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A review of reported effects of pelagic longline fishing gear configurations on target, bycatch and vulnerable species

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Abstract

1. A meta-analysis of 40 publications totalling 59 experiments was undertaken to review and assess the effects of changing the hook (circle vs. J-hooks or tuna hooks), bait (fish vs. squid) and leader (wire vs. nylon) type on retention and at-haulback mortality rates of teleosts (tunas and billfishes), elasmobranchs and sea turtles caught on shallow-set and deep-set pelagic longline fisheries.

2. Circle hooks are a promising approach to mitigate the impact of pelagic longline fisheries on sea turtles, as they reduced sea turtle retention rates. The adoption of circle hooks would, however, also lead to a decrease in swordfish retention, the main target species of shallow-set pelagic longlines.

3. Using fish as bait resulted in lower retention rates of sea turtles, highlighting that option as an additional measure to further mitigate sea turtle bycatch. The bait type had non-significant effects on sharks, except for blue shark and shortfin mako, for which at-haulback mortality rates were significantly higher with fish bait.

4. The use of nylon leaders instead of wire leaders could serve as a conservation measure for sharks, as they reduced the retention of blue shark without adversely impacting the catches of swordfish. The results on the effect of the leader material types should, however, be interpreted with caution owing to the limited information available reporting on leader material effects.

5. When considering future research directions, priority should be given to experimental field work on the effects of leader material and on deep-set longlines. Evaluating the post-release survival of species should also be a priority.

KEYWORDS
bycatch mitigation, conservation, fisheries management, fishing mortality, meta-analysis, pelagic longline

1 | INTRODUCTION

Commercial fishing has a major influence on marine systems worldwide, affecting both marine populations and ecosystems, and requires urgent and comprehensive management (Ortuño Crespo & Dunn, 2017). In particular, bycatch – the unintended capture of non-target organisms during fishing operations – is a major problem in pelagic longline fisheries (Hall, Alverson & Metuzals, 2000). While some species caught as bycatch are also of commercial value, and therefore retained, others with little or no economic value and/or protected under international legislation are discarded, often dead or in poor condition (Carruthers, Schneider & Neilson, 2009; Gilman, 2011).

Despite the existence of bycatch in most fisheries, the pelagic longline fishery targeting swordfish (*Xiphias gladius*) and tunas (*Thunnus* spp. and similar species) has received considerable attention

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as it has been identified as one of the main threats for several species of concern, including pelagic sharks, sea turtles, sea birds and marine mammals (e.g. Carranza, Domingo & Estrades, 2006; Garrison, 2007; Jiménez et al., 2010; Coelho et al., 2012; Gallagher et al., 2014). Pelagic longline fishing gear consists of a mainline suspended by floats with a series of baited hooks hanging vertically on branch lines (ICCAT, 2006-2016). While attempting to feed on the bait, animals are hooked or become entangled in the lines (Yeung, 2001; Watson & Kerstetter, 2006; Carlson et al., 2016). Some animals manage to escape the fishing gear; however, their fate after release is uncertain since there is a probability of delayed mortality owing to the high levels of stress associated with the capture and physical injuries inflicted while fighting to escape (Skomal, 2007; Ward et al., 2008; Afonso et al., 2011; Swimmer et al., 2014; Campana et al., 2016; Whitney et al., 2021). In general, the available information on post-release survival of non-target species caught in pelagic longlines is still limited and restricted to some of the most common and emblematic species captured (Chaloupka, Parker & Balazs, 2004; Kerstetter & Graves, 2008; Swimmer et al., 2014; Campana et al., 2016; Musyl & Gilman, 2018; Hutchinson & Bigelow, 2019; Orbesen et al., 2019; Schaefer et al., 2021). Electronic tagging has been widely used to investigate the post-release behaviour of marine animals; however, the goal of most studies using this type of tag is to understand the movements and habitat use of species rather than to assess their survival rates after release (Moyes et al., 2006; Hussey et al., 2015; Ellis, McCully Phillips & Poisson, 2017).

For conservation purposes, the ideal scenario would be to avoid interactions between pelagic longlines and non-target species, yet with the overlap of geographic ranges and habitats of target and non-target species it would be unrealistic to expect no interactions of non-target species with the fishing gear (Kerstetter & Graves, 2006; Zollett & Swimmer, 2019). In spite of that, it is crucial to implement measures that could minimize encounters of these animals with pelagic longlines, as well as measures that together with good handling practices could improve their at-haulback and post-release survival rates.

Bycatch reduction strategies include the implementation of fishing regulation and management measures such as the limitation of fishing effort and the protection of species through time–area closures, as well as the modification of fishing practices (Hall, 1996; Gilman, 2011; Swimmer, Zollett & Gutierrez, 2020). The latter strategy involves a variety of methods which include the reduction of pelagic longline soak time and changes in fishing gear (e.g. bait restrictions, the use of circle hooks instead of J-hooks and replacement of wire leaders for monofilament leaders; Gilman, 2011; Swimmer, Zollett & Gutierrez, 2020). Gear modification measures are generally regarded as relatively easy to implement and have low economic impact (Afonso et al., 2011; Favaro & Cote, 2015). Specifically, the use of circle hooks instead of J-hooks has been widely tested and is seen as one of the best measures to reduce the bycatch and mortality rates of some vulnerable fauna while maintaining or even increasing the catch rates of some target species (e.g. Diaz, 2008; Promjinda et al., 2008; Piovano, Swimmer &

Giacoma, 2009; Pacheco et al., 2011; Graves, Horodysky & Kerstetter, 2012). However, conflicting results between studies and species groups have created a lack of agreement between scientists and fisheries managers, preventing a wider implementation of this measure (Graves, Horodysky & Kerstetter, 2012). For instance, while there is a general consensus on the efficacy of circle hooks in reducing bycatch of sea turtles (e.g. Watson et al., 2005; Gilman et al., 2006; Read, 2007; Piovano, Swimmer & Giacoma, 2009; Sales et al., 2010; Santos et al., 2013), this type of hook has also been linked with higher catch rates of pelagic sharks (e.g. Kim et al., 2007; Ward et al., 2009; Afonso et al., 2011; Domingo et al., 2012; Saidi et al., 2020). Despite this, circle hooks have been associated with lower at-haulback mortality rates and higher chances of long-term survival of sharks (Godin, Carlson & Burgener, 2012; Favaro & Cote, 2015; Gilman et al., 2016; Reinhardt et al., 2018). This is because animals caught on circle hooks are usually hooked externally (i.e. in the mouth or jaw), whereas J-hooks tend to hook the fish in the throat or gut thereby increasing the risk of fatal injuries (Carruthers, Schneider & Neilson, 2009; Serafy, Kerstetter & Rice, 2009; Pacheco et al., 2011).

Besides hook type, bait species and leader material have also been reported to affect the catchability, retention and survival of bycatch species. Changing the bait type from squid to fish seems to be an effective measure to lower the bycatch of sea turtles and reduce their mortality rates (Watson et al., 2005; Yokota, Kiyota & Okamura, 2009; Foster et al., 2012; Coelho et al., 2015; Gilman & Huang, 2017; Swimmer et al., 2017). These outcomes might be because sea turtles tend to swallow the whole squid bait, which results in deep hooking and subsequent reduced likelihood of survival, in comparison with fish bait that is usually bitten off and ingested in pieces (Kiyota et al., 2004). On the other hand, using fish bait instead of the traditional squid resulted in inconclusive findings for sharks. In Foster et al. (2012), fish bait was suggested to cause higher catches of some vulnerable shark species, including the shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*), while catch rates were lower for blue shark (*Prionace glauca*). Contrarily, Coelho, Santos & Amorim (2012) reported higher catches of blue shark with fish bait as compared with squid.

The results have also been inconsistent as regards to the effect of leader material. Studies by Ward et al. (2008), Vega & Licandeo (2009), Afonso et al. (2012) and Santos, Lino & Coelho (2017) reported lower catch rates of pelagic sharks when using nylon instead of wire leaders, most likely because sharks are able to sever the nylon and escape. However, it was noted that bycatch on nylon leaders may be underestimated, as well as the mortality rates of sharks since the fate of the animals after escaping the gear is unknown. These studies also indicated that catch rates of some target species were higher with nylon leaders, probably owing to their low visibility in the water. The improved catch rates of valuable species together with the lower production costs associated with nylon leaders compared with wire leaders can contribute to increased financial returns. Smukall et al. (2021) presented contrary results to those described above, with nylon leaders having a higher

bycatch rate of sharks than wire leaders when thinner and lighter leaders were used. Similarly, Branstetter & Musick (1993) found that nylon leaders increased the catch rates of sharks in the Chesapeake Bight region of the US mid-Atlantic coast.

