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**A Meta- Analysis of Bycatch Mitigation Methods for Sea Turtles Vulnerable to Swordfish
and Tuna Longline Fisheries**

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ORIGINAL ARTICLE

A Meta-Analysis of Bycatch Mitigation Methods for Sea Turtles Vulnerable to Swordfish and Tuna Longline Fisheries

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ABSTRACT

Fisheries bycatch poses one of the most significant threats to sea turtles. Although various methodologies have been developed to mitigate sea turtle bycatch in swordfish and tuna longline fisheries, the effectiveness and interactions remain uncertain. In this study, we conducted a comprehensive meta-analysis, encompassing 41 studies focused on sea turtles and 36 studies on tunas, swordfish and sharks, all derived from well-controlled experimental research in swordfish and tuna longline fisheries. The objective was to systematically evaluate the relative effectiveness of species-specific mitigation strategies for sea turtles, particularly examining the impact of circle hooks and fish bait as alternatives to conventional longline fishing practices. While a nuanced hierarchy, characterised by species-specific patterns, was observed among the mitigation measures, circle hooks demonstrated great promise in reducing bycatch of loggerhead, olive ridley and leatherback turtles, with minimal impact on the catch rates of tuna, swordfish and sharks. We highlighted the broader applicability of fish bait in minimising sea turtle bycatch, noting that the effectiveness of bait may overlap with that of hooks, potentially making the additional benefits of the hooks less evident. The study also revealed regional variations in the effectiveness of these methods, emphasising the need for more detailed data collection. Given current data limitations that restrict extensive meta-analyses, a series of small-sample studies with promising innovations, exemplified by circle hooks with a wire appendage and blue-white lights, necessitates in-depth investigation and field tests.

1 | Introduction

Longline fishing is a globally prevalent technique, widely employed in swordfish and tuna fisheries across the Pacific, Indian and Atlantic Oceans (Gilman et al. 2006; Watson and Kerstetter 2006; Ward and Hindmarsh 2007). This method, which deploys long lines with numerous baited hooks, primarily targets high-value pelagic species such as swordfish (*Xiphias gladius*), bigeye tuna (*Thunnus obesus*), yellowfin tuna

(*T. albacares*) and albacore tuna (*T. alalunga*), while also capturing other species such as sharks (Gilman et al. 2007; Ward and Hindmarsh 2007; Gilman 2011; Favaro and Côté 2015). However, a significant issue arising from longline fishing is the incidental capture of sea turtles, which poses a major conservation challenge on a global scale (Watson and Kerstetter 2006; Doherty et al. 2014; Swimmer et al. 2017). The overlap between the diving depths of loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), olive ridley (*Lepidochelys olivacea*) and

green turtles (*Chelonia mydas*) with the operational depths of longline hooks increases their vulnerability to being caught in longline fisheries (Eckert et al. 1989; Seminoff, Resendiz, and Nichols 2002; Polovina et al. 2003; Martínez-Ortiz et al. 2015). This bycatch significantly impacts turtle populations, many of which are classified as vulnerable, endangered or critically endangered by the International Union for Conservation of Nature (IUCN 2024). While some sea turtle populations are showing positive signs of recovery, the majority continue to decline, largely due to the bycatch in large, industrialised pelagic longline fisheries (IUCN 2024). Some coastal artisanal and small domestic longline fleets that use shallow-set gear may also contribute to relatively high sea turtle catch rates, owing to the specific locations of their fishing grounds and fishing methods (Alfaro-Shigueto et al. 2011; Carpio et al. 2022). These smaller-scale operations, though significant, often receive less regulatory oversight and research focus, making their impact on sea turtle populations less visible but no less concerning (Alfaro-Shigueto et al. 2011; Andraha et al. 2013; Carpio et al. 2022). This ongoing threat makes it increasingly important to develop and implement effective bycatch mitigation strategies to protect these vulnerable species and support their recovery (Watson and Kerstetter 2006; Ward and Hindmarsh 2007; Wallace et al. 2010; Carpio et al. 2022).

To address this conservation challenge, significant progress has been made in reducing sea turtle interactions in both swordfish and tuna longline fisheries (Gilman et al. 2007; Swimmer et al. 2017). Commonly adopted methods include the adoption of circle hooks and the substitution of squid bait with fish bait, both of which have shown promise in various regions (Watson et al. 2005; Catarina, Rosa, and Coelho 2020). However, the effectiveness of these methods may vary depending on the species and bait type. For example, while circle hooks have been shown to benefit loggerhead turtles (Catarina, Rosa, and Coelho 2020), results for other species, such as olive ridley and green turtles, have been inconsistent (Andraha et al. 2013). Such variations suggest that species-specific factors play a crucial role in determining the success of bycatch mitigation methods. Much of the current research has focused on the impact of individual factors such as bait type or hook design, often overlooking how these factors might interact. The effectiveness of circle hooks, for instance, may vary depending on the bait used, as different bait types can influence how sea turtles interact with the hooks (Echwikhi et al. 2010; Stokes et al. 2011). The interactions between these methods have uncertain or potentially variable effects on sea turtles, resulting in a fragmented understanding of overall effectiveness and limiting the development of general recommendations for swordfish and tuna longline fisheries. To bridge these gaps, it is essential to integrate and analyse existing comparative experimental data. A meta-analysis can offer a comprehensive evaluation of mitigation methods, helping to establish generalised protective measures for various sea turtle species and improving overall conservation efforts.

