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Factors affecting elasmobranch escape from turtle excluder devices (TEDs) in a tropical penaeid-trawl fishery

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ABSTRACT

The use of turtle excluder devices (TEDs) has resulted in fewer elasmobranchs (i.e. sharks and rays) caught in tropical penaeid-trawl fisheries. However, very few studies in the primary literature have quantified the effects of various TED design aspects affecting the escape of elasmobranchs. Data collected by observers on board commercial trawlers operating in Australia's northern prawn fishery (NPF) during 2001 were re-examined to quantify the effect of TEDs on catches of various elasmobranchs. During this sampling, a total of 6204 elasmobranchs were caught from 1440 net trawls. The 34 species identified, from 15 families and four taxonomic orders, were dominated by small carcharhinids (n = 2160, median total length = 75 cm) and dasyatids (n = 2030, median disc width = 24 cm). The TEDs assessed significantly reduced the numbers of large elasmobranchs caught: increasing fish size was found to result in higher escape for all taxonomic orders. Further, top-shooter TEDs increased the escape of Carcharhiniformes, while bottom-shooter TEDs facilitated greater escape of Myliobatiformes. Grid orientation had no effect on the escape of Orectolobiformes or Rhinopristiformes. Decreasing bar space was found to increase the escape of only one species, the Australian blacktip shark (*Carcharhinus tilstoni*). The TEDs facilitated the escape of several species of conservation interest including the globally endangered scalloped hammerhead (*Sphyrna lewini*) and zebra shark (*Stegostoma fasciatum*). However, the rostrum of the narrow sawfish (*Anoxypristis cuspidata*) inhibited the escape of this globally important species. Fishery-specific research is required to determine the appropriate TED bar spaces that reduce catches of elasmobranchs while minimising the loss of commercially important species.

1. Introduction

Tropical penaeid trawling is recognised as a poorly selective form of fishing (Griffiths et al., 2006). Penaeids cohabit in demersal environments with various species that are susceptible to capture by trawls (Andrew and Pepperell, 1992) resulting in the highest discard rates of 25 gear types assessed by Perez Roda et al. (2019) at 54.9 %. The discarded portion of penaeid-trawl catches comprises hundreds of species (Courtney et al., 2006; Stobutzki et al., 2001) some of which have substantial conservation interest such as sea turtles and sawfish (Brewer et al., 1998; Robins-Troeger et al., 1995; Watson and Seidel, 1980). Concerns regarding the impacts of discarding unwanted animals on ecosystems are also recognised globally (Broadhurst, 2000; James et al., 2016). Consequently, quantifying and mitigating discards have been the subjects of significant research efforts since the early 1990s (Broadhurst et al., 2006; Kelleher, 2005).

The introduction of turtle excluder devices (TEDs) in tropical penaeid-trawl fisheries has led to beneficial flow-on effects (Jordan et al., 2013) including significant reductions in the capture of large elasmobranchs (e.g. Brewer et al., 1998; Robins-Troeger et al., 1995; Willems et al., 2016). Elasmobranchs (i.e. sharks and rays) are one component of penaeid-trawl discards that have received increasing attention in the last two decades (Dulvy et al., 2017). A major driver for this work is that elasmobranch life histories include late maturity, few offspring, long life spans and slow growth (Dulvy et al., 2008; James et al., 2016) making them vulnerable to overexploitation (Ellis et al., 2008).

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It has been estimated that 25 % of elasmobranchs are threatened with an elevated risk of extinction due to, for the most part, capture in marine fisheries, either as target species or by fishing gears targeting other species (Dulvy et al., 2014; Simpfendorfer and Dulvy, 2017). Research has shown that elasmobranchs caught by penaeid trawls are predominantly batoids and small demersal sharks (Courtney et al., 2006; Ellis et al., 2017; Robins and McGilvray, 1999; Shepherd and Myers, 2005; Stobutzki et al., 2002), although larger pelagic sharks (e.g. carcharhinids) are caught by larger, and/or fast moving penaeid and fish trawls (e.g. Brewer et al., 2006; Jaiteh et al., 2014; Raborn et al., 2012; Wakefield et al., 2016).

