match the assumptions for RUM modelling. A grid of points spaced at 0.1˚ x 0.1˚ degrees of latitude and longitude was created, covering the area in which all of the 185 demersal fishing locations were reported. This grid was then extended 0.05˚ beyond the furthest North, South and

West fishing locations, to allow for fishing which may have occurred beyond the spatial area recorded during boat ramp surveys. All points north of 22.55˚S were considered to be the Tantabiddi choice set, and all points south of this were in the Coral Bay choice set. Any of the locations in the 0.1˚ x 0.1˚ grid that had a depth >600 m were removed, as it was considered to be highly unlikely that recreational fishers would fish at these depths, because the deepest fishing location in the surveys was 500 m. The final grid therefore contained 81 site choice locations, with 27 for Tantabiddi boat ramp, and 54 for Coral Bay boat ramp (Fig. 4-1). The site chosen by each of the 185 fishers was determined to be the 0.1˚ x 0.1˚ point in the grid that was closest to the real location that fisher chose, i.e. each 0.1˚ x 0.1˚ point represented an area of approximately 6 nm^{-2} (~11 km^{-2}), within which the real fishing locations were located in order to be attributed to that point.

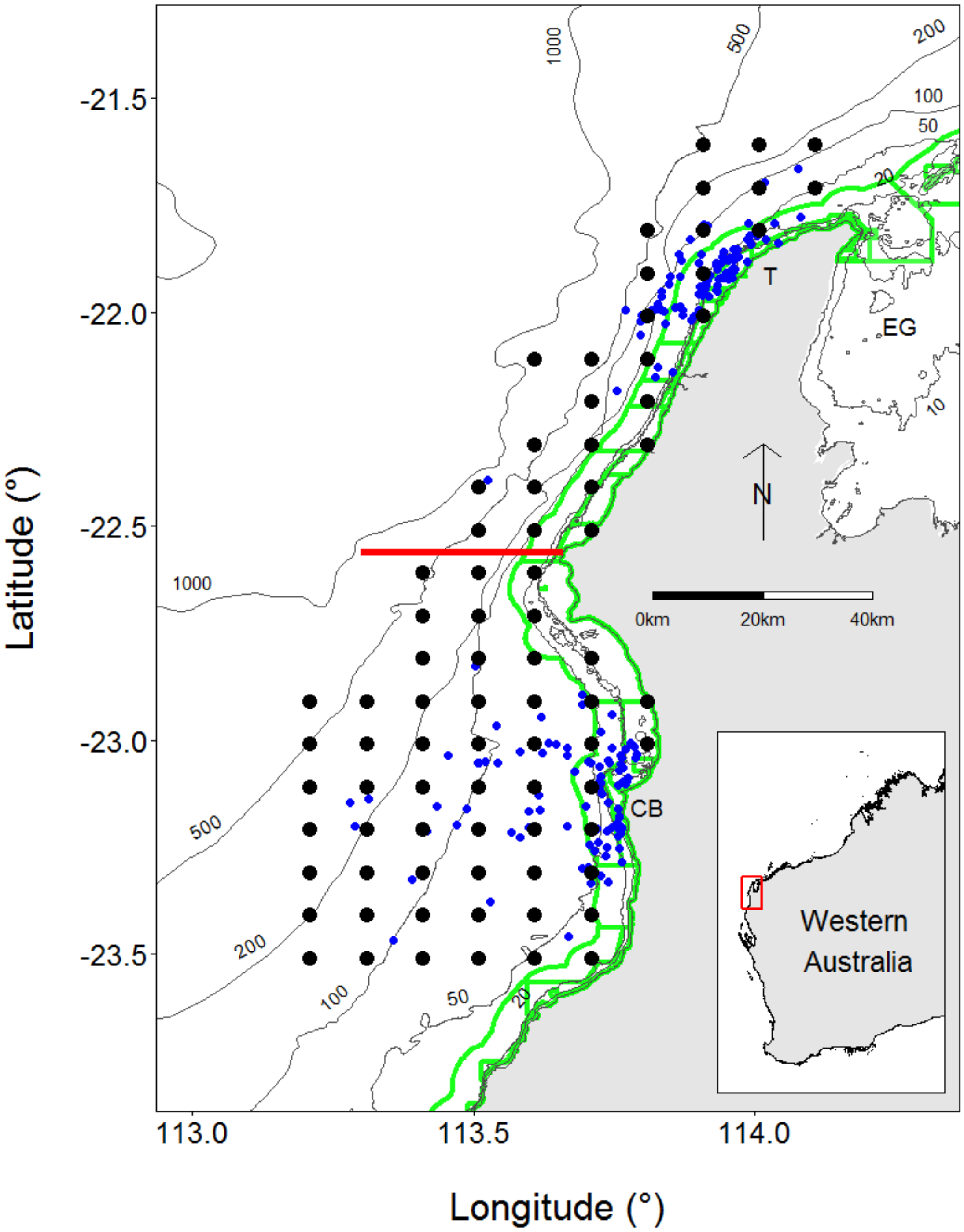

Fig. 4-1: Map of the 81 simulated site choice locations (black points) used for the Random Utility Model (RUM), with 27 for Tantabiddi boat ramp (T), which are north of the solid red line, and 54 for Coral Bay boat ramp (CB), south of the red line. The 185 fishing locations recorded in boat ramp surveys are shown as blue points. Labelled contour lines show depth in metres. Solid green lines indicate the boundary of the Ningaloo Marine Park (NMP). EG = Exmouth Gulf. Inset map shows the location of the study site in Western Australia.

4.3.5.2. Environmental data

Sea Surface Temperature (SST) data were acquired from The US National Oceanic and Atmospheric Administration (NOAA 2016). The data were high-resolution Optimum Interpolation (OI) of SST (see Reynolds et al. (2007)), collected by an Advanced Very High Resolution Radiometer (AVHRR) on polar orbiting satellites (NOAA 2016). Daily mean SST values were extracted, with a spatial resolution of 0.25° x 0.25° (NOAA 2016). A mean SST value across all of the 40 boat ramp survey sampling days was generated for each of the spatial locations that were to be used as site choices in the RUM.

A habitat type classification for each of the site choice locations was obtained from the Ningaloo Atlas (AIMS 2016). The site choice locations were in five different habitat types – 'Coral reef communities', 'Mixed filter feeding communities', 'Bare reef', 'Sand' and 'Pelagic' (AIMS 2016). These categories were assigned values of one to five, respectively. For deepwater locations which were unclassified in the Ningaloo Atlas, a value of five (corresponding to the 'Pelagic' category) was assigned, because these deepwater sites were adjacent to the areas classified as 'Pelagic' in the Atlas.

Depth data for the site choice locations were obtained from the General Bathymetric Chart of the Oceans (GEBCO) 2014 Grid, version 20150318 (GEBCO 2015). This dataset is a continuous global grid of depth data, with a spatial resolution of 30 arc-seconds (GEBCO 2015, Weatherall et al. 2015). Depth values were derived from verified ship-based soundings, with interpolation to areas with no data based on satellite-based gravity data (GEBCO 2015, Weatherall et al. 2015).

Windspeed data for Learmonth (~40 km from Tantabiddi and ~100 km from Coral Bay) was obtained from The Australian Government Bureau of Meteorology (BOM) Daily Weather Observations (BOM 2018). A daily mean windspeed value for each day where survey data collection took place was calculated from the 9am and 3pm values recorded in the Daily Weather Observations (BOM 2018). The deviation of each daily windspeed value from the overall mean windspeed across all survey days, was then generated for use in the RUM.

4.3.5.3. Travel cost data

Travel cost values for all of the site choice locations were generated, based on their distance from the boat ramp. This distance was then multiplied by a nominal value of AUD$0.5 per km. Travel distance was given a monetary value in this way to enable direct assessment of the economic costs to fishers. The value of AUD$0.5 per km was chosen because it represented an average fuel cost for a 5.1 m fibreglass recreational vessel with a 90 horsepower outboard engine, travelling at a speed of 35 kmh. This was representative of the vessels surveyed at boat ramps, which all had outboard engines and ranged from 3 m to 9 m in length, with a mean of 5.5 m. At 35 kmh, the engine would use 0.33 litres of fuel per km (best case scenario) (Honda 2009), with fuel costing approximately AUD$1.5 per litre in this location (Fuelwatch 2015). This would therefore equate to a cost of AUD$0.5 per km. The total travel cost incorporated this cost per km for both the outward and return trips to and from the site to the boat ramp. Whilst some studies have calculated the travel cost from fishers' home location to the fishing location (Kaoru et al. 1995, Lipton & Hicks 2003, Schuhmann & Schwabe 2004, Raguragavan et al. 2013), this was not possible in the current study, because no home location information was collected for the fishers interviewed during the boat ramp survey. As a result, the RUM presented here is conditional upon the assumption that fishers will fish in the NMP region at the particular ramp chosen, and the choice of sites is conditional upon being in this region i.e. it does not consider choice at the broader regional level.

4.3.5.4. Generating predicted values of catch rate and depredation rate

Although previous studies have modelled fishers' expected catch rates for different sites in RUMs (McConnell et al. 1995, Lipton & Hicks 1999, Van Bueren 1999, Schuhmann & Schwabe 2004), this study did not collect data on expected catch rates, therefore a different approach was used. It is important to note that the RUM requires an estimate of predicted catch rates, for each fisher, at all sites, not just those at which they fished. Generalised Additive Models (GAMs) (Hastie & Tibshirani 1986, Wood 2006) were, therefore, applied to generate predicted values of catch rate and depredation rate, which were based on actual values reported by fishers at Tantabiddi and Coral Bay boat ramps, during surveys by Mitchell et al. (2018a). Raguragavan et al. (2013) also used a predictive modelling approach to estimate catch rate in this way.

4.3.5.4.1. Generalised Additive Model for catch rate

The total fish hooked per hour was used as the response variable in the catch rate GAM. A range of error distributions were tested to find the most appropriate for this dataset. Negative binomial distribution was identified to be the most suitable for the response data, based on goodness of fit metrics, specifically the distribution of model residuals and the relationship between real and fitted values. This was due to the fact that the data was low-skewed, with many zeros and ones, as well as being over-dispersed. Negative binomial distribution has been widely used in GAMMs for modelling fisheries data that is over-dispersed (Bannerot & Austin 1983, O'Neill & Faddy 2003, Venables & Dichmont 2004, Irwin et al. 2013, Raguragavan et al. 2013). A wide range of predictor variables (see Table A1 in appendices) were tested in the GAM to assess which variables accounted for the highest percentage deviance explained, and therefore produced the model with the best predictive power and robustness. A forward stepwise process was used to identify predictor variables that explained >5% of deviance in the response, and which reduced the model Akaike Information Criterion (AIC) (Akaike 1974) value. Correlation between predictor variables was assessed, to ensure that all variables had Spearman rank correlation coefficients <0.5, as suggested by Booth et al. (1994) and Zuur et al. (2009). Any combination of predictor variables with coefficients >0.5 were therefore excluded from the GAM. Cubic regression spline smoothing was used for the continuous predictor variables. The best-fitting model that was generated had the following form:

Total fish hooked per hour = No. vessels within 5 km + Total hours fishing + No. years fishing + Lat, Long + Habitat type + No. days boat fishing in last year (6)

This model explained 31.7% of the deviance in the response (see Table A2 in appendices for the GAM output table showing variable coefficients and p-values), and the fit and robustness of the model was verified using visualisation of residual plots, which showed a normal distribution of the residuals, independent data points and an appropriate level of fit between the observed and fitted response values.

To generate predicted values of total fish hooked per hour, this GAM was applied to a new dataset, which contained values for all of the predictor variables for all 185 fishers, for each site within their choice set. This included the site-specific values for latitude, longitude and habitat type, and the individual-specific values for the number of vessels within 5 km, the total number of hours fishing, the number of years of fishing experience and the number of days of boat fishing in the last year. The predicted catch rate values were then used in the RUM.

4.3.5.4.2. Generalised Additive Model for depredation rate

The response variable for the depredation rate GAM was the number of fish depredated per hour, which was highly low-skewed due to many zero datapoints, and had a large range of values. Tweedie distribution (Tweedie 1984) was therefore used, because it was more effective than other distributions at handling the high level of zero-inflation in the data. A number of other fisheries studies have used this distribution to model zero-inflated catch rate data (Candy 2004, Shono 2008, Tascheri et al. 2010, Coelho et al. 2016). The same range of predictor variables were tested as in the catch rate GAM, using the same approach. This produced a best-fitting model with the following structure:

No. fish depredated per hour = Depth + Total fish hooked per hour + Vessel length + No. years fishing + Lat, Long + Habitat type (7)

This model explained 60.6% of the deviance in the response (see Table A3 in appendices for the GAM output table showing variable coefficients and p-values), and the fit and robustness of the model was verified using the same techniques as the catch rate GAM. Predicted values of the number of fish depredated per hour were produced by running the GAM with a new dataset, which included all site choice locations for each fisher, incorporating site-specific values for depth, latitude, longitude and habitat type, and individual-specific values for vessel length and the number of years of fishing experience. The individual-specific predicted values of total fish hooked per hour from the previous GAM, were used in this new dataset for predicting the depredation rate. The new predicted values for the number of fish depredated per hour generated by this GAM were then fed into the RUM.

GAMs were run in the R language for statistical computing (R Development Core Team 2015), using the 'mgcv' package (version 1.8-4) (Wood & Scheipl 2015).

4.4. Results

From the 92 fishers launching from Tantabiddi boat ramp, 10 of the 27 site choice locations in the RUM consideration set were selected at least once, with the most popular site (located at 21.91˚S, 113.91˚E - see Fig. 4-2) receiving 44 visits. The majority of the other sites received much fewer visits. For Coral Bay boat ramp, 23 of the 54 sites were selected by fishers, with the site located at 23.21˚S, 113.71˚E receiving the most visits (20).

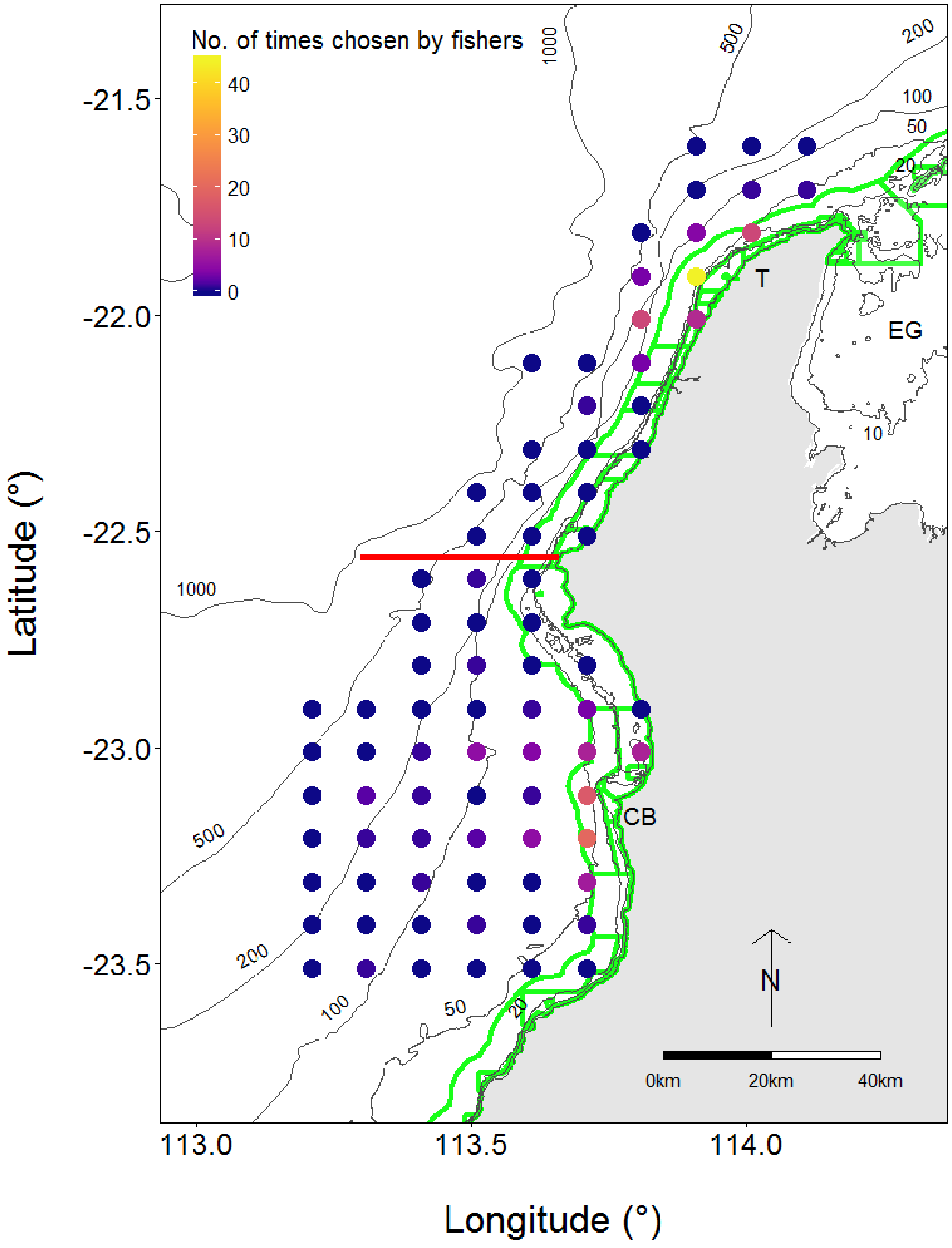

Fig. 4-2: Map of the 81 simulated site choice locations used for the Random Utility Model (RUM) and the number of times that each site was chosen by fishers, as indicated by the colour scale. The 27 points north of the solid red line represent the site choices for Tantabiddi boat ramp (T), and the 54 points south of the line are the site choices for Coral Bay boat ramp (CB). Labelled contour lines show depth in metres. Solid green lines indicate the boundary of the Ningaloo Marine Park (NMP). EG = Exmouth Gulf.

Travel cost and depth had a notably large range of values, from AUD$6.99 to AUD$81.89 and 1 m to 591 m, respectively (Table 4-1). The total number of fish hooked per hour ranged from 0.42 – 15.78, with a mean of 2.75, whereas the number of fish depredated per hour was notably lower, from 0.01 – 7.86, with a mean of 0.53.

Table 4-1: Descriptive statistics for variables used in the Random Utility Model (RUM).

Variable name	Mean	Std. Dev.	Min.	Max.
Travel cost (return) (AUD$)	40.96	18.16	6.99	81.89
Total number of fish hooked per hour	2.75	1.72	0.42	15.78
Number of fish depredated per hour	0.53	0.69	0.01	7.86
Depth (m)	154.13	138.34	1.00	591.00
Vessel length (m)	5.51	1.34	3.00	9.00
Deviation from mean windspeed (km h^{-1})	-2.52	5.80	-12.11	10.89

Travel cost had a significant ($p <0.01$) and strong negative effect on site choice (Table 4-2), with the largest value of all the coefficients (-0.38). The total number of fish hooked per hour (catch rate) had a non-significant influence on site choice, as did the number of fish depredated (depredation rate). Depth also had a non-significant effect. Both of the interaction terms including local fishing experience produced non-significant coefficient values, as did those where frequency of fishing was interacted with catch rate and depredation rate. There was a significant ($p < 0.01$) positive interaction between vessel length and travel cost (0.04), whereas there was a significant ($p <0.01$) negative interaction of travel cost and deviation from mean windspeed was negative (-0.01).

Table 4-2: Variables included in the Random Utility Model (RUM), with their coefficients, standard errors, t- and p-values. Variables labelled with a '*' were significant at the 99% level (p-value = <0.01).

Variable name	Coefficient	Std. Error	t-value	p-value
Travel cost (return)	-0.38	0.05	-8.15	<0.01*
Total number of fish hooked per hour	0.05	0.18	0.28	0.78
Number of fish depredated per hour	-0.02	0.53	-0.03	0.98
Depth	-0.001	0.002	-0.34	0.74
Total number of fish hooked per hour * local fishing experience	-0.04	0.05	-0.72	0.47
Number of fish depredated per hour * local fishing experience	-0.20	0.15	-1.30	0.19
Total number of fish hooked per hour * frequency of fishing	-0.04	0.06	-0.62	0.53
Number of fish depredated per hour * frequency of fishing	0.14	0.18	0.75	0.46
Travel cost (return) * vessel length	0.04	0.01	5.29	<0.01*
Travel cost (return) * deviation from mean windspeed	-0.01	0.002	-5.58	<0.01*

The hypothetical fisheries closure (indicated by the red 'X' in Fig. 4-3b), implemented as a management action to redistribute fishing effort away from the shark depredation hotspot adjacent to Tantabiddi boat ramp, had an overall mean negative impact on the utility of fishers of AUD$1.88 per trip, whereas the mean negative cost for just the fishers which visited this site would be AUD$2.29 per trip. This site received 44 visits and had a return travel cost of AUD$6.99. The predicted redistribution of fishing effort resulting from this fisheries closure indicated that the majority of fishers would choose sites that were relatively close to to the proposed closure (Fig. 4-3b), to minimise travel cost. As a result of the lower predicted depredation rates and higher catch rates at these adjacent sites, we predicted a mean increase in net catch rate as a result of the closure, which was equivalent to AUD$1.51 overall, but this was higher (AUD$1.74) for those fishers that originally chose the closed site.

