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Shark depredation in a commercial trolling fishery in sub-tropical Australia

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ABSTRACT: Shark depredation, whereby hooked fish are partially or completely consumed before they can be retrieved, occurs globally in commercial and recreational fisheries. Depredation can damage fishing gear, injure sharks, cause additional mortality to targeted fish species and result in economic losses to fishers. Knowledge of the mechanisms behind depredation is limited. We used a 13 yr dataset of fishery-dependent commercial daily logbook data for the Mackerel Managed Fishery in Western Australia, which covers 15° of latitude and 10 000 km of coastline, to quantify how fishing effort and environmental variables influence depredation. We found that shark depredation rates were relatively low in comparison with previous studies and varied across the 3 management zones of the fishery, with 1.7% of hooked fish being depredated in the northern Zone 1, 2.5% in the central Zone 2 and 5.7% in the southern Zone 3. Generalized additive mixed models found that measures of commercial fishing activity and a proxy for recreational fishing effort (distance from town centre) were positively correlated with shark depredation across Zones 1 and 2. Depredation rates increased during the 13 yr period in Zones 2 and 3, and were higher at dawn and dusk, suggesting crepuscular feeding in Zone 1. This study provides one of the first quantitative assessments of shark depredation in a commercial fishery in Western Australia, and for a trolling fishery globally. The results demonstrate a correlation between fishing effort and depredation, suggesting greater fishing effort in a concentrated area may change shark behaviour, leading to high rates of depredation.

KEY WORDS: Depredation · Fishing effort · Shark behaviour · Fisheries management · Generalized additive mixed models · Spanish mackerel · *Scomberomorus commerson*

1. INTRODUCTION

Depredation occurs when fisheries catch is partially or completely consumed by a predator before it can be retrieved (Gilman et al. 2006, Mitchell et al. 2018a,b). Depredation behaviour has been observed for several taxa including sharks (Mandelman et al. 2008, Mitchell et al. 2018a), teleosts (Shideler et al. 2015), cetaceans (Gilman et al. 2006, Ramos-Cartelle & Mejuto 2008, Hamer et al. 2012) and pinnipeds (Cook et al. 2015, van den Hoff et al. 2017). Depredation by sharks can have economic implications for commercial and recreational fisheries, potentially reaching losses of several hundred dollars per set in

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longline fisheries (Gilman et al. 2007, 2008). Shark depredation also has biological or ecological implications. Mortality of targeted fish species may be higher than expected in output-controlled fisheries, as depredated fish are not counted against quota (Nishida & Shiba 2005, Mitchell et al. 2018b). Mortality of sharks may also increase if they become hooked (Musyl et al. 2011, Butcher et al. 2015) or experience internal trauma caused by retained hooks and ingested fishing gear if released (Borucinska et al. 2002, Bansemer & Bennett 2010). The severity of depredation differs between fishery types and locations, with depredation rates (the percentage of hooked fish partially or completely taken by sharks) ranging from 1.5 to 20.7% in commercial longline fisheries (Dalla Rosa & Secchi 2007, MacNeil et al. 2009, Romanov et al. 2013, Hamer et al. 2015, Mitchell et al. 2018b) and from 7.2 to 13.7% in recreational fisheries globally (Labinjoh 2014, Mitchell et al. 2018a). The current shark depredation literature is primarily restricted to commercial longline fisheries, with some information on recreational fisheries, and only a recent study by Ryan et al. (2019a) included trolling fisheries.

Knowledge of the mechanisms that drive depredation is limited. Sharks may have the capacity for learning by associating fishing-related stimuli such as boat noise with food rewards (Dallas et al. 2010, Raby et al. 2014, Madigan et al. 2015, Mitchell et al. 2020) through provisioning in eco-tourism, for example (Bruce & Bradford 2013, Brunnschweiler & Barnett 2013). Increased site fidelity and/or abundances of sharks may occur in areas of high fishing activity due to the regular and consistent availability of hooked fish. The opportunity for sharks to depredate will potentially be enhanced in these areas. Evidence for the influence of environmental variables on depredation is also lacking, with current knowledge extending to what is known about shark activity patterns and how they change with depth (Simpfendorfer et al. 2002, Gilman et al. 2008, MacNeil et al. 2009, Espinoza et al. 2014), time of day (Nixon & Gruber 1988, Andrews et al. 2009), temperature (Sims et al. 2006, Speed et al. 2010, DiGirolamo et al. 2012) and lunar phase (Poisson et al. 2010), amongst other variables. Information on the shark species responsible for depredation is mostly anecdotal, with depredating species rarely being recorded. Mitchell et al. (2019) observed 4 species of carcharinid sharks depredating epinephelid and lethrinid fish in north-west Western Australia, although they also recorded 5 species from 4 other shark families interacting with fishing gear without depredating. Fotedar et al. (2019) identified 6 carcharinid species, as well as grey nurse sharks *Carcharias taurus*, depredating commercial line-caught demersal fish in the same region of Western Australia using trace DNA found at bite marks on recovered remains of hooked fish. Overall, the extent to which changes in the level of shark depredation may be caused by environmental influences, fluctuations in shark/shark prey or targeted species' populations, or changes in shark behaviour is uncertain.

To better understand the mechanisms behind shark depredation, we analysed 13 yr of logbook records, which include records of depredation events on hooked fish, from the Mackerel Managed Fishery (MMF). The MMF is a commercial trolling fishery in Western Australia with a substantial spatial range that covers 15° of latitude. Trolling fishers know instantly when a fish is hooked and thus also when a fish is also depredated, which is not the case for longline fisheries, where depredation is only recorded when damaged fish or fishing gear are retrieved to the vessel. Commercial fishers have suggested that the level of shark depredation within the MMF is increasing, but this has not been verified nor are the reasons for this possible change well understood. Considering that MMF data cover substantial spatial and temporal gradients in environmental and fishing variables, these data provide the opportunity to identify which of these variables are most associated with shark depredation, while also allowing for comparisons to be made in the level of depredation between commercial trolling fisheries and previous studies on longline and recreational fisheries.

The aims of this study were to: (1) quantify the depredation rates in the MMF and (2) assess how shark depredation correlates with gradients in fishing activity and environmental variables. We hypothesised that shark depredation had increased in the MMF especially in the southernmost zone of the fishery considering reports from mackerel fishers. We further hypothesised that depredation would be higher in areas with greater fishing effort, as it is possible that sharks have become conditioned to associate fishing vessels with the availability of hooked fish to feed on.

2. MATERIALS AND METHODS

2.1. The fishery

The MMF targets narrow-barred Spanish mackerel *Scomberomorus commerson* with minor catches of other pelagic species including grey mackerel

S. semifasciatus. This fishery is divided into 3 zones ranging from the Western Australia–Northern Territory (WA–NT) border to Augusta in the southwest, although the majority of fishing occurs north of Geraldton (Mackie et al. 2010; Fig. 1). Fishing primarily occurs in waters adjacent to reefs or the shore, generally in 30–80 m depths.