Building on the experience from previous meta-analyses (Reinhardt et al. 2018; Santos et al. 2019; Gilman et al. 2020), in addition to further validating the mitigation effects of these methods on various sea turtles, our study seeks to identify potential synergistic effects between different mitigation measures, particularly between bait and hooks and to explore

whether these methods might overlap or obscure the effectiveness of reducing sea turtle bycatch. This research focuses on the four aforementioned sea turtle species, which are the most commonly recorded in bycatch data, as well as the composite groups they form. We gathered the mitigation techniques or methods from peer-reviewed literature, grey literature and conference proceedings, encompassing both large-scale commercial fishing vessels and smaller coastal fishing fleets, along with data from control experiments. Through multiple quantitative assessments, our goal is to determine the most effective strategies for reducing the bycatch risk of individual or multiple sea turtle species and to evaluate their broader application (Eckert et al. 1989; Seminoff, Resendiz, and Nichols 2002; Polovina et al. 2003; Reinhardt et al. 2018). More broadly, to gain insights into the feasibility of promoting these mitigation measures, we conducted an initial assessment of their effectiveness in reducing sea turtle bycatch while maintaining the catch rates of target species, including both teleost fish and sharks. Our study not only aims to fill existing gaps in the current research but also seeks to propose more effective mitigation methods through a more holistic understanding of their potential benefits and limitations, ultimately balancing the needs of sea turtle conservation with the sustainability of fisheries.

2 | Methods

2.1 | Sources of Data and Screening

We employed a meta-analysis methodology to systematically evaluate the collective effectiveness of bycatch mitigation techniques used in swordfish and tuna longline fisheries for sea turtles. Our study primarily utilised data from publications featuring controlled experimental results. The principal source for these publications was the Bycatch Management Information System (BMIS; available at <https://www.bmis-bycatch.org>). The review adhered to the guidelines outlined in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 statement (Page et al. 2021).

The inclusion criteria established for the present study were threefold. Firstly, the publications needed to include experiments with a control group, providing data on both the unmodified longline fishing gear (control group) and the modified gear with turtle bycatch mitigation methods (experimental group). The publications had to clearly specify the number of treated and untreated hooks used, along with the corresponding number of sea turtles caught. Second, the bycatch mitigation methods had to be applicable to longline fishing gear without significantly altering fishing operations or increasing fishing costs, especially in swordfish and tuna fisheries. Third, only the data obtained from field experiments at sea were included; data from laboratory settings were excluded. Additionally, we considered mitigation methods designed to reduce bycatch of other species, like seabirds, if they also provided data on turtle bycatch from field experiments. Our study included all formally published literature, conference records and unpublished peer-reviewed literature that met the three established criteria and were discoverable through searching the BMIS database. We utilised the PRISMA Flow Diagram and adapted it to fit our screening process (Figure 1). To ensure comprehensive coverage and avoid missing