There are relatively few studies detailing the effects of TEDs and other bycatch reduction devices (BRDs) on the catch of elasmobranchs in the primary literature (some examples are: Brewer et al., 2006, 1998; Fennessy and Isaksen, 2007; Jaiteh et al., 2014; Noell et al., 2018; Wakefield et al., 2016). As these devices were adopted in penaeid-trawl fisheries, their effects on target catch and discards were a focus of research (see review by Broadhurst, 2000). Numerous studies from the 1990s reported the effects of TEDs and BRDs on penaeid and discard catches (e.g. Broadhurst et al., 1997; Isaksen et al., 1992), while others also confirmed the exclusion of turtles (Brewer et al., 1998; McGilvray et al., 1999; Robins-Troeger, 1994; Robins-Troeger et al., 1995). Most studies during the 1990s were conducted on known trawl grounds in an effort to replicate commercial conditions (Broadhurst et al., 1997; Robins-Troeger, 1994; Robins and McGilvray, 1999), resulting in sufficient quantities of both target species and bycatch to enable robust analyses from a relatively small number of trawls. However, given interactions with penaeid trawls are relatively rare for most species caught (Kyne et al., 2002; Wakefield et al., 2016), analyses regarding the effect of TEDs and BRDs on elasmobranchs were largely absent.

The lack of detailed information in the primary literature describing the effects of TEDs on elasmobranchs warrants attention. Although the composition of elasmobranch bycatch caught by penaeid trawlers is poorly understood (e.g. Molina and Cooke, 2012), previous research has shown it includes species groups of conservation value. Hammerhead sharks (Sphyrnidae: Raborn et al., 2012; Wakefield et al., 2016), sawfish (Pristidae: Brewer et al., 2006; Wakefield et al., 2016), guitarfish (Glaucostegidae: Garcıa-Caudillo et al., 2000; Robins-Troeger, 1994), wedgefish (Rhinidae: Brewer et al., 2006; Fennessy, 1994; Robins and McGilvray, 1999) and skates (Rajidae: Kyne et al., 2002) have all been shown to occur in penaeid-trawl bycatch.

The objective of the current study was to quantify the impact of TEDs on the catches of various elasmobranchs caught off northern Australia using data collected during a previous study (Brewer et al., 2006). The effect of fish size and various aspects of TED design such as grid orientation, grid angle and bar space were quantified to determine their effect on the escape of elasmobranchs from penaeid trawls. For the purposes of the current study, a TED was considered to be a barrier installed in a trawl designed to exclude any component of the discarded portion of a catch. Further, all care has been taken to provide updated species names when discussing previous studies.

2. Materials and methods

In the current study, data collected by Brewer et al. (2006) were reanalysed to determine factors affecting the escape of elasmobranchs from penaeid trawls. These data were recorded by scientific observers with the objectives of providing information regarding the impact of TEDs and BRDs on target and non-target catches within the NPF. Five observers collected data on board 23 vessels while fishing commercially during the tiger (*Penaeus semisulcatus* and *P. esculentus*) prawn season (August to November) of 2001. At this time, fishers primarily targeted tiger and endeavour (*Metapenaeus endeavouri* and *M. ensis*) prawns at night using one Florida Flyer ($> \sim 18$ m or 10 fathoms headline length) net towed from each side of the vessel. Fishers were required to have a TED and one of seven prescribed BRDs installed in each net. Of the seven prescribed BRDs, the bigeye and square-mesh panels (see Brewer et al., 2006 for illustrations) were the most popular during the sampling period. Observers spent approximately two weeks on board a vessel before moving to the next vessel (hereafter referred to as a ‘trip’). The two-week period was chosen as it approximated the time between visits to a refuelling barge: the barges anchored in calm inshore waters which facilitated the easy transfer of observers between vessels and negated the need to perform potentially dangerous transfers on the fishing grounds.

2.1. Sampling protocol

Once an observer boarded a vessel, the gear was left unaltered for one night in order to quantify between-net variation in catch, termed a ‘calibration night’. On the second night, the TED and BRD were removed from one net, chosen by the master of the vessel, resulting in a ‘control’ net and a ‘treatment’ net being towed simultaneously. After seven nights, the BRD in the treatment net was either removed or made ineffective by sewing trawl mesh over the escape opening, thereby providing information on the effects of the TED only. On the last night of sampling (typically night 14), a second calibration night was undertaken to ensure any between-net variation detected on the first night was consistent throughout the sampling period.

Various design aspects of the TEDs used were recorded by the observer at the start of each trip. Important information including grid size, orientation (top-shooter or bottom-shooter), angle, bar spacing and dimensions of the escape hole were documented in order to determine their effects, if any, on catches. The BRDs tested had no effects on the catch rates of elasmobranchs and, as such, we focus only on the effects of TEDs, used either in combination with a BRD, or individually.

During the sampling period, vessels completed up to four trawls per night. Each trawl was 3–4 h in duration depending on the amount of bycatch present. At the end of each trawl, the two codends were spilled onto the sorting tray ensuring the catches from each net were separated. All large animals (attaining > 30 cm in length) such as sea turtles, elasmobranchs, sponges and sea snakes, were removed from the catch and, where possible, identified to species, weighed, measured and released alive. The crew then commenced sorting, by removing all commercial penaeids and byproduct, including squid (Teuthoidea), Moreton Bay bugs (Scyllaridae: *Thenus australiensis* and *T. parindicus*) and scallops (Pectinidae: *Amusium pleuronectes*), for immediate processing and storage in on-board freezers. Generally, *P. semisulcatus* and *P. esculentus* ≥ 26 mm carapace length (CL) were retained, while *T. australiensis* and *T. parindicus* had a minimum legal size of 60 mm carapace width. All remaining bycatch was sorted into lug baskets and weighed by the observer.

