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

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ABSTRACT: Shark depredation, whereby a shark consumes an animal caught by fishing gear, can cause higher mortality for target species, injury to sharks and the loss of catch and fishing gear. A critical first step towards potential 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. We used line-mounted video cameras in a recreational fishery in the Ningaloo region of Western Australia to: (1) identify shark species responsible for depredation, (2) investigate behavioural interactions with fishing gear, (3) identify the prevalence of retained fishing gear in sharks and (4) quantify the influence of environmental variables and fishing methods on shark abundance 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 *C. amblyrhynchos* and spottail *C. sorrah* sharks were observed depredating lethrinid and epinephelid fishes. Five additional shark species from 4 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 retrieved. 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.

KEY WORDS: Depredation · Shark behaviour · Underwater video · Fisheries management · Deterrents

1. INTRODUCTION

Depredation, whereby a predator consumes a fish caught by fishing gear before it can be retrieved, occurs in commercial and recreational line fisheries around the world (Gilman et al. 2007, IOTC 2007, Mitchell et al. 2018a). This causes the loss of catch and fishing gear, higher mortality for target species and injury to the predators responsible (Gilman et al. 2007, Mitchell et al. 2018b). A range of taxa can be

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responsible for depredation, including sharks (Gilman et al. 2008), cetaceans (IOTC 2007), squid (Remeslo et al. 2015), teleost fishes (Shideler et al. 2015), pinnipeds (Meyer et al. 1992) and seabirds (Dieperink 1995). Depredation by sharks in commercial and recreational fisheries can result in 0.9–26% of the catch being lost (Mitchell et al. 2018b).

Identifying sharks involved in depredation events is important for fisheries management and for designing effective deterrent measures, which can be species-specific (Brill et al. 2009, Hart & Collin 2015). However, depredation by sharks remains relatively understudied (compared to cetacean depredation) (IOTC 2007, Hamer et al. 2012, Mitchell et al. 2018b) due to difficulties observing depredation events not occurring close to fishing vessels. Previous studies identified depredating shark species through observation of surface depredation events (Backus et al. 1956) or through the analysis of stomach contents (Celona et al. 2005, Romanov et al. 2007), but this may not be possible for a large proportion of depredation events.

The link between behaviour and catchability has been well demonstrated (Walsh et al. 2004, Alós et al. 2012, Young et al. 2019), although shark behavioural interactions with fishing gear are not well understood (Jordan et al. 2013). The specific behaviours of sharks around fishing gear may influence efficacy of measures designed to mitigate depredation, hooking and entanglement (Robbins et al. 2011). Understanding sharks' interactions with fishing gear, such as when and where sharks investigate and strike the bait, is therefore important.

Video cameras have not been used to investigate shark depredation, other than in 2 recent studies in the western Atlantic Ocean and Gulf of Mexico (O'Shea et al. 2015, Streich et al. 2018). Small, lightweight cameras mounted directly on fishing lines create new opportunities to investigate depredation by sharks and shark behaviours around fishing gear. We therefore designed this project to: (1) use line-mounted video cameras to identify the depredating shark species, (2) record shark behaviours when interacting with fishing gear, (3) provide an assessment of the proportion of sharks that retained hooks from previous fishing gear interactions and (4) quantify the influence of fishing methods and environmental variables on the abundance of sharks at fishing locations.

2. MATERIALS AND METHODS

2.1. Study location, vessel information and fishing methods used

We chose the Ningaloo region of Western Australia (Fig. 1) as a case study location because it is a popular area for recreational fishing (Sumner et al. 2002, Ryan et al. 2017), where shark depredation has been quantified (Mitchell et al. 2018a). It has also been designated by the United Nations as a World Heritage Site, and includes Ningaloo Marine Park, with 34% of its area designated as sanctuary zones where boat-based recreational fishing is prohibited (CALM & MPRA 2005).

Data were collected during 19 single-day fishing trips at 92 fishing locations (Fig. 1) from October 2016 to May 2017, aboard the recreational charter fishing vessels 'Osso Blue' and 'Blue Horizon' (Table 1). Fishers used hook-and-line fishing gear to target demersal fishes (e.g. lethrinids and epinephelids) at depths from 10–110 m.