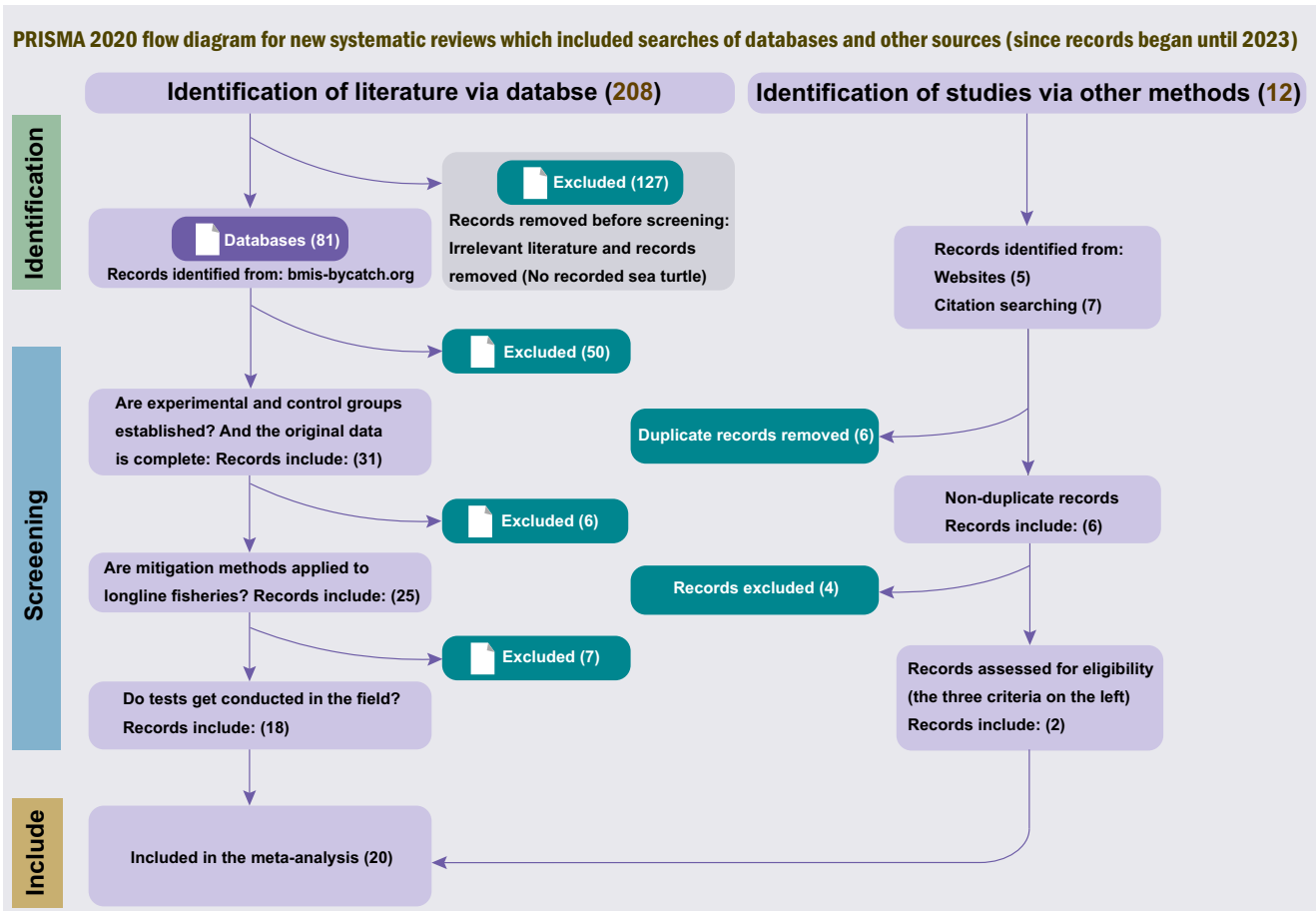


FIGURE 1 | Standard flow chart for screening meta-analysis publications.

any relevant publications, we used broad English keywords such as ‘turtle’, ‘longline’ and ‘bycatch’ in our search.

2.2 | Effect Sizes and Mitigation Methods

We used the relative risk ratio (RR) (Ospina, Nydam, and Diccio 2012) as the standard measure to quantify the effectiveness of turtle bycatch mitigation methods. A statistically significant effect on sea turtle bycatch was indicated if the 95% confidence interval of the model coefficient did not exceed 1 (excluding 1). To fully utilise the data included in our study, we recorded and processed all control experiment data from each publication. This included the number of hooks used in both the control and the experimental group, the total number of turtles caught on the hooks in both groups and the number of hooks that caught turtles, with species identification. The experimental group typically involved the use of circle hooks, fish bait and other unconventional designs in longline fisheries, while the control group employed J-type hooks, squid bait and conventional designs. The formula for calculating the relative risk ratio (RR) and its 95% confidence interval was as follows:

$$RR \text{ (Risk Ratio)} = (\text{event. } e / n. e) / (\text{event. } c / n. c) \quad (1)$$

$$\text{confidence interval lower} = \exp (\ln (RR) - 1.96 \times SE) \quad (2)$$

$$\text{confidence interval upper} = \exp (\ln (RR) + 1.96 \times SE) \quad (3)$$

The *event. e* and *event. c* represent the number of turtles caught with and without using bycatch mitigation methods, respectively; the *n.e* and *n.c* represent the total number of hooks used with and without mitigation methods, respectively.

Where SE is the standard error of the natural logarithm of RR and its calculation formula is as follows:

$$SE = \sqrt{(1 / \text{event. } e - 1 / n. e) + (1 / \text{event. } c - 1 / n. c)} \quad (4)$$

We calculated the relative risk ratio (relative bycatch rate) for each species to assess the practical impact of these methods on turtle populations. We chose the Risk Ratio (RR) over the Odds Ratio (OR) because it more accurately quantifies the effectiveness of mitigation techniques in reducing turtle bycatch, rather than merely indicating the strength of the association between the methods and incidental captures.

Eight different methods for mitigating turtle bycatch were identified (comprehensive data and illustration can be found in Tables S1–S6 and Figure 2), which are summarised as follows: (i) *Replacing J-style hooks with circle hooks* in longline fishing operations (Bolten et al. 2004; Yokota, Minami, and Nobetsu 2006; Boggs and Swimmer 2007; Mejuto, García-Cortés, and Ramos-Cardelle 2008; Piovano, Swimmer, and Giacomini 2009; Sales et al. 2010; Pacheco et al. 2011; Cambiè et al. 2012; Piovano et al. 2012; Domingo et al. 2012; Foster et al. 2012; Santos