2.2. Statistical analyses

For the purposes of the present study, a subset of the data obtained by Brewer et al. (2006), containing only those trawls where an elasmobranch was caught in either the control net or treatment net, was used. In accord with Brewer et al. (2006), the effect of TEDs on the elasmobranch catch was initially assessed using the exact binomial test. That is, the probability of an elasmobranch being caught in the treatment net is p and $1 - p$ for capture in a control net with a null hypothesis of $p = 0.5$. Retention of the null hypothesis implies that the TED failed to exclude elasmobranchs. The exact binomial test was performed using R statistical software (Version 3.3.3, R Foundation for Statistical Computing, Vienna, Austria, see https://www.R-project.org/, accessed 19 April 2018) via the “binom.test” function from the “stats” package.

In order to provide information on the factors affecting the escape of elasmobranchs via TEDs, the data were analysed using a logistic regression model of length data which relates the probability of capture in the treatment net to the size of the animal (Brewer et al., 2006). Assuming each net was equally likely to catch an elasmobranch, the expected number caught in a control net is n and $n(1 - e)$ in the treatment net, where e is the rate of escape due to the presence of the TED. Therefore, the probability of capture in the treatment net, t, is

$$t = n(1-e)/(n + n(1-e))$$

Where sample size permitted, t was estimated for each species, family and order. This probability was estimated via generalised linear mixed modelling using R statistical software via the 'glmer' function within the 'lme4' package (Bates et al., 2015). The probability of capture in the treatment net of each species or species group was modelled separately and datasets were restricted to cases where all relevant data were present. A vessel identifier was added as a random term while grid orientation (top-shooter or bottom-shooter), grid shape (circular, elliptical, tombstone or rectangular), the presence of a BRD (0, 1), the presence of bent deflector bars (0, 1) and the presence of an escape-hole cover (0, 1) were added as categorical fixed terms. Additionally, grid angle, bar space, area, and escape hole area and fish size (TL for all sharks and Rhinopristiformes, DW for all other rays) were added as covariates. Given their importance in the results reported by Brewer et al. (2006), fish size and grid orientation were added to all models. All other categorical terms and covariates were tested for significance and retained in the model only if their addition improved the Akaike Information Criteria (AIC). Relevant two-way interactions were also tested and excluded if their addition had no significant effect on the probability of capture in the treatment net. The 'bootMER' function within the 'lme4' package was used to calculate 95 % confidence intervals around the estimated probabilities.

Following Brewer et al. (2006), the probability of capture in the treatment net, t, was then converted to escape, e, with the equation $e = 1 - t(1 - t)$. A simple function in R converted the vectors of estimated probabilities and the associated confidence intervals to escape rates.

Preliminary analysis revealed that treatment nets caught more smaller elasmobranchs than control nets. This resulted in negative values of escape (i.e. $e < 0$). As such, the size at which escape and retention were equal (i.e. the size at which escape was zero, S_0) was calculated for each taxonomic order. This metric provided additional information on the effects of TED design on escape. The size at which 50 % escape (S_{50}) occurred was also calculated.

To ensure the nets were fishing similarly before and after each sampling period, the number of elasmobranchs caught during the calibration nights were analysed using generalised linear mixed modelling. For this analysis, a vessel identifier was added as a random term while trawl number, calibration period (0 = before sampling, 1 = after sampling) and vessel side were added as fixed effects. The number of elasmobranchs in each net was the variable of interest which was modelled as a Poisson distribution using R.

3. Results

During the sampling period, 720 trawls were undertaken on 22 vessels where a treatment net and a control net were towed simultaneously (i.e. 1440 net trawls). Results from one vessel were excluded due to the limited number of trawls conducted with treatment and control nets present. Various TED designs were used during the sampling period (Supplementary Table 1). Most devices were deployed as bottom-shooters: 430 trawls were undertaken with bottom-shooter TEDs; and 290 as top-shooters. Only two devices were tested in both top- and bottom-shooting configurations. TEDs were generally tombstone-shaped, rectangular or elliptical with a grid angle ranging between 40 and 72° from the horizontal. Bar space ranged between 95 and 120 mm, with 32 % of trawls completed using TEDs with the maximum permitted bar space of 120 mm. The majority of trawls were conducted with guiding panels installed (~79 %) and no deflector bars (~90 %). A BRD was installed during 427 (~59 %) trawls.