As reported above, discerning the true effect of gear modifications can be hampered by differing findings. To address this challenge, statistical methods such as meta-analysis have been used to summarize the existing research outcomes, helping scientists to reach conclusions on the effectiveness of a specific intervention (e.g. Koricheva, Gurevitch & Mengersen, 2013; Gurevitch et al., 2018). As regards meta-analyses on terminal gear modifications in pelagic longline fisheries, most studies have focused their attention on a single species group, except for those by Reinhardt et al. (2018) and Gilman et al. (2020), who examined the effects of hook and bait type, respectively, on both target and bycatch species. Specifically, Serafy, Kerstetter & Rice (2009) performed a quantitative review to evaluate the effect of hook shape on the catch, mortality, deep hooking and bleeding rates of billfishes, concluding that circle hooks would provide conservation benefits for billfishes; Godin, Carlson & Burgener (2012) conducted a meta-analysis to assess the impact of circle hooks on catch and at-vessel mortality rates of sharks. The results suggested that circle hooks do not significantly alter shark catch rates, but do contribute to a reduction in at-vessel mortality compared with J-hooks; Favaro & Cote (2015) examined the overall effect of bycatch reduction technologies, including changes in hook type and leader material, on the catch rates of elasmobranchs. It was noted that circle hooks did not significantly decrease the likelihood of capturing sharks and rays; however, they appeared to enhance the survival of discarded animals. The study also emphasized the necessity for further research to evaluate the implications of different leader materials; and finally, Gilman et al. (2016) analysed the effects of hook shape, leader material and bait type on elasmobranch catch and survival rates. The results indicated that circle hooks significantly increased catch rates of certain elasmobranch species while simultaneously reducing haulback mortality rates when compared with tuna and J-hooks of the same narrowest width. Additionally, using small fish species as bait, as opposed to squid species, led to increased catch rates and a higher incidence of deep hooking for some shark species, while wire leaders were associated with higher catch rates and potentially lower at-haulback survival rates for the majority of shark species.

The present review expands on previous analyses by presenting a species-specific meta-analysis on the effect of hook shape (circle vs. J-hooks and circle vs. tuna hooks), bait type (fish vs. squid) and leader material (wire vs. nylon) on the retention and at-haulback mortality rates of teleosts (tunas and billfishes), elasmobranchs and sea turtles captured in shallow-set (swordfish/sharks targeting sets) and deep-set (tropical tunas targeting sets) pelagic longlines. Additionally, methodological limitations and data gaps are discussed, highlighting research needs for the future. Ultimately, the information presented here can be applied to support decision-making processes aimed at enhancing fishery and ecosystem sustainability.

2 | METHODS

2.1 | Data collection

Information from studies that examined hook shape (circle, tuna or J-hook), bait type (squid or fish) and leader material (nylon or wire) effects on retention and at-haulback mortality in pelagic longline fisheries, for both shallow and deep sets, was compiled. The published literature, technical reports and unpublished data relevant to this search were identified based on electronic database searches, using relevant keywords ('circle hook', 'J-hook', 'tuna hook', 'bait type', 'leader material', 'pelagic longline', 'catch rates', 'retention rates', 'at-haulback mortality', 'fishing mortality'). Initial references were collected from a meta-analysis by Reinhardt et al. (2018). Further references in the available literature were also analysed if there was a match with the search criteria. Inclusion in the analysis required that studies used pelagic longlines, reported species-specific data for both hook/bait/leader types using the same experimental design and presented data on catch/at-haulback mortality numbers or catch/at-haulback mortality rates. References used included publications ranging from January 2005 to January 2022. Following Reinhardt et al. (2018), the term 'reference' is used to refer to a document; 'experiment' is used to refer to a unique dataset considered in this analysis. An experiment was considered unique if it differed with respect to attributes such as the year of study or season, location, gear, vessel size or fleet. Each unique experiment was assigned an identification number, and a unique reference could have more than one experiment (Table S2).

Data collected from each reference included date and location, set type, species name, hook type, size, offset and manufacturer, bait species, leader material, number of hooks, total catch and number of dead animals at haulback. The set type was classified as 'deep set' or 'shallow set' depending on the longline depth during the fishing operation. If this information was not available, the target species and number of hooks between floats were used to differentiate between set type. Typically, swordfish and shark targeting sets that tend to operate down to a maximum of around 100 m depth and are usually deployed during the nighttime were classified as shallow sets, while tropical-tuna targeting sets that tend to operate mainly between 100 and 300 m depth and are usually deployed during the daytime were classified as deep sets. The hook type was classified as 'circle', 'J' or 'tuna' hook (please see Figure S1 for further details). The bait type was classified as 'fish' or 'squid' depending on the bait species used. The leader material was classified as 'nylon' or 'wire'. Some values that were required, but not directly reported, were derived when possible. For example, the number of animals caught was often derived from retention rates and effort reported in the reference.

Data from the National Marine Fisheries Service Southeast Fisheries Science Center Pelagic Observer Program (Epperly et al., 2012; Foster et al. 2012) were obtained from Reinhardt et al. (2018). Data from Coelho, Santos & Amorim (2012), Amorim et al. (2015), Fernandez-Carvalho et al. (2015), Santos & Coelho (2016) and Santos, Lino & Coelho (2017) were used directly from the raw data provided by the authors.

2.2 | Meta-analysis

Differences in retention and at-haulback mortality rates for tuna and billfish species, elasmobranchs and sea turtles retained on different hook, bait and leader type on shallow-set and deep-set pelagic longlines were analysed through a meta-analysis (the complete list of species is described in detail in Table S1). This analysis follows the method used by Reinhardt et al. (2018) but expands the analysis to include bait type and leader type and to separate shallow-set from deep-set longlines. The difference between the calculated summary effect size (relative risk, RR) and a value of 1.0 represents the mean percentage change associated with the experimental treatment, such that an RR < 1.0 indicates lower values for treatment compared with the control (e.g. circle vs. J-hooks). The analysis was only conducted when at least three experiments were available for a given factor combination.

The RR is equal to

$$RR = \left(a_i/n_i^1\right)/\left(c_i/n_i^2\right)$$

where for the ith experiment, a_i is the number of animals retained on an experimental hook (circle hook), n_i^1 is the number of experimental hooks fished, c_i is the number of animals retained on control hooks (J-hooks) and n_i^2 is the number of control hooks fished for the analysis of retention rate.

For the comparison between bait type, for the ith experiment, a_i is the number of animals retained on experimental bait (fish), n_i^1 is the number of experimental hooks fished, c_i is the number of animals retained on control hooks (squid) and n_i^2 is the number of control hooks fished for the analysis of retention rate.

For the comparison between leader type, for the ith experiment, a_i is the number of animals retained on experimental leader (steel wire), n_i^1 is the number of experimental hooks fished, c_i is the number of animals retained on control hooks (nylon) and n_i^2 is the number of control hooks fished for the analysis of retention rate.

The same methods apply to at-haulback mortality, where the a_i and c_i are the numbers of animals dead at haulback for the experiment and control, respectively, and n_i^1 and n_i^2 are the numbers of animals retained for the experiment and control, respectively.

Retention and at-haulback mortality rates were estimated using the 'meta' (Balduzzi, Rücker & Schwarzer, 2019) and 'dmetar' (Harrer et al., 2019) packages in R 3.5.1 (R Core Team, 2018) for each species. The RR value is log-transformed to normalize the distribution of effect sizes around zero and to meet the assumption of normality for the analysis. A summary effect size was computed for all taxa that had at least three experiments. A two-sided Wald-type Z-test was used to test for differences between effects mean and zero. Effect sizes were estimated using a random effects model. The random effects model computes a global mean effect size based on a weighted mean of the studies' effect sizes. Weights were computed as the inverse of the sample variance and the between-study variance (τ^2). Sample variance, v_i, for ln(RR) of the ith experiment was calculated as

$$v_i = (1/a_i) - \left(1/n_i^1\right) + (1/c_i) - \left(1/n_i^2\right).$$

For the validation procedure, a multiple step approach was used. The first step was to calculate and test the heterogeneity (I^2) value, which represents the extent to which effect sizes vary within the meta-analysis. Values of I^2 vary from 0 to 100%, with higher values indicating greater heterogeneity between experiments. High values of I^2 can be problematic from a statistical point of view as they might mean that there are two or more subgroups of studies present in the data, which would have a different true effect; in such cases, it might be problematic to calculate and report pooled effects (Borenstein et al., 2011).