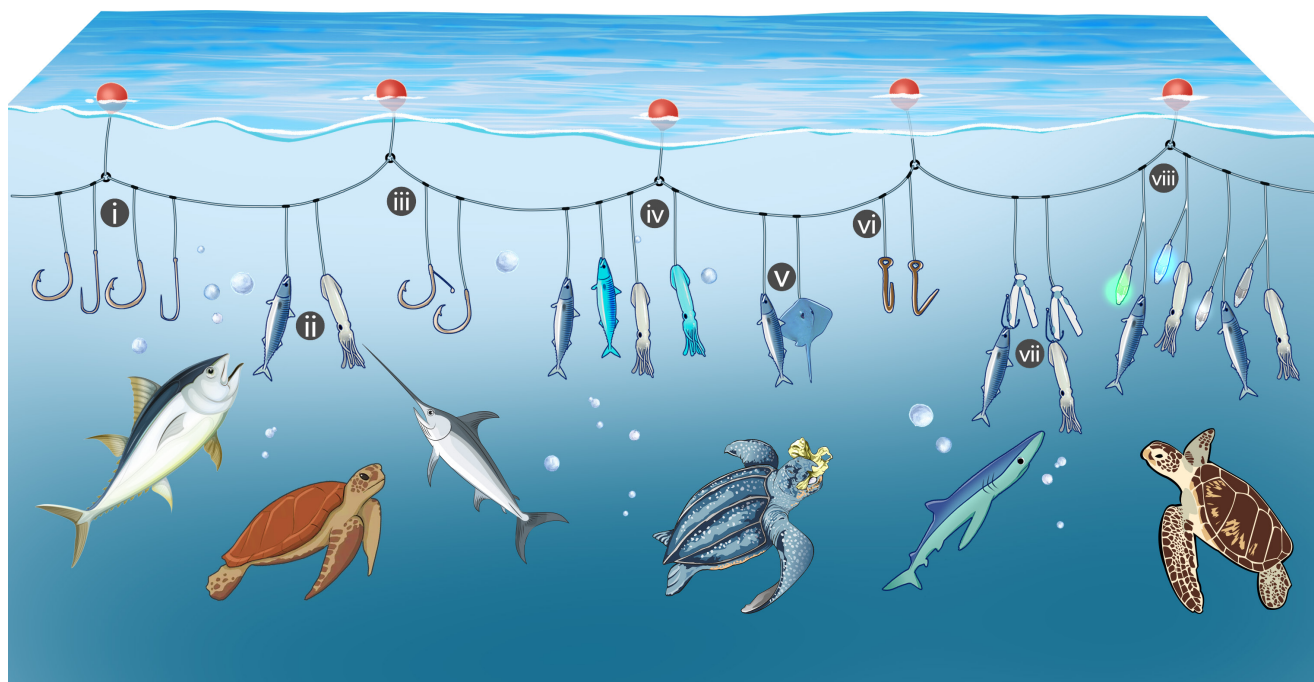


FIGURE 2 | Illustration of the mitigation methods: (i) Replacing J-style hooks with circle hooks in longline fishing operations (Bolten et al. 2004; Yokota, Minami, and Nobetsu 2006; Boggs and Swimmer 2007; Mejuto, García-Cortés, and Ramos-Cardelle 2008; Piovano, Swimmer, and Giacoma 2009; Sales et al. 2010; Pacheco et al. 2011; Cambiè et al. 2012; Piovano et al. 2012; Domingo et al. 2012; Foster et al. 2012; Santos et al. 2012; Andraha et al. 2013; Coelho et al. 2015); (ii) Using fish bait instead of squid bait, such as using mackerel (Yokota, Minami, and Nobetsu 2006; Boggs and Swimmer 2007; Mejuto, García-Cortés, and Ramos-Cardelle 2008; Foster et al. 2012; Santos et al. 2012; Coelho et al. 2015); (iii) Using circle hooks with a wire appendage (Boggs and Swimmer 2007; Swimmer et al. 2011); (iv) Dyeing the bait blue in longline fisheries (Swimmer et al. 2005; Yokota, Kiyota, and Okamura 2009) aims to reduce the visibility of by-catch species; (v) Further changing the bait by replacing fish bait with stingray bait (Echwikhi et al. 2010); (vi) Using offset hooks, where the bent part of the circle or J-style hook is not parallel to the connecting branch line and instead forms a certain angle, usually between 0° and 10° (Swimmer et al. 2010); (vii) The use of the Hookpod-mini device on branch lines, as discussed in the publication, reports instances of bycatch involving both turtles and seabirds (Gianuca et al. 2021); (viii) Using different light types at the end of longline fishing branch lines, including white, blue and green light, to improve gear selectivity (conducted in controlled experiments to determine the most effective light frequency) (Afonso et al. 2021).

et al. 2012; Andraha et al. 2013; Coelho et al. 2015). Circle hooks, commonly used in swordfish and tuna longline fisheries, are available in various sizes typically ranging from 14/0 to 18/0 (Watson et al. 2005; Gilman et al. 2006). Unlike traditional J-style hooks, circle hooks do not deeply hook sea turtles but rather catch them in their limbs or mouths. Numerous studies have recognised circle hooks for their ability to mitigate turtle bycatch and improve the survival rate of released turtles to some extent; (ii) *Using fish bait instead of squid bait*, such as mackerel (Yokota, Minami, and Nobetsu 2006; Boggs and Swimmer 2007; Mejuto, García-Cortés, and Ramos-Cardelle 2008; Foster et al. 2012; Santos et al. 2012; Coelho et al. 2015), can help mitigate the likelihood of turtles swallowing the hook whole. Fish bait tends to be easily bitten off by turtles when attracted to the longline hooks, whereas squid bait, due to its softer texture and tendency to entangle on the hook, is more difficult for turtles to remove, increasing the risk of capture (Stokes et al. 2011; Serafy et al. 2012); (iii) *Using circle hooks with a wire appendage* (Boggs and Swimmer 2007; Swimmer et al. 2011). The hook's width has been increased based on the circle hooks design, which prevents smaller marine organisms from easily swallowing it and becoming bycatch; (iv) *Dyeing the bait blue* in longline fisheries (Swimmer et al. 2005; Yokota, Kiyota, and Okamura 2009) aims to reduce the visibility of by-catch species; (v) *Replacing fish bait with stingray bait* (Echwikhi