Generalised linear mixed modelling revealed there was no significant between-net variation in the catches of elasmobranchs (all species) at each location during the calibration phase of each sampling trip ($P = 0.817$). This indicated that, for all vessels, any variability in catch between nets could not be attributed to the nets themselves.

From the 1440 net trawls, a total of 6204 elasmobranchs were identified representing 34 species from 27 genera, 15 families and four orders (Supplementary Table 2). The most common species caught was the whitecheek shark (*Carcharhinus coatesi*, $n = 1218$), while Australian blacktip sharks (*Carcharhinus tilstoni*, $n = 634$), brown whiprays (*Maculabatis toshi*, $n = 634$), painted maskrays (*Neotrygon leylandi*, $n = 627$), Australian butterfly rays (*Gymnura* australis, $n = 641$) and bottlenose wedgefish (*Rhynchobatus australiae*, $n = 571$) occurred frequently in catches. In contrast, ten or fewer individuals were caught for 15 of the remaining 28 (~54 %) species identified during sampling (Supplementary Table 2).

Generally, the most abundant species were small (Supplementary Table 2). Median TL of the most common sharks (*C. coatesi*, *C. tilstoni*, *Rhizoprionodon acutus* and *Chiloscyllium punctatum*) was ≤81 cm, while the median DW of the most common rays (*Maculabatis toshi*, *Neotrygon annotata*, *N. leylandi* and *Gymnura australis*) was ≤44 cm. Further, the median TL of the most common Rhinopristiform, *R. australiae*, was 65 cm. However, small numbers of large (≥3.0 m TL) *S. lewini*, tiger sharks (*Galeocerdo cuvier*) and *R. australiae* were caught in control nets.

3.1. Factors affecting escape

It should be noted that, for the most part, the low number of elasmobranchs encountered during the sampling resulted in a lack of power to isolate the effects of the various factors tested on the catches of elasmobranchs. The observational nature of the data, combined with the lack of control over the design factors of the TEDs tested (Supplementary Table 1), caused some issues when analysing these data. For example, only 20 trawls were undertaken with a circular TED compared to 234 and 188 trawls with elliptical and rectangular grids, respectively.

The GLMMs indicated fish size significantly affected the probability of capture in treatment nets and, therefore, escape for only three species (Table 1): *C. tilstoni* ($\beta = -0.031$, S.E. = 0.007: $P < 0.001$), *M. toshi* ($\beta = -0.019$, S.E. = 0.006: $P < 0.001$) and *R. australiae* ($\beta = -0.014$, S.E. = 0.003: $P < 0.001$). In all instances, increasing size was found to reduce the probability of capture in treatment nets. Further, top-shooter TEDs ($\beta = -0.360$, S.E. = 0.174: $P < 0.05$) reduced the probability of capture of *C. tilstoni*, while increasing bar space ($\beta = 0.022$, S.E. = 0.010: $P < 0.05$) had the opposite effect. For the remaining species, the respective GLMMs failed to attribute differences in the probability of capture in treatment nets to any factor or covariate tested.

At the family level, increasing fish size significantly reduced the probability of capture in treatment nets (Table 1) for carcharhinids ($\beta = -0.014$, S.E. = 0.003: $P < 0.001$), sphyrnids ($\beta = -0.028$, S.E. = 0.012: $P < 0.05$), dasyatids ($\beta = -0.024$, S.E. = 0.002: $P < 0.001$) and myliobatids ($\beta = -0.032$, S.E. = 0.013: $P < 0.05$). Top-shooter TEDs reduced the probability of capture in treatment nets for both carcharhinids ($\beta = -0.259$, S.E. = 0.099: $P < 0.01$) and sphyrnids ($\beta = -2.281$, S.E. = 1.038: $P < 0.05$). In contrast, the probability of capture in treatment nets was significantly greater ($\beta = 0.237$, S.E. = 0.117: $P < 0.05$) for dasyatids when top-shooter TEDs were used.

At the order level, increasing fish size significantly reduced the probability of capture ($P < 0.05$, Table 1). Top-shooter TEDs caught fewer Carcharhiniformes ($\beta = -0.214$, S.E. = 0.101: $P < 0.05$) and more Myliobatiformes ($\beta = 0.216$, S.E. = 0.105: $P < 0.05$). Grid orientation had no effect on the probability of capture in treatment nets for both Orectolobiformes and Rhinopristiformes ($P > 0.05$).

Escape from TEDs was greatest for large animals (Figs. 1 and 2).

Table 1

Beta parameters from the generalised linear mixed models testing the effects of fish size (cm, total length for all except the Myliobatiformes which are measured by disc width), TED grid orientation (bottom-shooter TED is the reference level) and bar spacing on the probability of capture in treatment nets undertaken for each species or species group. Numbers in parentheses represent the standard error around the beta parameter estimate. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; and ns $P > 0.05$.