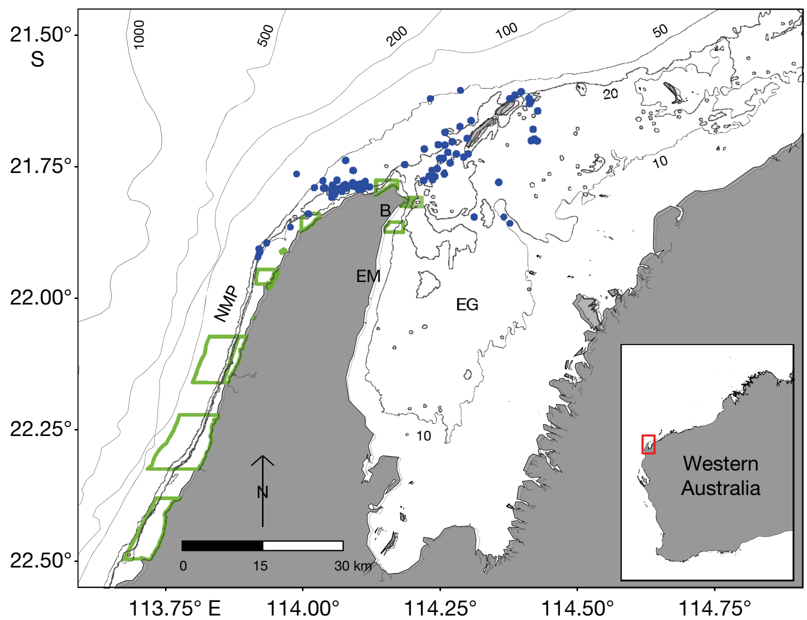

Fig. 1. Charter fishing locations (blue points, n = 92) in the Ningaloo region, Western Australia. Labelled contour lines show depth in metres. Solid green lines indicate the Ningaloo Marine Park (NMP) sanctuary zones, where boat-based fishing is prohibited. B: Bundegi boat ramp, EM: Exmouth marina boat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

Table 1. Vessel parameters and fishing methods used by the 2 charter fishing vessels in this study

	'Osso Blue'	'Blue Horizon'
Number of fishing days	14	5
Number of locations fished	59	33
Length of fishing day	08:00–17:00 h	07:00–17:00 h
Departure location	Bundegi boat ramp	Exmouth marina boat ramp
Length of vessel	8.4 m	16.8 m
Maximum number of lines in water	7	10
Fishing method	Demersal	Demersal
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
Number of hooks per line	1	1

2.2. Line-mounted video camera setup

We used high-definition video cameras (Water Wolf underwater camera kit 1.1; Svendsen Sport) to record shark depredation events and interactions with fishing gear, by mounting them on fishing lines approximately 1.5–2 m above the hook (Fig. 2a,b). Between 1 and 5 cameras were deployed on separate fishing lines at a time, for up to 4 h, recording continuously.

2.3. Fishing method and environmental data

We recorded location, number of lines in the water, whether vessels were fishing at anchor vs. drifting, fishing depth, gear and bait type, to assess the influence of fishing methods and environmental variables on the abundance of sharks at each fishing location. All data were collected on an Apple iPad, using the software application 'Collector for ArcGIS' (Environmental Systems Research Institute). We sourced sea surface temperature (SST) data for the dates and locations of fishing from the US National Oceanic and Atmospheric Administration, in the form of Optimum Interpolation (OI) SST (Reynolds et al. 2007), at a spatial resolution of 0.25° × 0.25° (NOAA 2016). We accessed lunar phase data for Exmouth, Western Australia, from an online database (https://www.timeanddate.com/moon/phases/@2079492?year=2017), and we assigned a lunar phase value to each fishing location based on the fishing date and corresponding quarter of the lunar cycle.

2.4. Video analysis

Video files were analysed using EventMeasure (version 4.42) (SeaGIS). All footage was viewed and analysed by the same observer to ensure standardisation, which was particularly important for behavioural data, due to potential subjectivity. We collected species identity and behavioural data every time a shark entered the field of view, and sharks were identified to the lowest taxonomic level possible. 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 hooked fish were: (1) identified to the lowest taxonomic level possible, (2) assessed as to whether they got off the hook themselves, or if they were depredated by sharks or (3) were retrieved undamaged to the fishing vessel. The shark depredation rate was calculated as the number of fish that were depredated out of the total number of fish hooked, and the time gap between a fish being hooked and then being depredated was calculated. We classified shark behaviours into 10 broad categories and then quantified the occurrence of each behaviour in a detailed ethogram (see Table 5). Behavioural sequences were also identified. We calculated 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, for each camera deployment at each fishing location. This avoided repeat counts of the same individual sharks. The highest

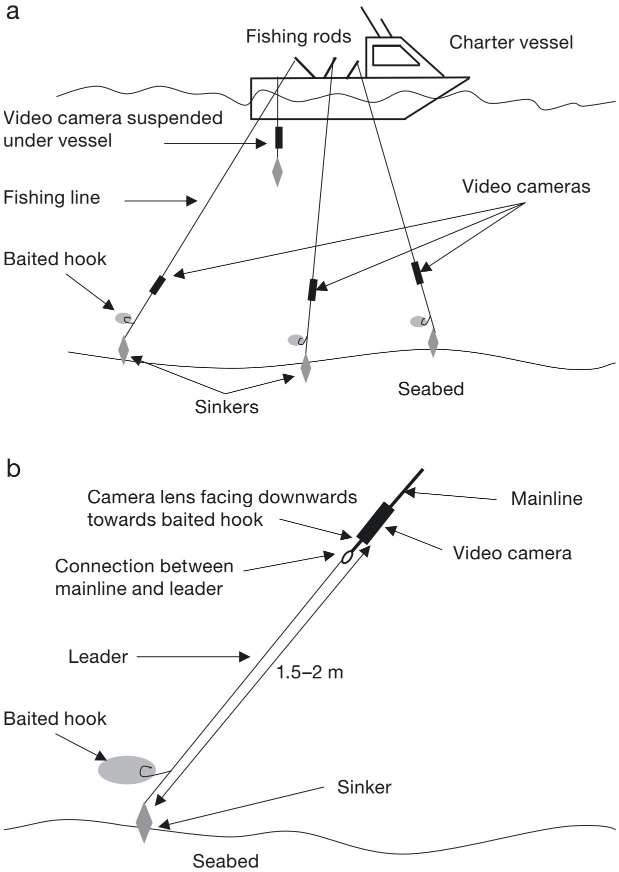

Fig. 2. (a) Video camera deployment on fishing lines close to the seabed and under the fishing vessel. (b) Close-up of the proximity of the video camera to the key components of the fishing gear, such as the baited hook and sinker. Diagrams not to scale