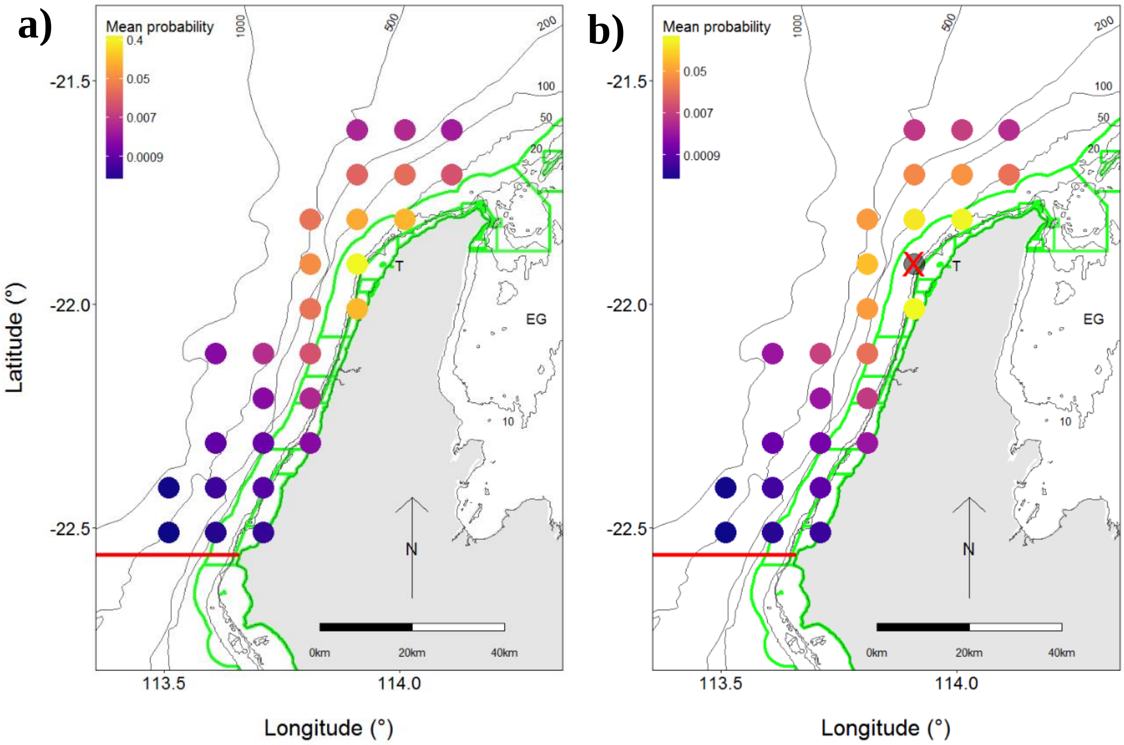

Fig. 4-3: Map of the mean (calculated across the 92 fishers who launched from Tantabiddi boat ramp (T)) site choice probabilities (indicated by colour scale) generated by the Random Utility Model (RUM) for the 27 Tantabiddi site choices **a)** before and **b)** after a site adjacent to Tantabiddi boat ramp is closed (site marked with a red 'X'), which represents the predicted redistribution of fishing effort after the closure. Solid red line indicates the southern extent of the Tantabiddi site choice locations used in the RUM. Labelled contour lines show depth in metres. Solid green lines indicate the boundary of the Ningaloo Marine Park (NMP). EG = Exmouth Gulf.

4.5. Discussion

Fishers covered a broad spatial area when choosing fishing locations in the NMP, travelling up to approximately 80 km from the boat ramp, although the majority (~70%) of fishing effort was concentrated close to (within a 15 km radius) Tantabiddi and Coral Bay boat ramps. This is particularly true for the former boat ramp, where a high number of fishers chose sites along the reef that were adjacent to the boat ramp. Conversely, whilst fishers launching from Coral Bay boat ramp also showed clustering in areas close to the boat ramp, they covered a greater space overall, travelling further offshore. Previous research has identified similar patterns of recreational fishing effort in the NMP, particularly with concentrations close to Tantabiddi boat ramp (Sumner et al. 2002, Smallwood & Beckley 2012). The fact that many fishers launching from these boat ramps were tourists, some of which would only have limited local knowledge of potential fishing sites, may have contributed to this clustering of fishing close to the boat ramps. Understanding these site choices is important for marine park and fisheries management, because the NMP is a key location for fishers targeting demersal species in the north-west of Australia (Sumner et al. 2002, Westera et al. 2003, Ryan et al. 2017). The value of recreational fishing in this region has been highlighted by Raguragavan et al. (2013), who found that Coral Bay and Exmouth (the two settlements serving the NMP), had the highest access values (AUD$14.46 and AUD$13.31 per trip, respectively) for recreational fishers out of 48 sites surveyed across Western Australia.

It has been suggested that sharks are forming behavioural associations between the presence of recreational fishing vessels and the availability of hooked fish to feed on in these regularly fished areas (Mitchell et al. 2018a). This is reflected by previous research, which identified an overlap between the area of highest fishing pressure and higher depredation rates, as well as the fact that measures of fishing pressure have been found to be important for predicting the number of fish depredated (Mitchell et al. 2018a). One potential option for mitigating depredation could be the creation of small, temporary fisheries closures in depredation hotspots, which would redistribute fishing effort away from areas of high depredation and potentially reduce the process of behavioural association occurring in these areas. These closed areas could be moved to new locations on an adaptive basis, if future fisher surveys indicated that depredation rates had increased in other areas. However, determining the necessary timeframe for these temporary closures to result in the breakdown of behavioural associations in the depredating sharks would be difficult. It is possible that the areas would need to be closed for at least one year, although research conducted in small periodically harvested closures found that timeframes of ~6 months were enough to increase naivety in small reef fish to the extent that their flight initation distance decreased and they were markedly easier for spearfishers to catch (Januchowski-Hartley et al. 2011, 2014). But, the learning processes in these small reef fish compared to large sharks are likely to be different, although the results do provide some insight into the possibility of using closures to change fish behaviour. These closures could be self-policed by fishers, because peer judgement and social norms have been shown to have a powerful influence on the likelihood of fishers following regulations (Thomas et al. 2015, Mackay et al. 2018).

The adoption of these closures may only be temporarily successful, depending on the movement patterns of the sharks responsible for depredation, which have been reported to be carcharhinid species, including sicklefin lemon *Negaprion acutidens*, blacktip/Australian blacktip *Carcharhinus limbatus/tilstoni*, grey reef *Carcharhinus amblyrhynchos* and spottail *Carcharhinus sorrah* sharks (Mitchell et al. *in review*). Whilst reef shark species such as *C. amblyrhynchos* and *N. acutidens* have been found to be resident within single reef systems or atolls year round (Filmalter et al. 2013, Espinoza et al. 2014, Heupel & Simpfendorfer 2015), and have relatively small activity spaces of <5 km^2 (McKibben & Nelson 1986), they can still undertake long distance movements >100 km (Heupel et al. 2010). The activity centre of *C. amblyrhynchos* in the Ningaloo region was found to be 19.6 km^2 (Speed et al. 2016). *C. limbatus*, which is classed as a coastal species (Compagno et al. 2005), has been recorded to have cumulative home ranges of 1.2-6.2 km^2, although this data was from juvenile animals (Heupel et al. 2004). *C. tilstoni* and *C. sorrah* tagged in Northern Australia, however, have been recorded moving >1000 km from their oringal capture location (Stevens et al. 2000). Therfore the closure, which represented an area of ~11 km^2, may be large enough to partially cover the home range area of the shark species found to be responsible for depredation, but may not cover their larger scale movements. It must also be considered that sharks in other areas may depredate hooked fish on an opportunistic basis, not just due to the occurrence of behavioural associations. A voluntary closure was trialled in the Protea Banks fishery in Kwa-Zulu Natal, South Africa, in an attempt to reduce shark depredation for recreational and charter fishers, but many fishers disregarded the closure, making it unsuccessful (Labinjoh 2014). It is, therefore, suggested that fisheries closures to mitigate shark depredation are applied as management actions by the state fisheries and marine park management agencies, rather than as a voluntary measure.

The RUM in this study has provided a detailed quantification of fisher site choice in the NMP. Travel cost was the most important factor, and had a significant negative influence on site choice, a pattern which has been reported in other studies that have applied RUMs to recreational fisheries data (Bockstael et al. 1989, McConnell et al. 1995, Van Bueren 1999, Whitehead & Haab 1999, Zhang 2003, Schuhmann & Schwabe 2004, Gao & Hailu 2011, Raguragavan et al. 2013, Camp et al. 2018). Whilst travel cost was significant in the RUM, this variable is a cost-based representation of travel distance, which is the true driver of site choice, because many fishers may not want to travel too far from the boat ramp due to time constraints on their fishing trip. The is especially the case for fishing parties with children, many of whom were surveyed in this study due to the data being collected predominantly during school holiday periods. The small cost associated with travelling further to a fishing location would be negligible when considering the thousands of dollars most fishers would likely have spent on land travel, vehicle and vessel maintenance and accommodation, to fish in the NMP, as many fishers travel >1000 km from Perth, or other states of Australia, to fish in this area (Wood & Glasson 2005, Jones et al. 2009, Beckley et al. 2010). However, these broader costs were not considered in the current RUM because no data was available on land-based travel costs. Therefore, the model only represented the estimated costs conditional upon fishers deciding to fish in this region, and from the particular boat ramp they chose.

The interaction between travel cost and vessel length produced a positive and significant coefficient in the RUM, indicating that distance and travel time had a lower marginal disutility for fishers with larger vessels. This likely reflects that larger vessels typically travel faster and can reach sites further offshore in less time. Additionally, larger vessels have greater stability and are able to handle adverse sea conditions better, thus enabling them to reach offshore sites more safely and efficiently. The influence of weather conditions on site choice was represented by the negative and significant result for the interaction between travel cost and deviation from mean windspeed, which indicated that higher windspeeds increase the disutility of distance. This meant that fishers would be less likely to travel further from the boat ramp when windspeeds were higher, as would be expected due to the increased difficulty and risks associated with doing so.

The fact that shark depredation had no effect on site choice was unexpected, and perhaps occurred because the majority of fishers had limited knowledge of how to avoid depredation on a spatial basis, or that they made a conscious decision to keep fishing in that location despite suffering depredation. Fishers may have perceived that depredation was equally likely to occur regardless of the site chosen, when in fact it can be highly spatially variable (Mitchell et al. 2018a). This would be especially likely for inexperienced fishers who had travelled to fish in the NMP from other regions. Depredation may, therefore, not have influenced fishers' site choice *ex ante*, but it likely had a negative effect *ex post*. Previous research by Swait et al. (2004), in Western Australia, demonstrated that by incorporating past behaviours and pereptions, as well as changes in behaviour over time, a more detailed and informative assessment of how different factors influence site choice can be produced. Future research could therefore investigate how changes in perceptions and knowledge of shark depredation influences site choice over time, in response to education and dissemination of information relating to the spatial variation of depredation rates.

Another potential reason why depredation had no effect on site choice in the RUM in the current study, is that fishers selected sites based on the presence of certain habitat which supports the mixed reef fish species they were targeting, as many fishers use their echosounder to locate suitable fishing habitat. These sites may have greater abundances of target species such as epinephelids and lethrinids due to the presence of certain benthic habitat types, but also more sharks, therefore leading to higher depredation rates. In support of this, habitat has been shown to have an important effect on the relative abundance of shark species identified to be responsible for depredation in this fishery, particularly *C. amblyrhynchos* (Wetherbee et al. 1997, Field et al. 2011, Rizzari et al. 2014b, Mitchell et al. *in review*). If sites with suitable fishing habitats were also relatively close to the boat ramp, then this combination of factors may have resulted in the fisher choosing to fish at that site, even if they knew depredation may occur there.

The high level of spatial variation in shark depredation rates recorded by Mitchell et al. (2018a), and the presence of discrete areas where shark depredation rates were higher, highlights the possibility that spatial management measures could be adopted to mitigate depredation. The hypothetical fisheries closure scenario investigated in this study indicated that closure of the site closest to the boat ramp, which had the highest visitation but also a high depredation rate, would negatively impact fishers, due to the increased costs incurred by having to travel further. This negative impact was higher for those fishers which chose this site, as would be expected, because this site had highest utility for them. The welfare change values produced in this study were similar, but lower, than some of the site closure costs reported by Raguragavan et al. (2013). However, these closures represented the cost of closing an entire boat ramp or fishing area, which would be expected to have a greater negative impact, and the sites we investigated in the NMP were small and relatively close together, resulting in minimal variation in utility between sites. Conversely, the cost values for closures reported by Van Bueren (1999) and Zhang (2003), for the majority of locations across Western Australia, were lower than the current study, although these studies did not include sites in the NMP. In the broader literature, where RUMs have been applied in other recreational fisheries around the world, the cost values are generally greater than the current study (Morey et al. 1991, Kaoru et al. 1995).

Although the effect of implementing such a fisheries closure may have a negative impact on travel cost, it could lead to lower depredation rates across the fishery, which fishers may value *ex post* if not *ex ante*, due to the reduction in behavioural association in sharks. This was partially reflected by the value of the increase in net catch rate after the redistribution of fishing effort caused by the introduction of the closure (Fig. 4-3), although this did not totally offset the welfare loss, likely because travel cost was strongly significant in the RUM and depredation rate was not. In addition, the cost of lost fishing gear as a result of depredation must also be considered, which Mitchell et al. (2018a) estimated to be between AUD$10 and AUD$200, with a mean value of AUD$38, albeit this was based on a small sample size (42 trips). Additionally, there would also be an improvement in the quality of the fishing experience for many fishers if depredation rates were reduced, yet this is difficult to quantify in monetary terms and has not been investigated in the current study. Overall, whilst such adaptive closures may result in some negative cost, the long-term net effect may therefore be positive for recreational fishers, leading to them supporting such closures. In general, recent research has indicated that the majority of recreational fishers in Australia support the adoption of areas closed to fishing within marine parks, and that their approval increases over time (Navarro et al. 2018). It is, however, important to consider the broader biological impacts of closures, because Gao & Hailu (2011) identified that the biomass of fish, coral cover and catch rates can either be positively or negatively impacted depending on complex feedback mechanisms linked to the redistribution of fishing effort after closures, using the NMP as a case study.

Past studies which have applied RUMs to recreational fishing data have reported a significant positive effect of catch rate (Kaoru et al. 1995, Shrestha et al. 2002, Lipton & Hicks 2003, Schuhmann & Schwabe 2004, Prayaga et al. 2010, Melstrom & Lupi 2013), including Raguragavan et al. (2013), who reported that catch rate had a highly significant positive effect on site choice for fishers launching from Coral Bay and Exmouth boat ramps. In contrast, the current study recorded no effect of catch rate, which was unexpected and may have been caused by the stronger overall influence of travel cost for recreational fishers in the NMP, which could have masked the effect of catch rate. In addition, it was possible that some fishers targeted particular ‘trophy’ species, which are generally lower in abundance, thereby leading to lower overall catch rates. Also, some inexperienced fishers may not have had enough knowledge of the local area to make informed site choices based on catch rate alone. Indeed, a large proportion of fishers in the NMP are tourists who travel to the area from other parts of Western Australia or interstate (Wood & Glasson 2005, Jones et al. 2009, Beckley et al. 2010), highlighting the potential lack of site-specific knowledge. In addition, there is evidence from recreational fisheries in Australia, North America and Europe that catch rate is not always the primary motivation for fishing, with social aspects also being important, such as being outdoors, having the opportunity to relax and being with family and friends (Fedler & Ditton 1994, Henry & Lyle 2003, Arlinghaus 2006, McManus et al. 2011, Young et al. 2016). Results from a past national survey of recreational fishers indicated that ‘relaxing and unwinding’ was the primary motivation for 37% of fishers, with only 8% reporting that ‘catching fish for food’ was their main reason for fishing (Henry & Lyle 2003). Likewise, it has been shown that some fishers still consider a fishing trip successful even if they catch few or no fish (Ormsby 2004, McManus et al. 2011). Amongst recreational fishers in Germany, motivations unrelated to catch also played a dominant role, with approximately 80% of recreational fishers being classed as having minimal catch orientation (Arlinghaus 2006). The occurrence of diverse motivations for fishing, other than catch rate, would therefore support the reason why catch and, potentially, depredation rate were non-significant in the current study. Lastly, the concentration of fishing effort at a small number of the sites considered in the RUM may have also contributed to the non-significant effects for both catch rate and depredation rate, because there was not enough variation in the catch rate and depredation rate values across all of the sites in the choice set to detect meaningful differences between sites.

4.6. Conclusion and future directions

This study is the first to investigate the influence of shark depredation on fisher site choice using RUMs, providing an important insight into the economic impact of this phenomenon on the recreational fishery in the NMP. Certain limitations of this study, including the relatively small sample size (185 fishers) and the use of predicted catch rate and depredation rate values, rather than expected values provided by fishers, reduce the robustness of the results. Future data collection surveys should therefore aim to collect expected catch rate and depredation rate data for each site, for every fisher, which would provide a more reliable assessment of how these variables may *ex-ante* affect site choice. Collection of data for other individual-specific parameters, such as age, income and group size, would offer further insights into the dynamics of fisher site choice in this fishery, as would including questions on fisher motivation in future surveys. This could involve multiple choice options for identifying which factors motivate fishers, and to what extent. Investigating the role of benthic habitat on site choice would be another interesting avenue for future research, as many fishers use their echosounder to identify suitable locations for fishing. Future collection of fine-scale habitat data, including continuous parameters such as benthic relief and/or rugosity, could enable such an assessment, which was not possible in the current study due to the coarse resolution of habitat classification data. Applying more comprehensive modelling techniques, such as the time-series approach used by Swait et al. (2004) and the integrated biophysical-economic agent-based model used by Gao & Hailu (2011), would enable a more holistic investigation of the socio-economic and biological impacts of depredation in this recreational fishery.

The results of this study build on those previously reported by Raguragavan et al. (2013), offering a socio-economic assessment of factors driving recreational fishing in the NMP. Additionally, this economic evaluation complements the data previously reported for the biological impacts of shark depredation in this fishery, which affect both the target fish species and the sharks involved (Mitchell et al. 2018a, *in review*). Generating this information is essential to inform management, due to the importance of recreational fishing to the local economies of Exmouth and Coral Bay, which are heavily dependent on tourism revenue (Jones et al. 2009, Beckley et al. 2010). Whilst studies in commercial fisheries have investigated the economic cost of depredation in terms of lost catch and fishing gear, which can reach hundreds or even thousands of dollars per longline set (Gilman et al. 2007, IOTC 2007), the impact on site choice has so far been overlooked. It is therefore hoped that the preliminary application of RUMs to shark depredation data in the current study, will provide impetus for further development and utilisation of this modelling approach in other recreational and commercial fisheries subject to depredation.

4.7. Ethics statement

The boat ramp survey data used in this study was collected with human ethics approval from The University of Western Australia (approval number RA/4/1/7462).

4.8. Acknowledgments

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Chapter 5: Shark depredation and behavioural interactions with fishing gear in a recreational fishery in Western Australia

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5.1. Abstract

Shark depredation, where a shark consumes an animal caught by fishing gear, can cause higher mortality for target species, injury to sharks and loss of catch and fishing gear. A critical first step to mitigation is understanding this behaviour and the shark species involved, because the identity of depredating shark species is unknown in many fisheries, and behavioural dynamics of shark interactions with fishing gear are not well understood. This study developed a novel application of line-mounted video cameras, to identify shark species responsible for depredation and investigate behavioural interactions with fishing gear, in a recreational fishery in the Ningaloo region, Western Australia. Data was collected during demersal fishing at 92 locations. The shark depredation rate was 9.1% and sicklefin lemon *Negaprion acutidens*, blacktip/Australian blacktip *Carcharhinus limbatus/tilstoni*, grey reef *Carcharhinus amblyrhynchos* and spottail *Carcharhinus sorrah* sharks were observed depredating lethrinid and epinephelid fishes. Five additional shark species from four families were recorded, but were not responsible for depredation. Sharks frequently investigated baited hooks and other fishing gear components, and

were observed following the fishing gear as it was reeled upwards to the vessel. The relative abundance of sharks at each fishing location was influenced by longitude, sea surface temperature and total number of fish hooked. By identifying the shark species responsible for depredation and investigating their behavioural interactions with fishing gear, this study provides important insights that have broader significance to other fisheries, particularly for understanding impacts on sharks and for developing effective deterrents to mitigate shark depredation and bycatch.

5.2. Introduction

Shark depredation, where a shark consumes a fish caught by fishing gear before it can be retrieved to the fishing vessel, occurs in commercial and recreational line fisheries around the world, causing loss of catch and fishing gear, and increased capture of, and injury to, sharks (Gilman et al. 2007, IOTC 2007, MacNeil et al. 2009, Mitchell et al. 2018b). A range of other taxa can also be responsible for depredation in fisheries, including cetaceans, squid, teleost fishes, pinnipeds, octopus, crabs and seabirds (Meyer et al. 1992, Dieperink 1995, Donoghue et al. 2003, Brock et al. 2006, IOTC 2007, Gilman et al. 2008, 2013, Briceño et al. 2015, Remeslo et al. 2015, Shideler et al. 2015). Shark depredation rates in commercial and recreational fisheries have been reported to range from 0.9 - 26% (Beerkircher et al. 2002, IOTC 2007, Romanov et al. 2007, Varghese et al. 2007, Gilman et al. 2008, Labinjoh 2014, Muñoz-Lechuga et al. 2016, Mitchell et al. 2018a, 2018b). However, despite these impacts, shark depredation remains relatively understudied. For example, there is little or no information on which shark species are responsible for depredation in many fisheries (Mitchell et al. 2018b). This is mainly due to the difficulty of observing sharks when this behaviour takes place, as it often occurs at depth and may be some distance from the vessel. Some studies in commercial and recreational fisheries have determined the species responsible based on observations of sharks depredating hooked fish close to the surface (Bullis 1955, Backus et al. 1956, Madigan et al. 2015), or through analysing their stomach contents (Celona et al. 2005, Romanov et al. 2007). However, these approaches require being able to observe or catch the sharks responsible, which may often not be possible. Determining the identity of depredating sharks is important for fisheries management, to assess whether these interactions are leading to substantial impacts on particular shark species, such as protected species. Furthermore, knowledge of the species involved is vital for designing mitigation measures, particularly shark deterrents, because their effectiveness can be highly species-specific (Brill et al. 2009, Tallack & Mandelman 2009, Robbins et al. 2011, Jordan et al. 2013, O'Connell et al. 2014, Hart & Collin 2015).