Species or species group	Size	Grid orientation	Bar spacing
Carcharhiniformes	−0.013 (0.002)***	−0.214 (0.101)*	ns
Carcharhinidae	−0.014 (0.003)***	−0.259 (0.099)**	ns
Carcharhinus tilstoni	−0.031 (0.007)***	−0.360 (0.174)*	0.022 (0.010)*
Sphyrnidae	−0.028 (0.012)*	−2.281 (1.038)*	ns
Orectolobiformes	−0.011 (0.002)***	ns	ns
Myliobatiformes	−0.018 (0.002)***	0.216 (0.105)*	ns
Dasyatidae	−0.024 (0.002)***	0.237 (0.117)*	ns
Maculabatis toshi	−0.019 (0.006)**	ns	ns
Myliobatidae	−0.032 (0.013)*	ns	ns
Rhinopristiformes	−0.012 (0.002)***	ns	ns
Rhynchobatus australiae	−0.014 (0.003)***	ns	ns

However, the GLMMs indicated that escape from treatment nets was negative for animals in smaller size classes across all species groups. It was prudent, therefore, to quantify the size at which retention and escape were equal (i.e. S_0): animals below S_0 experienced higher retention by treatment than control nets, while escape occurred for some proportion of those animals larger in size than S_0. The S_0 occurred at 17 and 31 cm DW for Myliobatiformes caught in treatment nets containing bottom- and top-shooter TEDs, respectively (Supplementary Table 3). In contrast, the estimate of S_0 was lower for Carcharhiniformes caught in top-shooter TEDs ($S_0 = 61$ cm TL) than those caught in bottom-shooter TEDs ($S_0 = 76$ cm TL). The S_0 was similar for the Orectolobiformes and Rhinopristiformes.