Fishing method varies substantially between the zones (Table 1). Both baits and lures are used by fishers, depending on crew preference, with bait used on approximately 70% of lines. Baits generally lie on or within 5 m of the surface, although the depth varies depending on use of lead core handlines and trolling speed (between 3 and 7 knots). Line length varies between 5 and 30 m (Mackie et al. 2010).

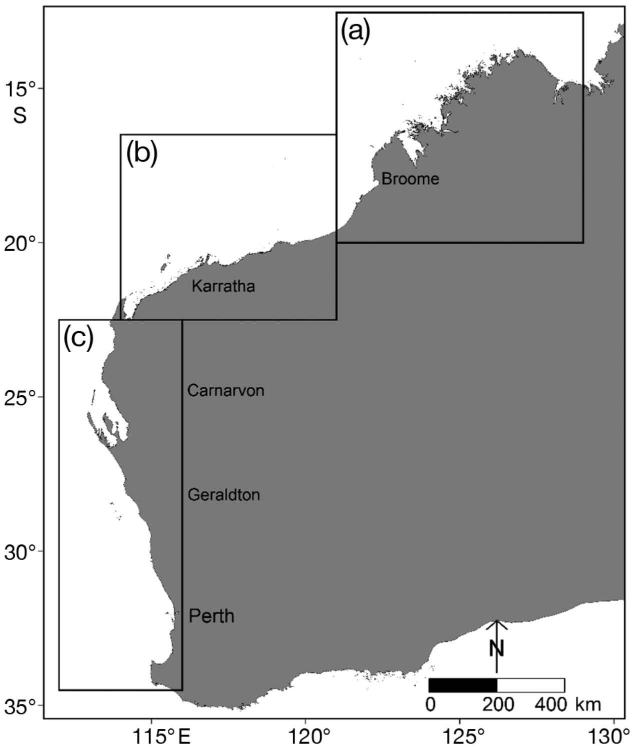

Fig. 1. Spatial extent of the commercial Mackerel Managed Fishery in Western Australia with 3 management zones (a: Zone 1; b: Zone 2; c: Zone 3)

Fishing effort and catch rates follow a strong north–south gradient, with highest catch rates and effort in Zone 1 (Kimberley), intermediate catch rates in Zone 2 (Pilbara) and lowest catch rates in Zone 3 (Gascoyne/west coast; Lewis & Jones 2016). Fishers troll for *S. commerson* alongside reefs in Zones 1 and 2 (Pilbara) or along the coastline in Zone 3 (Mackie et al. 2010). Each fishing day is broken up by session, defined as when lines first enter the water until they are retrieved to the vessel. These sessions last for as long as the schooling fish are biting, which could be several hours, with fishers operating across multiple locations daily, typically travelling between sites in the middle of the day when catch rates are lower. Peak fishing seasons vary between zones, with fishing effort peaking earlier in Zone 3 (May–June) compared to Zones 1 and 2 (August) (Mackie et al. 2010). Recreational fishing which also targets *S. commerson* peaks in all zones in austral autumn and winter (Ryan et al. 2019b).

The MMF is managed using a total allowable catch system, which is capped at 430 t for *S. commerson* across the 3 zones, in conjunction with annual catch tolerance levels. Catches of *S. commerson* in the MMF have remained relatively stable at 270–330 t following management changes in 2006, though the 2018 catch of 218 t was the lowest on record and fell below the lower limit of the annual catch tolerance level (246 t) (Lewis & Blay 2019). As *S. commerson* is heavily targeted by recreational and charter fishers, catches by these sectors are also considered in the management of the MMF, whereas the Total Allowable Catch system is only used for the commercial fishery. Catch in the charter fishery has remained stable at 17–37 t (22 t in 2018), while catch in the recreational fishery declined in 2017/2018 (37–

Table 1. Summary of differences in fishing methods between zones in the Mackerel Managed Fishery of Western Australia (Mackie et al. 2010)

Zone	Gear type	Line weight	Vessel size/ arrangement	Crew arrangement	No. lines used
1	Handlines/gunwale-mounted lines	200+ kg cord/mono line and wire trace	Main vessel (20 m) + 2–4 dories (5–6.5 m dinghies)	3–5 fishers	6–7 (main vessel) + 2–3 (dories)
2	Handlines/gunwale-mounted lines	180 kg mono line and wire trace	Main vessel (9–15 m)	2–3 fishers	6–7
3	Rod and reel	20–30 kg line and wire trace	Main vessel (7–15 m)	1–3 fishers	2–4

58 t) and 2015/2016 (35–54 t) compared to 2013/2014 (69–103 t) and 2011/2012 (78–108 t) (Ryan et al. 2019b). The breeding stock of *S. commerson* is assessed as 'sustainable-adequate' (Lewis & Blay 2019).

2.2. Logbook data

Daily logbook data provided to the West Australian Department of Primary Industries and Regional Development (DPIRD) give a record of depredated catch in the MMF on a 10 × 10 nautical mile (n mile) grid basis from 2006 to 2018 (13 yr). These data include details of catch and shark depredation events per fishing session, the reporting of which is mandatory for the fishery. Fishers recorded depredation events once they hooked a fish and noted a strong pull on the line, followed by either the retrieval of a partially consumed fish (e.g. the head) or the line snapping. Though fishers noted in the logbooks that large teleosts such as cod/grouper (*Epinephelus* spp.) were occasionally responsible (<1% of incidents), sharks were likely the primary depredating taxon as they were frequently observed depredating hooked *S. commerson* or were hooked themselves and retrieved to the vessel when depredating. Therefore, in subsequent analysis, it was assumed that sharks were responsible for all depredation events, although the potential for recall bias, whereby records of depredation events and their attribution to sharks occurred at the end and not during a fishing session, is noted.

Following Rabearisoa et al. (2018), we used 2 metrics to quantify rates of shark depredation: (1) interaction rate (IR, %) = total number of sessions where depredation occurred/total number of sessions. Calculated as a single value per zone for the entire 13 yr of data; (2) depredation rate (DR, %) = the mean number of fish depredated/number of fish hooked per session.

Depredation rate is used in most other depredation studies (Lawson 2001, Gilman et al. 2008, MacNeil et al. 2009, Labinjoh 2014, Mitchell et al. 2018a). The depredation rates only included fish taken while on the line, not fish predated after release (Raby et al. 2014). Economic loss due to depredation was also calculated as the product of the estimated weight of depredated fish (extrapolated from the average weight of fish caught for that session which was recorded by the fisher) and the market price of *S. commerson* ($8.08 AUD [USD $6.28] kg^{-1} beach price as of 2017; Gaughan & Santoro 2018).

Logbook data for each of the 3 zones were analysed separately due to differences in the fishing methods used. To improve reliability of the final analyses, we removed data for skippers who recorded fewer than 10 sessions and for 2 skippers known to DPIRD who made no record of depredation across their careers. As such, out of the total 48 skippers who had recorded catch in the fishery from 2006 to 2018, 16 were removed, leaving 32 in total. Only sessions targeting *S. commerson* were included, due both to a lack of sessions targeting *S. semifasciatus* and because the fishing methods differ substantially; sessions targeting *S. commerson* were identified as those in which 50% or more of the catch consisted of *S. commerson*. The final dataset consisted of 8125 sessions in Zone 1, 3634 sessions in Zone 2 and 1857 sessions in Zone 3.