value of MaxN for each species and for all species pooled, across all cameras deployed at each fishing location, was then taken as the estimate of relative abundance for that fishing location.

2.5. Generalised additive mixed model (GAMM) analysis

We used GAMMs (Lin & Zhang 1999) to quantify the influence of fishing methods and environmental variables on the relative abundance (MaxN) of sharks at each fishing location. GAMMs are a modified version of generalised additive models (Hastie & Tibshirani 1986), which apply smoothing techniques to address non-linearity in the predictor variables (Craven & Wahba 1978, Wood 2008), and include both fixed and random effects (Zuur et al. 2009).

The response data used in the GAMMs were the integer MaxN counts for all shark species combined, at each fishing location. The data were pooled for all species rather than assessing each species individually, due to the low number of observations for most species, which resulted in a high number of zeros. The GAMMs were run with a Poisson error distribution, which has been widely used for modelling catch rate data from fisheries (Gilman et al. 2012, Noack et al. 2017) and abundance data from baited camera studies (Willis et al. 2000, Espinoza et al. 2014).

Eight sites located <500 m from previous fishing locations were removed from the response data (resulting in n = 84 locations for the final GAMM), over concerns that sharks may have followed vessels, artificially inflating the relative abundance value. This minimum distance of 500 m is in line with studies that have used baited cameras to quantify shark abundance (Espinoza et al. 2014, Rizzari et al. 2014). Also, 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.

We tested fishing methods and environmental variables (Table 2) in the GAMM, to quantify their influence on relative abundance of sharks. The distribution of the predictor variables depth, time at fishing location, number of lines in the water and total number of 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). Vessel 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 between vessels. The number of cameras deployed at each fishing location was included as an offset term, because a higher number of cameras deployed simultaneously at a site results in a greater chance of recording a higher abundance of sharks.

We used a full-subsets approach for the GAMM, which identified the best-fitting, most parsimonious model from a range of possible predictor variable combinations, based on Akaike's information criterion (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 Zuur et al. (2009). 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

Table 2. 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 the relative abundance of sharks

Predictor variable	Importance
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 influence shark abundance and distribution. Latitude was therefore used as a proxy for these variables because data for habitat type were 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 were 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 (min)	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
Number of lines in water	Greater fishing effort will lead to more activity in the water, and therefore stronger sensory cues to attract sharks
Sea surface temperature (°C)	Temperature influences the activity patterns and feeding behaviour of sharks (Carey et al. 1990, Stevens et al. 2010); therefore, it may affect whether sharks are motivated to move towards the fishing vessel and depredate hooked fish
Total number of fish hooked	Sites where a greater number of fish are caught may be indicative of higher abundance, so 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 2 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 (West & Stevens 2001, 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	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 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	
Number of 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

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. Predictor variable importance values (Fisher et al. 2018) were 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).

3. RESULTS

3.1. Shark and teleost species identification

We recorded 1688 shark observations (Table 3), of which 37% (617) were identified to species level, recording 9 species belonging to 4 families. Sicklefin lemon shark *Negaprion acutidens* was the most frequently observed species, comprising 18% (301) of observations, followed by the blacktip/Aus-

Table 3. 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	Common name	Observ-ations (n)	Fishing locations (n)	Depreda-tions (n)	Observations with gear (n)
Carcharhinus spp.	Requiem sharks	711	36	3	12
Carcharhinidae spp.	Requiem sharks	359	39	1	1
Negaprion acutidens	Sicklefin lemon shark	301	25	5	7
Carcharhinus limbatus/tilstoni	Blacktip/Australian blacktip shark	138	21	4	1
Carcharhinus amblyrhynchos	Grey reef shark	85	13	1	1
Carcharhinus plumbeus	Sandbar shark	34	9	0	12
Carcharhinus sorrah	Spottail shark	28	10	1	0
Carcharhinus amboinensis	Pigeye shark	16	4	0	3
Hemitriakis falcata	Sicklefin houndshark	5	2	0	0
Nebrius ferrugineus	Tawny nurse shark	5	2	0	0
Rhynchobatus laevis	Smoothnose wedgefish	5	1	0	0
Triakidae sp.	Houndshark	1	1	0	0
Total		1688	-	15	37

tralian blacktip *Carcharhinus limbatus/tilstoni* (which is a species complex that was indistinguishable from the video footage), with 8% (138). *N. acutidens* and *C. limbatus/tilstoni* were recorded at 25 and 21 of the 92 locations, respectively (Table 3).