et al. 2010) may offer potential benefits in mitigating turtle by-catch, as suggested by data from the publications included in the analysis; (vi) *Using offset hooks*, where the bent part of the circle or J-style hook is angled relative to the connecting branch line, usually between 0° and 10° (Swimmer et al. 2010); (vii) *The use of the Hookpod-mini device on branch lines*, as discussed in the publication, reports instances of bycatch involving both turtles and seabirds (Gianuca et al. 2021); (viii) *Using different light types at the end of longline fishing branch lines*, including white, blue and green light, to improve gear selectivity (conducted in controlled experiments to determine the most effective light frequency) (Afonso et al. 2021).

2.3 | Statistical Analysis

2.3.1 | Data Classification

Our study aims to evaluate the effectiveness of mitigation methods on sea turtle species severely affected by longline fishing and to assess the interactive efficacy of these methods for vulnerable sea turtle species. While sea turtles are categorised into different subspecies, which can exhibit variations in life history, traits and population dynamics (Wallace et al. 2010),

most existing research and data collection have been conducted at the species level (Tables S1–S6). Our analysis mainly focused on the species level and assumed that bycatch mitigation methods performed similarly across the subspecies of sea turtle species. This assumption was anticipated to increase the heterogeneity of model results. Subsequently, the primary data for the meta-analysis were classified—among the 20 publications included in the meta-analysis (Figure 1), the data were categorised into three main groups: circle hooks, fish baits and other mitigation methods. Specifically, 34 studies provided data on the use of circle hooks versus J-hooks (further classified into four sea turtle species), seven studies focused on the use of fish baits as a mitigation method and seven additional studies on other mitigation methods, which necessitate larger sample sizes for a more robust meta-analysis. Additionally, data were gathered from 10 studies on tunas, 14 on swordfish and 12 on sharks. Most of the data for target species were derived from studies that utilised circle hooks in comparative experiments (Tables S7–S9).

2.3.2 | Heterogeneity and Other Enhanced Analyses

The eight analyses conducted did not evaluate the overall effect of other mitigation methods due to insufficient field-test data on sea turtles, which is necessary for a robust meta-analysis model. The sea turtles and target fish species, experimental locations and hook sizes varied across the eight analyses. Therefore, we need to conduct a heterogeneity test to determine if there is a significant difference between these study results and to check the compatibility of the outcomes of individual independent studies. Based on this, we can decide whether to use a common effect model or a random effects model. By understanding the extent of heterogeneity, it may be possible to explain and control potential confounding variables and covariates. Since all the data in our study were binary variables, heterogeneity tests were conducted using the *metabin* function in the meta package (Balduzzi, Rücker, and Schwarzer 2019) in RStudio, focusing primarily on the results of the *Q* test and the I^2 statistic (Huedo-Medina et al. 2006). Our study specifically examined the results of the I^2 statistic in analysing groups with a limited number of study groups. This is because the I^2 statistic has the potential to overestimate heterogeneity when the study sample is large (Huedo-Medina et al. 2006). For datasets with a larger number of studies on the circle hook mitigation method, the focus was on the *Q* test results. Although a meta-analysis might indicate no heterogeneity, the *Q* test can still show statistical significance when many studies are involved (Hoaglin 2016). Conversely, with fewer studies, the *Q* test might not be statistically significant despite the presence of heterogeneity (Hoaglin 2016). To ensure the reliability of our findings, these heterogeneity indicators were thoroughly reviewed. Additionally, the *H*-value was evaluated and compared with the *Q* test results to validate our heterogeneity analysis (Balduzzi, Rücker, and Schwarzer 2019; Huedo-Medina et al. 2006).

We generate a series of forest plots using the *forest* function from the meta package (Balduzzi, Rücker, and Schwarzer 2019). For the groups exhibiting high heterogeneity, we employed a random effects model. For groups with low heterogeneity,

both common effects and random effects models were used to ensure robust results. Significant variations in the sample sizes of the included studies were observed (Tables S1–S9). To ensure the robustness of the overall effect size and sensitivity to heteroscedasticity and to minimise the possibility of false-positive results, the Cluster-Robust Variance Estimator, Type 2 (CR2) method from the clubSandwich package was employed for robust variance estimation. The CR2 method provides more reliable estimates of standard errors, especially when the number of studies is small and heterogeneity is high (Viechtbauer 2010; Balduzzi, Rücker, and Schwarzer 2019; Pustejovsky 2024). After establishing a robust base model effect size, a sensitivity analysis was conducted using the *metainf* function from the meta package (Balduzzi, Rücker, and Schwarzer 2019). This involved excluding each dataset one by one to observe changes in heterogeneity or confidence intervals. If excluding a special study significantly altered the results, further investigation was conducted to identify potential sources of heterogeneity, such as experimental location and sample size. If results remain robust, we proceed with subgroup and meta-regression analysis.