The second step was to search and detect possible outliers. The method used was to define any study as an outlier if such study confidence intervals (CIs) do not overlap with the CIs of the pooled effect calculated from the meta-analysis. Finally, the third and final step was to use influence analysis. For this, several values were estimated and are presented, with each representing different influence measures. This type of influence analysis has been described by Viechtbauer & Cheung (2010), and the outcomes should be analysed in a comparative way. As a general rule, influential cases are studies that consistently present very extreme values in all or several of those measurements, that represent the following:

- Dffits – represents in standard deviations how much the predicted pooled effect changes after excluding each individual study;
- Cook's distance – calculated as the distance between the value once the study is included compared with when it is excluded;
- covariance ratio (cov.r) – this is the determinant of the variance–covariance matrix of the parameter estimates when the study is removed, divided by the determinant of the variance–covariance matrix of the parameter estimates when the full dataset is considered; values of cov.r < 1 indicate that removing the study will lead to a more precise effect size estimation (i.e. less heterogeneity).

The Baujat Plot analysis (Baujat et al., 2002), which is a diagnostic to detect studies that are overly contributing to the heterogeneity of a meta-analysis vs. their influence in the final estimations, was also used for the influence analysis. The plots show specifically the contribution of each study to the overall heterogeneity measured by Cochran's Q on the horizontal axis, and its influence on the pooled effect size on the vertical axis (Baujat et al., 2002). Studies represented on the right side are the main contributors to the heterogeneity observed, and it is even more significant if at the same time such studies are small contributors to the overall pooled effect, as in those cases they most likely have very low sample sizes. Finally, a leave-one-out-method was used, in which the meta-analysis is re-calculated $k - 1$ times, each time leaving out one study (with $k =$ number of studies available) (Viechtbauer & Cheung, 2010). This is then analysed in terms of the overall gains in homogeneity, as well as changes in the final model estimations.

The RR, CIs, I^2 and statistical significance were reported for each final analysis. Additional forest plots provided for a better visualization of results were created using the 'ggplot2' package (Wickham, 2016).

3 | RESULTS

Retention and at-haulback mortality rate meta-analyses between hook, bait and leader types were performed for teleosts (tunas and billfishes), elasmobranchs and sea turtle species captured in shallow- and deep-set longlines. For these analyses, 40 relevant references yielding 59 experiments were identified (Table S2). Individual forest plots of retention and at-haulback mortality rates of species included in the analysis are provided in the Supporting information. Note that it was not possible to conduct a meta-analysis on bait and leader type effects for deep-set pelagic longlines owing to the lack of references reporting retention data. The reported information on at-haulback mortality in deep-set pelagic longline fisheries was also insufficient/ unavailable.

3.1 | Retention rates – shallow set

3.1.1 | Hook shape

In general, retention rates with circle hooks (vs. J-hooks) were higher for shark and tuna species and lower for sea turtles and billfishes (Table 1 and Figure 1). Species with higher retention rates included the blue shark, oceanic whitetip, porbeagle, crocodile shark, shortfin mako, scalloped hammerhead, tiger shark, albacore, bigeye tuna, bluefin tuna and yellowfin tuna, although results were only significant for the crocodile shark, albacore and bluefin tuna, varying between increases of 26% for bluefin tuna (RR = 1.26; p = 0.0335) and 57% for the crocodile shark (RR = 1.57; p = 0.0123). On the other hand, the bigeye thresher, silky shark, longfin mako, smooth hammerhead, pelagic stingray, sea turtle species and billfishes had lower retention rates with circle hooks. Species with significant decreases in retention included the pelagic stingray, loggerhead sea turtle, leatherback sea turtle, olive ridley sea turtle, swordfish and blue marlin. Significant reductions in retention varied between 19% in swordfish (RR = 0.81; p < 0.0001) and 72% in the pelagic stingray (RR = 0.28; p < 0.0001).

Table 2 and Figure 2 summarize the results of the meta-analysis when changing from tuna hooks to circle hooks, which was only possible to perform for nine of the 25 species studied. The sailfish, tunas and sharks – including silky shark, the only species with a significant change in retention (RR = 1.41; p = 0.0377) – had higher retention rates with circle hooks, while sea turtles and swordfish had lower retention rates when caught on circle hooks.

3.1.2 | Bait species

Retention rates with fish bait (vs. squid bait) were lower for all sea turtle, tuna and billfish species considered, with significant differences found for the loggerhead sea turtle, olive ridley sea turtle, albacore, yellowfin tuna and sailfish (Table 3 and Figure 3). These reductions varied between 60% in yellowfin tuna (RR = 0.40; p = 0.0008) and 76% in albacore (RR = 0.24; p = 0.0127). In

contrast, and with the exception of the crocodile shark, elasmobranchs showed an increasing, although non-significant, trend in retention with fish bait.

3.1.3 | Leader material

Since the effect of leader material has received little attention, meta-analyses were conducted for eight species only (Table 4 and Figure 4). While retention rates tended to be lower with wire leaders (vs. nylon leaders), reductions were only significant for the yellowfin tuna (RR = 0.55; p = 0.0247) and blue marlin (RR = 0.62; p = 0.0362). Blue shark was the only species with a significant increase in retention when using wire leaders (RR = 1.45; p = 0.0238).

3.2 | Retention rates – deep set

3.2.1 | Hook shape

The only species for which it was possible to conduct a meta-analysis on the effects of circle vs. J-hooks on retention rates for deep-set longlines was the yellowfin tuna. The results showed a decrease in retention of 29% with circle hooks; however, this decrease was not statistically significant (RR = 0.71; CI: 0.10–4.96; I^2 = 44%; p = 0.5260).

Also for deep-set pelagic longlines, elasmobranchs, swordfish, albacore and the yellowfin tuna had lower retention rates with circle hooks when compared with tuna hooks, but these findings were not significant (Table 5 and Figure 5). On the other hand, retention rates of bigeye tuna were higher with circle hooks, albeit non-significant (RR = 1.08; p = 0.3265) (Table 5 and Figure 5).

3.3 | At-haulback mortality – shallow set

3.3.1 | Hook shape

Overall, at-haulback mortality rates with circle hooks (vs. J-hooks) were lower for tunas and billfishes and mixed for elasmobranchs and sea turtles (Table 1 and Figure 6). The risk of at-haulback mortality was significantly lower for bigeye tuna, yellowfin tuna, swordfish, blue marlin, white marlin, blue shark, shortfin mako and scalloped hammerhead, and varied between 4% lower for swordfish (RR = 0.94; p = 0.0416) and 22% lower for blue shark (RR = 0.78; p = 0.0150). The bigeye thresher was the only species that showed a significantly higher rate of at-haulback mortality with circle hooks with a 16% increase relative to the J-hook at-haulback mortality (RR = 1.16; p = 0.0332).

Regarding the comparison between the effects of circle vs. tuna hooks on at-haulback mortality rates, it was not possible to perform the analysis for any of the species studied owing to the lack of sufficient references.

TABLE 1 Results of the meta-analyses on retention and at-haulback mortality rates when changing the hook type (circle hooks vs. J-hooks) in shallow set pelagic longlines.