Investigating the behavioural dynamics of shark interactions with fishing gear will facilitate an understanding of how depredation occurs, as well as the likelihood of sharks taking the bait directly and becoming hooked. This is important, because behaviour has been shown to have a substantial effect on the catchability of, and impact upon, certain fish groups (Løkkeborg et al. 1989, Arreguín-Sánchez 1996, Walsh et al. 2004, Alós et al. 2012, Anders et al. 2016). Certain shark behaviours may also influence their susceptibility to measures designed to mitigate bycatch and depredation, such as sensory-based deterrents. However, there is currently a distinct lack of knowledge about shark behavioural interactions with fishing gear (Jordan et al. 2013). It is important to understand the factors influencing shark presence and abundance at fishing locations, as this can also affect the likelihood of shark depredation. Spatial and environmental variables, as well as fishing methods, may influence changes in shark abundance due to the role they have on feeding activity, as well as through the creation and propagation of sensory cues which may attract sharks to fishing vessels.

Video cameras have previously been used in net, trap, pot and line fisheries to observe the behaviour of target species around fishing gear (Løkkeborg et al. 1989, Renchen et al. 2012, Nguyen et al. 2014, Struthers et al. 2015, Anders et al. 2016, Gutowsky et al. 2017, Meintzer et al. 2017), as well as depredation by cetaceans and pinnipeds in commercial fisheries (Straley et al. 2007, Thode et al. 2016, van den Hoff et al. 2017, Santana-Garcon et al. 2018). However, this technology has not yet been used to investigate shark depredation in fisheries, other than two studies which opportunistically assessed a small number of depredation events in the Gulf of Mexico (Streich et al. 2018) and The Bahamas (O'Shea et al. 2015). The availability of small, lightweight cameras that can be mounted directly on fishing lines creates new opportunities to identify the shark species responsible for depredation, and learn about their behavioural interactions with recreational fishing gear.

A recent study in the Ningaloo region, Western Australia, quantified shark depredation in a recreational fishery, recording a rate of approximately 12% for demersal fishing, and whilst reef-associated carcharhinids were thought to be involved, it was largely unknown which shark species were responsible in many cases (Mitchell et al. 2018a). Due to this uncertainty, and the need to learn more about shark behavioural interactions with fishing gear, this study used line-mounted video cameras to identify the depredating shark species and record the range of their behaviour(s) when interacting with fishing gear. Identifying which teleost species were depredated was also an important goal. It was expected that the fish being depredated would be mainly lethrinids and epinephelids, which are commonly targeted in this fishery (Sumner et al. 2002, Westera et al. 2003, Ryan et al. 2017).

The study sought to provide a preliminary assessment of the proportion of sharks that had retained hooks and line in their jaw from previous interactions with fishing gear, which was expected to be relatively high due to the common occurrence of shark depredation in this fishery (Mitchell et al. 2018a). Quantifying the influence of fishing methods and environmental variables on the numbers of sharks observed at different fishing locations, was also a key aim of the study, to understand which processes may lead to a higher chance of fishers encountering sharks. Fishing locations which had a higher abundance, and therefore catch rate of target species, were expected to have a greater abundance of sharks, due to the increased availability of prey. The presence of suitable reef habitat would also be expected to drive variation in shark abundance, due to it supporting a greater abundance of prey. Environmental variables including temperature and lunar phase were predicted to influence shark presence/absence, due to the effect they may have on the feeding behaviour and movement patterns of sharks (Carey et al. 1990, Bigelow et al. 1999, West & Stevens 2001, Sims et al. 2006, Lowry et al. 2007, Cartamil et al. 2010). Additionally, the level of fishing effort, in terms of duration and the number of lines in the water, may affect the numbers of sharks present, as a higher level of fishing activity would result in an increased chance of attracting sharks. The integrated analysis of behavioural dynamics, quantitative assessment of depredation rates and the factors influencing depredation is crucial. This study provides a comprehensive investigation of shark interactions with fishing gear in this fishery, and reveals important insights for developing depredation mitigation strategies.

5.3. Methods

5.3.1. Study location, vessel information and fishing methods used

Data were collected during 19 single day fishing trips in the Ningaloo region, Western Australia (Fig. 5-1) in October 2016 and May 2017. These fishing trips visited 92 different fishing locations (Fig. 5-1). The Ningaloo region is a popular destination for recreational fishing between April and October (Sumner et al. 2002, CALM & MPRA 2005, Ryan et al. 2017, Mitchell et al. 2018a). The Ningaloo Marine Park is divided into different zones, with 33% designated as sanctuary zones where boat-based recreational fishing is prohibited (CALM & MPRA 2005).

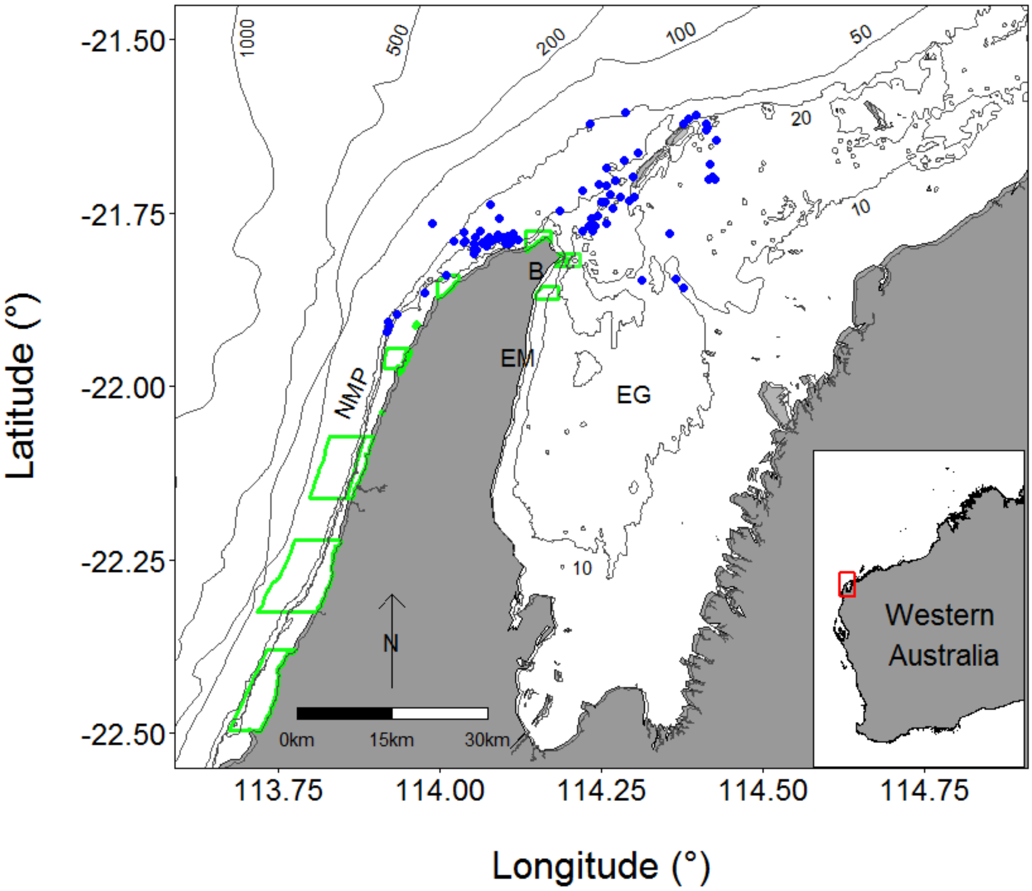

Fig. 5-1: Map of 92 charter fishing locations (blue points) in the Ningaloo region, Western Australia. Labelled contour lines show depth in metres. Solid green lines indicate the Ningaloo Marine Park (NMP) sanctuary zones, where boat-based fishing is prohibited. B = Bundegi boat ramp, EM = Exmouth marina boat ramp. EG = Exmouth Gulf.

Data were collected on the recreational charter fishing vessels 'Osso Blue' and 'Blue Horizon' (Table 5-1). Recreational fishers on both of these vessels use hook-and-line fishing gear to target demersal fish, such as lethrinids and epinephelids, at depths ranging from 10 – 110 m.

Table 5-1: Vessel parameters and fishing methods used by the two charter fishing vessels in this study.

	Vessel name	
	'Osso Blue'	**'Blue Horizon'**
No. of fishing days	14	5
No. of locations fished	59	33
Length of fishing day	8am – 5pm	7am – 5pm
Departure location	Bundegi boat ramp	Exmouth marina boat ramp
Length of vessel	8.4 m	16.8 m
Max. no. of lines in water	7	10
Fishing method	Demersal fishing	Demersal fishing
Depth range	15 – 110 m	10 – 45 m
Gear types used	Rods with spinning or overhead reels, handlines	Rods with Alvey reels
Mainline material and strength	Braided line - 36 kg	Monofilament line – 36 kg
Leader material and strength	Monofilament line – 36 kg	Monofilament line – 36 kg
Sinker weight	0.34 kg	0.57 kg
Bait type	Squid *Loligo spp.*, sardines *Sardinops sagax* and mixed demersal fish	Octopus *Octopus spp.*, squid *Loligo spp.*, sardines *S. sagax*, mixed demersal fish
Anchoring method	Drifting with sea anchor	Anchored on seabed or drifting without anchor
No. of hooks per line	1	1

5.3.2. Line-mounted video camera setup

High-definition video cameras (Water Wolf) were used to record shark depredation events and interactions with fishing gear. These cameras were 120 mm in length and weighed 58 g, and were cylindrical in shape to reduce drag as they moved through the water. Each camera was attached to a mount which had stainless steel wire running through it. The wire was then attached to the fishing line of a recreational fisher at the point where the leader was joined to the mainline, using two snap-swivel clips and two cable ties. Each camera was positioned approximately 1.5 – 2 m above the hook, with the lens facing downwards (Fig. 5-2a,b). This was determined to be the optimal distance for observing shark behaviour around the fishing gear and identifying sharks and teleost fishes.

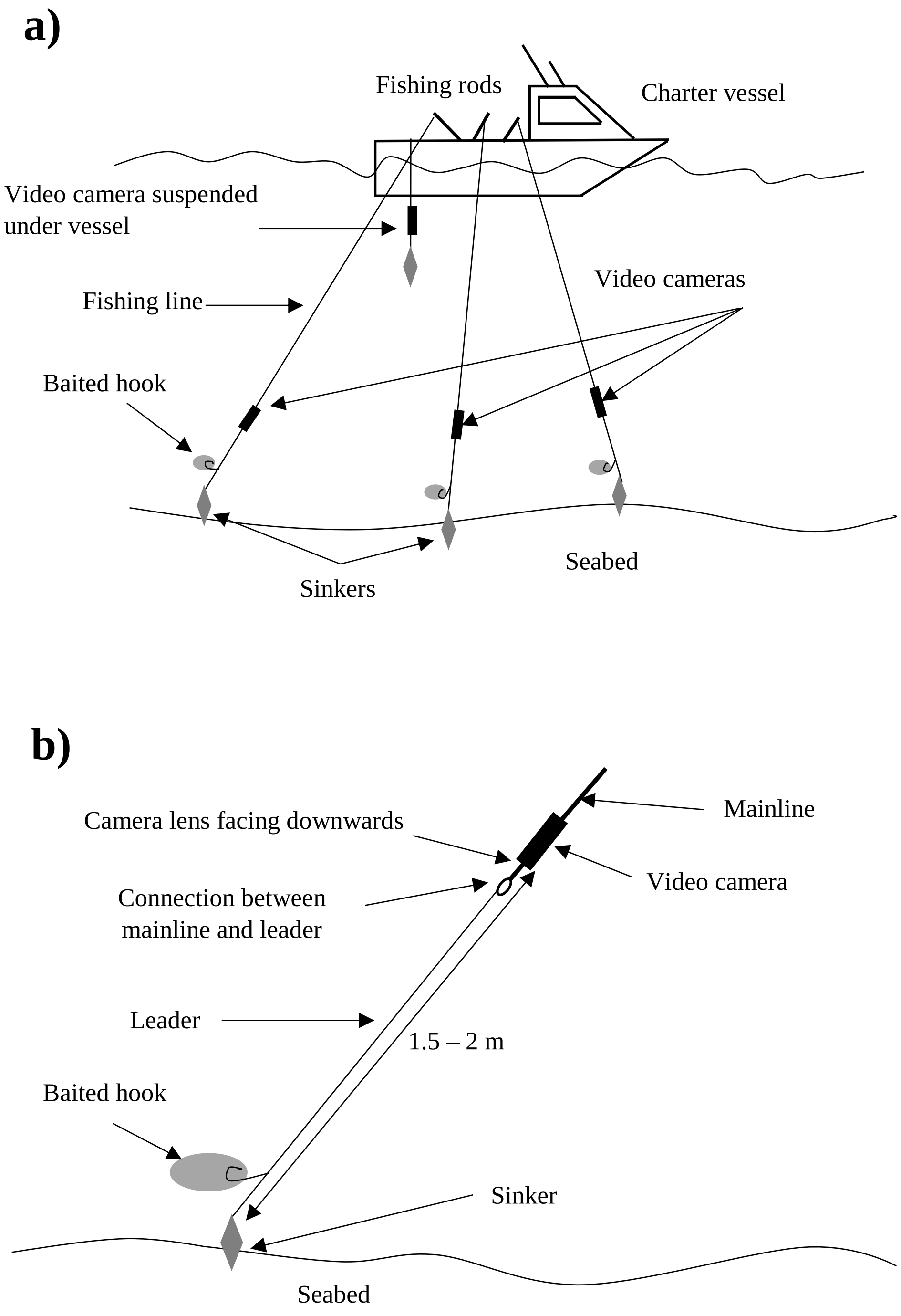

Fig. 5-2: Diagram showing **a)** how video cameras were deployed on fishing lines close to the seabed and under the fishing vessel, and **b)** a close-up of the proximity of the video camera to the key components of the fishing gear, such as the baited hook and sinker. Diagrams not to scale.

Video cameras were deployed at 92 fishing locations, with between one and five cameras deployed on separate fishing lines at a time, for up to four hours. The cameras recorded continuous colour video at 720p, with a wide angle of 120˚ x 90˚. Although these cameras were rated to 120 m depth, reliable footage could only be obtained until approximately 70 m, due to low light levels beyond this depth.

5.3.3. Fishing methods data

Data for fishing methods were also collected at each fishing location, including the latitude and longitude coordinates, the number of lines in the water, whether the vessel was anchored or drifting, the depth and the fishing gear and bait type used. These data were collected to allow later analysis of the influence of fishing methods and environmental variables on the number of sharks recorded at each fishing location. All data were collected on a tablet device, using the software application 'Collector for ArcGIS' (Environmental Systems Research Institute (ESRI) 2015, Redlands, CA).

5.3.4. Environmental variables

Remotely sensed Sea Surface Temperature (SST) data were retrospectively sourced from the US National Oceanic and Atmospheric Administration (NOAA 2016). These data were high resolution Optimum Interpolation (OI) of SST (see Reynolds et al. (2007) for detail on OI SST), collected by an Advanced Very High Resolution Radiometer (AVHRR) on polar orbiting satellites (NOAA 2016). The SST data used were daily mean values at a spatial resolution of 0.25˚ x 0.25˚ (NOAA 2016). The daily mean SST values were extracted for the dates on which charter fishing trips occurred, and for the latitude and longitude positions closest to each fishing location.

Lunar phase data for Exmouth, Western Australia, were also accessed retrospectively from an online database (Anon. 2018). Each of the fishing locations were assigned a lunar phase value based on the date they were fished and the corresponding quarter of the lunar cycle, i.e. either 'first quarter', 'full moon', 'third quarter' or 'new moon'.

5.3.5. Video analysis

Video files collected from the Water Wolf cameras were analysed using EventMeasure (version 4.42) (SeaGIS 2016). All footage was viewed and analysed by the same observer to ensure standardisation, which was particularly important for behavioural data, due to potential subjectivity. Species identification and behavioural data were collected every time a shark entered the field of view of the camera. Sharks were identified to the lowest taxonomic level possible, and all shark identifications were verified by a second experienced researcher with taxonomic training. Sharks with retained fishing gear in their jaw were also noted. All fish that were hooked were also identified to the lowest taxonomic level possible, as well as whether they got off the hook themselves, were depredated by sharks, or were retrieved to the fishing vessel undamaged. The shark depredation rate was calculated as the number of fish that were depredated out of the total number of fish hooked (not including fish that were hooked but then got off the hook shortly after). The time gap between a fish being hooked and then being depredated by a shark was calculated for all depredation events.

Shark behaviours were classified into 10 specific categories – 'biting', 'chasing', 'competition', 'consuming/depredating fish', 'following', 'hooked', 'investigating', 'nudging with head/mouthing', 'passing' and 'turning'. The 'biting' category included instances where sharks were observed biting any part of the fishing gear, but it did not cover where sharks depredated hooked fish, which was in the 'consuming/depredating fish' category. The 'chasing' category applied to where sharks chased either free-swimming fish or other sharks, whereas the 'following' category referred to where sharks followed the fishing gear or a hooked fish upwards as it was reeled towards the fishing vessel. The 'competition' group included behaviours where a shark made contact with another shark during attempts to feed on a hooked fish or the bait. 'Investigating' was defined as where the shark made a very close pass of the fishing gear or a hooked fish to investigate it, compared to the 'nudging/mouthing' category where the shark actively bumped the fishing gear or hooked fish with its head, or mouthed it. The 'passing' category included instances where sharks passed through the field of view at a distance from the fishing gear, with no interaction observed, and 'turning' referred to where a shark turned away from either the fishing gear, hooked fish or another shark. In most cases, it was clear which part of the fishing gear the shark was interacting with. However, for the 'investigating' category in particular, although the shark appeared to be investigating a particular part of the fishing gear, it may have also been assessing other parts of the fishing gear simultaneously, such as looking at the bait, sinker and camera as it swam past. A detailed behavioural ethogram based on these 10 categories was created from the video observations of shark behaviours, and key behavioural sequences were identified.

The maximum number of individuals (MaxN) (Priede et al. 1994, Cappo et al. 2004) of each shark species and of all shark species combined, that were visible together on video, were calculated for each camera deployment at each fishing location. This avoided repeat counts of the same individual sharks. The highest value of MaxN for each species and for all species pooled, across all the cameras deployed at each fishing location, was then taken as the estimate of relative abundance for that fishing location. Visibility was relatively consistent across all fishing locations, therefore it was unlikely to have influenced the variation in MaxN values between locations.

5.3.6. Generalised Additive Mixed Model analysis

To quantify the influence of fishing methods and environmental variables on the relative abundance (MaxN) of sharks at each fishing location, this study utilised Generalised Additive Mixed Models (GAMMs) (Lin & Zhang 1999). GAMMs are a modified version of Generalized Additive Models (GAMs) (Hastie & Tibshirani 1986, Wood 2006), which apply smoothing techniques to address non-linearity in the predictor variables (Craven & Wahba 1978, Wood 2008). GAMMs include both fixed and random effects, with the fixed effects quantifying the influence of each predictor variable on the response at different levels, and the random effects assessing the result of variation between levels for grouped data (Bolker et al. 2009, Zuur et al. 2009).

The response data used in the GAMM was the integer MaxN count data for all shark species combined, at each fishing location. The data was pooled for all species rather than assessing each species individually, due to the low sample size for most species, and the resulting high number of zeros. The relative abundance data for all species pooled had much fewer zeros (35% of data points), and a range of integer values between zero and eight. The GAMM was run with different error distributions, including Poisson and negative binomial, which are the most appropriate for count data (Zuur et al. 2009). Plots of goodness-of-fit metrics including the relationship between observed and fitted values and the distribution of residuals, as well as the percentage of deviance explained by the model, confirmed that the Poisson distribution produced the best-fitting model. This distribution has been widely used for modelling count-based catch rate data from fisheries (Gilman et al. 2012, Brodie et al. 2015, Gilman et al. 2016a, Noack et al. 2017) and abundance (MaxN) data from baited camera studies (Willis et al. 2000, Espinoza et al. 2014).

Eight sites were removed from the response data, because these fishing locations were <500 m from the previous fishing location, therefore sharks may have followed the vessel and been recorded at the new location, artificially inflating the relative abundance value. This distance or less between replicates, has been widely used in other studies where baited cameras have been deployed to quantify shark abundance (Goetze & Fullwood 2013, Espinoza et al. 2014, Rizzari et al. 2014a, Santana-Garcon et al. 2014a, Barley et al. 2017, Goetze et al. 2018). The mean distance between consecutive fishing locations in the current study was substantially higher, at 4.72 km, and the mean time spent at each fishing location was 39 minutes, which was less than the deployment time of baited cameras in these previous studies (Goetze & Fullwood 2013, Espinoza et al. 2014, Rizzari et al. 2014a, Santana-Garcon et al. 2014a, Barley et al. 2017, Goetze et al.

2018). Furthermore, no burley was used and only small baits were used on hooks, reducing the size of the potential bait plume. Once fishing ended at a location, the vessel moved on to the next location at relatively high speed (>30 km h^{-1}), reducing the chance that sharks would be able to follow the vessel. After removal of eight locations which were <500 m from the previous fishing location, the final GAMM had 84 response datapoints.