Subgroup analysis and meta-regression were primarily conducted based on the bait type, region and species used in the experiment. To ensure the stability and reliability of the meta-regression analysis results, we included at least 10 studies per regression (Higgins and Green 2008), thus allowing for single-variable analysis only for the loggerhead group (Table S1). Due to the limited number of variables and studies, only preliminary meta-analyses were conducted on target fish and sharks (Tables S7–S9). Special attention was paid to the *p*-values generated for the moderators in the meta-regression analysis. Both random and common effects models were employed in subgroup analysis to prudently identify studies with homogeneity. For subgroups with high heterogeneity, the results from random effects models were given precedence, whereas for those with low heterogeneity, the outcomes from common effects models were prioritised. If all subgroups exhibited heterogeneity, it suggested the absence of a significant source of heterogeneity.

2.3.3 | Publication Bias Tests

Following the guidelines from the Intervention Measures Systematic Review Manual (Higgins and Green 2008), we utilised the *funnel* function in RStudio to generate contour-enhanced funnel plots for studies with sample sizes of 10 or more. Funnel plots were not used for studies with fewer than 10 samples, as recommended. If the distribution of each study in the funnel plot is symmetric, with an even distribution on both sides of the dashed line in the middle, we considered no publication bias to be present. If the contour-enhanced funnel plot exhibits asymmetry, we employed the trim-and-fill method for adjustment (Balduzzi, Rücker, and Schwarzer 2019). The *trimfill* function in the meta package was used to estimate the number of missing studies and conduct a meta-analysis. If the enhanced funnel plot remained asymmetric and no missing studies were filled in, we considered heterogeneity to be the likely cause of the asymmetry (Peters et al. 2008; Balduzzi, Rücker, and Schwarzer 2019).

When heterogeneity is low, we used the Harbord test and Peters test (the Harbord test is recommended for fewer than 10 studies; Harbord, Egger, and Sterne 2006). When significant heterogeneity is present, to ensure that the meta-analysis was free from publication bias, we use the transformed test (AS-Thompson test with the 'AS' effect size in the meta package) after arcsine transformation (Harbord, Egger, and Sterne 2006; Sterne et al. 2011; Jin, Zhou, and He 2015; Balduzzi, Rücker, and Schwarzer 2019). The Arcsine-Begg test and Arcsine-Egger test were employed, with their p -values serving as indicators of publication bias (i.e., p -value > 0.05 indicates publication bias). It is preferable not to use the AS-Thompson test when heterogeneity is low, as its effect is smaller compared to the Peters test (Harbord, Egger, and Sterne 2006; Sterne et al. 2011; Jin, Zhou, and He 2015). All analysis in our study were conducted in R-4.3.3 using the meta, metafor and clubSandwich packages (Viechtbauer 2010; Balduzzi, Rücker, and Schwarzer 2019; Pustejovsky 2024).

3 | Results

3.1 | Meta-Analysis of Turtle Bycatch Mitigation Using Circle Hooks

3.1.1 | Loggerhead (*Caretta caretta*)

These 20 publications yielded 13 studies on mitigating the bycatch of loggerhead turtles using circle hooks, all meeting the inclusion criteria for our meta-analysis (Table S1). Significant heterogeneity was found ($I^2 = 81\%$, 95% CI = 67.8% to 88.3%; $\tau^2 = 0.1772$, 95% CI = 0.0509 to 0.7693; $H = 2.27$, 95% CI = 1.76 to 2.93; $Q = 61.98$, $df = 12$, $p < 0.01$). Circle hooks effectively reduced loggerhead turtle bycatch compared to J-style hooks (RR = 0.59, 95% CI = 0.44 to 0.79; Figure 3). Robust variance estimation (CR2 method) supported these results, albeit with wider confidence intervals (RR (CR2) = 0.59, 95% CI (CR2) = 0.42 to 0.83). Sensitivity analyses indicated that

the results remained robust, with no outliers after sequentially excluding each study (Figure S1). We conducted a meta-regression using the variables 'bait' and 'region' and found subgroups within the 'bait' group with p -values < 0.05 , indicating that the 'bait' group might be a significantly heterogeneous factor. Subsequent subgroup analysis using both common effects and random effects models revealed that while the combined bait group exhibited moderate heterogeneity, the other two groups had low heterogeneity (Figure 4). We suggested that bait type significantly influenced heterogeneity, though it was not the sole factor. The study demonstrated that distinct baits have varying effects on loggerhead turtle bycatch, with squid bait in conjunction with circle hooks failing to effectively mitigate this issue (Figure 4). The enhanced funnel plot displayed left-right asymmetry in the funnel plot and the trim-and-fill method did not fill any studies in the blank areas (statistically insignificant areas) of the funnel plot, suggesting that the asymmetry resulted from heterogeneity (Figure S2). The Arcsine-Begg and Arcsine-Egger tests for publication bias produced p -values > 0.05 (Arcsine-Begg: $p = 0.9029$; Arcsine-Egger: $p = 0.7256$), indicating no statistically significant publication bias in the data.