	Retention rate				At-haulback mortality rate			
Species	RR	CI	I^2	p-Value	RR	CI	I^2	p-Value
Elasmobranchs								
Blue shark	1.10	0.98–1.24	99%	0.1082	0.78	0.64–0.94	93%	**0.0150**
Bigeye thresher	0.88	0.67–1.17	78%	0.3133	1.16	1.02–1.33	28%	**0.0332**
Silky shark	0.95	0.63–1.42	91%	0.7607	0.76	0.48–1.21	80%	0.1976
Longfin mako	0.72	0.32–1.63	72%	0.3445	1.11	0.68–1.80	0%	0.5466
Oceanic whitetip	1.08	0.86–1.36	0%	0.4560	0.73	0.47–1.14	21%	0.1350
Porbeagle	1.13	0.80–1.60	74%	0.3731	—	—	—	—
Crocodile shark	1.57	1.14–2.15	77%	**0.0123**	1.52	0.50–4.62	63%	0.4050
Shortfin mako	1.18	0.99–1.40	75%	0.0597	0.89	0.80–0.99	34%	**0.0374**
Scalloped hammerhead	1.12	0.52–2.41	24%	0.7271	0.79	0.68–0.92	0%	**0.0212**
Smooth hammerhead	0.99	0.63–1.54	56%	0.9304	1.02	0.79–1.32	46%	0.8235
Tiger shark	1.38	0.53–3.58	39%	0.4480	1.47	0.62–3.51	0%	0.1967
Pelagic stingray	0.28	0.18–0.46	73%	**<0.0001**	3.04	0.12–73.81	0%	0.3488
Sea turtles								
Loggerhead sea turtle	0.51	0.43–0.60	42%	**<0.0001**	0.93	0.56–1.53	0%	0.7431
Leatherback sea turtle	0.39	0.32–0.49	30%	**<0.0001**	2.04	0.99–4.24	0%	0.0536
Olive ridley sea turtle	0.57	0.39–0.84	46%	**0.0094**	1.22	0.79–1.88	0%	0.2387
Green sea turtle	0.71	0.28–1.82	0%	0.3275	—	—	—	—
Hawksbill sea turtle	0.86	0.03–24.95	57%	0.8681	—	—	—	—
Teleosts								
Swordfish	0.81	0.74–0.88	99%	**<0.0001**	0.96	0.92–1.00	94%	**0.0416**
Albacore tuna	1.47	1.05–2.06	96%	**0.0285**	0.98	0.91–1.05	58%	0.4655
Bigeye tuna	1.25	0.99–1.58	98%	0.0593	0.80	0.72–0.88	48%	**0.0004**
Bluefin tuna	1.26	1.03–1.55	12%	**0.0335**	—	—	—	—
Yellowfin tuna	1.05	0.84–1.33	92%	0.6304	0.81	0.69–0.95	66%	**0.0167**
Blue marlin	0.72	0.59–0.88	46%	**0.0048**	0.81	0.74–0.90	14%	**0.0012**
Sailfish	0.62	0.27–1.44	55%	0.1887	—	—	—	—
White marlin	0.75	0.43–1.28	95%	0.2550	0.84	0.79–0.89	0%	**0.0007**

Note: I^2 represents the heterogeneity and describes the percentage of total variation caused by between-study heterogeneity; *p*-values shown in bold indicate significance (at a significance level of 0.05).
Abbreviations: CI, 95% confidence interval; RR, relative risk.

3.3.2 | Bait species

Generally, fish bait (vs. squid bait) was associated with higher at-haulback mortality rates of sharks, with significant increases found for blue shark (RR = 1.71; $p = 0.0039$) and shortfin mako (RR = 1.13; $p = 0.0270$) (Table 3 and Figure 7). The results were mixed and non-significant for the remaining 15 species evaluated, including sea turtles, tunas and billfishes (Table 3 and Figure 7).

3.3.3 | Leader material

The blue shark, bigeye tuna, swordfish and blue marlin were the only species with a sufficient number of references available to perform a meta-analysis (Table 4 and Figure 8). The results showed a slight decrease in at-haulback mortality rates for blue shark, bigeye tuna and swordfish with wire leaders (vs. nylon leaders); however, this was non-significant. Blue marlin had a higher rate of at-haulback mortality with wire leaders, but this result was also non-significant.

3.4 | Data gaps

An overview of the current data gaps with detailed information on the number of available studies for every factor and species evaluated is provided in Table 6. In summary, information available for shallow set pelagic longlines is far more numerous when compared with deep-set pelagic longlines. This is particularly evident when analysing factors
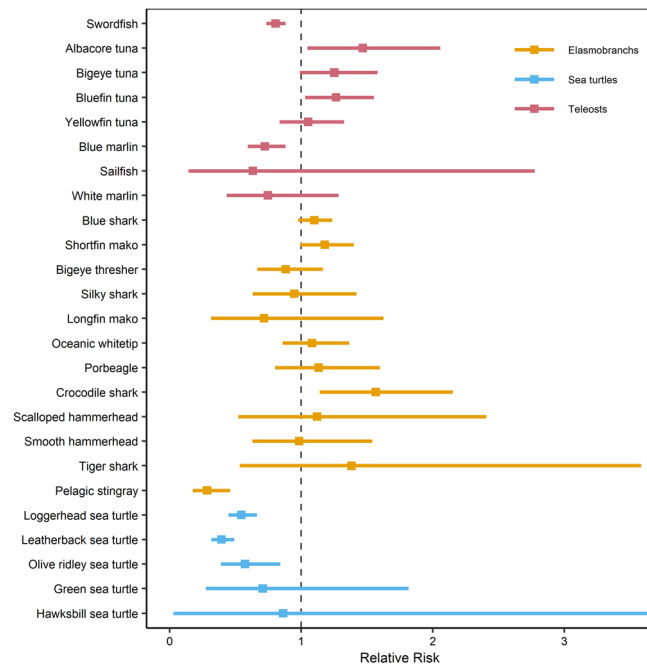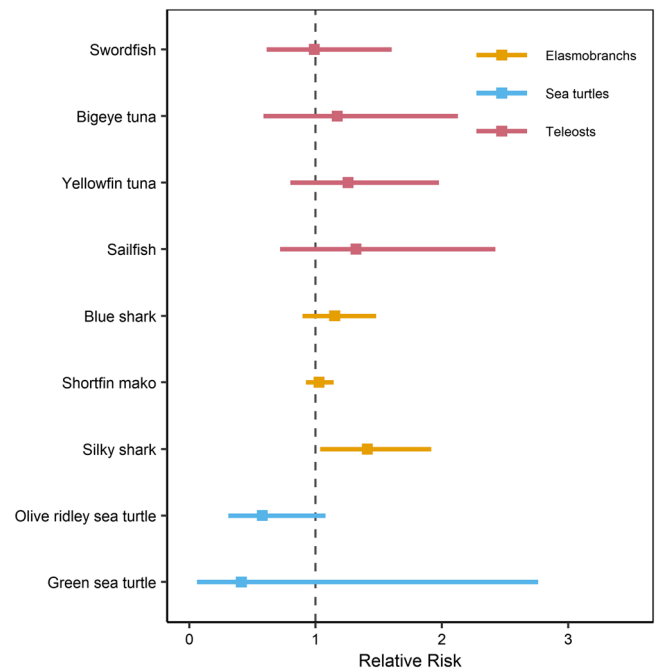
FIGURE 1 Results of the meta-analysis on retention rates when changing the hook type (circle vs. J-hooks) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: J-hooks are considered the control and circle hooks the experimental hook; a relative risk (RR) > 1 indicates retention is higher with circle hooks).

FIGURE 2 Results of the meta-analysis on retention rates when changing the hook type (circle hooks vs. tuna hooks) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: tuna hooks are considered the control and circle hooks the experimental hook; a relative risk (RR) > 1 indicates retention is higher with circle hooks).

TABLE 2 Results of the meta-analyses on retention rates when changing the hook type (circle hooks vs. tuna hooks) in shallow set pelagic longlines.

	Retention rate			
Species	**RR**	**CI**	I^2	**p-Value**
Elasmobranchs				
Blue shark	1.15	0.90–1.48	94%	0.2241
Silky shark	1.41	1.04–1.92	73%	**0.0377**
Shortfin mako	1.03	0.92–1.14	0%	0.5185
Sea turtles				
Olive ridley sea turtle	0.58	0.31–1.08	78%	0.0678
Green sea turtle	0.41	0.06–2.76	68%	0.2347
Teleosts				
Swordfish	0.99	0.61–1.60	89%	0.9597
Bigeye tuna	1.17	0.59–2.33	65%	0.4283
Yellowfin tuna	1.26	0.80–1.98	88%	0.2329
Sailfish	1.32	0.72–2.42	33%	0.1883

Note: I^2 represents the heterogeneity and describes the percentage of total variation caused by between-study heterogeneity; p-values showed in bold indicate significance (at a significance level of 0.05). Abbreviations: CI, 95% confidence interval; RR, relative risk.

such as hook shape (especially circle vs. J-hooks) and bait type, whereas leader material effects were less explored. For deep-set pelagic longlines, while there are a few studies reporting catches on circle and tuna hooks, studies that tested the effects of changing bait type and leader material are absent or practically non-existent. In terms of species representation, information on target (tunas and swordfish) and desirable bycatch species (blue shark and shortfin mako) was the most frequently reported, along with data on the commonly captured pelagic stingray, loggerhead and leatherback sea turtles. In contrast, species with narrower geographic distributions (e.g. white marlin) and higher risk status (most pelagic sharks) were less well represented.