A range of fishing methods and environmental variables were tested in the GAMM, to quantify their influence on relative abundance of sharks (Table 5-2). The distribution of the predictor variables 'depth', 'time at fishing location', 'no. lines in the water' and 'total no. fish hooked' were low-skewed, so they were log(x + 1) transformed to achieve an even distribution for more robust model fitting (Zuur et al. 2009). The vessel name was included as a random factor in the model, rather than a fixed factor, because the focus of the study was on the larger scale environmental and spatial factors and fishing methods influencing relative abundance of sharks, rather than variation at the vessel level. The number of cameras deployed at each fishing location was included as an offset term, because the higher the number of cameras deployed simultaneously at a particular site, the greater the chance of recording a higher relative abundance.

Table 5-2: List of predictor variables tested in the full-subsets Generalised Additive Mixed Model (GAMM) for the relative abundance (MaxN) of sharks at each fishing location, and the hypothesised importance of these variables to relative abundance of sharks.

Predictor variable	Hypothesised importance to relative abundance of sharks
Smoothed continuous predictor variables	
Latitude	Change in latitude will reflect variation in other spatial parameters not included in the model, such as habitat type and oceanographic features, which may be influencing shark abundance and distribution. Latitude was therefore used as a proxy for these variables because data for habitat type was not available.
Longitude	Longitude represents the spatial change between fishing locations on the Ningaloo Reef and in the Exmouth Gulf, which have markedly different bathymetry and habitat types. Longitude was used instead of a direct habitat variable because no habitat data was available for this area.
Depth (m)	Depth can influence the habitat type and species present at a particular location, and may therefore influence shark abundance and distribution
Time at fishing location (mins)	The longer the time spent at a fishing location, the higher the chance of attracting sharks, due to the increased opportunity for them to detect sensory cues from the fishing activity and move towards the vessel
No. lines in water	Greater fishing effort will lead to more activity in the water, and therefore stronger sensory cues to attract sharks

Predictor variable	Hypothesised importance to relative abundance of sharks
Sea surface temperature (SST; °C)	Temperature influences the activity patterns and feeding behaviour of sharks (Carey et al. 1990, Sims et al. 2006, Cartamil et al. 2010, Stevens et al. 2010), therefore it may affect whether sharks are motivated to move towards the fishing vessel and depredate hooked fish
Total no. fish hooked	Sites where a greater number of fish are caught may be indicative of higher abundance, therefore sharks may also be more abundant, due to the availability of prey. Also, more fish being hooked will create more disturbance in the water, as well as fish blood and oil, both of which may attract sharks
Categorical factor predictor variables	
Month/Year	Video cameras were deployed on fishing lines from charter vessels on two trips, the first in October 2016 and the second in May 2017. Therefore, there may have been seasonal differences in shark abundance and distribution between these times of year
Lunar phase	Lunar phase may affect the activity patterns and feeding behaviour of sharks due to changes in light levels and tidal dynamics, thus it may have a localised effect on shark movements and distribution (Bigelow et al. 1999, West & Stevens 2001, Lowry et al. 2007, Hammerschlag et al. 2017). In this sense it would likely impact upon shark presence/absence in a particular area, rather than abundance.
Random factor	
Vessel name	The fishing practices and experience levels of the skipper on each fishing vessel may influence the nature of the fishing activity, and therefore the chance of attracting sharks. Vessel name was included as a random factor rather than a fixed factor because the focus of the study was on the larger scale environmental and spatial factors and fishing methods influencing relative abundance of sharks, rather than variation at the vessel level
Offset term	
No. cameras deployed at each fishing location	A greater number of line-mounted video cameras deployed at once will increase the likelihood of sharks being recorded during fishing activity

A full-subsets approach was used for the GAMM, which identifies the best-fitting, most parsimonious model from a range of possible predictor variable combinations, based on Akaike Information Criteria (AIC) (Akaike 1974) values (see Fisher et al. (2018) for a detailed description of this method). The predictor variable combinations were tested for correlation, to check that Spearman rank correlation coefficients were <0.35, which was a more conservative threshold than <0.5 suggested by Booth et al. (1994) and Zuur et al. (2009) to reduce the chance of multiple correlations occurring between predictor variables, which can result in unreliable model outputs. Any predictor variable combinations with values >0.35 were therefore excluded from the GAMM. The robustness and goodness-of-fit of the final model chosen by the full-subsets approach was also verified by checking residual plots, which indicated normally distributed residuals, independent data points and an appropriate level of fit between the model fitted values and the observed values. Plots were created for the most parsimonious model, to show how each predictor variable affected the response across its range of values. Predictor variable importance values (Fisher et al. 2018) were also calculated to indicate the relative importance of each predictor variable tested in the full-subsets GAMM. The ‘full.subsets.gam’ function (version 1.9) (Fisher et al. 2018) was run in the R language for statistical computing (R Development Core Team 2015).

5.4. Results

5.4.1. Shark and teleost species identification

There were 1688 observations of sharks on video camera imagery (Table 5-3), of which 36.6% (617) were identified to species level. Nine species from four families were recorded. Sicklefin lemon shark *Negaprion acutidens* was the species observed most frequently, comprising 17.8% (301) of the observations, followed by the blacktip/Australian blacktip *Carcharhinus limbatus/tilstoni* (which is a species complex that was indistinguishable from the video footage), with 8.2% (138). *N. acutidens* and *C. limbatus/tilstoni* were also the two species recorded at the highest number of fishing locations, being observed at 25 and 21 of the 92 locations, respectively (Table 5-3). It is important to note that within each fishing location, it was likely that individual sharks were recorded multiple times. Recording the same individual at more than one fishing location, however, was unlikely due to the distance between locations and the fact that the vessel transited at speed.

Table 5-3: List of shark species recorded and the number of times they were observed by line-mounted video cameras during fishing activity, the number of fishing locations at which they were recorded (out of 92), the number of times they depredated hooked fish, and the number of times they were observed with retained fishing gear. Species are ordered by number of observations, from highest to lowest.

Species	No. times observed	No. fishing locations recorded at	No. times depredated hooked fish	No. times observed with retained fishing gear
Carcharhinus spp.	711	36	3	12
Carcharhinidae spp.	359	39	1	1
Negaprion acutidens	301	25	5	7
Carcharhinus limbatus/tilstoni	138	21	4	1
Carcharhinus amblyrhynchos	85	13	1	1
Carcharhinus plumbeus	34	9	0	12
Carcharhinus sorrah	28	10	1	0

Carcharhinus amboinensis	16	4	0	3
Hemitriakis falcata	5	2	0	0
Nebrius ferrugineus	5	2	0	0
Rhynchobatus laevis	5	1	0	0
Triakidae sp.	1	1	0	0
Total	**1688**	**-**	**15**	**37**

Throughout the video footage collected, 165 teleost fishes were hooked, with 90.3% (149) of these identified to the species level (Table 5-4). Eighteen teleost species from eight families were identified. Chinaman rockcod *Epinephelus rivulatus* was the most frequently hooked species, comprising 33.9% (56) of the fish hooked, followed by redthroat emperor *Lethrinus miniatus*, with 16.4% (27).

Table 5-4: List of teleost fish species that were hooked and retrieved to the boat undamaged, or depredated by sharks, during fishing activity. Species are ordered by number of observations, from highest to lowest.

Species	**Total no. fish hooked**	**No. individuals retrieved to boat undamaged**	**No. individuals depredated by sharks**	**Percentage depredation**
Epinephelus rivulatus	56	54	2	3.57
Lethrinus miniatus	27	27	0	0
Lethrinus nebulosus	19	16	3	15.79
Lethrinus spp.	13	10	3	23.08
Lethrinus rubrioperculatus	10	10	0	0
Lethrinus punctulatus	8	7	1	12.5
Lethrinus laticaudis	5	5	0	0
Pentapodus porosus	4	4	0	0
Plectropomus maculatus	3	3	0	0
Epinephelus coioides	3	2	1	33.33
Epinephelus multinotatus	3	2	1	33.33
Lutjanus carponotatus	2	2	0	0
Lutjanus sebae	2	2	0	0
Cephalopholis sonnerati	2	2	0	0
Choerodon cyanodus	1	1	0	0
Lethrinus genivittatus	1	1	0	0
Gnathanodon speciosus	1	1	0	0
Gymnothorax undulatus	1	1	0	0
Rachycentron canadum	1	0	1	100
Lethrinidae sp.	1	0	1	100

Carangidae sp.	1	0	1	100
Unidentified sp.	1	0	1	100
Total	**165**	**150**	**15**	**9.09**

5.4.2. Shark depredation

Out of the 165 teleost fishes hooked, 15 of these were depredated by sharks, resulting in a depredation rate of 9.09% (Table 5-4). The depredated fish belonged to seven different species, with spangled emperor *Lethrinus nebulosus* and *E. rivulatus* being the most frequently depredated. All shark depredation events were caused by sharks from the carcharhinid family, and predominantly by sharks from the genus *Carcharhinus* (9 out of 15 events; 60%). Four different shark species depredated hooked fish (Table 5-3), with *N. acutidens* (Fig. 5-3) responsible for 33.3% (5) of the depredation events, followed by *C. limbatus/tilstoni* with 26.7% (4), grey reef shark *Carcharhinus amblyrhynchos* (6.7%; 1 event) and spottail shark *Carcharhinus sorrah* (6.7%; 1 event). The time gap between a fish getting hooked and then being depredated by a shark ranged from 3.6 - 16.8 seconds, with a mean time of 11.0 seconds. Most depredation events occurred close to the seabed, although a small number occurred in mid-water. The length of time between the start of fishing at a location (lines entering the water) and the first depredation event, ranged from approximately 5 – 40 mins. In addition to shark depredation, there were four instances where large teleosts, including blackspotted rockcod *Epinephelus malabaricus*, estuary cod *Epinephelus coioides* and shark mackerel *Grammatorcynus bicarinatus*, attempted to depredate hooked fish, but were unsuccessful.

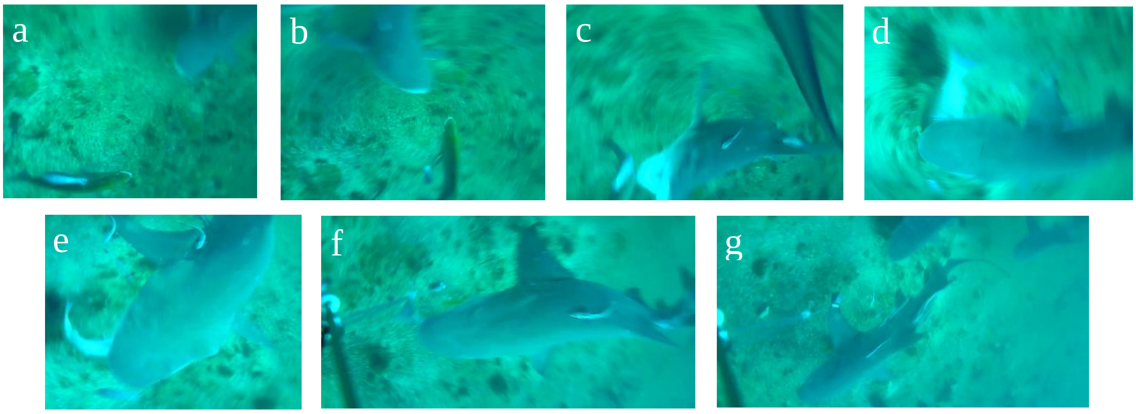

Fig. 5-3: Image sequence of a shark depredation event. **a)** a sicklefin lemon shark *Negaprion acutidens* approaches a hooked lethrinid fish, **b)** shark investigates hooked fish, **c)** shark about to bite hooked fish, **d-e)** shark bites hooked fish and shakes head, **f)** shark snaps off fishing line, **g)** shark swims away and is chased by two other sharks.

5.4.3. Behavioural interactions with fishing gear

Across the 10 behaviour categories, a total of 64 behaviour types were observed (Table 5-5). It must be noted, however, that some behaviours may have been recorded multiple times for the same individual shark in the same fishing location. Depredation events made up only a small fraction (2.9%) of the shark interactions with fishing gear, with a wide range of other behaviours recorded. In particular, sharks frequently investigated (Fig. 5-4a), nudged or followed the bait (212 occurrences; 40.3% of all interactions with fishing gear), with *N. acutidens* having the highest number of bait investigations. Sharks also commonly investigated or nudged the sinker (110 occurrences, 20.9%), or less frequently, the camera itself (46 occurrences, 8.7%). On 20 occasions (3.8% of all interactions), sharks were recorded following fishing gear up towards the surface as it was being reeled in to the vessel (Fig. 5-4b).

Table 5-5: Ethogram of behaviours recorded by line-mounted video cameras, along with the total number of times they were observed and the number of times per species. *N.a. = Negaprion acutidens*, *C.l/t. = Carcharhinus limbatus/tilstoni*, *C.amb. = Carcharhinus amboinensis*, *C.p. = Carcharhinus plumbeus*, *C.s. = Carcharhinus sorrah*, *C.a. = Carcharhinus amblyrhynchos*, *H.f. = Hemitriakis falcata*, *N.f. = Nebrius ferrugineus*, *R.l. = Rhynchobatus laevis*, *C. = Carcharhinus spp.*, *Ch. = Carcharhinidae spp.*, *T. = Triakidae sp.*

		No. of times recorded per species											
Behaviour description	**Total no. times recorded**	***N.a.***	***C.l/t.***	***C.amb.***	***C.p.***	***C.s.***	***C.a.***	***H.f.***	***N.f.***	***R.l.***	***C.***	***Ch.***	***T.***
Biting													
Biting and snapping stationary sinker off line	1	0	0	0	0	0	0	0	0	0	1	0	0
Biting at stationary bait but not becoming hooked	1	0	0	0	0	0	0	0	0	0	1	0	0
Biting stationary camera	3	1	0	0	0	0	0	0	0	0	2	0	0
Biting stationary sinker	4	1	0	0	0	0	1	0	0	0	2	0	0
Chasing													
Chasing free swimming fish	5	1	3	0	0	1	0	0	0	0	0	0	0
Competition													
Attempting to bite remains of hooked fish in another shark's mouth	1	0	0	0	0	0	0	0	0	0	1	0	0
Nudging remains of hooked fish in another shark's mouth	1	0	0	0	0	0	0	0	0	0	1	0	0
Turning away to avoid other shark trying to steal partially depredated fish out of its mouth	1	1	0	0	0	0	0	0	0	0	0	0	0
Following/chasing other shark	22	2	0	0	1	0	1	0	0	0	16	2	0
Consuming/depredating fish													
Depredating a hooked fish	15	5	4	0	0	1	1	0	0	0	3	1	0
Consuming fish that has just been released	2	0	0	0	0	0	0	0	0	0	1	1	0

		No. of times recorded per species											
Behaviour description	**Total no. times recorded**	***N.a.***	***C.l/t.***	***C.amb.***	***C.p.***	***C.s.***	***C.a.***	***H.f.***	***N.f.***	***R.l.***	***C.***	***Ch.***	***T.***
Attempting to consume fish swimming down but is unsuccessful because fish evades it	1	0	1	0	0	0	0	0	0	0	0	0	0
Attempting to depredate hooked fish but is unsuccessful because fish evades it	7	6	1	0	0	0	0	0	0	0	0	0	0
Following													
Following baited hook as it is being reeled up to the boat	8	2	0	0	0	0	0	0	0	0	5	1	0
Following hooked fish as it is being reeled up to the boat	26	7	3	0	2	0	1	0	0	1	9	3	0
Following hooked shark as it is being reeled up to the boat	2	0	0	0	0	0	2	0	0	0	0	0	0
Following sinker as it is being reeled up to the boat	1	0	0	0	0	0	0	0	0	0	1	0	0
Following snapped off fishing line as it is being reeled up to the boat	2	0	0	0	0	0	0	0	0	0	2	0	0
Following unbaited hook as it is being reeled up to the boat	7	3	1	0	1	0	0	0	0	0	2	0	0
Hooked													
Taking stationary bait and becoming hooked	15	7	1	0	0	1	0	1	0	0	3	2	0
Got off the hook without breaking line	7	4	0	0	0	0	0	0	0	0	1	2	0
Hooked and being reeled up to the boat	22	9	3	0	0	0	0	0	0	0	5	5	0
Retrieved to the boat	1	0	0	0	0	0	0	1	0	0	0	0	0
Broke off line and swam away	26	11	6	0	0	2	1	0	0	0	5	1	0
Investigating (a singular approach and pass of the fishing gear rather than sustained following)													
Investigating stationary bait – contact with part of the shark's body other than the head	54	18	3	0	1	3	0	0	0	0	13	16	0

		No. of times recorded per species											
Behaviour description	**Total no. times recorded**	***N.a.***	***C.l/t.***	***C.amb.***	***C.p.***	***C.s.***	***C.a.***	***H.f.***	***N.f.***	***R.l.***	***C.***	***Ch.***	***T.***
Investigating stationary bait - no contact	94	23	13	0	1	5	1	1	1	0	35	14	0
Investigating bait as it is being reeled up to the boat - contact with part of the shark's body other than the head	2	0	0	0	0	0	0	0	0	0	2	0	0
Investigating bait as it is going down to seabed - contact with part of the shark's body other than the head	1	0	0	0	0	0	0	0	0	0	1	0	0
Investigating bait as it is going down to seabed - no contact	2	0	1	0	0	0	0	0	0	0	1	0	0
Investigating stationary camera - contact with part of the shark's body other than the head	20	0	0	0	0	0	0	0	0	0	12	8	0
Investigating stationary camera - no contact	16	0	0	4	0	0	1	0	0	0	7	4	0
Investigating hooked fish as it is being reeled up to the boat - contact with part of the shark's body other than the head	1	1	0	0	0	0	0	0	0	0	0	0	0
Investigating hooked fish as it is being reeled up to the boat - no contact	11	6	0	0	1	1	1	0	1	0	0	1	0
Investigating hooked shark as it is being reeled up to the boat – no contact	3	0	0	0	1	0	0	0	0	0	2	0	0
Investigating stationary sinker - contact with part of the shark's body other than the head	12	1	1	0	1	0	2	0	0	0	3	4	0
Investigating stationary sinker - no contact	73	4	6	3	4	0	15	0	0	0	38	3	0
Investigating sinker as it is going down to seabed - contact with part of the shark's body other than the head	2	1	0	0	0	0	0	0	0	0	1	0	0
Investigating sinker as it is going down to seabed - no contact	1	0	0	0	0	0	0	0	0	0	1	0	0

		No. of times recorded per species											
Behaviour description	**Total no. times recorded**	***N.a.***	***C.l/t.***	***C.amb.***	***C.p.***	***C.s.***	***C.a.***	***H.f.***	***N.f.***	***R.l.***	***C.***	***Ch.***	***T.***
Investigating sinker as it is being reeled up to the boat - no contact	1	0	0	0	0	0	1	0	0	0	0	0	0
Investigating stationary unbaited hook - contact with part of the shark's body other than the head	6	5	0	0	0	1	0	0	0	0	0	0	0
Investigating stationary unbaited hook - no contact	9	5	0	0	0	0	0	0	0	1	2	1	0
Investigating unbaited hook as it is being reeled up to the boat - no contact	2	0	1	0	0	0	0	0	0	0	0	1	0
Swimming up to investigate stationary fishing gear in midwater	6	0	1	1	1	0	2	0	0	0	1	0	0
Circling stationary bait	11	0	0	0	2	0	0	0	0	0	9	0	0
Nudging with head/mouthing													
Nudging stationary bait with head	22	8	1	0	1	3	0	0	0	0	9	0	0
Nudging bait with head as it is being reeled up to the boat	2	1	0	0	0	0	0	0	0	0	1	0	0
Nudging stationary camera with head	5	0	0	1	0	0	0	0	0	0	2	2	0
Nudging camera with head as it is being reeled up to the boat	1	0	1	0	0	0	0	0	0	0	0	0	0
Nudging camera with head as it is going down to seabed	1	0	0	0	0	0	0	0	0	0	0	1	0
Nudging stationary sinker with head	15	3	1	0	3	2	4	0	0	1	1	0	0
Nudging sinker with head as it is being reeled up to the boat	1	0	0	0	0	0	1	0	0	0	0	0	0
Nudging stationary unbaited hook with head	1	0	0	0	0	0	0	0	1	0	0	0	0
Mouthing hooked fish but not depredating it as it is being reeled up to the boat	4	2	1	0	0	0	1	0	0	0	0	0	0
Passing													
Passing	1036	117	80	7	10	7	43	1	2	1	486	281	1
Swimming down after being released	1	0	0	0	0	0	0	1	0	0	0	0	0

Behaviour description	Total no. times recorded	No. of times recorded per species											
		N.a.	***C.l/t.***	***C.amb.***	***C.p.***	***C.s.***	***C.a.***	***H.f.***	***N.f.***	***R.l.***	***C.***	***Ch.***	***T.***
Turning													
Turns and starts chasing free-swimming fish	1	0	1	0	0	0	0	0	0	0	0	0	0
Turns away and stops following baited hook as it is being reeled up to the boat	5	1	0	0	0	0	0	0	0	0	3	1	0
Turns away and stops following hooked fish as it is being reeled up to the boat	20	3	2	0	2	0	2	0	0	1	7	3	0
Turns away and stops following hooked shark as it is being reeled up to the boat	1	0	0	0	0	0	1	0	0	0	0	0	0
Turns away and stops following sinker as it is being reeled up to the boat	1	0	0	0	0	0	0	0	0	0	1	0	0
Turns away and stops following unbaited hook as it is being reeled up to the boat	4	1	0	0	1	0	0	0	0	0	2	0	0
Turns away from bait to chase free swimming fish	1	0	0	0	0	1	0	0	0	0	0	0	0
Turning tightly to try and depredate hooked fish which is trying to evade it	5	5	0	0	0	0	0	0	0	0	0	0	0
Turns away and stops following snapped-off fishing line	1	0	0	0	0	0	0	0	0	0	1	0	0

Fig. 5-4: Shark behavioural interactions with fishing gear, including **a)** a sandbar shark *Carcharhinus plumbeus* investigating but not biting a bait, **b)** a *Carcharhinus sp.* following fishing gear upwards as it is reeled to the vessel, **c)** inter-specific competition where a grey reef shark *Carcharhinus amblyrhynchos* attempted to steal a partially depredated fish out of the mouth of a sicklefin lemon shark *Negaprion acutidens*.