To supplement the logbook data, interviews of experienced MMF fishers (>30 yr in the fishery) were also carried out to help understand perceptions of depredation. Only a small sample of skippers were able to be interviewed, hence the methods and results of these interviews are included in Supplement 1 at www.int-res.com/articles/suppl/m676p019_supp.pdf and are not the focus of this paper. The questionnaire for these interviews can be found in Supplement 2.

2.3. Fishing effort variables

Measures of fishing effort were calculated to test the hypothesis that consistent fishing effort in a small area, whether commercial or recreational, has a positive relationship with depredation rates. Commercial fishing effort was quantified as the number of fishing sessions which occurred within each respective 10 × 10 n mile block from 2006 to 2018. Spatial data on recreational fishing effort is not available for this region. We therefore identified a proxy that may capture broad spatial patterns in recreational fishing effort. Recent studies on this coastline suggest that proximity to towns is a major driver of recreational fishing effort (Ryan et al. 2017). Hence, distance from town centre was included separately in addition to commercial fishing effort to assess any relationship between depredation and proximity to towns. Shorter distances from population centres were assumed to be related to greater recreational fishing activity, which is supported by recreational fisher surveys (Ryan et al. 2017). This relationship is particularly important to test in conjunction with commercial fishing effort, considering that in some areas of the MMF, recreational effort was equal to or greater than that of commercial effort (Ryan et al. 2017, Gaughan & Santoro 2019). Because commercial fishers are not as limited in site choice (for Zones 1 and 2 particularly) as recreational fishers, who typically return to port for every fishing event and can spend multiple days fishing, there is unlikely to be significant correlation between commercial fishing effort and distance from town centre. This was tested as described in Section 2.5. Data were collected retrospectively using the Urban Centre and Locality dataset (Australian Bureau of Statistics 2016), which listed all towns in Western Australia or the Northern Territory (for those Catch and Effort System blocks close to the WA–NT border) which had a population of 200 or more people as of 2016. This variable was calculated by finding the distance of the nearest town centre in the Urban Centre and Locality dataset to the centroid of each 10 × 10 n mile block. Distance from town centre did not account well for known patterns in recreational fishing effort (Smallwood & Gaughan 2013) within Zone 3, where popular recreational fishing locations such as Steep Point and Dirk Hartog Island are extremely remote from town centres. No other suitable metrics were found to account well for recreational fishing effort in this zone. Longitude was initially tested to investigate whether it would capture known gradients in recreational fishing effort, with high fishing effort at 112.5° E (where there are known recreational fishing 'hotspots' both shore-based and boat-based) to lower fishing effort at 114.5° E (Smallwood & Gaughan 2013). However, it was later removed from analyses, as any influence of longitude was confounded by the limited availability of data in the MMF from 112.5 to 114° E. Latitude was initially tested as another spatial variable, but it was highly correlated with measures of commercial fishing effort and the proxy of recreational fishing effort, and thus was not included in the final analyses.

Fish size may influence depredation, as it takes longer for larger fish to be retrieved to the vessel, increasing the chances of depredation occurring. For this study, the weight of fish lost to depredation was unknown and could not be included in analyses. Fishers only recorded estimated total weight of the catch and total number of fish caught at the end of a fishing session, with no records kept for the weights of individual fish caught. No other suitable metric for fish weight could be included.

2.4. Environmental variables

Environmental variables were calculated based on the 10 × 10 n mile grid in which depredation events were reported. Daily mean satellite sea surface temperature (SST) records at 0.25 × 0.25° degree resolution were obtained from the US National Oceanic and Atmospheric Administration (NOAA 2019). We used high-resolution optimum interpolation SST (Reynolds et al. 2007) based on advanced very high-resolution radiometer (AVHRR) instruments on polar orbiting satellites (NOAA 2019). SST values were extracted for the date and nearest location of each logbook record. Lunar phase in the form of percentage of lunar illumination were obtained from the United States Naval Observatory (USNO 2019) and were matched to the logbook data by date. Average depth across the 10 × 10 n mile grids was obtained from Geoscience Australia (Whiteway 2009).

2.5. Generalized additive mixed model analysis

Generalized additive mixed models (GAMMs) (Lin & Zhang 1999) were used to model the count of fish depredated per session as a function of fishing and environmental variables. Separate models were fit to each zone due to the differing fishing methods between them. GAMMs were chosen as they allow fitting of random effects and the identification of non-linear relationships between dependent and smoothed predictor variables (Craven & Wahba 1978, Wood 2008). A random effect of skipper ID was included to account for any skipper-dependent variation. The total number of fish hooked was included as an offset in the model to account for differences in overall catch, as the number of fish depredated was assumed to be correlated with the total number of fish hooked as found in previous research (Mitchell et al. 2018a). The observed number of fish depredated per session was used as the response variable and was assumed to follow a Tweedie distribution (Tweedie 1984) with a log-link to account for the over-dispersed and zero-inflated logbook data. The appropriateness of this distribution was confirmed through visualization of residual plots and percentage of deviance explained. Log $(x + 1)$ transformations were applied to the offset variable, commercial fishing effort and hours fished to achieve uniformity in the distribution of x-variables (Zuur et al. 2009). The offset further needed to be log transformed considering a log-link was used and that the number of fish depredated was proportional to the total catch per fishing session. Most smoothed predictor variables were treated as continuous; however, time of day and month were treated as circular variables (Downs & Mardia 2002) using a cyclic cubic regression spline as the basis spline function (bs = 'cc') in 'mgcv' (Wood 2011), while year was treated as a linear variable and vessel configuration as a categorical factor (Table 2).

A full subsets approach was used for model selection (Fisher et al. 2018). To avoid overfitting, we limited the complexity of the models by setting the basis dimension (k) of the cubic regression splines to 4 and restricting the models to a maximum of 3 predictor variables (Burnham & Anderson 2002). To avoid multicollinearity, predictor variables with Spearman rank correlations greater than 0.28 were not included in the same model (Graham 2003). The most parsimonious model was defined as the model within 2 units of the lowest Akaike's information criterion (AIC) value with the lowest number of predictor variables (Raftery 1995, Burnham & Anderson 2002). Weighted AIC values (ωAIC) outlined by Fisher et al. (2018) were included to give further strength to model selection. Predictor variable importance scores, which represent the average ωAIC of all the models containing a particular predictor, were generated and plotted to compare the relative importance of all variables tested. The fit and robustness of the best-fitting, most parsimonious model of depredation for each zone was checked through visualization of residual plots, allowing confirmation of normal distribution of residuals, data point independence and goodness-of-fit of the fitted to the observed response data. Checks for spatial auto-correlation using Moran's I were also completed, with no models showing significant Moran's I p-values and all expected Moran's I outputs being close to 0 (Tiefelsdorf 2006). The R language for statistical computing (R Core Team 2017) was used for all data manipulation ('tidyr', Wickham & Henry 2017; 'dplyr', Wickham et al. 2017), GAMMs