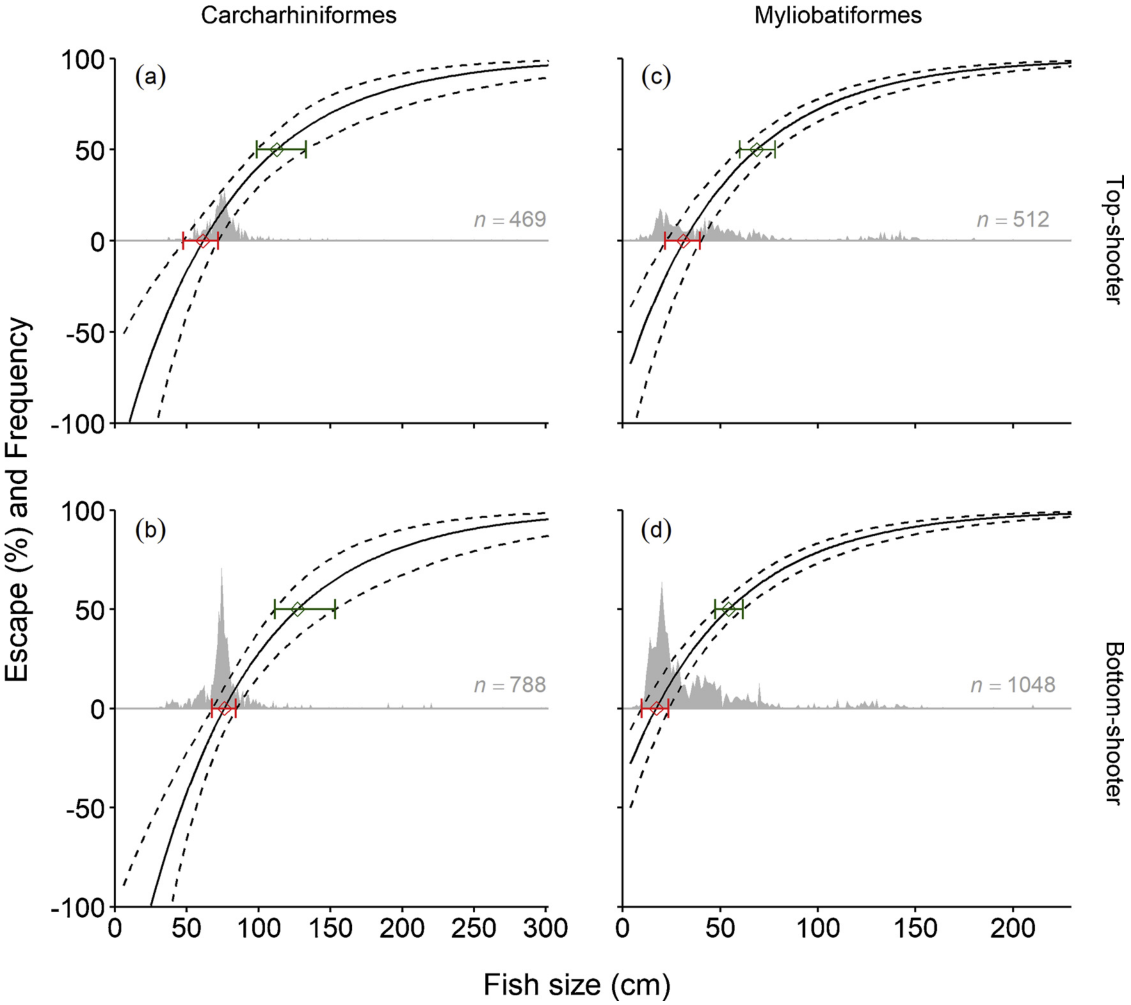

Fig. 1. Escape of Carcharhiniformes (a, b) and Myliobatiformes (c, d) as a function of fish size (total length for Carcharhiniformes and disc width for Myliobatiformes) and turtle excluder device (TED) grid orientation. Dashed lines represent 95 % confidence intervals. Also shown are the length frequencies of the respective species groups, as a function of grid orientation, caught in control nets (i.e. no TEDs) only. Sample sizes represent the number of individuals assessed in the respective reduced generalised linear mixed models. The red points show the sizes at which escape and retention were equal (i.e. S_0) and the green points represent the size at which 50 % escape (i.e. S_{50}) occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

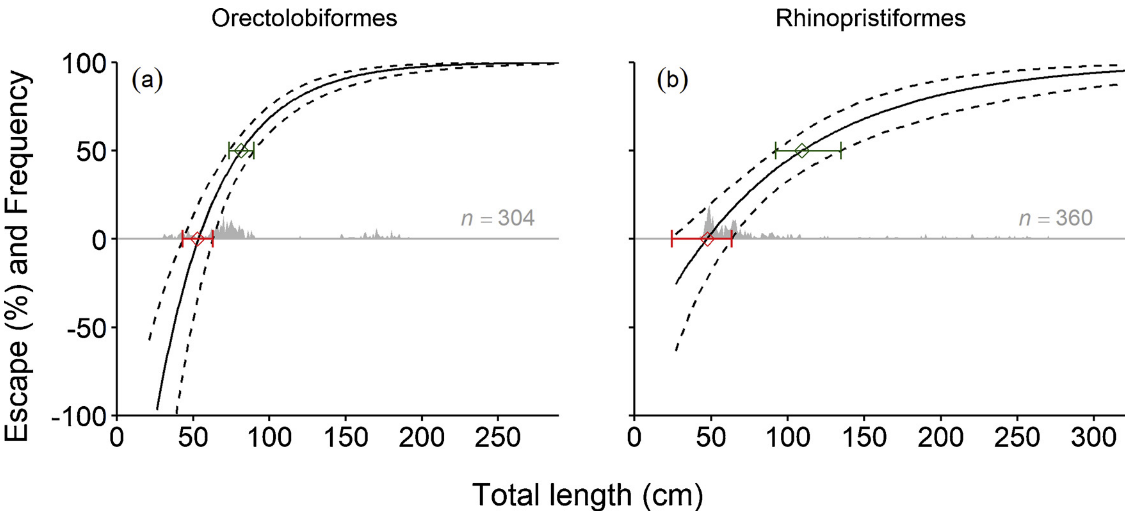

Fig. 2. Escape of Orectolobiformes (a) and Rhinopristiformes (b) as a function of total length, in centimetres. Dashed lines represent 95 % confidence intervals. Also shown are the length frequencies of the respective species groups caught in control nets (i.e. no TEDs) only. Sample sizes represent the number of individuals assessed in the respective reduced generalised linear mixed models. The red points show the sizes at which escape and retention were equal (i.e. S_0) and the green points represent the size at which 50 % escape (i.e. S_{50}) occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The TEDs used throughout the sampling period facilitated the escape of a high proportion of species of conservation interest. Importantly, the TEDs significantly reduced the number of Endangered *S. lewini* (Baum et al., 2009) and *S. fasciatum* (Dudgeon et al., 2016). This is the first study to demonstrate that TEDs reduce the catch of these species in penaeid-trawl fisheries. In contrast, the TEDs used throughout the sampling period had no effect on catches of the Endangered (D'Anastasi et al., 2013) narrow sawfish (*Anoxypristis cuspidata*), although sample size was low (*n* = 16). Similar to observations by Wakefield (2016), TEDs failed to exclude four narrow sawfish due to entanglement of the rostrum forward of the TED.