When a fish was hooked and a shark was present, a range of different behavioural sequences were recorded (Fig. 5-5), including 26 instances (4.9% of all shark-fishing gear interactions) where sharks closely followed a hooked fish as it was being reeled upwards towards the vessel. There were also two instances where sharks chased and consumed free-swimming fish after they had been released. One of these instances involved a *C. limbatus/tilstoni* chasing and consuming an *E. rivulatus*.

Sharks of different species were seen together at 21 of the 92 (22.8%) fishing locations, with five different species – *N. acutidens*, *C. limbatus/tilstoni*, *C. amblyrhynchos*, sandbar shark *Carcharhinus plumbeus* and pigeye shark *Carcharhinus amboinensis*, being recorded together at two separate locations. There were also a number of instances of inter- and intra-specific competition, especially where sharks chased after another shark which had just depredated a hooked fish (Fig. 5-4c).

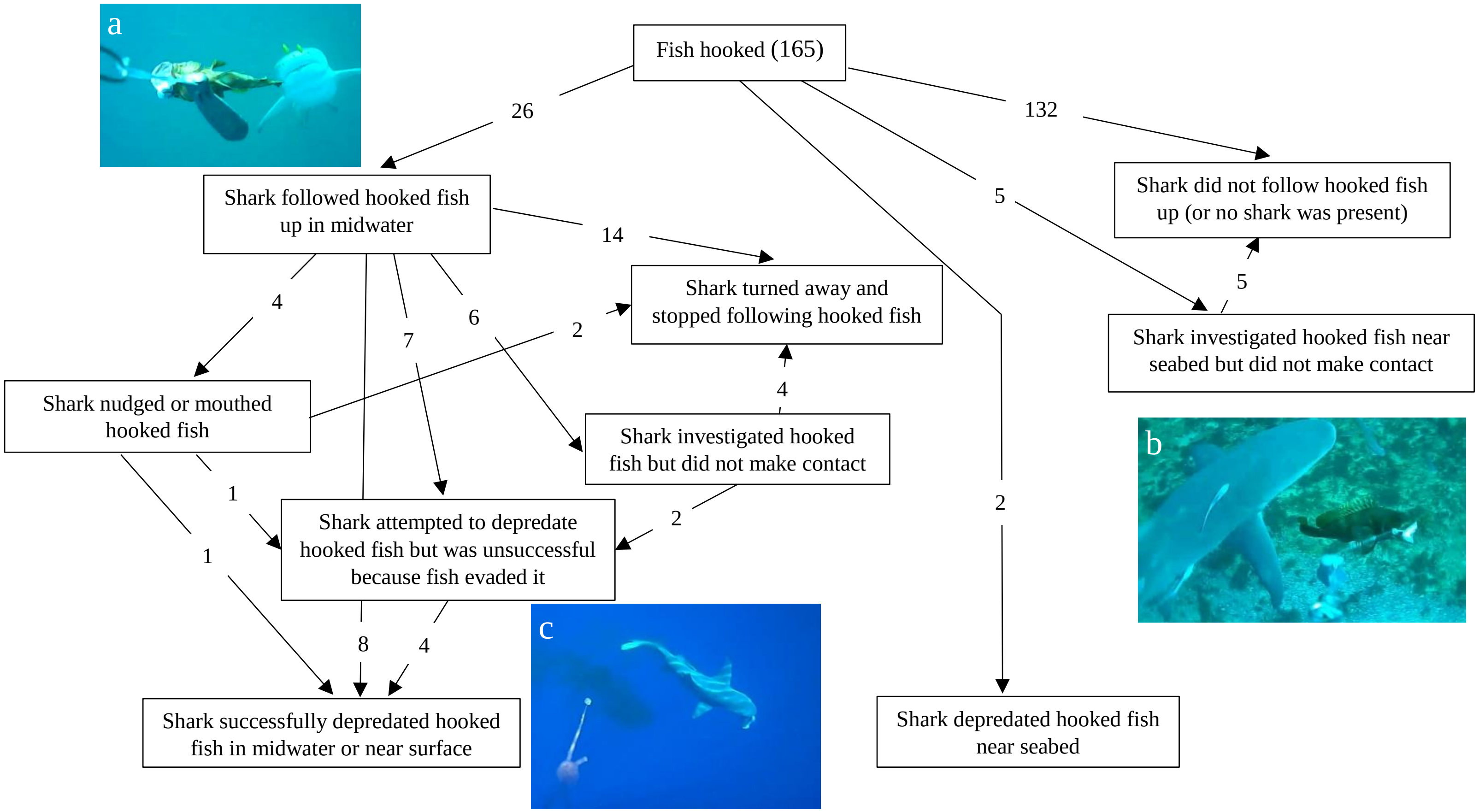

Fig. 5-5: Behavioural sequence diagram showing the range of behaviours displayed by sharks when a fish was hooked and being reeled up to the boat during recreational fishing. Images show examples of key behaviours, including **a)** a sicklefin lemon shark *Negaprion acutidens* following a hooked Chinaman rockcod *Epinephelus rivulatus*, **b)** a *Carcharhinus sp.* investigating a hooked *E. rivulatus* and **c)** a *N. acutidens* with a partially depredated cobia *Rachycentron canadum* in its mouth. Numbers on the diagram indicate the total number of times each behaviour was recorded, across all shark species.

5.4.4. Sharks with retained fishing gear

There were 37 observations of sharks with retained fishing gear (Fig. 5-6, Table 5-3), which represented 2.2% of the total number of shark observations. However, some of these observations may have been the same individual shark being seen multiple times. Four shark species were recorded with visible evidence of fishing gear, with *C. plumbeus* being the most commonly observed.

Fig. 5-6: A *Carcharhinus sp.* with a hook lodged in its jaw from a previous interaction with fishing gear.

5.4.5. Influence of fishing methods and environmental variables on relative abundance of sharks

The best-fitting, most parsimonious GAMM contained the predictor variables ‘longitude’, ‘SST’ and ‘log(total number of fish hooked + 1)’, and explained 55% of the deviance in the relative abundance of sharks. Longitude had the highest relative importance value of all the predictor variables (Table 5-6), and had an increasingly positive effect on the relative abundance of sharks up to a peak at 114.04˚ (Fig. 5-7a). At higher longitudes, there was a decreasing effect on relative abundance, followed by a plateau. SST also had a high relative importance value, and showed a markedly increasing positive effect on relative abundance, which peaked at 25.25 ˚C (Fig. 5-7b). Above this temperature, however, the effect on relative abundance decreased markedly. Lastly, the total number of fish hooked had an initially neutral effect on relative abundance, followed by an increasingly positive effect, up to a peak at 3.91 (Fig. 5-7c). This predictor variable had the third highest relative importance value, with the remaining predictor variables having substantially lower values (Table 5-6).

Table 5-6: Relative importance values for the predictor variables tested in the full-subsets Generalised Additive Mixed Model (GAMM), ordered from highest importance to lowest. Predictor variables that featured in the best-fitting, most parsimonious GAMM are marked with an (X).

Predictor variable	**Relative importance value**
Longitude	0.1260 (X)
Sea surface temperature	0.0668 (X)
log(total no. fish hooked + 1)	0.0413 (X)
log(no. lines in water + 1)	0.0074
log(depth + 1)	0.0035
log(time at fishing location + 1)	0.0025
Lunar phase	0.0003
Latitude	0.0003
Month/Year	<0.0001

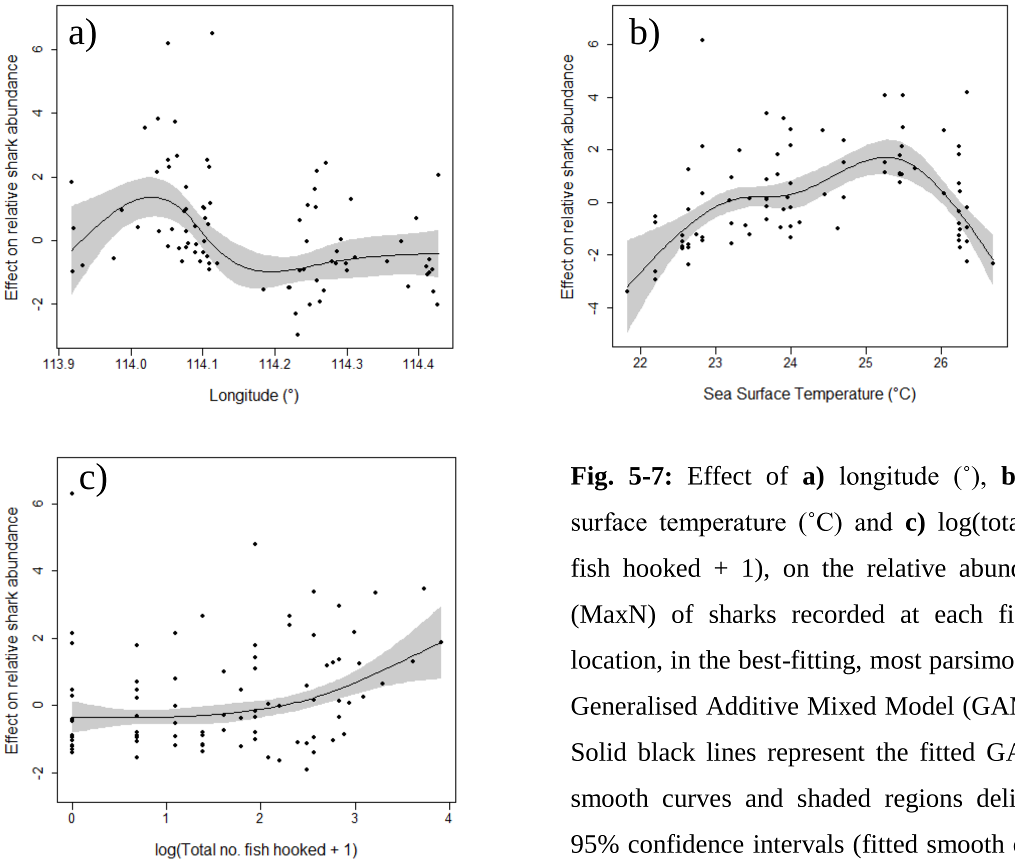

Fig. 5-7: Effect of **a)** longitude (˚), **b)** sea surface temperature (˚C) and **c)** log(total no. fish hooked + 1), on the relative abundance (MaxN) of sharks recorded at each fishing location, in the best-fitting, most parsimonious Generalised Additive Mixed Model (GAMM). Solid black lines represent the fitted GAMM smooth curves and shaded regions delineate 95% confidence intervals (fitted smooth curve +/- 2 Standard Errors). Points represent model residuals.

5.5. Discussion

5.5.1. Shark and teleost species identification

A range of shark species interacted with fishing gear in this study, which was expected due to the relatively high diversity and abundance of sharks in this region (Last & Stevens 2009, Stevens et al. 2009, Speed et al. 2012a, 2016, Oh et al. 2017). *N. acutidens* and *C. limbatus/tilstoni* were the most common species, and they were also commonly recorded during previous elasmobranch research in the Ningaloo region, which utilised dive, longline and baited camera surveys (Stevens et al. 2009, Schifiliti 2014).

Whilst the use of cameras enabled the identification of sharks, only 36.6% were identified to species level, due to restrictions in visibility or because the shark was too far away from the camera. The similarity of many carcharhinid species, which can only be differentiated using subtle features such as fin shape and position, tooth morphology and the presence or absence of an interdorsal ridge (Compagno 1984), exacerbated this difficulty. This limitation has also been acknowledged by other studies that have used underwater video to identify sharks (Brooks et al. 2011, Santana-Garcon et al. 2014b), although camera-based identification is useful for behavioural observations and is non-damaging, compared to catching the sharks to identify them.

The teleost species hooked and either retrieved to the vessel or depredated by sharks, were mostly common demersal reef-associated species, from the lethrinid and epinephelid families. This target species composition reflects that reported in past large-scale surveys of recreational fishing in this region (Sumner et al. 2002, Westera et al. 2003, Williamson et al. 2006, Ryan et al. 2017).

5.5.2. Shark depredation

The shark depredation rate recorded in this study (9.1%) was lower, but relatively similar to, recent research by Mitchell et al. (2018a), which reported rates of 13.7% and 11.5% for recreational demersal fishing in the Ningaloo Marine Park and Exmouth Gulf, respectively. The depredation rate in the current study may have been lower because it was collected on board charter vessels, therefore the skippers had extensive local knowledge and knew where to fish to minimise depredation, compared to the fishers surveyed by Mitchell et al. (2018a), many of which had limited local knowledge and less fishing experience so would not have the spatial knowledge required to avoid depredation. Additionally, the depredation rate in this previous study may have been overestimated due to fishers mistaking depredation events for where sharks took the bait directly and snapped off the fishing line, or because fishers deliberately exaggerated depredation rates due to negative perceptions of sharks and the desire for mitigation measures to be introduced. Because the depredation rate in the current study was based on the depredation events confirmed during video analysis, it is therefore considered more reliable, although the smaller sample size must be considered. Earlier surveys in this region produced depredation rates of 5% for some key demersal species, although the majority of species had rates <2% (Sumner et al. 2002, Williamson et al. 2006). In a South African recreational fishery, the depredation rate for demersal fishing was 1.9% (Labinjoh 2014). Globally, depredation rates in commercial and recreational fisheries have been found to vary between 0.9 – 26% (Lawson 2001, IOTC 2007, Gilman et al. 2008, MacNeil et al. 2009, Mitchell et al. 2018b, Rabearisoa et al. 2018).

Since depredation often occurs at depth, the predator responsible may not have been sighted, as was the case for the majority of depredation events reported by Mitchell et al. (2018a). It is therefore necessary to determine whether sharks were responsible, or if other predators also depredated hooked fish. All depredation events in the current study were caused by sharks, although large predatory teleosts were observed attempting to depredate hooked fish. The footage of these unsuccessful depredation events suggested that the teleosts were unable to remove the hooked fish, perhaps due to their smaller size, different jaw and teeth morphology and feeding technique, compared to sharks. This is especially the case for the *Epinephelus spp.*, which generally use ram or suction feeding to swallow their prey whole (Wainwright & Bellwood 2002, Oufiero et al. 2012, Collins & Motta 2017), as opposed to large carcharhinid sharks, which predominantly bite and tear their prey (Motta & Wilga 2001, Motta 2004). However, teleost species including goliath grouper *Epinephelus itajara*, greater amberjack *Seriola dumerili*, great barracuda *Sphyraena barracuda* and Warsaw grouper *Hyporthodus nigritus*, have been recorded successfully depredating hooked fish in US fisheries (Collins 2014, Shideler et al. 2015, Streich et al. 2018).

Mitchell et al. (2018a) theorised that reef-associated carcharhinids were the main group responsible for depredation, as the Ningaloo region is important for a number of reef shark species (Stevens et al. 2009, Speed et al. 2011, Oh et al. 2016, Ferreira et al. 2017), and because fishers mainly target reef-associated teleost species when demersal fishing. The current study confirmed that sharks from the carcharhinid family were the only group involved, with sharks from the *Carcharhinus* genus responsible for the majority of depredation events. *N. acutidens*, *C. amblyrhynchos* and *C. sorrah* are all considered to be reef-associated sharks, whereas *C. limbatus/tilstoni* are classed as a coastal species, although they can occur in reef environments in parts of their range (Heupel et al. 2004, Compagno et al. 2005). In terms of the individual species identified, *N. acutidens* were responsible for the most depredation events, followed by *C. limbatus/tilstoni*. Schifiliti (2014) also reported *N. acutidens* to be the species that interacted most frequently with baited cameras deployed in the Ningaloo region. It is possible that either this species is more common than others in the habitats fished in this study, that it may be bolder and more inclined to investigate fishing gear and/or is differentially attracted to the types of bait used by fishers. The sensory abilities of this species may also be adapted/sensitive to the baits used and the teleosts hooked (Collin 2012, Collin et al. 2015). Indeed, *N. acutidens* investigated bait and fishing gear more times than other species in the current study, and other research has found that it can be aggressive and opportunistic in nature (Compagno 1984, Clua et al. 2010). However, this species was only rarely caught in previous longline surveys in the Ningaloo region (Stevens et al. 2009), and it has not been reported to depredate hooked fish in past literature on depredation in other fisheries (Mitchell et al. 2018b). *C. limbatus* was recorded depredating hooked fish in a recreational fishery in South Africa (Labinjoh 2014) and in a commercial longline fishery in the Indian Ocean (Romanov et al. 2007). Oceanic whitetip sharks *Carcharhinus longimanus* depredated hooked pelagic fish in a recreational fishery in The Bahamas (Madigan et al. 2015), and in commercial longline fisheries, blue *Prionace glauca* and shortfin mako *Isurus oxyrinchus* sharks, and *C. longimanus* (Secchi & Vaske 1998, Ward et al. 2004, Gilman et al. 2007, MacNeil et al. 2009, Muñoz-Lechuga et al. 2016, Mitchell et al. 2018b), are thought to be the key species responsible. In total, 27 shark species from seven families have been reported to depredate hooked fish (Mitchell et al. 2018b), suggesting that this behaviour is not restricted to a few species, but is a broadly opportunistic behaviour displayed by many species.

Depredation events predominantly occurred at least 10 minutes after the start of fishing at a location, indicating that it took time for sharks to detect and locate the fishing vessel. Sharks may have used auditory and chemical cues, including the vessel engine noise and fish blood in the water, respectively, because sharks can detect these cues hundreds of metres from the source (Myrberg et al. 1972, Corwin 1989, Collin & Marshall 2003, Chapuis 2017). It is also possible that in this area, sharks have become conditioned to associate the sound of vessels with the availability of hooked fish (Schifiliti 2014, Mitchell et al. 2018a), as has been suggested in other regions where depredation occurs in recreational fisheries (McCord & Lamberth 2009, Labinjoh 2014, Madigan et al. 2015). Vibrations in the water created by struggling hooked fish, which would be detected by the shark's lateral line system (Boord & Campbell 1977, Collin 2012, Hart & Collin 2015), also likely played an important role in enabling sharks to locate and depredate hooked fish. Additionally, sharks have been found to be attracted by the irregular, low frequency sounds produced by injured fish (Nelson & Johnson 1970, Evans & Gilbert 1971, Banner 1972, Chapuis 2017). Vision may have also been used, with the sharks being attracted by the movement of the fish (Collin 2012, 2018), with electroreception used to guide the shark from a range of <0.5 m (Kalmijn 1972, Haine et al. 2001, Collin et al. 2015, Collin 2017), when moving in to bite the hooked fish.

Sharks sometimes followed hooked fish upwards but did not depredate them (Fig. 5-5), suggesting that they may have been selective of which fish they depredated. This did not appear to be linked to the species of teleost hooked, because lethrinid and epinephelid species that were depredated, including *E. rivulatus* and bluespotted emperor *Lethrinus punctulatus*, were also followed by sharks but not depredated. However, Streich et al. (2018) found that *C. plumbeus* only depredated hooked red snapper *Lutjanus campechanus*, although this was based on only eight depredation events and *L. campechanus* was the most commonly hooked species. Selectivity was not reported in past studies of depredation in commercial fisheries (Lawson 2001, Gilman et al. 2007, IOTC 2007, Romanov et al. 2007, Mandelman et al. 2008, Mitchell et al. 2018b), or in recreational fisheries (Labinjoh 2014, Madigan et al. 2015, Mitchell et al. 2018a). There was also no evidence of selectivity based on the size of the hooked fish in the current study, with fish of similar size being depredated on some occasions, but not others. However, the majority of fish hooked during this study were <50 cm in length.

5.5.3. Behavioural interactions with fishing gear

Sharks displayed many different forms of interaction with fishing gear, expanding our knowledge of behaviour. Interactions with the bait were the most common form recorded, including where sharks investigated the bait from a distance of approximately 1-2 m, which likely involved assessing the bait using visual and olfactory cues. Closer inspections of the bait were also observed, where the shark made contact with either its body, head (nudging) or mouth (mouthing/biting). Nudging and mouthing of the food source was also reported by O'Shea et al. (2015), and this may have involved mechanoreception, because past research has provided evidence that the teeth and gums of sharks contain sensory endings that act as mechanoreceptors (Roberts & Witkovsky 1975, Hammerschlag et al. 2012b). Gustation may also allow sharks to assess whether an object is palatable (Sheldon 1909, Cook & Neal 1921, Tester 1963, Whitear & Moate 1994, Hueter et al. 2004, Collin et al. 2015, Hart & Collin 2015, Atkinson et al. 2016).

