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

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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.

KEY WORDS: Shark depredation · Recreational fishing · Fisheries management · Generalised additive mixed models · GAMMs · Tweedie distribution

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). This occurs in commercial and recreational fisheries worldwide (Sumner et al. 2002, Nishida & Shiba 2005, 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,

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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 20% (Lawson 2001, IOTC 2007, Gilman et al. 2008, MacNeil et al. 2009). 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 northwest Western Australia (see Fig. 1a), 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, 55 000 boat fishing days were recorded across the northwest (Gascoyne) region of Western Australia over a recent 12 mo survey period (2011 to 2012) (Ryan et al. 2013). In this time, an estimated 16 884 ± 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. 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, 2016, 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, the depth of fishing 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. 2014). 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.

MATERIALS AND METHODS

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. 1a). 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).

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 3 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 3 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 2 weekdays for each weekend day (Jones & Pollock 2012, Smallwood & Gaughan 2013). All boats were interviewed 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' (ESRI) which was downloaded onto a tablet device. Each interview consisted of 20 short-answer questions, including boat level questions and individual fisher questions (see the Appendix for list of survey questions), and lasted 3 to 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 4 main access points (boat ramps) serving the west coast and Exmouth Gulf. Boats ranging from 3 to 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 1).

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).

Table 1. Fishing methods, fisher demographics and boat sizes that were in scope and 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 3 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	

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.

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 2 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 2 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 (<30 data points) for other methods such as squid jigging or fishing with stationary lures floating on the surface. The sample size for these 2 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 mo 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.

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 2-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 tests all possible combinations of the specified predictor variables to identify the best-fitting, most parsimonious model (McLean et al. 2016). The predictor variables tested in these GAMMs (Table 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 (Julian Day) 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.) was 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 2 AIC values of the lowest AIC and having the smallest number of predictor variables (Burnham & Anderson 2002). The maximum number of predictor variables

Table 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 4 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
Depth of fishing	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 time of 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. 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

allowed in this approach was 3 (to prevent potential overfitting), and the AIC criteria of being within 2 units of the lowest AIC was used because models that have less than 2 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 McLean et al. (2016). 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 0 and 1 and multiplied by the R^2 value for the most parsimonious model (McLean et al. 2016), were also generated and plotted to identify the relative importance of all the predictor variables tested in both models.

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).

RESULTS

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.

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. 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. 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. 1b). Additionally, this area included 7 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. 1b) were approximate, especially in the case of trolling trips where boats covered distances ranging from 1 to 20 km.

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). This variable showed a distinctly non-linear relationship with number of fish depredated per trip, with a peak at 60 m (Fig. 2). 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. 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.

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

Table 3. Relative importance of the predictor variables tested in generalised additive mixed models (GAMMs) (see Table 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 '×' 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 0 and 1 and multiplied by the R^2 value for most parsimonious model. SST: sea surface temperature

Predictor variable	West coast boat ramps	Exmouth Gulf boat ramps
Latitude	0.07	0.55 (×)
Max. hook depth	0.38 (×)	<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 (×)	0.07
Fishing pressure	<0.01	0.17 (×)
Survey period	0.18 (×)	0.03