Additionally, 165 teleost fishes were hooked, with 90% (149) of these identified to the species level (Table 4). Eighteen species from 8 families were identified, with halfmoon grouper *Epinephelus rivulatus* being the most frequently hooked species (34% of all fish hooked).

Table 4. Teleost fishes 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	Common name	Hooked (n)	Retrieved (n)	Depredated (n)	% depredation
Epinephelus rivulatus	Halfmoon grouper	56	54	2	3.57
Lethrinus miniatus	Trumpet emperor	27	27	0	0
Lethrinus nebulosus	Spangled emperor	19	16	3	15.79
Lethrinus spp.	Emperors	13	10	3	23.08
Lethrinus rubrioperculatus	Spotcheek emperor	10	10	0	0
Lethrinus punctulatus	Pinkear emperor	8	7	1	12.5
Lethrinus laticaudis	Grass emperor	5	5	0	0
Pentapodus porosus	Northwest Australian whiptail	4	4	0	0
Plectropomus maculatus	Spotted coralgrouper	3	3	0	0
Epinephelus coioides	Orange-spotted grouper	3	2	1	33.33
Epinephelus multinotatus	White-blotched grouper	3	2	1	33.33
Lutjanus carponotatus	Spanish flag snapper	2	2	0	0
Lutjanus sebae	Emperor red snapper	2	2	0	0
Cephalopholis sonnerati	Tomato hind	2	2	0	0
Choerodon cyanodus	Blue tuskfish	1	1	0	0
Lethrinus genivittatus	Longspine emperor	1	1	0	0
Gnathanodon speciosus	Golden trevally	1	1	0	0
Gymnothorax undulatus	Undulated moray	1	1	0	0
Rachycentron canadum	Cobia	1	0	1	100
Lethrinidae sp.	Emperor	1	0	1	100
Carangidae sp.	Jack	1	0	1	100
Unidentified sp.	-	1	0	1	100
Total		165	150	15	9.09

3.2. Shark depredation

Fifteen fish (9%) belonging to 7 species were depredated (Table 4). Four different shark species depredated hooked fish (Table 3), with *N. acutidens* (Fig. 3) responsible for 33% (5) of the depredation events, followed by *C. limbatus/tilstoni* with 27% (4), grey reef shark *C. amblyrhynchos* (7%; 1 event) and spottail shark *C. sorrah* (7%; 1 event). The time gap between a fish getting hooked and then being depredated by a shark ranged from 4–17 s (mean = 11 s). The timeframe between the start of fishing and the first depredation event ranged from 5–40 min. We recorded 4 instances where large teleosts, including blackspotted rockcod *E. malabaricus*, orange-spotted grouper *E. coioides* and shark mackerel *Grammatorcynus bicarinatus*, attempted to depredate hooked fish, but were unsuccessful (Fig. 4).

3.3. Behavioural interactions with fishing gear

We observed 64 behaviour types across the 10 categories (Table 5), and depredation events made up only a small fraction (3%) of the shark interactions with fishing gear. Sharks frequently investigated, nudged or followed the bait (212 occurrences; 40% of all interactions with fishing gear), with *N. acutidens* having the highest number of bait investigations. On 20 occasions (4% of all interactions), sharks were recorded following fishing gear up towards the surface as it was retrieved. When a fish was hooked and a shark was present, different behavioural sequences were recorded (Fig. 5), including 26 instances (5% of all shark–fishing gear interactions) where sharks closely followed hooked fish. Sharks were also observed chasing and consuming free-swimming fish after they had been released, including an instance