Table 2. Predictor variables tested in the full-subsets generalized additive mixed models (GAMMs) for shark depredation in the Mackerel Managed Fishery of Western Australia, the metric used to represent that variable within the models and their hypothesised influence on shark depredation. All predictors were smoothed continuous unless stated otherwise

Predictor variable	Metric used in GAMM	Hypothesised importance to shark depredation
Fishing-related predictors		
Fishing period for that session	Fishing trip duration (hours from lines in to lines out of the water)	Longer fishing times provide greater opportunity for sharks to locate fishing vessels and depredate on hooked fish
Commercial fishing effort	Total number of fishing sessions per 10 × 10 n mile block across the 13 yr period	Greater fishing effort may condition sharks to associate these areas with feeding opportunities or reduce the time it takes for sharks to locate fishing vessels
Distance from town centre	Distance from the nearest town centre to the centroid of each 10 × 10 n mile block	Locations closer to population centres are likely to experience more recreational fishing effort which has the same impact as commercial fishing effort
Vessel configuration (categorical factor)	Whether dories or just main vessels were used. Applicable to Zone 1 only	Greater concentration of fishing effort when fishing solely from large vessels may be more attractive to sharks to depredate. Sharks may be more attracted to low-frequency engine noise from larger vessels with inboard motors (Myrberg 2001)
Environmental predictors		
Temperature	Sea surface temperature (°C)	Temperature influences the activity patterns (including feeding behaviour) of sharks (Sims et al. 2006, Digirolamo et al. 2012)
Lunar phase	Percentage of moon illuminated	Lunar phase influences the activity patterns (including feeding behaviour) of both sharks and fish (Poisson et al. 2010)
Time of day (circular)	Median time between time of lines in and time of lines out	Activity patterns of sharks, especially for feeding, will vary through diel periods (Nixon & Gruber 1988, Garla et al. 2006, Andrews et al. 2009)
Depth of fishing	Average depth of 10 × 10 n mile blocks	Depth influences habitat and distribution patterns of sharks (Espinoza et al. 2014)
Month (circular)	Month in which fishing session occurred (January–December)	Time of year will influence the distribution of shark species due to seasonal movements (Braccini et al. 2017). Weather patterns and currents which influence fishing dynamics will also change across the year (Tink 2015)
Year (linear)	Year in which fishing session occurred (2006–2018)	Temporal fluctuations in shark behaviours or populations will influence shark depredation

('mgcv', Wood 2011, Fisher et al. 2018) and graphing ('ggplot2', Wickham 2009; 'viridis', Garnier 2018).

3. RESULTS

3.1. Shark depredation rates

The shark depredation rates for the MMF generally varied between 0 and 20% across fishing sessions, although in some sessions up to 100% of the hooked catch was depredated. Total interaction and average depredation (±95% CI) rates were highest in Zone 3 (IR 37.4%, DR 5.7 ± 0.5%) compared to Zones 1 (IR 20.4%, DR 1.7 ± 0.12%) and 2 (IR 18.3%, DR 2.4 ± 0.26%). The overall economic loss in terms of mackerel depredated for the entire fishery from 2006 to 2018 equated to $517 900 AUD (USD $402 357). Per year, this was approximately $40 000 AUD (USD $31 076) across the fishery, which is 1.5% of the average yearly value ($2.73 million AUD [USD $2.12 million]) to the fishers.

3.2. Spatial variation in depredation rates

Within each of the zones there were considerable differences in the level of depredation (Fig. 2), with spatially explicit hotspots observed throughout. In the northern region (Zone 1), depredation was con-

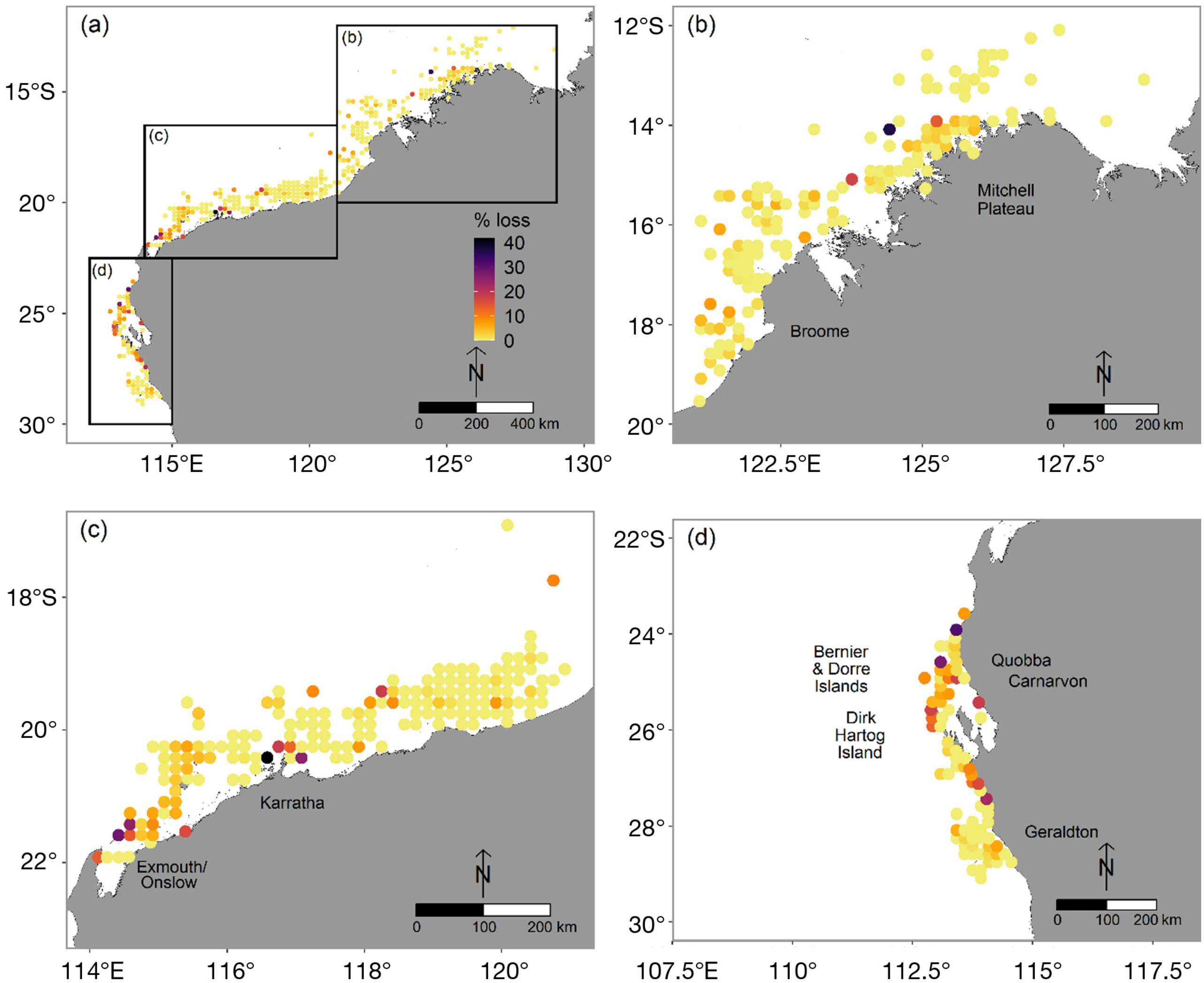

Fig. 2. Spatial variation in average shark depredation rates for the Mackerel Managed Fishery of Western Australia: (a) overall, (b) Zone 1, (c) Zone 2, (d) Zone 3. Depredation rates (% loss; colour key in panel a) are the average rates per Catch and Effort System 10 × 10 nautical mile fishing block for the years 2006–2018. Scale in panel (d) (Zone 3) is reduced to areas where fishing was recorded between 2006 and 2018 rather than the full zone

centrated offshore north off Broome and offshore from the Mitchell Plateau. Higher rates were observed in the central region (Zone 2) at the top of Exmouth Gulf and around Karratha. For the southern region (Zone 3), rates were highest off the west coast of Dirk Hartog Island, around Bernier and Dorre Islands and nearshore at Quobba and the coastline north of Geraldton.