3.1.2 | Green Turtles (*Chelonia mydas*)

Six studies on green turtles were included in our meta-analysis (Table S2). Although the heterogeneity was less than 50% ($I^2 = 47\%$, close to 50%, 95% CI = 0% to 78.9%; $\tau^2 = 0.2762$, 95% CI = 0.000 to 6.904; $H = 1.37$, 95% CI = 1.00 to 2.18; $Q = 9.38$, $df = 5$, $p = 0.0948$), the combined results showed a marginal effect. To assess the stability of the common effects model results, we applied a random effects model, which yielded results inconsistent with those of the common effect model, with a confidence interval spanning 1 (Figure 5). Sensitivity analysis revealed that excluding study 6 reversed the results of the common effect model and significantly affected heterogeneity, identifying it as the source of heterogeneity

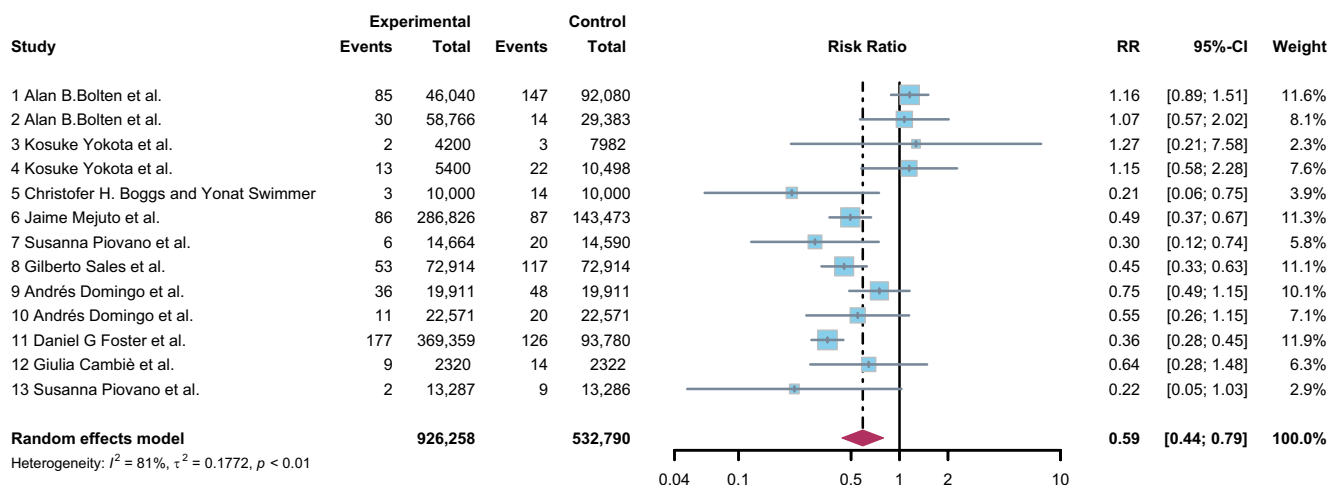


FIGURE 3 | Effect of replacing J-hooks with circle hooks on the risk of capturing loggerheads. RR > 1 or RR < 1 indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights of each study and random-effects model are shown. The experiments in the references are ordered from top to bottom by publication date and are distinguished by numerical identifiers.