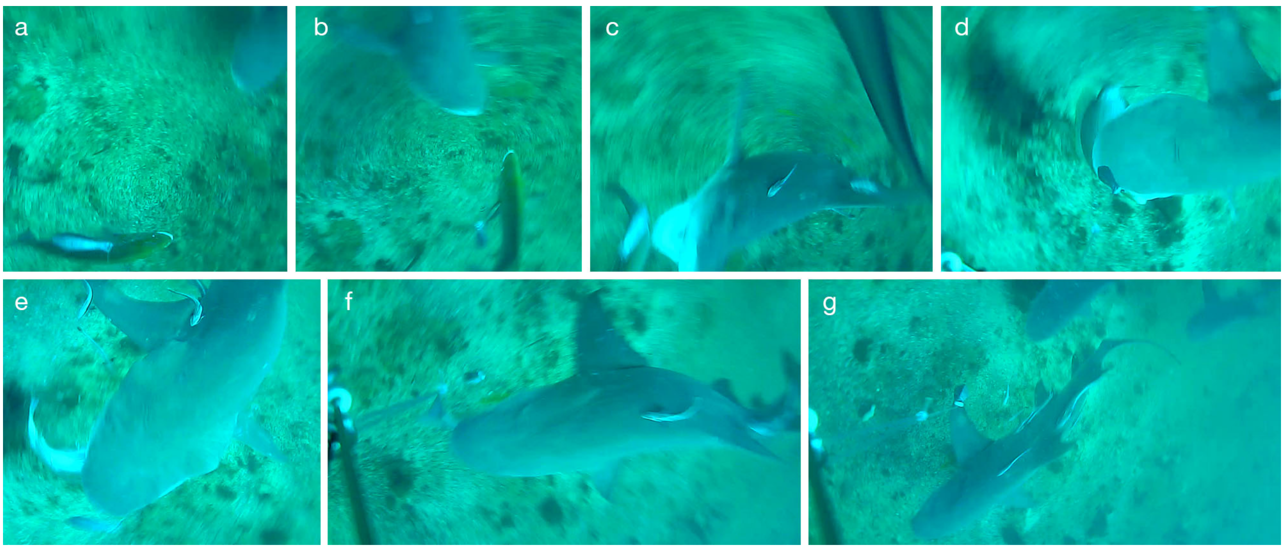

Fig. 3. Sequence of a shark depredation event. (a) A sicklefin lemon shark *Negaprion acutidens* approaches a hooked lethrinid fish; (b) shark investigates hooked fish; (c) shark about to bite hooked fish; (d,e) shark bites hooked fish and shakes head; (f) shark snaps off fishing line; (g) shark swims away and is chased by 2 other sharks

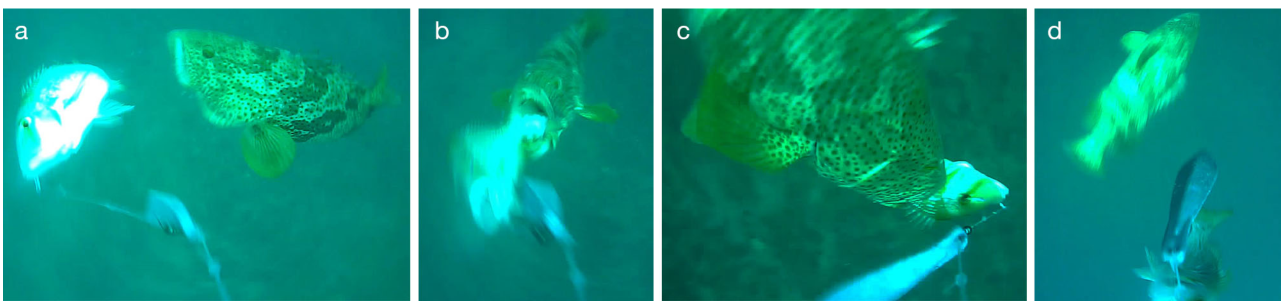

Fig. 4. Sequence of a teleost fish unsuccessfully attempting to depredate a hooked fish. (a) An orange-spotted grouper *Epinephelus coioides* investigates a hooked lethrinid fish; (b) *E. coioides* attempts to bite the hooked lethrinid; (c) *E. coioides* mouths the hooked lethrinid; (d) *E. coioides* turns and swims away after unsuccessfully attempting to depredate the hooked fish

Table 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.

Behaviour	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.*
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
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
Getting 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
Breaking off line and swimming 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
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

(Table continued on next page)

Table 5 (continued)

Behaviour	No. of times recorded per species												
	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 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
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
Turning away													
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