4 | DISCUSSION

The global deterioration of marine ecosystems has been repeatedly connected, in part at least, to industrial fisheries and their impact on marine life (Ortuño Crespo & Dunn, 2017). Recently, the removal of vulnerable species through bycatch in pelagic longlines has been regarded as a priority conservation concern, motivating several investigations to evaluate capture risk and test possible bycatch reduction strategies (e.g. Pacheco et al., 2011; Coelho et al., 2015; Santos, Lino & Coelho, 2017).

Modifications to traditional gear designs, like changing from J-shaped hooks to circle hooks or using fish for bait instead of squid, are some of the most well-explored methods of bycatch mitigation in pelagic longline fisheries (Clarke et al., 2014; Hall et al., 2017; Swimmer, Zollett & Gutierrez, 2020). However, the different

TABLE 3 Results of the meta-analyses on retention and at-haulback mortality rates when changing bait type (fish vs. squid) in shallow set pelagic longlines.

Species	Retention rate				At-haulback mortality rate			
	RR	CI	I^2	p-Value	RR	CI	I^2	p-Value
Elasmobranchs								
Blue shark	1.07	0.70–1.63	100%	0.7093	1.71	1.39–2.11	70%	**0.0039**
Bigeye thresher	1.09	0.78–1.52	46%	0.5000	1.03	0.80–1.34	38%	0.7127
Silky shark	1.06	0.37–3.05	78%	0.8683	1.05	0.52–2.14	84%	0.8278
Longfin mako	1.95	0.10–39.12	97%	0.5290	0.82	0.31–2.19	4%	0.5678
Oceanic whitetip	1.03	0.56–1.90	63%	0.8710	1.15	0.81–1.62	0%	0.2942
Crocodile shark	0.72	0.10–5.47	99%	0.6423	1.48	0.24–9.23	94%	0.5441
Shortfin mako	1.29	0.83–2.01	87%	0.1902	1.13	1.03–1.24	0%	**0.0270**
Smooth hammerhead	2.04	0.30–13.69	91%	0.3203	0.91	0.73–1.14	34%	0.2847
Tiger shark	1.63	0.02–161.43	87%	0.6911	—	—	—	—
Pelagic stingray	1.07	0.54–2.12	87%	0.7829	—	—	—	—
Sea turtles								
Loggerhead sea turtle	0.28	0.21–0.37	32%	**<0.0001**	1.16	0.80–1.67	0%	0.3433
Leatherback sea turtle	0.57	0.32–1.02	85%	0.0576	0.60	0.27–1.34	0%	0.1550
Olive ridley sea turtle	0.32	0.15–0.70	51%	**0.0185**	1.04	0.42–2.56	0%	0.9082
Teleosts								
Swordfish	0.99	0.79–1.24	98%	0.9344	1.00	0.95–1.06	68%	0.7862
Albacore tuna	0.24	0.09–0.63	96%	**0.0127**	1.04	0.97–1.11	0%	0.1630
Bigeye tuna	0.61	0.14–2.65	99%	0.4231	0.99	0.88–1.12	0%	0.8840
Yellowfin tuna	0.40	0.33–0.50	0%	**0.0008**	1.11	0.65–1.88	83%	0.5904
Blue marlin	0.97	0.31–3.02	87%	0.9357	1.00	0.78–1.27	26%	0.9787
Sailfish	0.38	0.30–0.49	0%	**0.0011**	—	—	—	—
White marlin	0.69	0.08–6.18	91%	0.6305	1.11	0.73–1.69	75%	0.3897

Note: I^2 represents heterogeneity and describes the percentage of total variation caused by between-study heterogeneity; p-values showed in bold indicate significance (at a significance level of 0.05).
Abbreviations: CI, 95% confidence interval; RR, relative risk.

outcomes between studies and distinct responses across taxa have resulted in the lack of clear scientific advice (Graves, Horodysky & Kerstetter, 2012). In such cases, meta-analyses are often used to synthesize the results of a set of independent studies, providing estimates with greater accuracy over single experiments (Koricheva, Gurevitch & Mengersen, 2013; Gurevitch et al., 2018). The present meta-analysis attempts to quantify species' relative risk of retention and at-haulback mortality on different pelagic longline gear configurations.

4.1 | Tunas and billfishes

Overall, the meta-analysis for tunas caught in shallow pelagic longlines showed that retention rates were higher with circle hooks (vs. J and tuna hooks), with significant increases found for albacore and bluefin tunas. In contrast, billfishes including the swordfish – the main target species in most shallow-set pelagic longlines – showed lower retention rates with circle hooks, in particular when these were

compared with J-hooks. However, at-vessel mortality rates of both species groups seemed to be reduced when using circle hooks. The review by Serafy, Kerstetter & Rice (2009), which incorporated recreational and pelagic longline fishery studies, revealed that the mean catch rate of istiophorid billfishes across pelagic longline fishery studies was lower with circle hooks. Data also pointed to lower at-vessel mortality, rates of deep hooking and bleeding rates with circle hooks (Serafy, Kerstetter & Rice, 2009). Previous studies reported that the quality of fish flesh is affected by numerous factors and biochemical changes that take place during the capture process (e.g. Arthur et al., 1992; Lowe et al., 1993; Addis et al., 2013; Anders et al., 2020). For instance, for yellowfin tuna, being boarded alive was found to be one of the factors correlated with higher flesh quality (Foster et al., 2015). Therefore, in addition to handling practices, chilling and storage conditions, and environmental factors such as water temperature that can also influence the quality of fish flesh, converting to circle hooks and minimizing at-haulback mortality rates have the potential to enhance the profitability of the fishery, especially for deep-set pelagic longlines targeting tunas.

Despite evidence of opposing effects on the catch rates of target species, the purpose of maximizing/minimizing catches of certain species may be achieved by combining specific gear characteristics. The results showed that using squid bait as well as nylon leaders might result in a better fishing performance and increased financial gains since commercial catch rates were generally higher with these features. Based on a literature review, Gilman et al. (2020) stated as well that tunas and billfishes seem to have higher catch rates on squid relative to fish bait. In addition, nylon is assumed to be less detectable in the water (Ward et al., 2008), which in turn could explain the higher
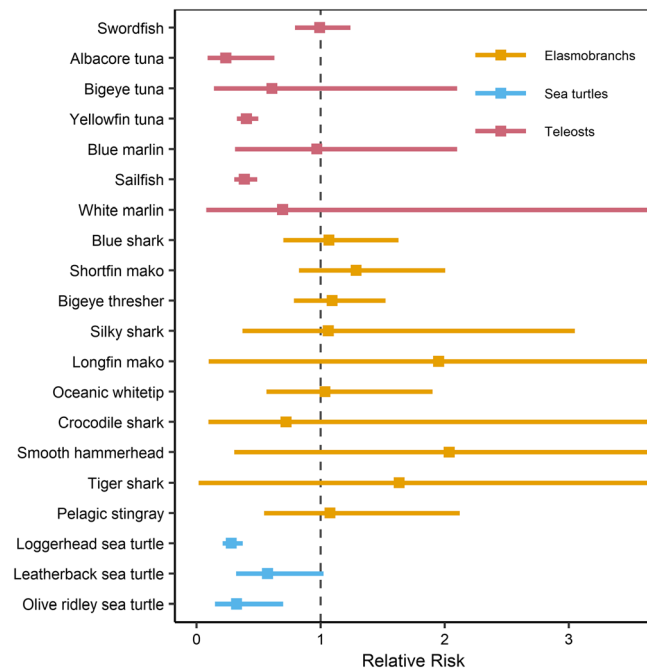
FIGURE 3 Results of the meta-analysis on retention rates when changing the bait type (fish vs. squid) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: squid is considered the control and fish the experimental bait; a relative risk (RR) > 1 indicates retention is higher with fish bait).
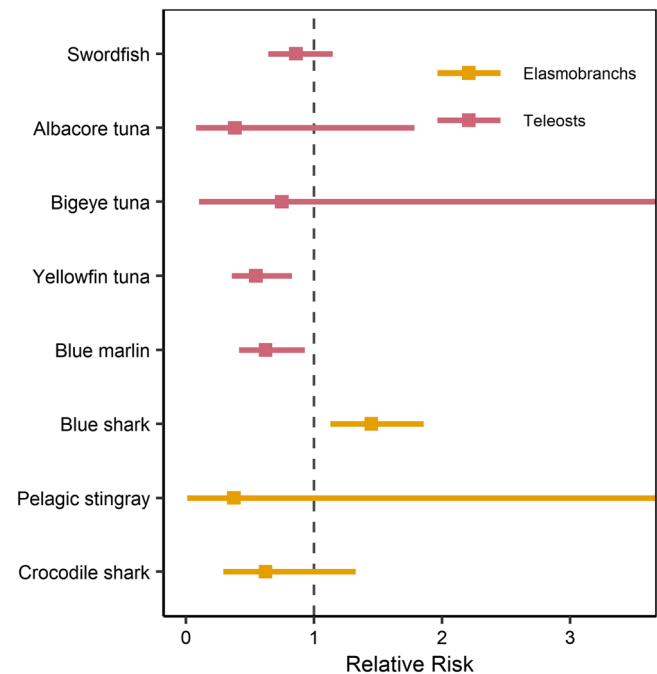
FIGURE 4 Results of the meta-analysis on retention rates when changing the leader type (wire vs. nylon) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: nylon leader is considered the control and wire leader the experimental leader; a relative risk (RR) > 1 indicates retention is higher with wire leaders).