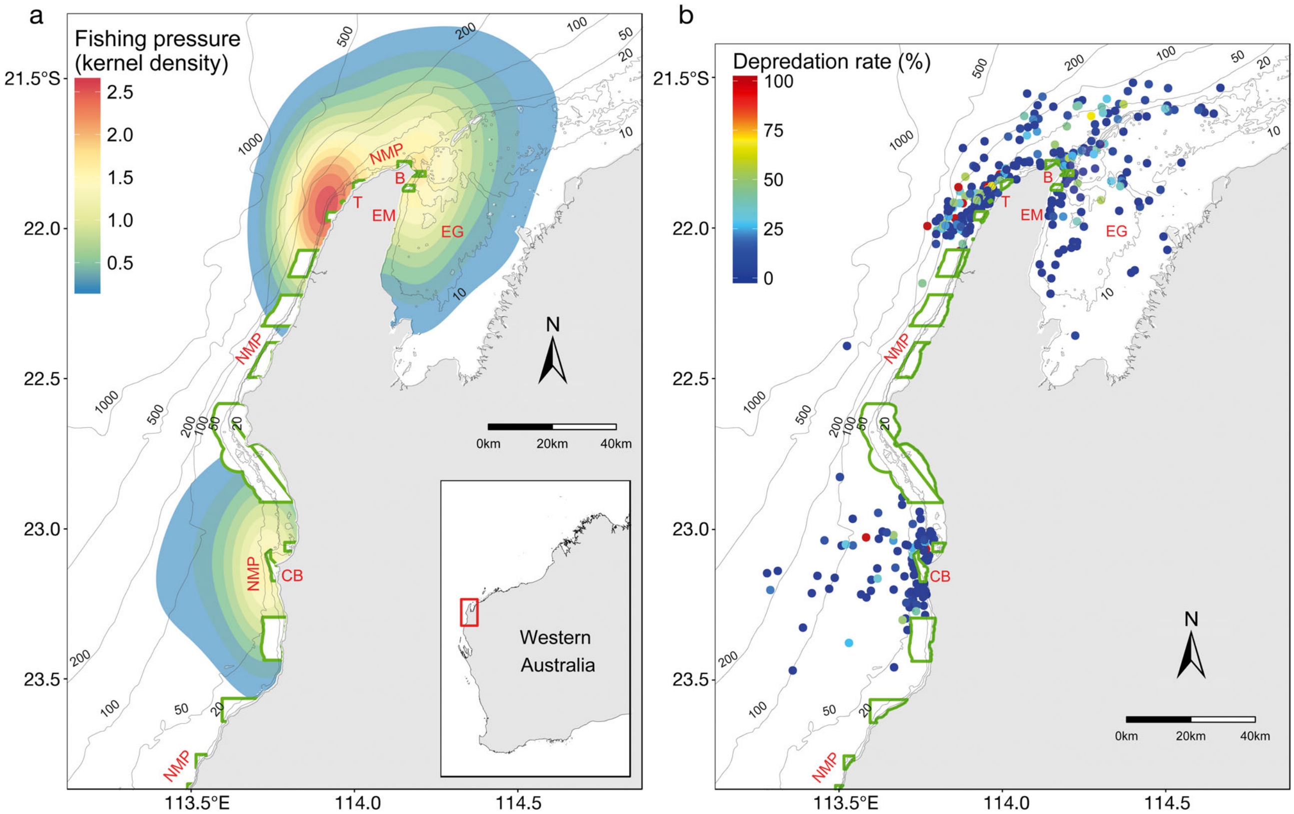

Fig. 1. (a) Spatial variation in estimated fishing pressure, calculated using kernel density estimation to analyse the density distribution of the 248 and 155 (403 total) boat-based fishing locations (for both demersal fishing and trolling) reported by boats launching from west coast boat ramps (Coral 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

with increasing number of fish depredated (Fig. 2), and had a relatively high level of importance across all of the Exmouth Gulf GAMMs (Table 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. 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).

DISCUSSION

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 understanding of the full range of impacts and potential underlying factors driving shark depredation.

Previous research conducted recreational fishing surveys in the northwest (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