3.3. Influence of fishing effort and environmental variables on shark depredation rates

The most parsimonious GAMMs for each zone are shown in Table 3. These were the only models which had AIC scores within 2 of the lowest AIC.

The most parsimonious GAMM for Zone 1 comprised commercial fishing effort ($F_{2.93}$ = 171.84, p < 0.001), distance from town centre ($F_{2.93}$ = 35.53, p < 0.001) and time of day ($F_{1.96}$ = 132.66, p < 0.001) (Table 3). This model explained 35.6% of the deviance for the number of fish depredated (the response variable) within Zone 1, of which 27.5% was accounted for by the random effect of skipper ID, meaning the 3 variables in the top model accounted for 8.1% of the total deviance. Commercial fishing effort, distance from town centre and time of day were important across all models in Zone 1 (importance scores of 1, 1 and 0.834, respectively), as was vessel configuration but only to a minor degree (0.166) (Fig. 3). Depredation showed a non-linear but mostly positive trend with commercial fishing effort, peaking where effort was most intense (Fig. 4a). Depredation was highest within 50 km of town centres, declining considerably beyond this distance. In terms of time of day, depredation was highest before dawn and after dusk but was lower during the middle of the day (Fig. 4c). For vessel configuration,

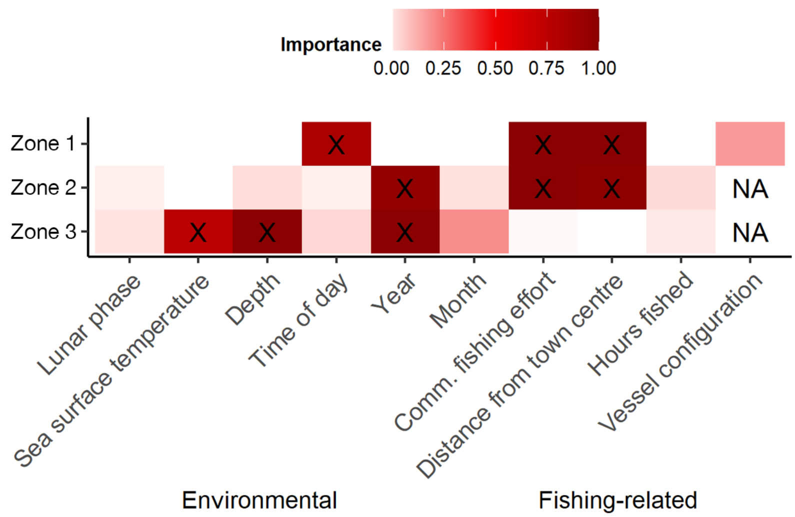

Fig. 3. Importance scores for environmental and fishing-related variables tested within generalized additive mixed model (GAMM) analysis (see Table 2) for predicting the number of fish depredated by sharks in Zones 1, 2 and 3 of the Mackerel Managed Fishery in Western Australia. Predictor variables which were in the most parsimonious models for each zone are denoted by (X). NA: not applicable for vessel configuration in Zones 2 and 3, as this predictor was only relevant for Zone 1

Table 3. Top Tweedie generalized additive mixed models (GAMMs) for predicting the depredation of *Scomberomorus commerson* by sharks from full-subset analyses for each zone of the Mackerel Managed Fishery of Western Australia. Differences between the lowest reported Akaike's Information Criterion (ΔAIC), weighted AIC values (ωAIC), deviance explained by total model (R^2), deviance explained by random effect (Skipper ID, RE R^2), p-values for each smooth term as calculated by the GAMM (p), *F*-/*t*-values for each smooth/linear term as calculated by the GAMM (*F*/*t*; in order of terms listed under best models) and effective degrees of freedom (EDF) for the total model are reported for model comparison. Model selection was based on parsimony, with only the most parsimonious model (fewest variables) within 2 units of the lowest AIC included. No zones had more than 1 model with a ΔAIC score <2. SST: sea surface temperature. *denotes significance (p < 0.05)

Zone	Best models	ΔAIC	ωAIC	R^2	RE R^2	p	*F*/*t*	EDF
1	Log fishing effort + Time of day + Distance from town centre	0	0.834	0.356	0.27	All <0.001*	171.84, 132.66, 35.53	15.73
2	Log fishing effort + Year + Distance from town centre	0	0.95	0.29	0.25	All <0.001*	16.68, 6.08, 22.48	19.58
3	SST + Year + Depth	0	0.76	0.416	0.39	SST 0.0035* Others <0.001*	5.09, 5.69, 19.12	18.54