TABLE 4 Results of the meta-analyses on retention and at-haulback mortality rates when changing leader type (wire vs. nylon) in shallow set pelagic longlines.

Species	Retention rate				At-haulback mortality rate			
	RR	CI	I^2	*p*-Value	RR	CI	I^2	*p*-Value
Elasmobranchs								
Blue shark	1.45	1.13–1.86	42%	**0.0238**	0.86	0.58–1.28	43%	0.2513
Crocodile shark	0.62	0.29–1.32	0%	0.1138	—	—	—	—
Pelagic stingray	0.37	0.01–13.87	92%	0.3617	—	—	—	—
Teleosts								
Swordfish	0.86	0.64–1.15	57%	0.1511	0.99	0.70–1.39	89%	0.9080
Albacore tuna	0.38	0.08–1.82	0%	0.1171	—	—	—	—
Bigeye tuna	0.75	0.10–5.46	82%	0.5945	0.98	0.60–1.62	26%	0.8838
Yellowfin tuna	0.55	0.36–0.83	0%	**0.0247**	—	—	—	—
Blue marlin	0.62	0.42–0.93	0%	**0.0362**	1.37	0.16–11.83	49%	0.5911

Note: I^2 represents heterogeneity and describes the percentage of total variation caused by between-study heterogeneity; *p*-values showed in bold indicate significance (at a significance level of 0.05).
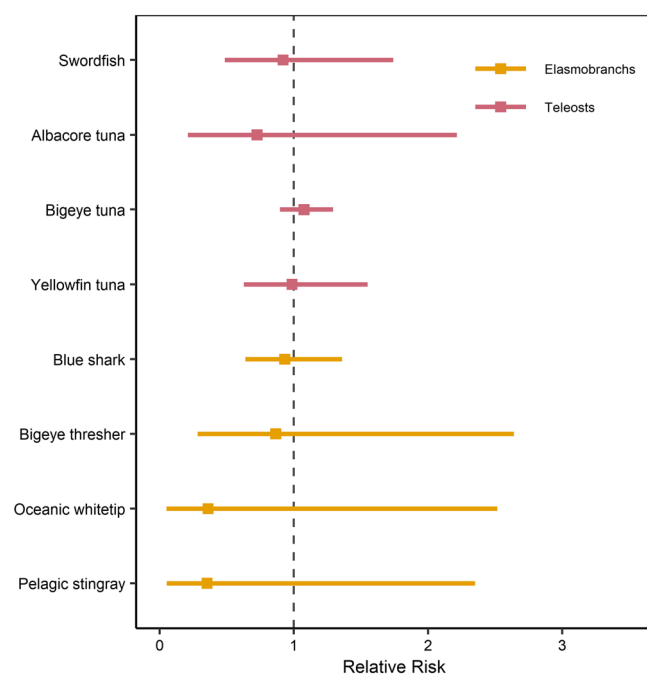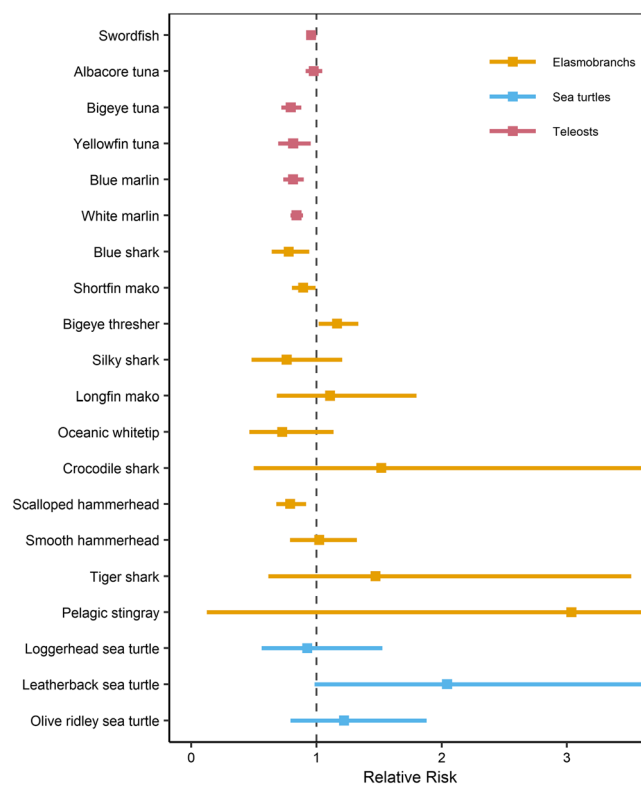Abbreviations: CI, 95% confidence interval; RR, relative risk.

TABLE 5 Results of the meta-analyses on retention rates when changing the hook type (circle hooks vs. tuna hooks) in deep set pelagic longlines.

	Retention rate			
Species	RR	CI	I^2	p-Value
Elasmobranchs				
Blue shark	0.93	0.64–1.36	80%	0.6331
Bigeye thresher	0.87	0.28–2.64	66%	0.6347
Oceanic whitetip	0.36	0.05–2.51	16%	0.1525
Pelagic stingray	0.35	0.05–2.35	83%	0.1788
Teleosts				
Swordfish	0.92	0.49–1.74	94%	0.7338
Albacore tuna	0.73	0.21–2.51	82%	0.5134
Bigeye tuna	1.08	0.90–1.29	80%	0.3265
Yellowfin tuna	0.99	0.63–1.55	75%	0.9371

Note: I^2 represents heterogeneity and describes the percentage of total variation caused by between-study heterogeneity.
Abbreviations: CI, 95% confidence interval; RR, relative risk.

FIGURE 5 Results of the meta-analysis on retention rates when changing the hook type (circle hooks vs. tuna hooks) in deep set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: tuna hooks are considered the control and circle hooks the experimental hook; a relative risk (RR) > 1 indicates retention is higher with circle hooks).

catches reported on nylon leaders. In terms of at-haulback mortality with different bait and leader types, the results were mixed and non-significant for all species considered.

FIGURE 6 Results of the meta-analysis on at-haulback mortality rates when changing the hook type (circle hooks vs. J-hooks) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: J-hooks are considered the control and circle hooks the experimental hook; a relative risk (RR) > 1 indicates at-haulback mortality is higher with circle hooks).