Sharks also investigated the sinker, camera and unbaited hooks. Vision may have been important where sharks investigated larger objects, particularly the sinker, and electroreception may have been used when investigating metal objects (Kalmijn 1966, 1971, Collin 2017), particularly unbaited hooks. Sharks investigated, nudged or mouthed the cameras attached to fishing lines, perhaps because they were able to detect electrical signals within them. Certain shark species have been shown to be sensitive to very weak electric fields (Murray 1962, Kalmijn 1966, 1971, 1972, Collin 2017), down to ≤ 5 nV cm^{-1} (Kalmijn 1982, Johnson et al. 1984, Kajiura & Holland 2002), therefore it might be expected that they could detect the cameras, which had a 3.7 V internal battery. However, previous testing has indicated that both remotely powered cameras, and those with an internal battery, had little or no effect on shark behaviour (Heithaus et al. 2001, Cappo et al. 2004, Robbins et al. 2011). Another notable form of behaviour was where sharks followed the fishing gear upwards as it was reeled to the vessel, but did not strike it. This behaviour was observed in five different species and perhaps occurred because the sharks were attracted to the visual and hydrodynamic cues created by the movement of the object in the water. In most of these cases, the sharks followed and briefly inspected the fishing gear, before turning away, suggesting that they may have been evaluating whether it was a potential food source.

Despite the many interactions with fishing gear, sharks rarely struck the bait and become hooked, with this representing only 2.9% of all the behavioural interactions with fishing gear. In contrast, a past study on grey nurse sharks *Carcharias taurus* reported that sharks took the bait on the first approach on 33% of occasions, with blue mackerel *Scomber australasicus* baits being taken significantly more often than Australian sardine *Sardinops sagax* or squid *Loligo sp.* (Robbins et al. 2013). Another study by Robbins et al. (2011), which also used underwater video cameras, noted that Galapagos sharks *Carcharhinus galapagensis* took the *S. sagax* bait in the majority of instances, with a mean time to strike of <30 seconds (Robbins et al. 2011). The low level of sharks striking bait in the current study may have been linked to the type and size of bait, which consisted of small pieces of squid *Loligo spp.*, octopus *Octopus spp.*, *S. sagax* and mixed demersal fish, because bait size as well as type has been shown to influence shark catch rates (Foster et al. 2012, Robbins et al. 2013, Amorim et al. 2015, Gilman et al. 2016b, Kumar et al. 2016). It is also possible that sharks were wary of the fishing gear due to previous negative interactions where they were hooked and injured. Mourier et al. (2017) found that sharks that had been captured on hook and line previously, were less likely to be caught again, and Backus et al. (1956) reported that *C. longimanus* regularly consumed floating scraps of bait, but were much more wary of bait on a hook.

Competitive behaviour was also observed, particularly before and after depredation events. In one instance, a *N. acutidens* was pursued by three carcharhinid sharks after it depredated a hooked fish. Competition linked to shark depredation was also reported in The Bahamas, where a bull shark *Carcharhinus leucas* and a tiger shark *Galeocerdo cuvier* fed on a hooked Caribbean reef shark *Carcharhinus perezi*, whilst they competitively excluded another *C. perezi* and a great hammerhead shark *Sphyrna mokarran*, preventing them from feeding on the hooked shark (O'Shea et al. 2015). Robbins et al. (2011) recorded competition between multiple *C. galapagensis*, where sharks displayed a lower level of cautiousness and were faster to strike baits when there was a higher number of conspecifics present. Competition has also been noted to drive higher feeding motivation in groups of *C. amblyrhynchos* (Nelson & Johnson 1980) and *N. acutidens* (Brena et al. 2018). This would suggest that sharks would be more likely to depredate hooked fish if other competitors were present, although in the current study, sharks were still observed following up hooked fish but not depredating them, even with other sharks present.

5.5.4. Sharks with retained fishing gear

When sharks depredated hooked fish or took the bait and became hooked, they almost always snapped off the fishing line, apart from one occurrence of a hooked shark being retrieved to the vessel, which was a small (~1 m) sicklefin houndshark *Hemitriakis falcata*. When sharks snap off the fishing line, it can lead to them retaining fishing gear in their jaw. This study found that 2.2% of all sharks observed had retained fishing gear, which was lower than the value of 9.2% reported by Whitney et al. (2012) for whitetip reef sharks *Triaenodon obesus*, and 16.8% for *C. taurus* (Bansemer & Bennett 2010). However, this value in the current study was likely underestimated, because retained fishing gear could only be identified if sharks were close to the camera. Likewise, sharks may have had hooks lodged inside their mouth, or deeper in their digestive tract, which were not observable. This is supported by the fact that Otway & Burke (2004) found that six out of eight dead *C. taurus* had internal hook injuries, without any external signs visible.

Retained fishing gear can cause sub-lethal impacts to sharks, including tissue necrosis, abscesses, perforations of the gastric wall and internal infections (Borucinska et al. 2001, 2002, Bansemer & Bennett 2010). This can lead to reduced feeding, lack of fitness, disease and possibly death (Borucinska et al. 2001, 2002, Bansemer & Bennett 2010, Whitney et al. 2012, Adams et al. 2015). Whitney et al. (2012) reported an observation of an unhealthy and emaciated *T. obesus*, which had a hook embedded in its jaw and was trailing fishing line, perhaps preventing it from feeding. The size and shape of fishing hooks, and the material they are made from, can also influence the degree of injury they cause to sharks (Godin et al. 2012, Jordan et al. 2013, Campana et al. 2015). Fishers could reduce injury to sharks by using small circle hooks made from material other than stainless steel, to reduce the chance of gut hooking sharks and the time it takes for hooks to corrode.

Understanding the impact of retained fishing gear on sharks is important because although targeted recreational fishing for sharks is uncommon in this region (Sumner et al. 2002, Ryan et al. 2013, 2017), and commercial fishing for sharks is prohibited (Simpfendorfer & Donohue 1998, McAuley & Simpfendorfer 2003, McAuley et al. 2005), depredation has been reported to occur on ~40% of fishing trips (Mitchell et al. 2018a). Therefore, across the ~4200 boat fishing trips that were estimated to occur in the Ningaloo Marine Park annually (Mitchell et al. 2018a), there may be a substantial cumulative impact on sharks due to retained fishing gear. Future research should therefore aim to investigate the effects at a wider temporal and spatial scale, and across populations of the key shark species identified here.

5.5.5. *Influence of fishing methods and environmental variables on relative abundance of sharks*

In the best fitting, most parsimonious GAMM, the relative abundance of sharks was higher at lower longitudes, as opposed to further east. This likely reflected the fact that there is a greater area of reef habitat in this part of the Ningaloo region, which is characterised by a shallow lagoon fringed by a large, continuous reef system (CALM & MPRA 2005), compared to further east in the Exmouth Gulf, which has predominantly bare substrate with only isolated patches of reef and seagrass (Kenyon et al. 2003). This reef habitat likely supported higher abundances of prey for reef-associated carcharhinids, which were the key group observed in this study, and thus resulted in the higher relative abundance values recorded in these fishing locations. Past research has indicated that reef shark abundance and diversity is higher at locations close to reef habitat, which have greater coral cover and higher complexity (Chin et al. 2012, Espinoza et al. 2014). *N. acutidens* and *C. amblyrhynchos*, in particular, have been found to have a high level of site fidelity to reef habitats, with year-round residence (Clua et al. 2010, Filmalter et al. 2013, Mourier et al. 2013, Vianna et al. 2013, Espinoza et al. 2015). However, *C. limbatus/tilstoni* are a coastal species and can travel long distances (Heupel et al. 2004, Compagno et al. 2005), for example a shark tagged in Northern Australia was reported to travel >1000 km (Stevens et al. 2000). In the Ningaloo region, past research that applied GAMMs to abundance data collected using baited camera surveys, indicated that *C. amblyrhynchos* abundance was influenced by seabed relief, with highest abundances at intermediate levels of relief (Babcock et al. 2017). Additionally, results from dive surveys reported that *C. amblyrhynchos* was widely abundant in reef habitats (Stevens et al. 2009). More broadly, previous longline surveys found that the abundance of *C. amblyrhynchos*, *C. limbatus/tilstoni* and *C. sorrah* was highest in the central and northern portions of the NMP (Stevens et al. 2009).

Sea surface temperature also affected relative abundance of sharks, which was expected because temperature has been shown to influence the feeding activity and movement patterns of sharks (Carey et al. 1990, Sims et al. 2006, Cartamil et al. 2010, Stevens et al. 2010, DiGirolamo et al. 2012, Schlaff et al. 2014), due to its impact on metabolism (Fry 1971, Bernal et al. 2012). For reef-associated sharks in particular, this link between temperature and shark abundance and distribution has been clearly demonstrated (Speed et al. 2012b, Brooks et al. 2013, Vianna et al. 2013), and SST has also been shown to have significant effects on the catch rate of sharks in commercial (Bigelow et al. 1999, Gilman et al. 2007, Bromhead et al. 2012, Brodziak & Walsh 2013) and recreational (Mitchell et al. 2014) fisheries. The peak in relative abundance at intermediate temperatures of ~25 ˚C in the current study, may have represented an overlap in the optimum temperature ranges of the different shark species recorded in this study.

The positive relationship between total number of fish hooked and relative abundance of sharks, may have indicated that fishing locations with a higher catch rate had higher abundance of demersal teleost species, which in turn supported a greater number of sharks. It is also possible that in locations where more fish were being caught, there was a higher chance of attracting sharks from a wider area due to the sensory cues being created, particularly fish blood in the water and low frequency hydrodynamic and acoustic disturbances created by struggling hooked fish. This is particularly important if sharks have learnt to associate certain sensory cues from vessels and fishing activity with the availability of hooked fish to feed on, which is theorised to occur in this recreational fishery (Schifiliti 2014, Mitchell et al. 2018a, 2018b), and others around the world (McCord & Lamberth 2009, Labinjoh 2014, Madigan et al. 2015). Mitchell et al. (2018a) also found that the higher the level of fishing pressure in a certain area, as well as a greater number of vessels fishing in close proximity, led to higher levels of depredation, possibly because this increased the likelihood of attracting sharks. Despite this possibility for attracting sharks, the >500 m distance between consecutive fishing locations (and a mean distance of 4.72 km), was believed to be enough to prevent duplicate counts of the same individual sharks, due to the relatively short time spent at each fishing location (mean of 39 mins) and the fact that the vessel travelled at speed (>30 km h^{-1}) between locations. The findings of the current study are important because they provide fishers with information about which factors may increase their likelihood of encountering sharks. This may allow them to fish in areas with a lower probability of shark interactions, thus reducing loss of catch and fishing gear due to depredation, as well as injury to sharks.

5.6. Conclusion and future directions

To mitigate negative impacts that occur when sharks interact with fishing gear, particularly depredation and bycatch, it is vital to identify the shark species involved, as well as understand their behavioural dynamics and the sensory mechanisms being used (Jordan et al. 2013, Mitchell et al. 2018b). The current study showed that despite certain limitations, the deployment of underwater video cameras on fishing lines has great potential for generating targeted knowledge to fill these research gaps. Cameras could also be deployed in commercial longline fisheries to collect similar data, as they have been to observe depredation by sperm whales *Physeter macrocephalus* and southern elephant seals *Mirounga leonina* (Straley et al. 2007, van den Hoff et al. 2017). This could be complemented by molecular approaches to identify depredating shark species, such as the collection of predator DNA from bite marks on damaged catch (Drymon et al. 2015, Fotedar et al. 2019). From a fisheries management perspective, the findings of this study, which reveal that multiple species of sharks interacted with fishing gear and depredated hooked fish, are important, because they highlight the potential vulnerability of these specific shark species to negative impacts from recreational fishing. In addition to injuries from capture and retained fishing gear, there is also the potential that depredation could lead to human-wildlife conflicts, similar to those reported to occur between fishers and other depredating taxa, including dolphins (Powell & Wells 2011), *E. itajara* (Collins 2014, Shideler et al. 2015), sea lions (Cook et al. 2015) and seabirds (Dieperink 1995), around the world. This could lead to retaliatory killing of sharks in an attempt to reduce depredation, which has occurred, or has been proposed, for these other depredating taxa (Read 2008, Frias-Torres 2013, Cook et al. 2015).

Based on the behavioural observations of this study, sharks were often wary of baited hooks, and would investigate them but not take the bait. The addition of a deterrent device to fishing gear could therefore build on this wariness to further reduce bait strikes and bycatch within the fishing industry. Since sharks integrate information from multiple sensory modalities when investigating fishing gear and hooked fish, a deterrent which targets multiple sensory modalities has a greater chance of successfully deterring sharks. For example, a combined light and sound deterrent recently tested on white *Carcharodon carcharias*, Port Jackson *Heterodontus portusjacksoni* and epaulette *Hemiscyllium ocellatum* sharks, reduced the time spent close to the bait for *C. carcharias*, and the number of bait strikes for both *H. portusjacksoni* and *H. ocellatum* (Ryan et al. 2018). Preliminary testing of a small, microprocessor-based electrical deterrent, also showed promise as a potentially practical and cost-effective deterrent that could be deployed on fishing gear (Howard et al. 2018). However, the finding from this study that multiple shark species are involved in depredation, may reduce the likelihood that a deterrent targeting only a specific sensory modality would be effective, due to species-specific variation (Brill et al. 2009, Tallack & Mandelman 2009, Robbins et al. 2011, O'Connell et al. 2014). The development of a deterrent that targets more than one sensory system and/or a physical deterrent, similar to those tested by Moreno et al. (2008) and Rabearisoa et al. (2012), is thus an approach worth investigating. Overall, the development and testing of deterrents for a range of fishing scenarios is a vital step towards the goal of mitigating shark depredation and bycatch, which currently have potentially large biological and economic impacts worldwide (Gilman et al. 2007, Mandelman et al. 2008, Worm et al. 2013, Dulvy et al. 2014, Mitchell et al. 2018b).

5.7. Ethics statement

This work was carried out under animal ethics approval from The University of Western Australia (approval number F 18979).

5.8. Acknowledgements

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Chapter 6: General discussion

6.1. How shark depredation in the Ningaloo region fits into a global context

Shark depredation presents a complex management issue for fisheries managers that may be influenced by a range of biological, environmental and fishing related factors. The interdisciplinary approach used here to investigate depredation in the Ningaloo region of Western Australia has provided important insights into such complexities. This study has presented the first quantitative assessment of shark depredation in a recreational fishery globally, enabling comparison with depredation in large scale commercial fisheries. For example, the rate of depredation recorded here, which was approximately 12% from boat ramp surveys and 9% from video camera deployments, falls centrally within the global range of 0.9% - 26% reported in chapter two for commercial and recreational fisheries. However, this rate is higher than the majority of values for commercial longline fisheries, which are generally <10% (Hoey & Moore 1999, Lawson 2001, Beerkircher et al. 2002, Clark et al. 2007, Gilman et al. 2007, Rabearisoa et al. 2007, Romanov et al. 2007, Varghese et al. 2007, MacNeil et al. 2009).

There are a number of key differences in the dynamics of shark depredation in the recreational fishery in the Ningaloo region, compared to typical commercial longline fisheries. For example, the recreational fishery in the Ningaloo region covers a relatively small area, and involves vessels fishing with a small number of individual lines and hooks. This is in stark contrast to the industrial scale of many longline fisheries, where lines can range from 2 – 100 km in length, with 100 – 2500 hooks per line (Gilman et al. 2007). Longlines may also be deployed for a number of hours, giving sharks a long timeframe to locate and depredate hooked fish, compared to in recreational fisheries, where sharks generally have less than 5 minutes to depredate a fish, between when the fish is hooked to when it is retrieved to the vessel. The nature of depredation in large-scale longline fisheries is therefore more similar to scavenging, especially when the hooked fish are already dead, compared to in a recreational fishery, where it more closely resembles chasing down and consuming injured prey. Considering this short timeframe in recreational fisheries, it is perhaps surprising that the depredation rate was higher in this recreational fishery, compared to the rates in the majority of pelagic commercial longline fisheries. However, a potential reason for this is that commercial pelagic longline fishing generally occurs in deeper, offshore waters, where the line is set in midwater or near the surface. Sharks may be relatively uncommon in this ecosystem, especially in areas where declines have occurred due to overfishing in recent decades (Baum & Myers 2004, Ward & Myers 2005, Dulvy et al. 2008, Camhi et al. 2009), compared to the shallow reef habitats found in the Ningaloo region (Stevens et al. 2009, Speed et al. 2011, Babcock et al. 2017). Likewise, the concentration of fishing effort in small areas relatively close to the boat ramp, was shown in the current research to be an important factor explaining the higher depredation rates in these discrete areas. Conversely, in commercial longline fisheries, the effort is spread over much larger areas, with less fishing in the same locations. Due to the differences in the spatial scale of fishing in commercial and recreational fisheries, it is possible that depredation in the former is mainly an opportunistic behaviour, whereas in small-scale recreational fisheries there is more scope for behavioural associations to occur for sharks.

The application of RUMs in chapter four indicated that the rate of shark depredation did not influence fisher site choice, despite the known socio-economic impacts of lost fishing gear and the associated decrease in the recreational fishing experience. Costs of shark depredation in commercial fisheries may be far higher, i.e. hundreds or even thousands of dollars per set (Gilman et al. 2007), due to lost/damaged catch and fishing gear. However, the impact of depredation on site choice has not yet been quantified in commercial fisheries. RUMs could thus be applied to commercial fisheries data, whilst also investigating the importance of other factors that may influence site choice, such as catch rate, weather conditions, environmental features and travel cost. In particular, the large volume of data collected globally through commercial fishery logbooks could offer a valuable opportunity to conduct such analyses.

The research presented in chapter five recorded two shark species that had not previously been identified as being responsible for depredation, i.e. the sicklefin lemon shark *Negaprion acutidens* and the grey reef shark *Carcharhinus amblyrhynchos*. These species are known to be associated with reef habitats and are only found in coastal waters (Wetherbee et al. 1997, Compagno et al. 2005, Field et al. 2011, Vianna et al. 2013, Rizzari et al. 2014b, Speed et al. 2016), which explains why they have not been identified in other depredation studies, which have mainly focused on offshore pelagic longline fisheries. The other two species that were identified depredating hooked fish in the Ningaloo fishery, i.e. the blacktip/Australian blacktip *Carcharhinus limbatus/tilstoni* and spottail *Carcharhinus sorrah* sharks, were previously reported by Romanov et al. (2007) as being potentially responsible for depredation, although this was based on stomach contents analysis rather than direct observation. In general, it is clear that the shark species involved in depredation vary substantially, depending on spatial and temporal patterns of fishing. Likewise, the results presented in chapter five, where longitude was found to be an important factor influencing the relative abundance of sharks, suggest that habitat was an important driver of the shark species involved. This thesis represents a vital case study, because it has generated a multi-disciplinary assessment of shark depredation in a regionally important fishery, combining aspects of biology, fisheries management, behaviour and socio-economics. The novel research covered here also has broader application to the global context of shark depredation in fisheries.

6.2. Study limitations

Whilst this research presents an in-depth investigation of shark depredation in this particular recreational fishery, there are a number of limitations which must be considered. Firstly, the temporal scope of the study was restricted, due to the logistical difficulties of conducting fieldwork in this remote region over multiple years. Whilst some level of seasonal variation was incorporated into the boat ramp surveys for chapters three and four, replication across multiple years was not possible. Likewise for chapter five, the results only represented a snapshot of the shark interactions with fishing activity in a constrained area, over a short timescale. The research was therefore not able to address one of the key questions relating to shark depredation in this region, which is whether there has been an increase in depredation rates in recent decades, as is reported anecdotally. However, the results of this thesis can be used as a baseline against which future research can quantify temporal changes.

The methodologies used in chapters 3 - 5 had a number of inherent limitations. Firstly, the boat ramp surveys may have been biased by the negative attitudes of many recreational fishers towards sharks in the Ningaloo region, leading to the fishers reporting exaggerated shark depredation rates. However, this possibility was minimised by not using data from repeat interviews of the same fisher, as it was judged to be less reliable. Also, the survey was not framed as a shark depredation study, but instead was introduced as a survey of recreational fishing catch and effort to avoid fishers immediately becoming biased towards sharks and providing exaggerated data. There was likely to be a degree of inaccuracy in the data due to fishers only being able to recall estimated numbers for how many fish they caught or lost. Fishers may have also mistaken depredation events for where sharks took the bait directly and snapped off the fishing line, or where a large fish got hooked and snapped off the line, thereby contributing to inaccuracies in the data for depredation rates. This possibility was observed during data collection on charter vessels for chapter five. Another limitation is that although a concerted effort was made to collect fishing location data that was as accurate as possible, the spatial locations of fishing sites reported by some fishers may have been unreliable, due to them not wanting to provide their exact fishing locations. The extent of this inaccuracy was, however, difficult to determine. Also, the spatial locations for those fishers that were trolling for pelagic species may have been somewhat inaccurate, due to them covering a large area.

A limitation of the use of line-mounted cameras in chapter five was that the ability to identify sharks and record behavioural interactions with fishing gear was restricted due to the rapid movement of the camera, which was caused by vibrations of the fishing line it was attached to. Whilst the results in chapter five enabled ground-truthing of the depredation rate reported in chapter three, as well as identification of the species involved, this was only based on a small sample size of 15 depredation events out of the 165 fish hooked at 92 fishing locations, limiting the conclusions that could be drawn from the data and the extent to which it can be considered representative of the depredation occurring across the whole fishery The low frequency of depredation events in that study suggest that a larger sampling effort and number of camera deployments would be needed to generate more robust results. The preliminary and experimental nature of the data presented in chapter five, meant that a more controlled, quantitative analysis of behavioural interactions with fishing gear was not possible. However, the descriptive data on behavioural types and frequency of occurrence is nonetheless an novel addition to the field of shark behavioural ecology, especially because very little information exists about their interactions with fishing gear and hooked fish.