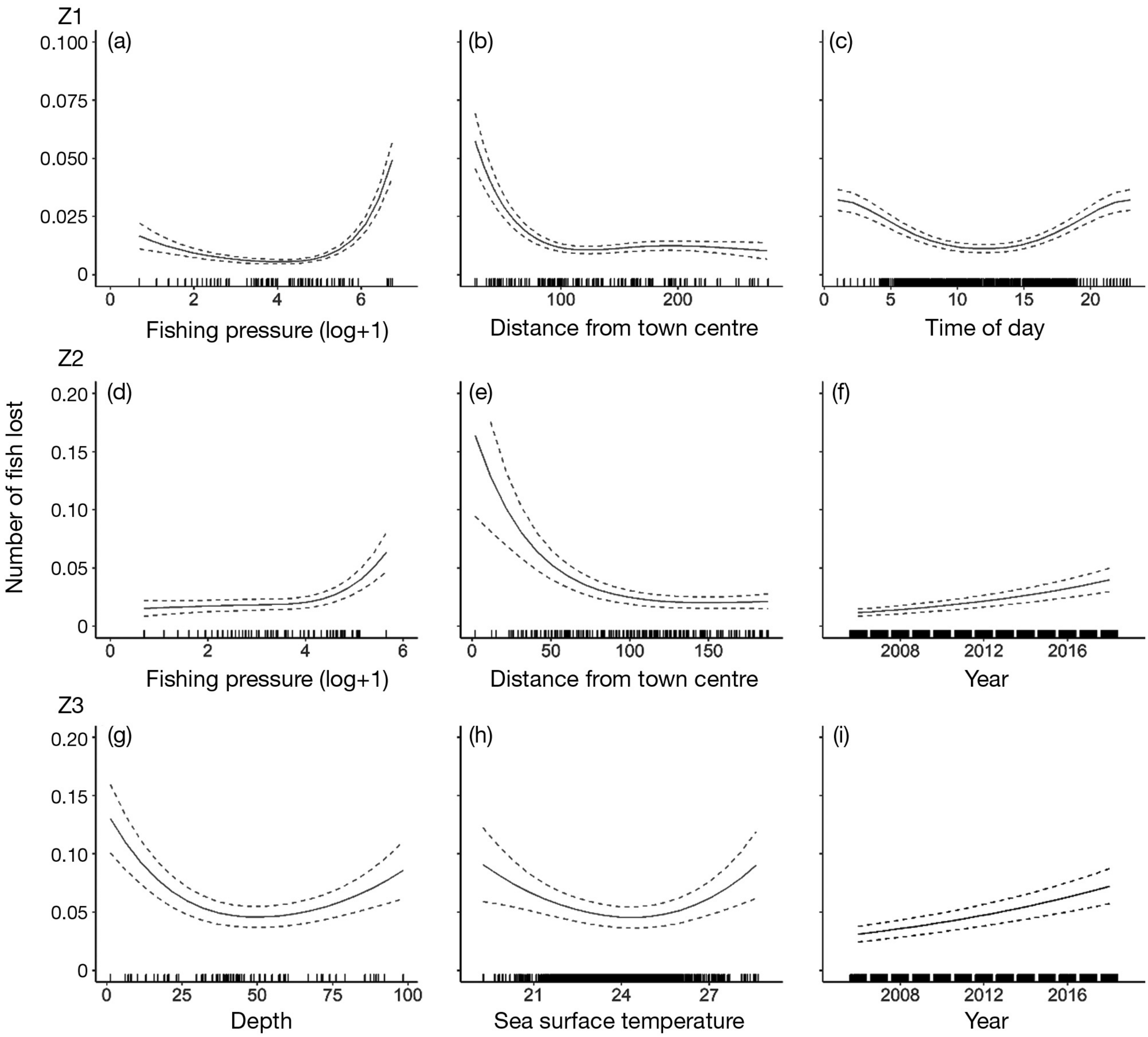

Fig. 4. Effect of predictors on the average number of fish depredated per fishing session for (a–c) Zone 1, (d–f) Zone 2 and (g–i) Zone 3 of the Mackerel Managed Fishery in Western Australia. The models shown are the most parsimonious Tweedie generalized additive mixed models (GAMMs). Solid black lines are fitted GAMM smooth curves; dashed lines are 95% pointwise confidence intervals (fitted smooth curve ± 2SE); black dashes on the *x*-axis are rug plots representing the distribution of the variable across all its values

depredation was higher when effort was concentrated on the main vessels compared to when it was dispersed across multiple smaller vessels (dories).

In Zone 2, commercial fishing effort ($F_{2.62}$ = 16.68, p < 0.001; Fig. 4d), distance from town centre ($F_{2.49}$ = 22.48, p < 0.001; Fig. 4e) and year (t_{12} = 6.07, p < 0.001; Fig. 4f) were important across all models (importance scores of 0.998, 0.98 and 0.958, respectively), with only minor scores for the other predictors. These variables were in the most parsimonious model which explained 29% of the deviance in the response, of which 24.5% was accounted for by the random effect of skipper ID. Thus, the 3 variables accounted for 4.5% of the total deviance in the response. Depredation rates showed a similar trend to that observed in Zone 1, with high depredation positively related to high commercial fishing effort. Depredation was highest close to town centres before declining considerably between 25 and 50 km. Depredation rates showed a positive linear trend with year, with the model indicating that rates almost doubled over the 13 yr study period.

Depth (importance score of 1, $F_{2.74}$ = 19.12, p < 0.001; Fig. 4g), SST (0.76, $F_{2.5}$ = 5.09, p < 0.0035; Fig. 4h) and year (1, t_{12} = 5.69, p < 0.001; Fig. 4i) were the most important predictors in Zone 3, with month the only other predictor with an importance score above 0.1 (0.19). The most parsimonious GAMM for Zone 3 included the 3 most important predictors and explained 41.6% of the deviance for the response variable. Skipper ID accounted for 39.4% of this deviance, meaning the 3 predictors accounted for only 2.2% of the total deviance. In terms of depth, depredation decreased substantially from a maximum at 0 to 25 m, with little or no change beyond that limit. Depredation showed a strong increasing linear trend from 2006 to 2018, peaking in 2018 at a level that was almost double that estimated for 2006. Depredation was highest at temperatures above 26°C and below 21°C, and during the months August–September.

4. DISCUSSION

This study is one of the first globally to quantify shark depredation rates in a commercial trolling fishery, to quantify depredation in a Western Australian commercial fishery, and to assess how gradients in fishing activity and environmental variables correlate with depredation across large spatial scales (the MMF ranges across 15° of latitude). We found that depredation rates in the MMF were at the lower end of the range recorded in commercial longline and recreational fisheries worldwide (Gilman et al. 2008, Mitchell et al. 2018b). We also found that depredation in the MMF is correlated with gradients of commercial fishing effort and a proxy of recreational fishing effort, which could suggest a behavioural response, whereby sharks associate fishing activities with feeding opportunities.

4.1. Shark depredation rates

The low rate of depredation in the current study compared to other studies in Western Australia (7.2–13.7% in a recreational fishery; Mitchell et al. 2018a) and in commercial longline fisheries elsewhere (1.9–20.74%; Lawson 2001, Dalla Rosa & Secchi 2007, Gilman et al. 2007, Rabearisoa et al. 2012, Hamer et al. 2015, Mitchell et al. 2018b) may be due to differing fishing practices. For instance, sharks have greater opportunity to depredate in longline fisheries where fish are hooked over a period of several hours (Gilman et al. 2008, MacNeil et al. 2009), whereas in the MMF, sharks only have up to 5 min to depredate before the fish are retrieved to the continuously moving/trolling vessel. Differences in the shark depredation rates may also be attributed to variation in biological and ecological factors (e.g. relative abundances of shark and prey species) between the regions in which the fisheries operate. Further research into how depredation varies with fishing practices, particularly within the same region where biological and ecological factors are more consistent, will help ascertain the true impact fishing practices have on shark depredation rates.

The analysis of depredation rates assumes fishers recorded depredation events accurately. It is possible that depredation events are under-recorded rather than overestimated due to the speed at which they occur and the possibility of skippers not recording all depredation events if they are not reported to them immediately by the deckhands or not observed directly by the skipper. Depredation might also be over-reported if fishers believe it may justify certain management interventions. Any associated error with this was reduced with the removal of known irregularly reporting skippers and those with minimal experience in the fishery who may not record events accurately. The assumption that sharks were the depredating taxa has minimal error, as even if incidents of depredation from other taxa (which fishers suggested made up <1% of depredation incidents) were removed, the shark depredation rates recorded would still fall within the error ranges given. The current study of depredation rates in a commercial trolling fishery expands on the existing literature, which has focussed on commercial longline or recreational line fisheries, and provides a basis for future studies of depredation in other commercial fisheries in Western Australia where anecdotal reports suggest that depredation is an issue.