4.2 | Elasmobranchs

There were mixed results when comparing retention rates of elasmobranchs caught on circle hooks relative to J-hooks in shallow pelagic longlines. Species with higher retention rates with circle hooks included the blue shark and shortfin mako, although this increase was only significant for the crocodile shark. In contrast, the pelagic stingray was the only species with a significant reduction in retention when using circle hooks. The reviewed literature included observations of higher catch rates of elasmobranchs with circle hooks (e.g. Kim et al., 2007; Ward et al., 2009; Afonso et al., 2011; Domingo et al., 2012; Saidi et al., 2020), as well as studies that found that circle hooks were effective in reducing elasmobranchs' bycatch (e.g. Gilman et al., 2007; Curran & Bigelow, 2011). A previous meta-analysis by Reinhardt et al. (2018) described similar trends to those presented here, reporting significantly higher catch rates of six shark species with circle hooks, including the blue shark, shortfin mako, porbeagle and crocodile shark. Gilman et al. (2016) also found that sharks had a higher relative risk of capture on circle hooks, including the crocodile shark. In Godin, Carlson & Burgener (2012), the results suggested that there was no significant difference in catchability between hook types, although most species had higher overall estimates when using
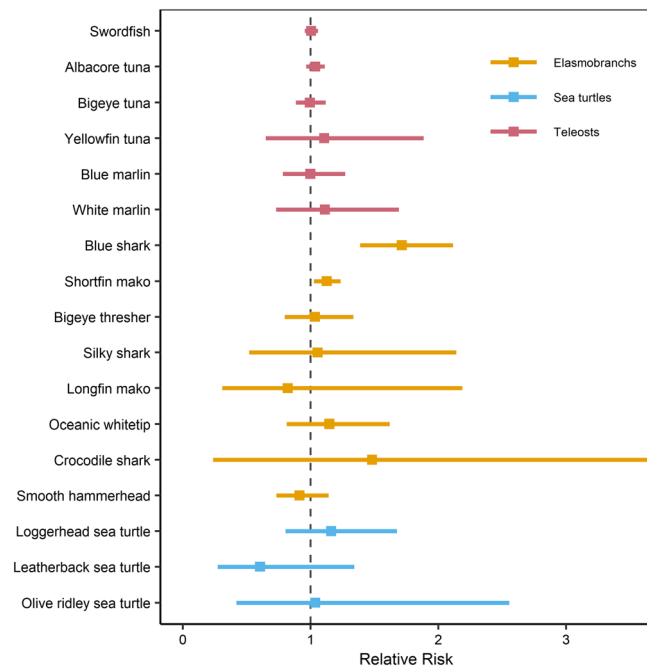
FIGURE 7 Results of the meta-analysis on at-haulback mortality rates when changing the bait type (fish vs. squid) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: squid is considered the control and fish the experimental bait; a relative risk (RR) > 1 indicates at-haulback mortality is higher with fish bait).

FIGURE 8 Results of the meta-analysis on at-haulback mortality rates when changing the leader type (wire vs. nylon) in shallow set pelagic longlines. The box represents the point estimate and error bars represent the 95% confidence intervals. (*Note*: nylon leader is considered the control and wire leader the experimental leader; a relative risk (RR) > 1 indicates at-haulback mortality is higher with wire leaders).

circle hooks. It was also explained that the lower catch rate of pelagic stingray on circle hooks is possibly justified by their morphology and different feeding behaviour (i.e. suction feeding) compared with other shark species. Furthermore, it is important to acknowledge the relationship between hook type and bite-offs. The circular design of circle hooks tends to promote hooking in the jaw/corner of the mouth, thereby reducing the probability of the fishing line being bitten off by the shark during the fight or escape attempts. In turn, J-hooks tend to deeply hook the sharks, potentially facilitating their escape and leading to a potential underestimation of catch rates.

Results were also mixed in terms of at-haulback mortality. The blue shark, shortfin mako and scalloped hammerhead showed significant decreases in at-haulback mortality rates when using circle hooks instead of J-hooks, while the bigeye thresher was the only species evaluated with a significantly higher at-haulback mortality rate with circle hooks. Generally, circle hooks have been associated with lower at-vessel mortality rates and improved chances of survival after release (Godin, Carlson & Burgener, 2012; Favaro & Cote, 2015; Gilman et al., 2016; Reinhardt et al., 2018). Although much remains unclear owing to the inherent difficulties of studying post-release survival of marine animals, it is assumed that circle hooks are less likely to cause fatal injuries since they tend to hook the animals in the jaw/corner of the mouth rather than internally (Montrey, 1999). Consequently, the survival of jaw-hooked sharks is primarily influenced by the length of time they spend on the line before being released. When testing circle
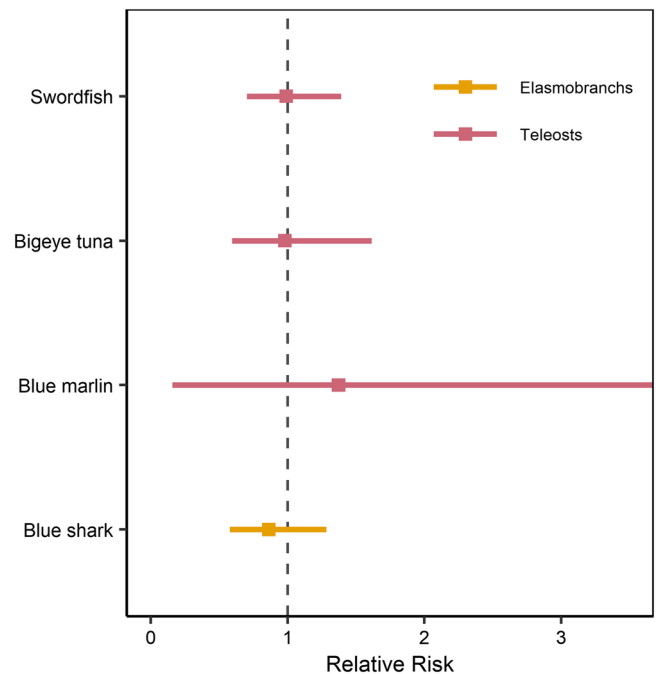
vs. tuna hooks in shallow pelagic longlines, the overall evidence of the current study pointed to a tendency for higher retention rates with circle hooks. On the contrary, and although no significant differences were found, in deep-set pelagic longlines all species tested had lower retention rates when circle hooks were used. However, these results should be interpreted with caution. It is important to note that, except for blue shark, the species assessed in these analyses were not the same and there was only a limited number of studies available reporting catches on deep-set longlines (see Table 6).

Although differences were not statistically significant, using fish as bait instead of squid in shallow pelagic longlines did not seem to be beneficial for elasmobranchs as retention rates were generally higher. At-haulback mortality rates with fish bait were also higher for most species, particularly for blue shark and shortfin mako. These results are consistent with the increasing trend in both catch and deep hooking rates when using fish reported in Gilman et al. (2016). In Gilman et al. (2020) results were inconclusive for combined pelagic shark species, but blue shark showed lower relative risk of capture on fish bait compared with squid bait. Even though most pelagic sharks are typically defined as generalist feeders (Simpfendorfer, Goodreid & McAuley, 2001; Flores-Martínez et al., 2017; Klarian et al., 2018), the various authors suggested that there might be species-specific responses to changes in bait type owing to distinct prey preferences and predatory behaviour, which might explain the observations for blue shark.

SANTOS et al.

TABLE 6 Summary table of data gaps.

Species	Shallow-set longlines								Deep-set longlines							
	Retention				At-haulback mortality				Retention				At-haulback mortality			
	Hook J	Hook T	Bait	Leader	Hook J	Hook T	Bait	Leader	Hook J	Hook T	Bait	Leader	Hook J	Hook T	Bait	Leader
SWO	25	6	7	3	11	6	4	3	2	5	0	0	1	2	0	0
BET	14	3	6	3	11	0	4	3	2	5	0	0	1	2	0	0
BFT	5	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0
YFT	12	5	4	3	10	0	4	2	3	5	0	1	1	2	0	0
ALB	17	1	6	3	10	0	3	2	1	5	0	1	1	2	0	0
BUM	10	2	4	3	8	0	4	3	1	1	0	0	1	1	0	0
SFA	5	3	4	2	5	0	3	2	1	0	0	0	0	0	0	0
WHM	6	0	4	1	6	0	3	1	0	0	0	0	0	0	0	0
BSH	22	8	6	3	11	2	4	3	2	5	0	0	1	2	0	0
SMA	17	5	5	2	10	2	4	2	0	2	0	1	0	0	0	0
OCS	9	2	4	2	8	0	4	2	0	3	0	1	0	0	0	0
POR	5	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0
FAL	8	4	4	2	7	0	4	2	1	1	0	1	0	0	0	0
BTH	7	2	5	2	7	0	4	2	2	3	0	1	1	1	0	0
LMA	6	1	4	1	4	0	4	1	0	1	0	0	0	0	0	0
PSK	8	1	4	3	8	0	4	2	0	2	0	0	0	0	0	0
SPL	7	0	2	0	3	0	1	0	0	2	0	0	0	0	0	0
SPZ	5	0	4	2	5	0	4	1	0	2	0	0	0	0	0	0
PLS	15	2	5	3	4	0	1	1	1	4	0	0	0	1	0	0
TTL	23	2	11	2	12	0	6	0	1	1	0	0	0	1	0	0
DKK	14	1	8	1	7	0	5	0	1	1	0	0	0	1	0	0
LKV	10	4	4	1	4	0	4	1	1	1	0	0	0	1	0	0
LKY	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
TUG	4	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0