6.3. Future directions

6.3.1. Quantifying temporal trends in shark depredation

6.3.1.1. In large-scale commercial fisheries

Whether shark depredation is increasing or decreasing over time is a significant question that remains to be addressed, both in this fishery, and in many others around the world. Increasing effort and greater spatial coverage of fishing activities globally (Anticamara et al. 2011, Watson et al. 2013, Tickler et al. 2018) may be leading to increases in depredation rates, because the chance of sharks encountering fishing operations would be higher. Likewise, reduction in natural prey species due to fishing activity (Srinivasan et al. 2010, Froese et al. 2012), may lead to an increase in sharks opportunistically depredating hooked fish, a pattern which has been reported for livestock depredation in the terrestrial world (Madhusudan 2003, Madhusudan & Mishra 2003, Polisar et al. 2003, Miquelle et al. 2005). In recreational and artisanal fisheries that are concentrated in small areas, the formation of behavioural associations in sharks between the presence of vessels and the availability of hooked fish to feed on, may lead to increasing depredation rates over time, a process which has been observed for cetacean depredation in some fisheries (Read 2008, Clark & Agnew 2010, Powell & Wells 2011, Peterson et al. 2013). Conversely, depredation could be decreasing globally, due to marked declines in the main pelagic species identified in chapter two to be responsible for depredation, such as blue sharks *Prionace glauca*, shortfin mako sharks *Isurus oxyrinchus* and oceanic whitetip sharks *Carcharhinus longimanus* (Baum et al. 2003, Ward & Myers 2005, Dulvy et al. 2008, Ferretti et al. 2010, Clarke et al. 2013).

Apart from a few studies which have investigated temporal trends, i.e. Romanov et al. (2013) found increases from 3% in 2011 to 9% in 2013 and MacNeil et al. (2009) reported no increase or decrease in depredation rates between 1992 and 2006, there is very little information to address this question. A newly published study by Muñoz-Lechuga & Coelho (2018) reported annual increases in depredation rates of 0.26% and 0.85% in the Atlantic and Indian Oceans, respectively, from 1.1% to 2.1% between 2011 and 2015 in the former and from 1.5% to 4.9% in the latter. However, depredation rates decreased in 2016 in both oceans and only 21% of the total depredation was confirmed to be caused by sharks in the Indian Ocean, with no recording of the predators responsible in the Atlantic Ocean. Similar long-term data collection protocols should therefore be implemented to enable analysis of temporal change in depredation rates in other large-scale commercial fisheries, alongside more detailed collection of data on the predators responsible for depredation. This could follow the example of the Indian Ocean Tuna Commission, which committed to ensuring its members continue to collect detailed data on depredation in coming years (IOTC 2007, Romanov & Bach 2009).

6.3.1.2. In the Ningaloo region

Prior to the current research, the only data that existed for shark depredation in Western Australia was from Sumner et al. (2002) and Williamson et al. (2006), which only provided estimated numbers of fish depredated per target species, which likely contained a large degree of uncertainty because quantifying depredation was not the main objective of these studies. Future data collection should therefore be conducted to replicate the methods used in chapter three, and enable reliable comparison of depredation rates over multi-year timescales. This is particularly important because there are regular anecdotal accounts that shark depredation has increased in recent decades in the Ningaloo Marine Park and Exmouth Gulf, as well as in the broader north-west region of Western Australia.

Shark depredation may also be strongly influenced by seasonal variation, due to changes in levels of fishing effort, weather, the occurrence of phenomena such as cyclones, and the movement patterns of sharks. Past research has shown that *C. amblyrhynchos* and *N. acutidens* show strong site fidelity to certain areas in the Ningaloo Marine Park, and are present all year round, although some *C. amblyrhynchos* individuals were recorded making movements of up to 80 km from the original tagging location (Speed et al. 2016). These species have also been found to show inter-annual site fidelity to key nursery areas in the Ningaloo region (Speed et al. 2011). Ongoing telemetry research on *N. acutidens* suggests that whilst this species does undertake movements on an annual basis, likely linked to parturition and mating, they remain in the broader Ningaloo region all year round (R. Pillans, unpubl. data). Whilst dusky *Carcharhinus obscurus* and sandbar *Carcharhinus plumbeus* sharks were not observed depredating hooked fish in the research presented in chapter five, they cannot be ruled out as a potential species responsible, as they have been anecdotally reported to depredate hooked fish in this region. These species are known to undertake extensive north-south migrations in Western Australian waters (McAuley et al. 2005, Braccini et al. 2017), and if they were implicated it would likely generate seasonal variation in depredation rates. Therefore, in addition to investigating inter-annual variation, future research should seek to analyse seasonal variation in depredation rates. Quantifying depredation rates in the high season (April – October), when the majority of fishers visit the Ningaloo region, compared to in the low season, would be another interesting avenue for research. This would provide further insights into how variation in the level of fishing pressure in certain areas may be influencing shark behaviour and depredation rates.

6.3.2. Analysing temporal patterns of shark abundance in the Ningaloo region

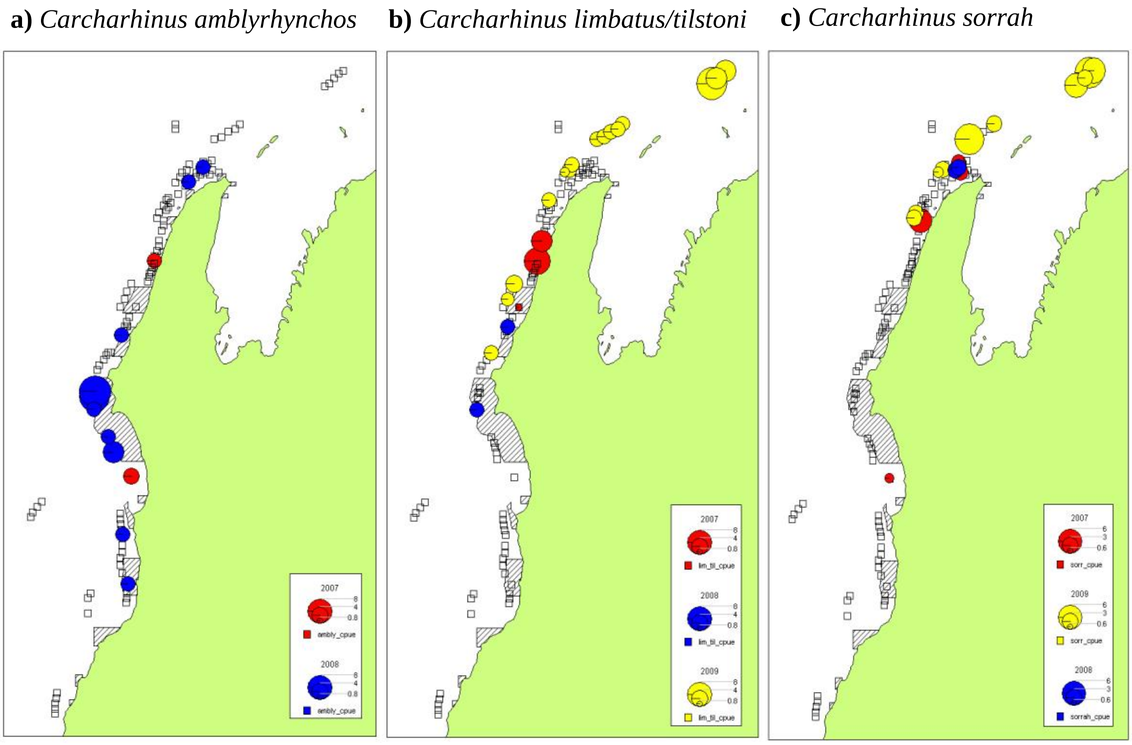
In addition to monitoring changes in depredation rates over time, it is necessary to quantify changes in the abundance of sharks in the Ningaloo region. It is a common perception amongst fishers that depredation is increasing due to rising numbers of sharks, as a result of the closure of commercial shark fisheries in the Gascoyne, Pilbara and Kimberley regions of north-west Western Australia (Mercer 2015). However, the k-selected life history traits of many large carcharhinid species (Carrier et al. 2004, Cortés 2004, Compagno et al. 2005, Camhi et al. 2009), particularly the species identified in chapter five to be responsible for depredation, suggest that whilst a small degree of population growth may have occurred since the prohibition of shark fishing was introduced in this region in 2005 (McAuley et al. 2005), substantial population increases are unlikely. For example, *C. amblyrhynchos* only produce litters of 1-6 pups, and do not reach maturity until 7 - 7.5 years old (Compagno et al. 2005). Determining changes in the population sizes of these species is currently difficult due to a lack of data on their stock size, natural mortality rates and juvenile survival rates.

The only historical data on shark abundance that exists for the Ningaloo region comes from longline surveys that were conducted between 2001 and 2009 (Stevens et al. 2009). Results from these surveys showed fluctuating catch rates, from 2.74 – 16.54 sharks per 100 hooks, with no clear increasing or decreasing trend over the period (Stevens et al. 2009). The trends for each individual species were also variable, although there was evidence of a decline in *C. plumbeus* catch rates (Stevens et al. 2009). It must be noted, however, that the locations of longline sampling and the methods used were not fully standardised across the time period, making meaningful comparison between years difficult. However, data from commercial fisheries in northern Western Australia suggest that some larger shark species declined between 1998 and 2006, including *C. plumbeus,* tiger shark *Galeocerdo cuvier* and hammerhead sharks *Sphyrna spp.* (Heupel & McAuley 2007). Of the species identified in chapter five to be responsible for depredation, *N. acutidens* was only rarely caught in these previous longline surveys, whereas *C. amblyrhynchos*, *C. limbatus/tilstoni* and *C. sorrah* were caught more frequently (Stevens et al.

2009). Catch rates for *C. amblyrhynchos* were higher than *C. limbatus* and *C. sorrah* in <50 m depth, with the reverse relationship in waters >50 m depth (Stevens et al. 2009).

On a spatial basis, overall catch rates were relatively even across the NMP (Fig. 6-1) (Stevens et al. 2009). *C. amblyrhynchos* was caught more widely across the NMP, whereas *C. limbatus/tilstoni* and *C. sorrah* were only caught in the northern section of the NMP (Fig. 6-1) (Stevens et al. 2009). Dive surveys were also conducted between 2007 and 2008 to assess shark abundance, which indicated that *C. amblyrhynchos* was the most abundant species overall, particularly in areas of reef habitat (Stevens et al. 2009). This historical data allows comparison with recent data collected using Baited Remote Underwater Video systems (BRUVs) in 2015, which showed that *C. amblyrhynchos* abundance was markedly higher than other shark species, especially in reef habitats (Babcock et al. 2017). The central portion of the NMP was found to have the highest abundance of *C. amblyrhynchos*, with areas close to the Tantabiddi and Coral Bay boat ramps having notably lower values (Fig. 6-2) (Babcock et al. 2017). Interestingly, the areas that had higher numbers of *C. amblyrhynchos* had low levels of fishing pressure according to the boat ramp surveys conducted in this study (see Fig. 3-1 in chapter three), which partly supports the theory that shark depredation is being driven by behavioural changes in sharks rather than simply reflecting changes in shark abundance. However, *C. amblyrhynchos* was only one of the four species identified to be responsible for depredation, so spatial abundance data for the other three species would be needed to verify this. For *C. amblyrhynchos*, there is also a degree of overlap in the areas of greater abundance recorded in both the longline surveys and the more recent BRUVs data (Stevens et al. 2009, Babcock et al. 2017). GAMMs identified that distance to the shelf edge and seabed relief were key factors influencing the observed patterns of *C. amblyrhynchos* abundance (Fig. 6-3) (Babcock et al. 2017). Abundance peaked at approximately 20 km from the shelf edge, which likely reflected the location and depth of suitable habitat (Babcock et al. 2017). Highest abundance also occurred at intermediate levels of seabed relief, again suggesting that the complexity of the benthic habitat is important for this species (Babcock et al. 2017). This reflects the results reported in chapter five, where higher shark abundance was found in the westerly portion of the study area on the Ningaloo reef, compared to at fishing locations in the Exmouth Gulf, which is further east. Surprisingly, *N. acutidens* was only recorded infrequently in both of these studies, contrary to the findings in chapter 5.

Whilst this past data does provide important insights into patterns of shark abundance in the Ningaloo region, the lack of consistent, repeated sampling protocols prevents meaningful assessment of temporal abundance trends. Future work should therefore aim to develop a rigorous approach to sampling shark abundance on a multi-year basis, using consistent methodology. The use of BRUVs is preferred to the previous approach where longlines were used, as it is a non-damaging technique. Increasing our understanding of the role that shark abundance plays in determining depredation rates is vital, as it is necessary to identify whether depredation solely reflects the abundance of sharks in an area, or if it is more complex and driven by other mechanisms, particularly the formation of behavioural associations. If the latter has a more important influence on depredation rates, then overall changes in shark abundance in the wider region may have little effect on depredation rates in those discrete areas where sharks have become accustomed to feeding opportunities from fishing.



a) *Carcharhinus amblyrhynchos* **b)** *Carcharhinus limbatus/tilstoni* **c)** *Carcharhinus sorrah*

Fig. 6-1: Catch rates (no. sharks per 100 hooks) for **a)** grey reef shark *Carcharhinus amblyrhynchos*, **b)** blacktip/Australian blacktip shark *Carcharhinus limbatus/tilstoni*, and **c)** spottail shark *Carcharhinus sorrah*, recorded from longline surveys between 2007 and 2009. Data collected by the Western Australia Department of Fisheries, figures taken from Stevens et al. (2009).

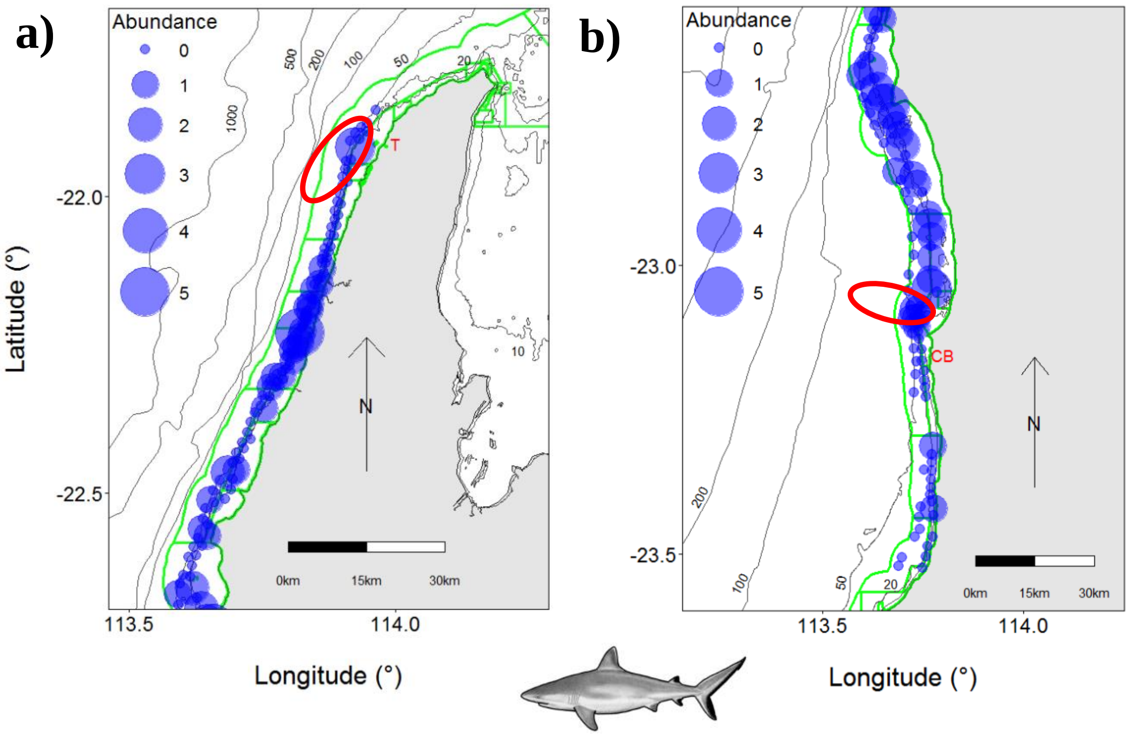


Fig. 6-2: Abundance (blue circles) of grey reef shark *Carcharhinus amblyrhynchos* in the **a)** northern and **b)** southern portions of the Ningaloo Marine Park (NMP), as recorded from Baited Remote Underwater Video Surveys (BRUVs) in 2015. Red ovals indicate areas which were identified by Mitchell et al. (2018a) to have high shark depredation rates. Labelled contour lines show depth in metres. Solid green lines delineate the boundary of the NMP. CB = Coral Bay boat ramp, T = Tantabiddi boat ramp. Modified from Babcock et al. (2017).

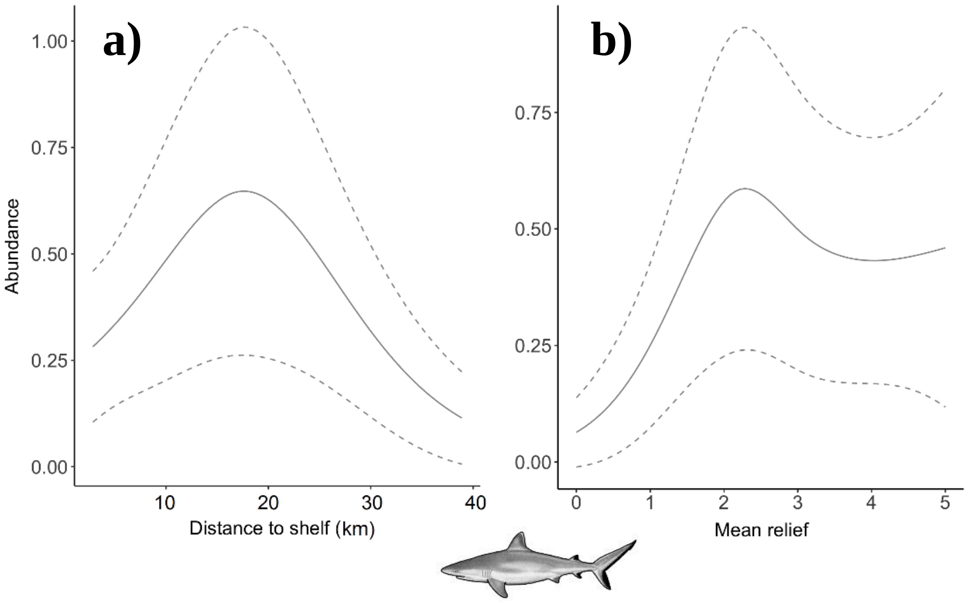


Fig. 6-3: Effect of **a)** distance to shelf edge and **b)** mean seabed relief on the abundance of grey reef shark *Carcharhinus amblyrhynchos* in the Ningaloo Marine Park. Solid lines represent fitted GAMM smooth curves. Dashed lines indicate 95% confidence intervals (fitted smooth curve ±2 S.E.). Taken from Babcock et al. (2017).

6.3.3. Quantifying shark depredation in other recreational fisheries

6.3.3.1. In Western Australia

In addition to the Ningaloo region, shark depredation is also reported to occur in other areas of north-west Western Australia (Mercer 2015, Kagi 2016). This has been confirmed by preliminary surveys conducted at recreational fishing tournaments in Denham, Carnarvon and Broome (Fig. 6-4) (Mitchell et al. unpubl. data). The rates of depredation in these areas were 4.43%, 4.59% and 10.99%, respectively, and the percentage of trips which experienced at least one depredation event in these areas were 27%, 22% and 25%, respectively. Whilst these data were only based on a small sample size (~150 trips for Carnarvon and ~100 trips each for Denham and Broome), they indicate that Denham and Carnarvon have depredation rates lower than Broome, and that the values for all of these areas were lower than the Ningaloo Marine Park and Exmouth Gulf. This is especially the case for the number of trips which experienced at least one depredation event, which was ~40% in the Ningaloo Marine Park and Exmouth Gulf, i.e. almost twice as high as the other locations surveyed. This clearly indicates that shark depredation is occurring across the wider north-west and northern regions of Western Australia and that future surveys should aim to replicate the methods described in chapter three, to create larger, more robust regional datasets. This would allow reliable comparison with the data in chapter three, and would also enable similar modelling using Generalised Additive Mixed Models (GAMMs). Other important recreational fishing locations in the west, north-west and northern regions of Western Australia, such as Geraldton, the Abrolhos Islands, Kalbarri, Karratha and Port Hedland (Fig. 6-4), could also be surveyed to create an holistic regional assessment of depredation rates. This information could then be disseminated to recreational fishers and the general public through a range of channels, including print and online media, similar to coverage of the research presented in chapter three (see Fig. 6-5) (Butler 2018, PerthNow 2018), as well as through social media and fishing club bulletins.