Because the bar spacing of a TED dictates what can physically pass through to the codend, it is an important factor influencing the escape of elasmobranchs. In the current study, reducing bar space resulted in significantly fewer *C. tilstoni* caught in treatment nets (Table 1). This was the only species where sufficient individuals were caught at appropriate sizes (37–159 cm TL) to isolate the effects of bar space on escape. This result is consistent with Noell et al. (2018), who found reducing bar space from 45 to 35 mm resulted in significantly lower numbers and weights of elasmobranchs with no loss of the targeted western king prawns (*Melicertus latisulcatus*). Similarly, Garstin and Oxenford (2018) reported a 40 % reduction in catches of elasmobranchs using a modified TED (4.45 cm bar space) compared to standard TEDs (10.2 cm bar space) used in the Atlantic seabob (*Xiphopenaeus kroyeri*) fishery in Guyana. These authors reported significant reductions for various batoids including the smooth butterfly ray (*Gymnura micrura*), longnose stingray (*Hypanus guttatus*) and sharpsnout stingray (*Fontitrygon geijskesi*). Further, in a simulation study, Brčić et al. (2015) suggested that reducing the bar spacing of a TED from 90 to 70 mm would significantly reduce the number of blackmouth catsharks (*Galeus melastomus*) whilst maintaining the catch rates of the targeted Norway lobster (*Nephrops norvegicus*).

While the use of narrower bar spaces is a logical modification to improve the escape of elasmobranchs from penaeid trawls, the size of the target and other commercially important species determines the appropriate bar space. Acceptable bar spaces have been shown to range between 1.9 cm, for targeting *Pandalus* sp. (Hannah et al., 2011; Isaksen et al., 1992), and 15–20 cm for targeting fish in Western Australia (Jaiteh et al., 2014; Wakefield et al., 2016). Assessing the loss of target species is important when quantifying the effects of TEDs in penaeid-trawl fisheries because fishers are likely to resist any modification to a net that reduces their catch (Gullett, 2003). However, fishers may accept small catch losses if this is offset by improved quality (Eayrs, 2007; Noell et al., 2018; Salini et al., 2000). For example, Salini et al. (2000) estimated the reduction in damage to *P. semisulcatus* and *P. esculentus*, due to the introduction of TEDs and BRDs in the NPF, would result in increased revenue to the fleet of ~$AU1 million per annum.

In addition to fish size, other morphological characteristics of individual species influence escape. For example, significantly fewer brown whiprays (*Maculabatis toshi*) were caught in treatment nets, while no significant reductions were detected for Australian butterfly rays (*Gymnura australis*), despite broadly similar sizes (Supplementary Table 2). This result is consistent with Willems et al. (2016) who reported greater escape for longnose stingrays (*Hypanus guttata*) than smooth butterfly rays (*Gymnura micrura*). These authors attributed this result to the contrasting morphology of the two species: while *H. guttata* possess a thick, rigid disc, *G. micrura* has a flexible, smooth disc which allows for easy passage through the TED bars and into the codend. Similarly, *M. toshi* is much thicker through the trunk than *G. australis*, which is extremely flattened (Last and Stevens, 2009), making the latter more likely to pass through the bars of a TED and into the codend at similar disc widths.

Grid orientation was the only other factor tested that was found to affect the escape of elasmobranchs in the current study (Table 1 and Fig. 1). Top-shooter TEDs facilitated greater escape of Carcharhiniformes while bottom-shooter TEDs improved the escape of Myliobatiformes. These results are likely a function of the escape response, and the resultant position in the trawl, of the respective species groups. Wakefield et al. (2016) and Jaiteh et al. (2014) observed carcharhinids attempting to exit a fish trawl in an upward direction during field trials using underwater video equipment. Considering these results, the use of top-shooter TEDs in the Raborn et al. (2012) study may have resulted in greater escape of *R. terraenovae* in the Gulf of Mexico penaeid-trawl fishery.

Top-shooter TEDs were less effective for Myliobatiformes. This outcome was particularly the case for smaller (S_0 = 31 cm DW) individuals, with 36 % of animals in control nets of a size where escape did not occur (Fig. 1 and Supplementary Table 3). This contradicts the previous study by Brewer et al. (2006), who used exact binomial tests to demonstrate grid orientation had no effect on the escape of

Myliobatiformes and Rhinopristiformes combined (what they refer to as "rays"). However, these species groups were analysed separately here.

The greater escape of small Myliobatiformes from bottom-shooter TEDs may be a result of the location of these animals in the net. Their morphology suggests that the majority of these animals live on the sea floor and are, therefore, more likely to escape in a downward direction. Main and Sangster (1982) found that skates (Rajidae) and spotted dogfish (*Scyliorhinus canicula*) were more likely to be caught in the lower level of a fish trawl net divided by a horizontal separator panel. Escape holes placed in the bottom of the net may allow more animals to escape before passing through the bars of a bottom-shooter TED.