Note: The value within each cell represents the number of studies available for that specific component. The colour gradient from green to red quantifies the number of studies available (upper limit ($n = 25$) = dark green; lower limit ($n = 0$) = dark red; middle colour ($n = 8$) = yellow). 'Hook J' refers to studies assessing the effects of changing hook type from J-hooks to circle hooks; 'hook T' refers to studies assessing the effects of changing hook type from tuna hooks to circle hooks; 'bait' refers to studies assessing the effects of changing bait type from squid to fish; 'leader' refers to studies assessing the effects of changing leader type from nylon to steel wire leaders. Species abbreviations are described in Table S1.

The catch data available on both wire and nylon leaders were limited, and therefore the analysis was only performed for three elasmobranch species caught on shallow pelagic longlines. Differences found were only significant for the blue shark, which had higher retention rates with wire leaders. Additionally, leader material did not have a major effect on blue shark at-haulback mortality rate. Despite the highlighted concerns about the limited number of available references, both the literature review by Gilman et al. (2016) and the meta-analysis by Favaro & Cote (2015) indicated that wire leaders may contribute to increased catch and mortality rates for most shark species captured in pelagic longline fisheries. While nylon leaders can be torn by most sharks, wire leaders are less prone to breaking, resulting in a higher number of retained animals (Ward et al., 2008). Nevertheless, higher bite-off rates with nylon leaders do not necessarily mean lower fishing mortality. Assuming the survival of specimens that escape the gear is a speculative interpretation since their fate remains largely unknown.

4.3 | Sea turtles

The results indicated that interactions of sea turtles in shallow-set pelagic longlines seemed to be reduced when circle hooks were used instead of the J-hooks or tuna hooks, although at-haulback mortality rates did not seem to be highly influenced by hook type. These findings were consistent with previous studies that suggested that circle hooks are an effective measure for reducing retention rates of sea turtles (e.g. Watson et al., 2005; Gilman et al., 2006; Read, 2007; Piovano, Swimmer & Giacoma, 2009; Sales et al., 2010; Santos et al., 2013). While tuna and J-hooks have the end point of the hook parallel to the shank, on a circle hook the point is generally perpendicular to the shank, making it less exposed to contact (Cooke & Suski, 2004). It is also believed that circle hooks tend to slide out of the gut/throat without engaging with soft tissues when the tension of the fishing line increases, resulting in fewer deep-hooked animals (Domeier, Dewar & Nasby-Lucas, 2003).

Likewise, the results showed that changing the bait species from squid to fish does not affect at-haulback mortality but seems to decrease the retention rates of sea turtles. Numerous studies have documented the same trend (e.g. Watson et al., 2005; Yokota, Kiyota & Okamura, 2009; Foster et al., 2012; Coelho et al., 2015; Gilman & Huang, 2017; Swimmer et al., 2017), which is probably explained by diet preferences and feeding behaviour. Despite being omnivorous, soft-bodied prey (including jellyfish and squid) were described as the main food source of loggerhead and leatherback sea turtles (Revelles et al., 2007; Dodge, Logan & Lutcavage, 2011). Moreover, Kiyota et al. (2004) suggested that feeding behaviour varies with bait texture, explaining that sea turtles tend to swallow the whole squid bait, in contrast to fish, which is usually ingested piece by piece. Accordingly, using squid bait is expected to cause higher hooking rates of sea turtles.

4.4 | Data gaps and limitations

In addition to evaluating the effects of fishing gear configurations on different species groups, this study had the purpose of identifying data gaps in the current literature and providing direction for future research.

It was observed that most studies available were related to shallow-set pelagic longlines and tested the effects of hook shape on retention and at-haulback mortality rates, especially the performance of circle hooks vs. J-hooks. While there were also a considerable number of studies on bait type effects in shallow-set longlines, information on leader material effects was very limited and restricted to a maximum of three studies. Data gaps were even more significant for deep-set pelagic longlines. Apart from a few studies that reported catches on circle and tuna hooks, the absence of suitable information made it impossible to perform the analysis for most factors and species at this time.

Tunas, billfishes, blue shark and shortfin mako were the best represented species in the analysis. This is mainly because these are target or desirable bycatch species and as such data are available from several sources. The number of experiments reporting on species such as the loggerhead and leatherback sea turtles and the pelagic stingray – species commonly caught in pelagic longline fisheries – was also better represented, while rarer species like most pelagic sharks were less represented.

The high heterogeneity values detected for some species, mainly caused by variations in fishing practices among experiments, is noteworthy. Although most studies were designed to evaluate the effects of a single factor, those effects can be confounded by other potentially significant explanatory variables. For example, when comparing hook shape effects on the catchability, a potential hook-size effect may be masked owing to the fact that most commonly used J-hooks (7/0, 8/0 and 9/0) are slightly smaller than 16/0 and 18/0 circle hooks. In this study, although information on hook size, hook offset, bait species and study area was collected, it was not accounted for as fixed effects. Since that kind of detail is not reported consistently across studies, its inclusion in the model would have limited the available data and hindered the analysis.

Given the gaps highlighted above, it is essential to emphasize the importance of standardizing study designs, data collection procedures and data reporting, as this standardization is critical to increase the power of future meta-analyses and therefore obtain a more accurate depiction of the impacts of pelagic longline fisheries on the ecosystem. Moreover, it is recommended that future research directs its focus towards species that are known to be more vulnerable and for which little information is available, including pelagic sharks. Testing the effects of different gear configurations on species at-haulback and post-release mortality should also be prioritized, as well as studies comparing the effects of less explored strategies (e.g. changing leader material) and sea trials assessing combined effects of different mitigation measures (e.g. changing baits within the various hook shapes).

4.5 | Conclusions

Every bycatch reduction strategy assessed seems to have its pros and cons, triggering different responses across different species groups. The main outcomes of this work indicate that the adoption of circle hooks mitigates incidental catches of sea turtles. However, if circle hooks are implemented in pelagic longline fleets, their effects on other species groups should be considered. For instance, they seem to increase the catchability of some target species like the albacore tuna, but reduce others like swordfish – the main target species of the shallow-set pelagic longline fishery. Furthermore, the circular hook shape is associated with lower at-haulback mortality rates of sharks, which is particularly beneficial for non-retention species that are released if captured. On the other hand, its effect on the retention rates of sharks remains unclear. The results also indicate that using fish bait also benefits sea turtles by reducing their catch rates, but might cause the opposite effect on sharks as higher at-haulback mortality rates for blue shark and shortfin mako have been noted. Despite the limited information available, the current evidence demonstrates that nylon leaders are an effective conservation tool for sharks by significantly reducing retention without adversely affecting, and in some cases even slightly increasing, retention rates of the main target species.

In terms of recommendations for future research, it is important to acknowledge that certain bycatch mitigation measures have received extensive study, while others remain poorly investigated and require prioritization. Specifically, the materials used in the leaders of pelagic longlines represent a bycatch mitigation option that has received limited attention; therefore, it is crucial to allocate greater efforts towards conducting experimental field work to further understand and assess the effectiveness of these materials. Additionally, the work conducted thus far regarding deep-set pelagic longlines has been notably insufficient, so it should also be the focus of future research priorities. In addition, although small-scale pelagic longline fisheries have received much less scientific scrutiny than industrial-scale operations, their impact on species should not be ignored. Finally, priority should be given to the evaluation of post-release mortality in order to assess the real survival rates of species upon release, as well as to the standardization of methodological procedures to improve the power and soundness of future meta-analyses.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

There are no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.