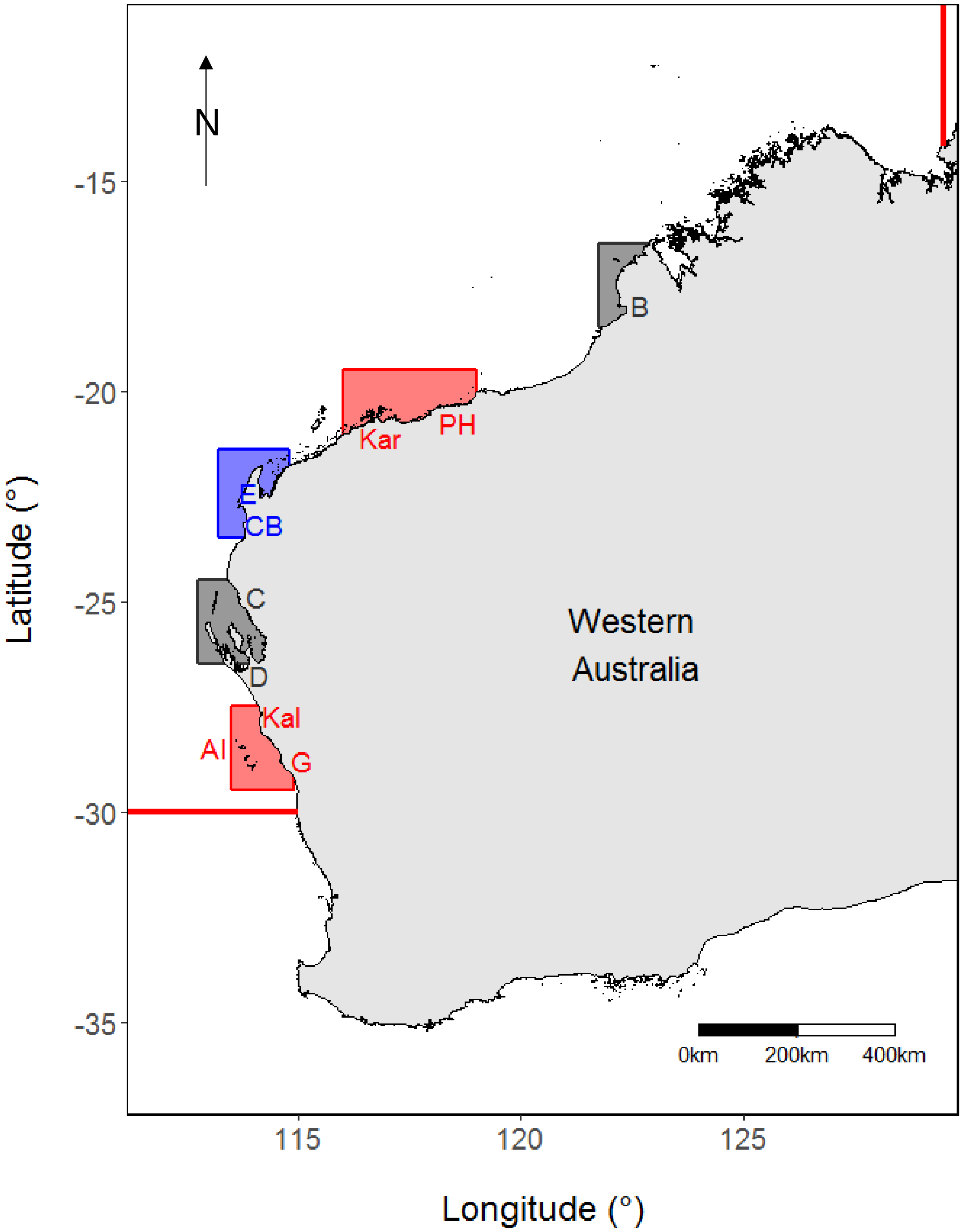


Fig. 6-4: Map of locations where shark depredation data has been collected by this study (shown in blue) and locations where pilot data has been collected (shown in grey; Mitchell *et al.* unpubl. data). Locations where future data collection is recommended are shown in red. Solid red lines represent the area of Western Australia across which shark depredation is theorised to occur in fisheries. G = Geraldton, AI = the Abrolhos Islands, Kal = Kalbarri, D = Denham, C = Carnarvon, CB = Coral Bay, E = Exmouth, Kar = Karratha, PH = Port Hedland, B = Broome.

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Fish spots easy food for sharks

Steve Butler

Sharks appear to be targeting popular recreational fishing spots in search of easy meals, according to a world-first study by University of WA researchers.

The research, led by PhD student Jonathan Mitchell, found that 40 per cent of more than 400 anglers fishing in the Ningaloo Marine Park and the Exmouth Gulf had lost hooked fish in their most recent fishing trip.

It amounted to 12 per cent of caught fish being taken by sharks. Mr Mitchell said it appeared shark behaviour was changing because they knew easier food was on offer where boats congregated.

It is believed to be the first time such a study, which had been prompted by a growing number of complaints of sharks taking hooked fish, had been undertaken in a recreational fishery.

"We wanted to get some numbers to estimate the scale of what's happening out there from a scientific point of view," Mr Mitchell said.

"We found the areas that are fished more frequently have higher bite-off rates. Basically, it suggests a change in the behaviour of sharks in these areas where they've come to associate regular fishing and the presence of fishing boats to the availability of food.

"On top of that, there is also the prospect of opportunistic behaviour in the sharks."

Mr Mitchell said a paper would soon be published outlining the types of sharks involved.

He said the research, conducted in collaboration with the Department of Primary Industries and Regional Development, would help lower the number of bite-offs as well as prevent injuries to fish and sharks.

"We're working on being able to identify the shark species and also learn more about their behaviour," Mr Mitchell said.

"Recreational fishers are losing out because they are losing fish and gear, so that's damaging their experience.

"But there's also an extra mortality of fish because of shark bite-offs and often when the sharks take the fish, they get hooked themselves. We're trying to develop research to combat all three of those things."

Mr Mitchell said modifying techniques by spending less time at each site and moving to a different location when a fish was taken could prevent sharks from learning to associate fishing activities with food.

The research was funded by the Gorgon Barrow Island Net Conservation Benefits Fund and the Jock Clough Marine Foundation.

The remains of a golden trevally.

A sweetlip after a shark bite-off.

UWA researcher Jonathan Mitchell, right, interviews a fisherman.

Fig. 6-5: Media coverage of the shark depredation research presented in chapter three of this thesis. Taken from Butler (2018).

6.3.3.2. In other Austalian states

The boat ramp survey methodology could be replicated in other states, as depredation has been anecdotally reported in Queensland (Fraser Coast Chronicle 2012, ABC 2018, Daily Mercury 2018). In particular, it is recommended that shark depredation is investigated and quantified across the Great Barrier Reef Marine Park, where fishing takes place across a wide range of habitats, with many different species being targeted (Mapstone et al. 2008, GBRMPA 2014). Quantifying depredation across this large marine park would produce valuable information about the drivers of shark depredation, and how it may vary due to a range of spatial and temporal factors, as well as fishing methods. In addition to collecting data on depredation, the spatial maps presented in chapter three are of substantial value for assessing the distribution of fishing activity in the Ningaloo Marine Park, and highlighting the heterogeneous distribution of fishing effort. Minimal information previously existed for patterns of fishing effort in either this marine park, or others around Australia, which demonstrates the value of data collected through targeted boat ramp surveys, and could be useful for addressing a range of management and research questions in the Great Barrier Reef Marine Park.

6.3.3.3. In other locations around the world

On a broader level, shark depredation has been anecdotally reported in a number of other recreational fisheries around the world, especially in The Bahamas (Madigan et al. 2015) and South Africa (McCord & Lamberth 2009, Labinjoh 2014), as well as in parts of the USA including the Gulf of Mexico, North Carolina (Fig. 6-6), and Guam (Stelter 2012, Quintanilla 2014, McNally 2017). There is already a long-standing and robust survey scheme used by the National Oceanic and Atmospheric Administration (NOAA) in the USA to collect data on catch and effort in recreational fisheries (NOAA 2018). Additions to these surveys could be made to collect data on shark depredation, similar to that presented in chapter three. The simplicity and transferability of the methodology used in chapter three would enable it to be used in recreational fisheries in many other countries. This should also include developing countries in which shark depredation occurs in recreational fisheries, such as in Kenya (Ndegwa & Makogola 2007).

Fig. 6-6: A carcharhinid shark depredating a hooked tuna during recreational fishing in North Carolina, USA. Credit: Anon., taken from McNally (2017).

The principle of using RUMs to evaluate how depredation may affect fisher site choice could also be applied in other recreational fisheries around the world. In US recreational fisheries, this approach would build on the large amount of existing research that has been conducted using RUMs (Bockstael et al. 1989, Greene et al. 1997, Lipton & Hicks 1999, Hunt 2005). The existing recreational fishing survey framework used by NOAA (NOAA 2018) could provide valuable opportunities to do this. This work could improve on the RUMs presented in chapter four by collecting detailed data for expected catch rates and depredation rates, at a range of site choice locations. Including extra individual-specific variables like age, income and home postcode would improve the power of the RUMs to investigate how fishers trade off travel cost, catch rate and depredation rate on an individual- and site-specific basis.

6.3.4. Investigating depredation in Western Australian commercial fisheries

Shark depredation is also known to occur in certain line-based commercial fisheries in Western Australia, such as the Mackerel Managed Fishery (MMF) and the Gascoyne pink snapper *Chrysophrys auratus* wetline fishery (G. Jackson, pers. comm.). Some basic data is available for depredation rates in these fisheries, although it is inconsistent due to its spatial and temporal patchiness (DPIRD, unpubl. data). A dedicated program of data collection could therefore be established in these fisheries to provide quantitative data on the rates of shark depredation, as well as spatial and temporal variation. This is of particular significance because these fisheries operate on a larger scale to recreational fisheries, so the loss of catch due to depredation may represent an important extra mortality for certain target species. In the Gascoyne *C. auratus* fishery in particular, dense spawning aggregations have historically been targeted in the Shark Bay region (Moran et al. 2003, Jackson 2008, Norriss et al. 2012), and the occurrence of depredation when fishing these spawning aggregations is anecdotally reported to be high (G. Jackson, pers. comm.), likely because the sharks would naturally associate with these areas of high prey density. As the fishers have specific quotas for *C. auratus* in this area, they will aim to catch a certain volume of fish and those lost to depredation will be an additional mortality on top of this quota. Since these aggregations occur over relatively small spatial scales, there is limited scope for avoiding depredation by modifying spatial fishing practices, therefore the adoption of shark deterrent devices could be particularly useful. Alternatively, a solution to depredation could be the use of fish traps, like those used by commercial fisheries in other parts of north-west Australia (Whitelaw et al. 1991), instead of hook and line fishing gear, which would largely eliminate shark depredation altogether. The high commercial value of *C. auratus* (DEH 2004) highlights the benefit of conducting research into understanding and mitigating shark depredation in this fishery.

6.3.5. Investigating shark movement patterns and overlap with fishing activity

Due to the possibility that sharks have come to associate the presence of fishing vessels with the availability of hooked fish to feed on, there may be a change in their movement patterns and residency if they are regularly depredating hooked fish. In order to investigate this, tagging methods could be utilised to determine the movement patterns and habitat use of individuals from the species that were confirmed to be responsible for depredation in chapter five. This could involve both acoustic and satellite tags to provide fine scale movement data, which could be analysed in conjunction with vessel tracks from recreational and charter fishing vessels, to assess the level of overlap. This technique has been used in recent research to assess the overlap between different shark species and fishing activity, in order to determine their potential vulnerability

(Queiroz et al. 2016, Calich et al. 2018). Conducting this research across seasonal and inter-annual timescales would allow identification of whether certain individual sharks spend large portions of time in the areas where recreational fishing is concentrated. It would also determine the extent to which these species undertake seasonal movements, which could lead to seasonal variation in depredation rates.

6.3.6. Development and application of depredation mitigation measures

From the research presented, it is clear that shark depredation is a highly complex issue which is influenced by a range of spatial and environmental factors, as well as differences in fishing methods, and involves different shark species. As a result, developing effective mitigation measures will be challenging and requires a comprehensive and multi-faceted approach. Understanding the factors driving fisher site choice is vital to enable implementation of strategies for moderating the spatial distribution of fishing effort. In particular, introducing fisheries closures is one such way that the predictability of fishing can be reduced, to minimise the occurrence of behavioural association in sharks and thus reduce overall depredation rates. Fisher education and dissemination of information can play a vital role in mitigating depredation, by providing fishers with detailed knowledge to make informed decisions about specific locations to avoid when fishing. This ‘mitigation through information’ approach can be implemented rapidly and cost-effectively to reduce depredation rates, and regular surveys could be conducted and spatial predictions of depredation rate produced, to keep fishers updated on where current depredation hotspots are. Such information could be provided to fishers through interactive platforms such as smartphone software applications (‘apps’), as well as more traditional sources including leaflets and information boards at boat ramps. These changes can be applied in combination with different fishing gear configurations, e.g. using fewer hooks on each line, and adopting systems that allow faster retrieval of hooked fish, particularly through the use of hydraulic or electric powered winches/reels, to give fishers multiple options for mitigating depredation.

Despite the large and growing body of research on shark deterrent devices, there has been minimal success at developing a deterrent that is both effective and practical for use in either commercial or recreational fisheries. Electrical deterrents appear to offer the most promise, such as the SharkShield, which has been demonstrated to be effective on white sharks *Carcharodon carcharias* (Kempster et al. 2016, Huveneers et al. 2018b), as well as certain configurations of electo-positive metals and/or magnets, which may be effective on some shark species (Kaimmer & Stoner 2008, Brill et al. 2009, O'Connell et al. 2011, 2014). However, a substantial amount of work is still needed to convert such deterrents into a small and practical device for large-scale application to commercial and recreational fisheries. In light of this, an approach worth investigating is the development of deterrents that target multiple sensory systems, as this would address some key limitations of the deterrents that have been tested so far, i.e. that there is a high degree of variability in sensitivity between species and that habituation needs to be taken into account. By producing a deterrent that targets two or more senses, for example by combining flashing lights and loud irregular sounds with a strong electric current, the stimulus created would be more powerful and noxious to an approaching shark. Those species that are less sensitive to one of these sensory stimuli may be more sensitive to the others, therefore increasing the likelihood of it being successful. Devices which physically protect the hooked fish, similar to those tested previously (Moreno et al. 2008, Rabearisoa et al. 2012, Hamer et al. 2015), are also worth investigating further, as they eliminate the issue of varied sensitivity to sensory stimuli, and are likely to be more cost-effective. A combined approach where physical and/or multi-sensory deterrents are deployed whilst also adopting changes to fishing methods, may offer a substantially higher chance of successfully reducing shark depredation rates, in comparison to each method in isolation. Whilst it is highly unlikely that depredation rates could ever be reduced to zero, the development and testing of non-lethal options for mitigating shark depredation is necessary as the perceived impact of shark depredation is very high in Western Australia, and currently many fishers are calling for shark culls or commercial shark fisheries as a means of mitigating depredation, which would be environmentally and socially unacceptable.

6.4. Conclusion

This study has made a substantial contribution to our understanding of shark depredation in Western Australia, and provides important information for management of this issue. Also, when considering the highly contentious nature of shark management in Australia, this research is timely in filling a key research gap. Additionally, knowledge of how depredation influences fisher site choice, as well as which shark species are responsible for depredation, will inform future efforts to mitigate depredation. On a broader level, this study also brings together a diverse range of data and information on shark depredation from around the world, which will hopefully stimulate targeted research into newly identified research gaps. In particular, it is recommended that future research should prioritise the development and testing of novel strategies for mitigating depredation, since, if successful, this will have far reaching benefits for target species populations, the shark species responsible for depredation, and commercial and recreational fishers. The principles underlying mitigation of depredation also have important relevance to reducing shark bycatch, which is a significant threat to many shark populations worldwide. Collaboration between researchers focusing on shark depredation, bycatch and conservation is therefore encouraged, as it could substantially increase the chances of designing effective mitigation measures for both of these fisheries issues.

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Appendices

Appendix A – List of boat ramp survey questions (chapter three)

Boat questions – apply to all the fishers on the boat:

- What time did lines enter the water?

- What time did lines leave the water?

- What fishing method was used?

- What type of bait/lure was used?

- Was burleying used?

- What was the maximum depth of hooks?

- What was the minimum depth of hooks?

- Approximate fishing location (recorded as a point location on the ‘Collector for ArcGIS map)?

- How many fish did you catch, including both those kept and those returned?

- Did you experience shark depredation?

- If yes, how many fish were partly or completely depredated by sharks?

- Were these fish consumed completely or was part of the fish (e.g. the head) retrieved?

- Boat name/number?

- Boat length?

- Time of interview?

Individual fisher questions – apply to just the fisher being interviewed:

- Have you been interviewed about shark bite-offs before?

- How many times have you fished from this boat ramp before?

- How many days have you fished from a boat in the last year?

- How many years have you been fishing?

Appendix B – Predictor variables tested in the predictive GAMs used to generate catch rate and depredation rate values for the RUM, and the resulting output tables from the best-fitting GAMs (chapter four)

Table B1: List of predictor variables tested in Generalised Additive Models (GAMs) for predicting the total number of fish hooked per hour and the number of fish depredated per hour, in the Ningaloo Marine Park (NMP) recreational fishery, along with their hypothesised importance.

Predictor variable	Hypothesised importance to total number of fish hooked and number of fish depredated
Smoothed continuous predictor variables	
Latitude, Longitude	Change in latitude and longitude acts as a proxy for spatial variation in other parameters not included in the model, such as oceanographic features and bathymetry, which may influence the abundance and distribution of target fish species and sharks
Depth (m)	Depth influences the habitat type present, as well as the distribution and abundance of different target fish species and sharks
Distance from boat ramp (km)	Sites that are further away from the boat ramp may have been less impacted by fishing, therefore the abundance of target species may be higher and there would be a greater total number of fish hooked. Sharks would be less likely to associate fishing vessels with the availability of hooked fish in these locations, resulting in a lower risk of depredation occurring
Length of fishing trip (hours)	Longer fishing trips would be expected to lead to a higher total number of fish caught, due to the higher fishing effort. The likelihood of depredation occurring may also be higher, due to the greater chance of attracting sharks to the vessel over a longer fishing trip, through sensory cues such as fish blood in the water and the sound of the engine
Density of fishing vessels within 5 km radius	A higher density of fishing vessels may lead to a greater chance of sharks being attracted to the area, because of the sensory cues created by fishing. The total number of fish hooked may be lower, however, due to more vessels targeting fish in close proximity
Fishing pressure (kernel density of all fishing locations)	Areas that have received higher levels of fishing pressure due to many vessels regularly fishing there, may be expected to have lower abundance of target species, resulting in smaller values for the total number of fish hooked per hour. Additionally, sharks may spend more time in these areas that are regularly fished, because they associate the presence of fishing vessels with the availability of hooked fish to feed on, leading to a higher risk of depredation

Predictor variable	Hypothesised importance to total number of fish hooked and number of fish depredated
Sea surface temperature (SST; °C)	Temperature likely affects the activity levels and feeding activity of sharks and target fish species, therefore it will influence the likelihood of fish striking the bait and being hooked, as well as whether sharks are motivated to depredate hooked fish
Total no. fish hooked per hour	The total number of fish hooked will influence the depredation rate, because more fish being hooked will create stronger sensory cues that attract sharks, such as disturbances in the water and fish blood
Vessel length (m)	The size of the fishing vessel will determine the level of fishing effort, with larger vessels potentially carrying more fishers. This higher fishing effort would therefore likely lead to a higher catch rate and a greater chance of attracting sharks
Fishing experience (number of years fishing)	More experienced fishers are likely to catch a greater number of fish because they use more effective fishing techniques and they have a greater knowledge of which sites to choose. Also, they may understand how to avoid or minimise depredation rates, such as by reeling fish to the vessel quicker or moving sites as soon as a hooked fish is depredated by sharks
Categorical factor predictor variables	
Month/Year	Data was collected across three survey trips in July/August 2015, September/October 2015 and April 2016, hence the seasonal change may influence the activity and distribution of target fish and shark species
Habitat type (5 categories)	Habitat has a strong influence on the distribution and abundance of target fish species and sharks, especially in reef habitats such as the NMP
Local fishing experience (Number of times launched from that boat ramp before; 5 categories)	Greater local fishing experience may lead to higher catch rates, because the fishers would know which sites are likely to yield more fish. Also, fishers would know which sites have a higher risk of shark depredation, so these areas would be avoided, leading to lower depredation rates
Frequency of fishing (Number of times fished from a boat in the last 12 months: 5 categories)	This is another indicator of avidity and fishing experience, as fishers that fish from a boat more regularly may be expected to have better technique and knowledge, resulting in a higher catch rate and lower depredation rate

Table B2: Variables included in the best-fitting Generalised Additive Model (GAM) for catch rate, with their estimated degrees of freedom (Est. d.f.), reference degrees of freedom (Ref. d.f.), f- and p-values for smoothed continuous predictor variables, and estimated coefficient values, standard errors, t- and p-values for factor variables. Variables marked with a '*' were significant (p-value = <0.05).

Smoothed continuous predictor variables	**Est. d.f.**	**Ref. d.f.**	**f-value**	**p-value**
No. vessels within 5 km	2.13	2.58	1.86	0.15
Total no. hours fishing	1.00	1.00	0.43	0.51
No. years fishing	1.00	1.00	5.47	0.02*
Latitude, Longitude	2.00	2.00	2.17	0.12
Factor variables	**Est. coeff.**	**Std. error**	**t-value**	**p-value**
Habitat type	0.42	0.37	1.14	0.27
No. days boat fishing in last year	0.73	0.38	1.86	0.08

Table B3: Variables included in the best-fitting Generalised Additive Model (GAM) for depredation rate, with their estimated degrees of freedom (Est. d.f.), reference degrees of freedom (Ref. d.f.), f- and p-values for smoothed continuous predictor variables, and estimated coefficient values, standard errors, t- and p-values for factor variables. Variables marked with a '*' were significant (p-value = <0.05).

Smoothed continuous predictor variables	**E.d.f.**	**Ref d.f.**	**f-value**	**p-value**
Depth	3.72	3.92	6.80	<0.01*
Total no. fish hooked per hour	2.44	2.82	5.12	<0.01*
Vessel length	1.00	1.00	1.11	0.30
No. years fishing	1.57	1.89	0.56	0.57
Latitude, Longitude	5.19	6.86	0.91	0.51
Factor variable	**Est. coeff.**	**Std. error**	**t-value**	**p-value**
Habitat type	-1.85	0.90	-2.23	0.13