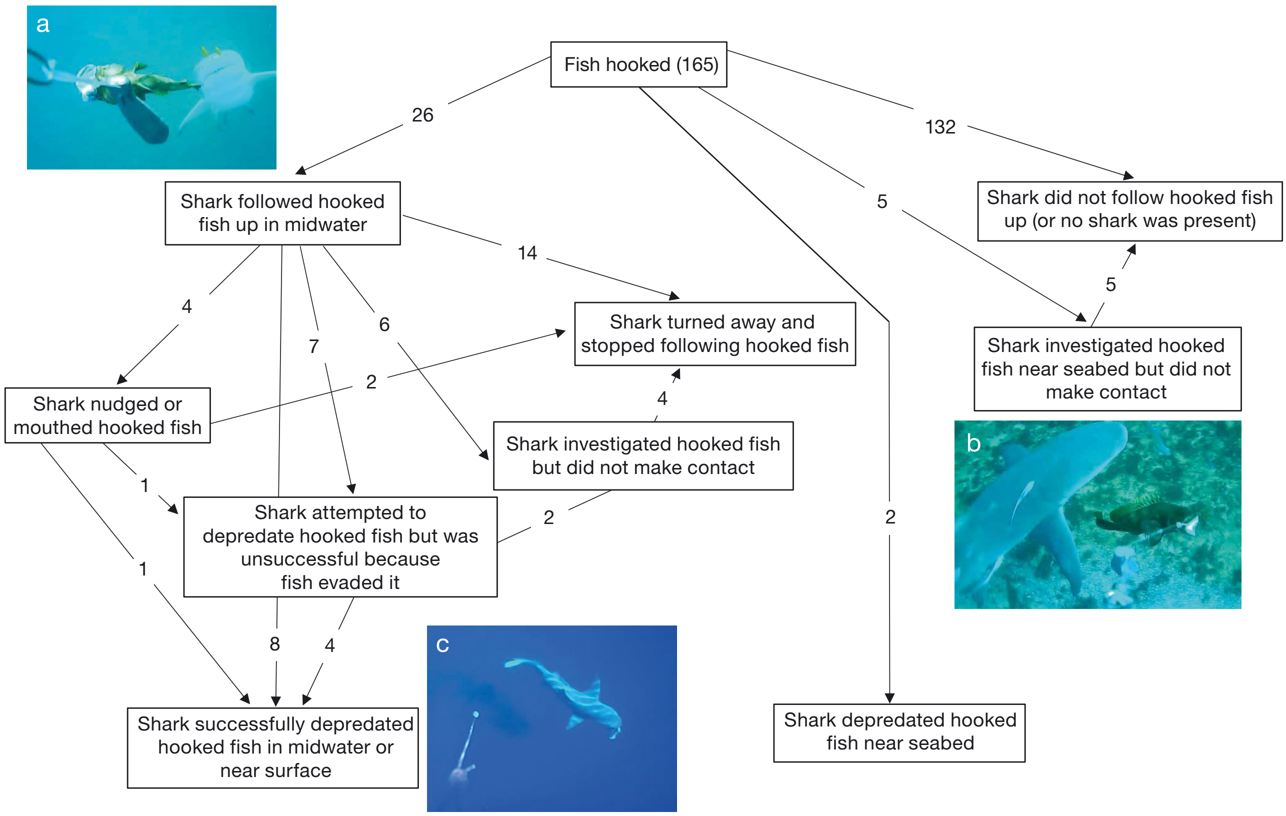

Fig. 5. Behavioural sequence diagram showing the range of behaviours displayed by sharks when a fish was hooked and being reeled up to the boat during recreational fishing. Images show examples of key behaviours, including (a) a sicklefin lemon shark *Negaprion acutidens* following a hooked halfmoon grouper *Epinephelus rivulatus*; (b) *Carcharhinus* sp. investigating a hooked *E. rivulatus*; and (c) *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 (see Table 5 for complete ethogram)

when a *C. limbatus/tilstoni* consumed an *E. rivulatus*. Multiple shark species were seen at 21 of the 92 (23%) fishing locations, with 5 different species, i.e. *N. acutidens*, *C. limbatus/tilstoni*, *C. amblyrhynchos*, sandbar shark *C. plumbeus* and pigeye shark *C. amboinensis*, being recorded together at 2 separate locations. Inter- and intra-specific competition also occurred, particularly before and after depredation events. Of the total number of shark observations, 2% were sharks with retained fishing gear (Table 3), although some of these observations may have been the same individual shark being seen multiple times.

3.4. 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 fishes hooked + 1), and explained 55% of the deviance in shark abundance. Longitude had the highest relative importance value of all predictor variables (Table 6) and had an increasingly positive effect on the relative abundance of sharks up to a peak at 114.04° (Fig. 6a). At higher longitudes, there was a decreasing effect on relative abundance, followed by a plateau. SST showed a markedly in-

Table 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 in **bold**

Predictor variable	Relative importance value
Longitude	**0.1260**
Sea surface temperature	**0.0668**
Log(total no. fish hooked + 1)	**0.0413**
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