Grid orientation is fishery specific (Eayrs, 2007). In areas where sedentary organisms (e.g. sponges) or slow moving heavy animals (e.g. turtles or rays) are present, bottom-shooter TEDs are more appropriate (Mitchell et al., 1995). In 'cleaner' areas, top-shooter TEDs can be more suitable (Eayrs, 2007). Where large animals are absent from catches and the escape-hole cover remains closed throughout the trawl, top-shooter TEDs are able to maintain penaeid catch compared to control nets (Courtney et al., 2014).

There is scant information in the primary literature regarding the effect of grid orientation on the catches of elasmobranchs in penaeid-trawl fisheries. Two studies (Chosid et al., 2012; Wakefield et al., 2016) discussed the effects of grid orientation on the escape of elasmobranchs in fish trawls and provide some information on this important factor. Chosid et al. (2012) attempted to assess the effectiveness of top- and bottom-shooter TEDs on the exclusion of spiny dogfish (*Squalus acanthias*) from fish trawls in Massachusetts, USA. Their results were inconclusive due to the low number of trawls undertaken. However, retention rates were lowest in nets containing bottom-shooter TEDs.

Wakefield et al. (2016) tested the effects of a TED on various Endangered, Threatened and Protected species (ETP) species, including elasmobranchs, in a fish-trawl fishery in Western Australia. These authors assessed behaviour at a TED using underwater cameras. In accordance with the current study, Wakefield et al. (2016) reported that a top-shooter TED allowed a significantly greater number of carcharhinids to escape trawls compared to a bottom-shooter TED. These authors also reported that significantly fewer Rhinopristiformes were caught in trawls with top-shooter TEDs, while grid orientation had no effect on Myliobatiformes, Rajidae, Scyliorhinidae or Orectolobiformes.

Similarly, grid orientation had no effect on the escape of Orectolobiformes in the current study. Fewer individuals of the dominant species, *C. punctatum* and *S. fasciatum*, were caught in treatment nets. Given the size of *S. fasciatum*, the only effect grid orientation is likely to have is to increase the speed at which the animals escape the trawl. Wakefield et al. (2016) reported that the escape times were lower when bottom-shooter TEDs were used, which was likely to reduce blockages at the grid and any resultant catch loss (McGilvray et al., 1999).

Since the 2001 fishing season, advancements in TED design have occurred to minimise catch loss. The effect of these advancements on the escape of elasmobranchs remains unquantified. For example, double escape-hole covers were developed in the early 2000s (Mitchell, 2006) to allow the escape of leatherback turtles (*Dermochelys coriacea*). The covers are designed to close quickly, due to the extra material used, which prevents the loss of target catch. Further research is required to quantify the effect of this and other modifications on the escape of elasmobranchs.

In the original study, Brewer et al. (2006) found that nets with a BRD only reduced the capture of *C. tilstoni* by 23.8 % compared to control nets. In contrast, the current study indicates that the BRDs used throughout the sampling period were ineffective for *C. tilstoni*, and all other elasmobranchs, when used in combination with a TED. Since 2001, the bigeye BRD has been removed from the list of approved devices with several others added after at-sea testing revealed their efficacy in reducing bycatch. For example, Raudzens (2007) reported that a modified fisheye BRD reduced bycatch whilst simultaneously maintaining penaeid catches, compared to a control net. Importantly, the device reduced the number of elasmobranchs caught in nets containing the device.

In conclusion, this research has shown that TEDs facilitate the escape of large elasmobranchs including several species of conservation interest. Bar space and orientation are important TED design factors affecting the escape of elasmobranchs. Top-shooter TEDs enable more Carcharhiniformes to escape penaeid trawls while bottom-shooter TEDs increase the escape of Myliobatiformes. However, the bar space that facilitates maximum escape of elasmobranchs, while maintaining the catches of target species, is more difficult to quantify given the relatively low catch rates of elasmobranchs in penaeid trawls. Experiments using TEDs with reduced bar spacing, such as those conducted by Noell et al. (2018), should be undertaken to quantify the effect on penaeid loss. This is especially the case for the NPF where the maximum regulated bar space remains at 12 cm. Any loss in target catch is likely to be offset by improved quality resulting from less damage in the codend. Further, the mitigation of the ecological risk posed to elasmobranchs by penaeid trawling, via less bycatch, is a beneficial result of reduced bar space.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Matthew J. Campbell: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Mark L. Tonks:** Conceptualization, Writing - review & editing. **Margaret Miller:** Data curation. **David T. Brewer:** Validation, Investigation, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition. **Anthony J. Courtney:** Writing - original draft, Writing - review & editing. **Colin A. Simpfendorfer:** Writing - original draft, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2019.105456.

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