4.2. Spatial variation and influence of fishing and environmental variables on shark depredation rates

The current study found that fishing effort, or proxies of fishing effort, had a consistent correlation with shark depredation across the northern and central zones of the MMF. Sharks may associate feeding opportunities with fishing activities via sensory signals that can include boat noise, fish oil and blood, as well as hydrodynamic disturbances created by struggling fish (Kalmijn 1988, Corwin 1989, Dallas et al. 2010, Collin 2012, Chapuis et al. 2019). The importance and trend of increasing depredation with increasing commercial fishing effort and proximity to town centre in Zones 1 and 2 suggest that areas of high commercial and recreational fishing effort are correlated with greater rates of depredation. This can be seen in the spatial pattern of depredation in the central region where several depredation hotspots occur in proximity to Karratha and Exmouth (Zone 2), areas which are subject to substantial recreational fishing effort (Smallwood & Gaughan 2013, Ryan et al. 2017). In fact, survey data suggest recreational fishing effort in these regions may be equal to or greater than commercial fishing effort in the MMF (Ryan et al. 2019b).

Though relatively minor, the importance of vessel deployment in the northern region (Zone 1) could also be explained by sensory cues associated with fishing activities. Depredation rates were lower when fishing effort was concentrated on one larger vessel in a small area compared to when it was dispersed across a larger area between multiple smaller vessels. When fishing effort is concentrated, the sensory cues associated with fishing activities are enhanced. This result is like that observed by Mitchell et al. (2018a), whereby depredation was greater when multiple vessels were fishing in close proximity. Fishers on the larger vessels also discard filleted carcasses overboard at the end of each fishing session, further enhancing the association of fishing activities with sensory cues for sharks. The observed pattern in this study could also be influenced by differences in boat noise, with the larger vessels using lower-pitched diesel inboard motors which may be more attractive to sharks then the higher-pitched outboard motors of the smaller vessels (Myrberg 2001). Although both types of vessels generally operate in similar habitats, the effects of variation in environmental conditions on the observed pattern cannot be discounted.

The capacity for conditioning of shark behaviour by food rewards has been recorded in laboratory (Guttridge & Brown 2014) and wild experiments (Mitchell et al. 2020), as well as in provisioning by ecotourism (Bruce & Bradford 2013, Brunnschweiler & Barnett 2013, Brena et al. 2015), though some provisioning studies found no change in behaviour (Laroche et al. 2007, Hammerschlag et al. 2012). The results of the current study suggest that the conditioning of sharks by feeding opportunities may play a role in influencing depredation rates across the MMF. This could be because feeding opportunities are more predictable and regular in areas of greater fishing effort, as both commercial and recreational fishers consistently return to known sites. Alternatively, the correlations between shark depredation rates and metrics of fishing effort could be explained by the natural ecological association between *Scomberomorus commerson* and depredating shark species, as observed historically in shark fisheries in northern Australia (Stevens 1999). In this sense, MMF fishers specifically target areas where *S. commerson* aggregate, and thus where depredating shark species may also co-occur. Future research should include quantitative data rather than proxies for recreational as well as commercial fishing effort where available. This research will help indicate whether the correlation between fishing effort and depredation rates observed in this study is consistent with actual patterns of fishing effort. In turn this may provide information for fishery managers as to how they can best reduce depredation, for example by reducing the spatial and/or temporal concentration of fishing effort where feasible.

Other long-term studies of depredation have found seasonal but not long-term trends in shark depredation (MacNeil et al. 2009, Rabearisoa et al. 2018). In the current study, we found a trend of increasing depredation from 2006 to 2018 in the central and southern areas of the fishery (Zones 2 and 3), where rates were estimated to have almost doubled in both zones. This trend is supported only partially by recent survey data where 50, 36 and 28% of charter, commercial and recreational fishers, respectively, suggested depredation in these areas had increased over a 2 yr period (Ryan et al. 2019a). Increasing rates of depredation could be explained by trends in commercial and/or recreational fishing effort over time. Commercial effort within the MMF, and more broadly across most fisheries operating in the relevant area, has fluctuated between 2006 and 2018; however, the available data do not suggest a consistent increase or decrease overall (Gaughan & Santoro 2019, Lewis and Blay 2019). Boat-based recreational fishing effort, as assessed by surveys of boat-based fishing, recorded lower estimates for the 2015/2016 and 2017/2018 periods in comparison to the 2011/2012 and 2013/14 periods in the north-west and Gascoyne coast regions of Western Australia in which the MMF operates (Ryan et al. 2019a).

Alternatively, increasing depredation rates could be explained by increasing shark abundances. Commercial shark fishing has been very limited in the north-west of Western Australia since 1993 (Zone 3) and 2005 (Zone 2) due to management closures and low effort (Simpfendorfer & Donohue 1998, McAuley et al. 2005, McAuley & Sarginson 2011). Life-history information for the sharks within this region suggests that populations would not have substantially increased over this period (McAuley et al. 2006, Harry et al. 2013, 2019, Braccini et al. 2018, 2020), indicating that increasing depredation rates are not correlated with increasing shark abundances. Catches of *S. commerson* within the MMF remained relatively consistent across the 13 yr. Although in 2018 they were the lowest on record, this decline can be partially attributed to a significant change in operators in combination with widespread environmental changes in northern Australia, with catches of *S. commerson* also declining in other states (Lewis & Blay 2019). As such, any relationship between depredation rates and indicative estimates of *S. commerson* population abundances from catch rates is currently unclear. Catch per unit effort reductions directly related to shark depredation (Peterson et al. 2014) should be estimated to further evaluate any relationship between depredation rates, *S. commerson* abundances and fishing effort within the MMF.