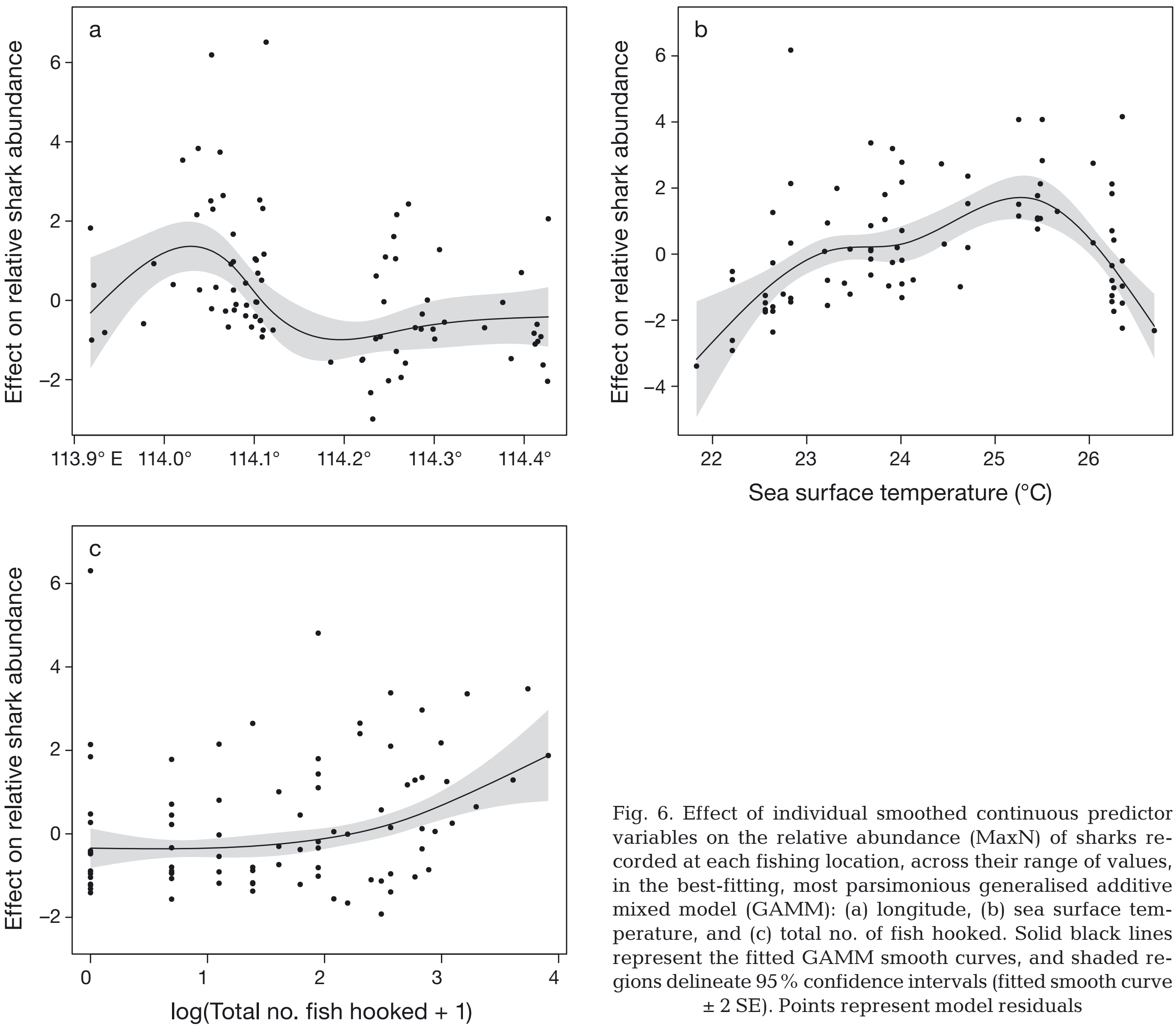

Fig. 6. Effect of individual smoothed continuous predictor variables on the relative abundance (MaxN) of sharks recorded at each fishing location, across their range of values, in the best-fitting, most parsimonious generalised additive mixed model (GAMM): (a) longitude, (b) sea surface temperature, and (c) total no. of fish hooked. Solid black lines represent the fitted GAMM smooth curves, and shaded regions delineate 95% confidence intervals (fitted smooth curve ± 2 SE). Points represent model residuals

creasing positive effect on relative abundance, which peaked at 25°C (Fig. 6b). Above this temperature, however, the effect on relative abundance decreased markedly. Lastly, the total number of fishes hooked had an initially neutral effect on relative abundance, followed by an increasingly positive effect, up to a peak at 3.91 (Fig. 6c). The remaining predictor variables had minimal influence on relative abundance (Table 6).

4. DISCUSSION

4.1. Shark and teleost species identification

Sicklefin lemon *Negaprion acutidens* and blacktip/Australian blacktip *Carcharhinus limbatus/tilstoni* sharks were the most commonly observed species in the current study, reflecting the results of previous dive, longline and baited camera surveys in the Ningaloo region (Stevens et al. 2009, Schifiliti 2014). The species composition of the teleost fishes we observed was similar to the range of fish species recorded in past large-scale surveys of recreational fishing in this region (Sumner et al. 2002, Ryan et al. 2017).

4.2. Shark depredation

The shark depredation rate we recorded was similar to the rate of approximately 12% reported by Mitchell et al. (2018a). We argue, however, that the rate of depredation we report is more reliable than that recorded by Mitchell et al. (2018a) and earlier surveys by Sumner et al. (2002), because the depredation events were confirmed by video footage rather than being retrospectively reported by fishers through surveys, which can be subject to bias and unreliability. This is especially the case if fishers deliberately exaggerate depredation rates to justify calls for mitigation measures to be introduced. The shark depredation rate in our study was notably higher than that recorded on charter fishing vessels in a South African recreational fishery (1.9%) (Labinjoh 2014). Globally, depredation rates in commercial and recreational fisheries have been found to vary between 0.9 and 26% (Mitchell et al. 2018b).

Teleost species, including Atlantic goliath grouper *Epinephelus itajara* (Collins 2014, Shideler et al. 2015), greater amberjack *Seriola dumerili*, great barracuda *Sphyraena barracuda* and Warsaw grouper *Hyporthodus nigritus* (Streich et al. 2018), have been recorded depredating hooked fish in US fisheries. In our study, we were able to confirm that all depredation events were caused by sharks, although large predatory teleosts attempted to depredate hooked fish. Reef-associated carcharhinid sharks were the main group responsible for depredation, because they are the most abundant species in the areas of the Ningaloo region where recreational fisheries operate (Stevens et al. 2009, Speed et al. 2011). *N. acutidens*, although only rarely caught during longline surveys in this region (Stevens et al. 2009), was the most frequently observed species in the current study. Schifiliti (2014) reported that *N. acutidens* interacted regularly with baited camera systems deployed in this region. Also, this species has been observed to be aggressive and opportunistic (Clua et al. 2010), which may explain why it was responsible for the highest number of depredation events in the current study. However, *N. acutidens* has not been reported to depredate hooked fish in past literature (Mitchell et al. 2018b). Concurrent with our data, *C. limbatus* have also been 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). Of the other species we observed to be responsible for depredation, spottail sharks have been identified as a depredating species by Romanov et al. (2007), whereas grey reef sharks have never been observed depredating hooked fish (Mitchell et al. 2018b). The only other study on shark depredation in recreational fisheries reported oceanic whitetip sharks *Carcharhinus longimanus* depredating hooked pelagic fish in The Bahamas (Madigan et al. 2015). In total, 27 shark species from 7 families have been reported to depredate hooked fish in both commercial longline and recreational fisheries (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.