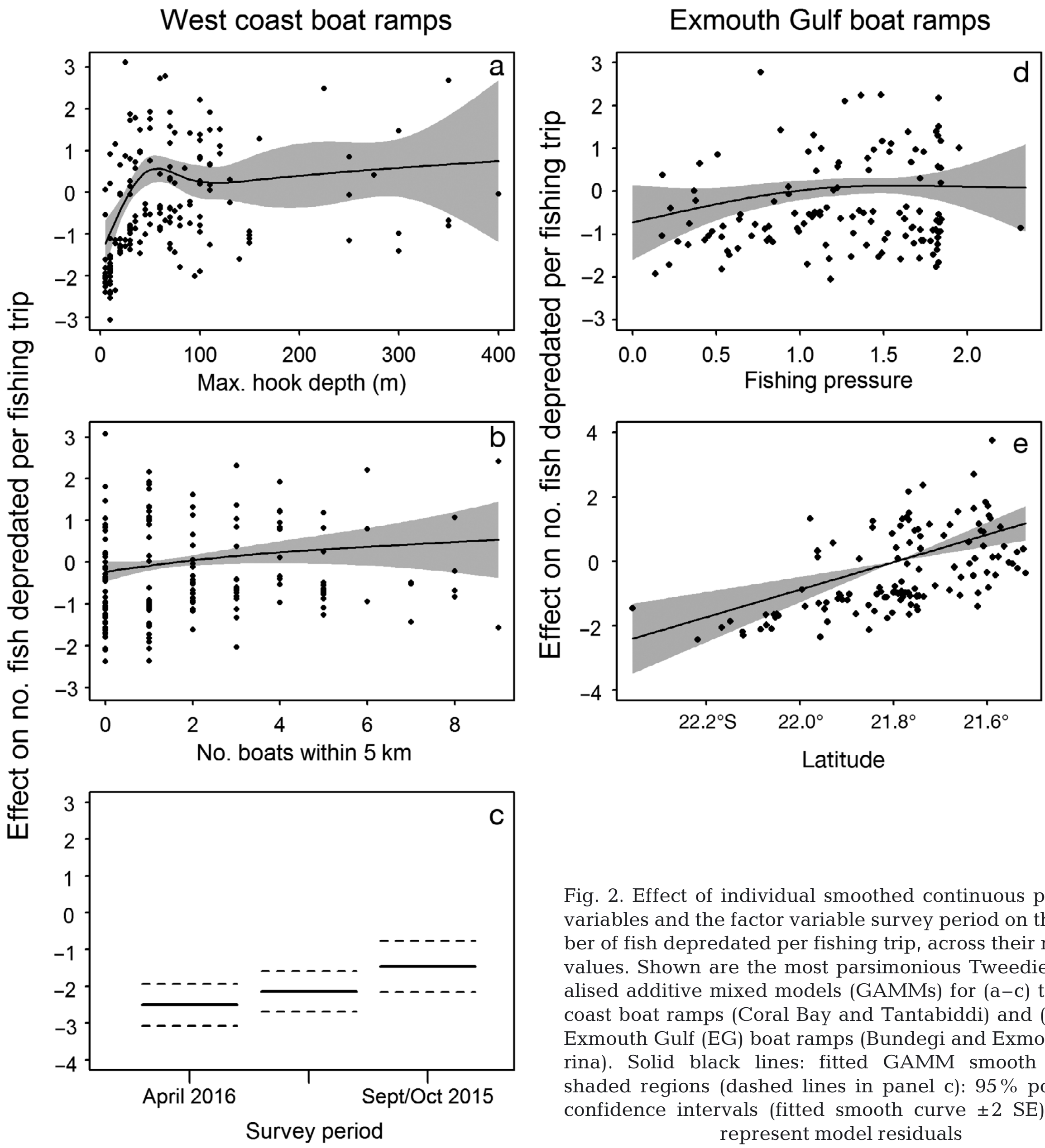

Fig. 2. Effect of individual smoothed continuous predictor variables and the factor variable survey period on the number of fish depredated per fishing trip, across their range of values. Shown are the most parsimonious Tweedie generalised additive mixed models (GAMMs) for (a–c) the west coast boat ramps (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

values varied widely by species, with spangled emperor *Lethrinus nebulosus*, the most commonly caught demersal species, having an estimated catch of 22 575 individuals retained, 25 056 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 northwest 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 2 fisheries, including their fisher demographics, methods and equipment used, may have contributed to disparate results. The small temporal scale (3 mo 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 *Sousa 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 sandbar sharks *Carcharhinus 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 2016). 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 1).

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, such as locally in 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 *C. 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 *C. 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. 2012), 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 serranids were more likely to be caught. Indeed, research by Schifiliti (2014) recorded sicklefin lemon *Negaprion acutidens*, pigeye *C. amboinensis*, tiger *Galeocerdo cuvier*, blacktip *C. limbatus* and dusky *C. obscurus* sharks 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 *N. acutidens*, *C. amblyrhynchos* and *C. melanopterus*, in the Ningaloo Marine Park (Speed et al. 2011, 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. 2014). 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 model (Table 3, Fig. 2) 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). 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.

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 5 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 (J. D. Mitchell unpubl. data), 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 and 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 $200, with a mean value of $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.

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.

CONCLUSIONS

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 larger-scale commercial line-based fisheries around the world, both of which may be impacted by shark depredation.

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Appendix. List of boat ramp survey questions

Boat questions – answers cover 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 berleying 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 – answers 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 for?

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