Environmental variables including time of day, SST, month and depth were found to correlate with depredation rates. Higher depredation rates during crepuscular periods, observed in Zone 1, are unsurprising considering the diel activity patterns of sharks. Various studies have found those species observed depredating in north-west Western Australia (Mitchell et al. 2019) hunt and/or range further at night, including grey reef sharks *Carcharhinus amblyrhynchos* (Barnett et al. 2012, Papastamatiou et al. 2018), blacktip sharks *C. limbatus* (Legare et al. 2018) and sicklefin lemon sharks *Negaprion acutidens* (Byrnes et al. 2021). Considering the depredating species observed by Mitchell et al. (2019) cannot be confirmed as the responsible depredating species in the MMF with the data currently available, other explanations for the higher depredation rates during crepuscular periods are possible. The greater depredation rates at higher temperatures in Zone 3 could also be explained by shark activity patterns. Studies have shown that *C. amblyrhynchos* and *C. limbatus* selectively move to and reside in areas where water temperatures are physiologically optimal, either on daily or seasonal scales (Heupel & Hueter 2002, Vianna et al. 2013). This behaviour is suggested to potentially help biological functions such as growth, gestation and digestion (Speed et al. 2010, 2012). Sharks may increase their feeding activity during periods of more optimal temperature (on a daily scale) or have greater site fidelity in areas of optimal temperature (on a seasonal scale). In turn, this could result in the relationship between higher temperatures and depredation rates, with sharks depredating more when temperatures are higher on a daily scale. On a seasonal scale, if sharks have greater site fidelity in areas of higher temperatures, then depredation rates will more likely by association be higher in these areas. The higher depredation rates at lower temperatures are potentially an exaggerated effect considering only 26 of the 1857 fishing sessions analysed for Zone 3 occurred at temperatures below 21°C (Fig. 4h), with this also true to a lesser extent for higher temperatures where 116 sessions occurred when temperatures were above 26°C. Depredation rates were highest in Zone 3 during August, which does not appear to correlate with peak fishing seasons (May–June). It is possible that this trend reflects environmental influences beyond temperature, considering there are marked differences in environmental conditions between seasons in this zone associated with the Leeuwin Current (Pattiaratchi & Woo 2009, Ridgway & Godfrey 2015). Considering there are multiple factors which show inter-annual variability within these 2 zones, and these are unaccounted for directly within the modelling, it is unknown which or what combination of these factors correlate with the trend with month shown in this study. Depredation in the southernmost region (Zone 3) was greater in shallower waters (<25 m). A number of factors may influence this trend. For example, it may be easier for sharks to depredate in shallow waters where they are more likely to detect fish hooked on the surface, or aggregations of the sharks responsible for depredation may be concentrated in shallow waters. With the data available, however, this explanation cannot be confirmed and it is reasonable to expect other factors may influence this trend. Overall, although environmental variables had some importance in the current study, metrics of fishing effort were consistently more important at predicting depredation rates across the MMF.

The deviance explained by the random effect of skipper ID in each of the 3 zones was substantial, suggesting that the level of depredation experienced differs between skippers. This pattern is possibly due to a combination of reporting/recall accuracy, method used, areas fished, skipper experience and associated responses to depredation. The number of fish depredated are only recorded at the end of a session, and it is likely some skippers are more accurate at this recall than others. As yet there has been no onboard validation of these data. Even though commercial vessels fish for several days and over a wide area, many skippers fish the same blocks regularly within the vicinity of their home port, which differ within and between zones. Some skippers reported that they modified their fishing methods in response to depredation (Supplement 1) and this may not be consistent or viable for some operators. Further exploration is required to ascertain if these factors are responsible for the variation in reported depredation rates between skippers in this study.

The low percentage deviance explained beyond the random factor for the most parsimonious models for each zone indicates that either other factors beyond those explored in this study are influencing depredation rates in the MMF, or that the complexity of depredation as a behaviour limits the consistent influence of any particular factor. The low percentage deviance explained in the modelled results is not surprising considering the broad spatial scale of the MMF. Significance values calculated by the GAMMs indicate that the influencing factors identified in this study do have a statistically significant correlation with depredation rates. As such, we can indicate which factors are correlated with depredation and warrant further exploration to increase understanding of their role, in combination with other environmental variables, such as habitat type or proximity, which could affect depredation but could not feasibly be included in this current study given its large scale and paucity of existing information.

4.3. Impacts of depredation within the MMF

Shark depredation, although currently at levels <10%, could have implications for the management of the MMF. To some degree the fishery relies on targeting *S. commerson* aggregations that occur in the higher fishing effort blocks with significant amounts of the catch coming from only a few blocks (e.g. 4 blocks in Zone 3 and 12 blocks in Zones 1 and 2). The higher depredation in these blocks and annually increasing rate of depredation are cause for concern, particularly in Zone 3, where fishing site choice is limited compared to the other zones, meaning it will be difficult for fishers to adapt their site selection to avoid depredation hotspots.

Direct loss of mackerel from depredation totalled an estimated $517 900 AUD (USD $402 357) across the 13 yr. Not all costs of depredation are captured by this figure. Firstly, the cost of replacing lost fishing gear was not included. Secondly, fishers noted that they moved sites and often reduced the number of lines used for trolling in response to depredation; this is motivated both by the direct depredation, and the fact that fishers perceive catch rates to be lower when sharks are depredating. Moving sites adds potential fuel costs and decreases available fishing time, while reducing lines reduces operational efficiency, though at an individual operator level these losses can be partially offset by continuing to fish until quotas are full. Even so, fishers in this case can be exposed to increased fuel and other operational costs considering they are having to increase their fishing effort to fill their quotas, especially if this continues beyond the traditional fishing season when aggregations of *S. commerson* become harder to find and inclement weather can reduce available fishing time. Furthermore, in the southern region (Zone 3) fishers noted that shark depredation had made it unprofitable to fish shallow-water sites, effectively reducing site access. These uncaptured and potentially substantial sources of economic losses due to depredation, coupled with the fact that shark depredation is increasing in parts of the MMF, makes shark depredation a pressing issue for the economic viability of the MMF, particularly in the southern region.

Depredation could have biological impacts across this region. The extra mortality associated with depredation in this fishery (1.7–5.7%), coupled with unknown but likely higher losses from recreational fishers, could negatively impact *S. commerson* stocks. Although the stock status of *S. commerson* is currently considered 'sustainable-adequate' (Lewis & Blay 2019), increasing losses associated with depredation could exacerbate any impacts from environmental events such as marine heatwaves, which have been suggested to be detrimental to the *S. commerson* stocks in the northern parts of the MMF if they coincide with the spawning season (Lewis & Blay 2019). Depredation increases human–wildlife conflicts in fisheries globally, often leading to the retaliatory killing of the predator(s) responsible (Drymon & Scyphers 2017, Carlson et al. 2019). Fishing gear retained by sharks has also been reported to restrict feeding capacity, cause lesions in the jaw, perforate the gastric wall and liver and result in bacterial infections (Borucinska et al. 2002, Bansemer & Bennett 2010).

5. CONCLUSIONS AND FUTURE DIRECTIONS

Our study suggests the rates of shark depredation in the MMF are low but increasing in some areas, with mitigation measures potentially needed where fishing effort is high to help reduce depredation and its effects on the MMF. Most of the previous depredation research has explored modifications to fishing gear to prevent depredation (Moreno et al. 2008, Rabearisoa et al. 2012, Hamer et al. 2015), yet generally these modifications can hamper fishing efficiency without reducing depredation completely (Rabearisoa et al. 2012, Hamer et al. 2015). Our study indicates that fishers are already reducing the number of lines to reduce losses but may be able to decrease depredation further by reducing fishing effort during dusk and dawn periods when sharks are more active and by reducing their visitation to heavily fished sites. In doing so, they could mitigate potential behavioural associations between fishing activities and feeding opportunities for sharks.

This study is one of the first to quantify shark depredation in a commercial fishery in Western Australia and in a commercial trolling fishery globally, creating a baseline for future research. The considerable spatial and temporal scale of this study enabled us to show that areas of greater fishing effort, where feeding opportunities for sharks from hooked catch are provided regularly and predictably, were consistently correlated with higher rates of depredation. This suggests changes in shark behaviour may partially explain both the temporal increases and spatial pattern of depredation observed in this fishery. With consideration for the low percentage deviance explained in the modelled results, more research is required to investigate experimentally the findings of a correlation between fisher behaviour and depredation here and to better understand depredation dynamics.

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