4.3. Behavioural interactions with fishing gear

Sharks displayed many different forms of interaction with fishing gear. Interactions with the bait were the most common form recorded, which likely involved the shark assessing the bait using visual and olfactory cues. We also observed nudging or mouthing of the bait, a behaviour also reported by O'Shea et al. (2015). Sharks also investigated the cameras, perhaps because they were able to detect emitted electrical signals, as elasmobranch species can detect electric field gradients down to ≤5 nV cm^{-1} (Kalmijn 1982, Kajiura & Holland 2002). Five shark species were also observed following the fishing gear upwards as it was reeled to the vessel, but not striking it, perhaps because the sharks were attracted to the visual and hydrodynamic cues created by the movement of the object, which may have mimicked a potential prey item.

We observed that sharks rarely struck the bait and became hooked. In contrast, Robbins et al. (2011, 2013) reported that grey nurse sharks *Carcharias taurus* took the bait on the first approach on 33% of occasions, and Galapagos sharks *Carcharhinus galapagensis* had a mean bait strike time of <30 s. 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., Australian sardine *Sardinops sagax* and mixed demersal fish, because bait size and type have been shown to influence shark catch rates (Foster et al. 2012). Sharks may have also been 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.

We also recorded competitive behaviour between individuals, particularly before and after depredation events; therefore, competition may have an influence on which shark species depredate hooked fish if larger, more aggressive species outcompete others. This form of competitive exclusion was reported in The Bahamas, where 4 shark species competed to access a hooked shark (O'Shea et al. 2015). Robbins et al. (2011) also 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.

We may have underestimated the frequency of retained fishing gear because: (1) this could only be identified when sharks were close to the camera and (2) sharks may have had hooks lodged inside their mouth, or deeper in their digestive tract. This is likely to explain why the prevalence of sharks with retained fishing gear in the current study was lower than expected, considering that Mitchell et al. (2018a) reported that 40% of fishing trips experienced shark depredation. This is supported by Otway & Burke (2004), who found that 6 out of 8 necropsied *C. taurus* had internal hook injuries, with no visible external signs. Our observed prevalence of sharks with retained fishing gear was lower than the 9% reported by Whitney et al. (2012) for whitetip reef sharks *Triaenodon obesus*, and 17% for *C. taurus* (Bansemer & Bennett 2010). Retained fishing gear can cause sublethal impacts to sharks, including tissue necrosis, abscesses, perforations of the gastric wall and internal infections (Borucinska et al. 2002, Bansemer & Bennett 2010). This can lead to reduced feeding, lack of fitness, disease and possibly death (Borucinska et al. 2002, Bansemer & Bennett 2010, Adams et al. 2015).

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

Most likely because there was a greater area of reef habitat at lower longitudes (CALM & MPRA 2005), which supported higher abundances of prey species, the relative abundance of reef-associated carcharhinid sharks was higher in these areas. This is supported by past research which has reported higher reef shark abundance and diversity 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 a high level of site fidelity to reef habitats, with year-round residence (Filmalter et al. 2013, Vianna et al. 2013) and in the Ningaloo region, *C. amblyrhynchos* was most abundant in areas with intermediate levels of relief (Babcock et al. 2017) and in reef habitats (Stevens et al. 2009). SST also affected relative abundance of sharks. For reef-associated sharks, the link between temperature and shark abundance and distribution has been clearly demonstrated (Brooks et al. 2013, Vianna et al. 2013), including in the Ningaloo region (Speed et al. 2012). SST has also been shown to have marked effects on the catch rate of sharks in recreational fisheries (Mitchell et al. 2014). The positive relationship between the number of fish hooked and shark abundance likely reflected that areas with a higher catch rate of teleosts supported greater numbers of prey species for the sharks identified. It is also possible that sharks were attracted to these areas which had higher catch rates of target species due to the sensory cues created by fishing activity, including auditory and chemical cues. Mitchell et al. (2018a) 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.

5. CONCLUSION AND FUTURE DIRECTIONS

To mitigate negative impacts that occur when sharks interact with fishing gear, particularly depredation and bycatch, it is necessary to identify the shark species involved, as well as to understand species-specific behaviours and the sensory mechanisms affecting these (Jordan et al. 2013, Mitchell et al. 2018b). We 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 on depredation by sharks and other taxa, as previously used to observe depredation by sperm whales *Physeter microcephalus* (Straley et al. 2007) and southern elephant seals *Mirounga leonina* (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 (Fotedar et al. 2019).

We observed that 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 reduce bait strikes and bycatch. Because 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 amount of time that *C. carcharias* spent close to the bait, and the number of bait strikes by 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). The development of physical deterrents which shield hooked fish from sharks attempting to depredate them, similar to those tested by Moreno et al. (2008), is thus another approach worth investigating further. 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, Dulvy et al. 2014, Mitchell et al. 2018b).

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