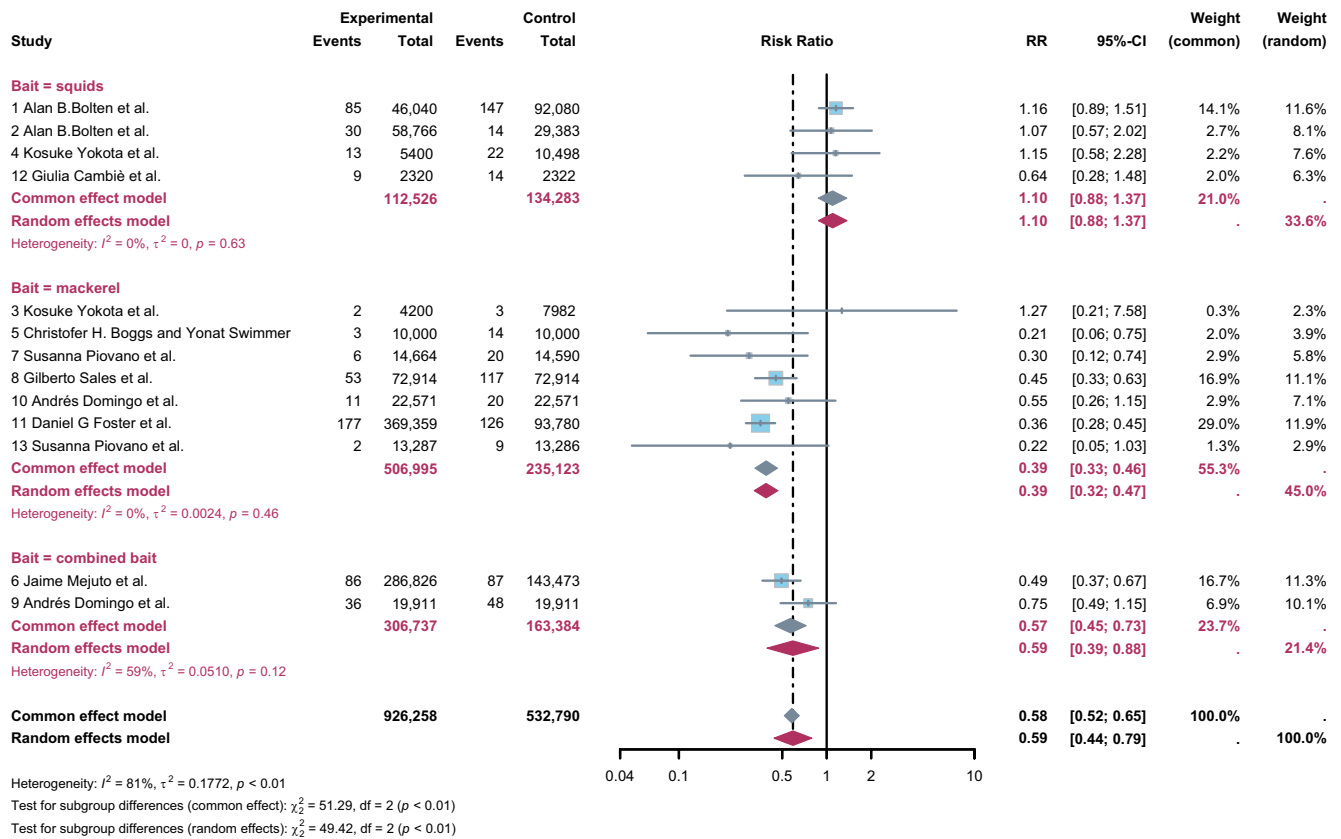


FIGURE 4 | Subgroup analysis of 13 studies on loggerheads, $RR > 1$ or $RR < 1$ indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

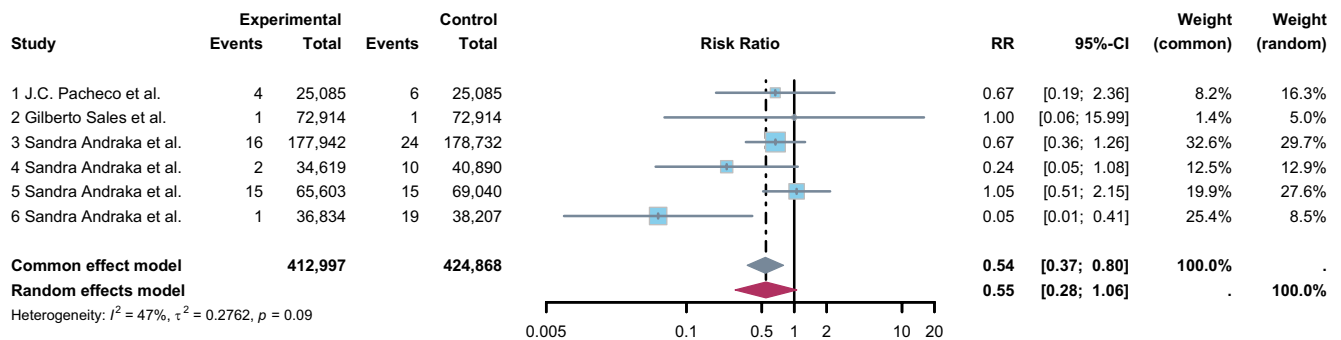


FIGURE 5 | Effect of replacing J-hooks with circle hooks on the risk of capturing green turtles. $RR > 1$ or $RR < 1$ indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights of each study and random-effects model are shown. The experiments in the references are ordered from top to bottom by publication date and are distinguished by numerical identifiers.

in our analysis (Figure S3). Study 6 meets our inclusion criteria and should not be excluded, despite its impact on heterogeneity and the combined effect size. The random effects model suggested that circle hooks do not significantly reduce the bycatch of green turtles ($RR = 0.55$, 95% CI = 0.28 to 1.06; Figure 5), with the p -value of the combined effect size being 0.0721, which is greater than 0.05. Robust variance estimation also supported this conclusion: RR (CR2) = 0.55, 95% CI (CR2) = 0.21 to 1.41. Given the sample size of less than 10 and

no significant heterogeneity (for which a funnel plot is inadvisable), we used the Harbord test, which yielded a p -value greater than 0.05 (p -value = 0.7568).

3.1.3 | Leatherback (*Dermochelys coriacea*)

We conducted heterogeneity tests on eight studies and found significant heterogeneity, leading us to use a random effects

model ($I^2=82\%$, 95% CI=65.0% to 90.4%; $\tau^2=0.1910$, 95% CI=0.0340 to 0.8666; $H=2.34$, 95% CI=1.69 to 3.23; $Q=38.21$, $df=7$, $p<0.01$). The results indicated that replacing J-type hooks with circle hooks significantly reduced the bycatch of leatherback turtles (RR=0.47, 95% CI=0.32 to 0.71; Figure 6). Robust variance estimation confirmed the robustness of these results: RR (CR2)=0.47, 95% CI (CR2)=0.28 to 0.80. The sensitivity analysis identified study 1 as a potential source of heterogeneity, but no result reversal was observed, confirming the robustness of the results (Figure S4). With fewer than 10 studies, meta-regression was not conducted. Sub-group

analysis based on bait and regional factors indicated that bait composition might contribute to the observed heterogeneity, with combined baits showing higher heterogeneity than single bait treatments (Figure 7). The combination of fish bait and circle hooks proved more effective in mitigating leatherback turtle bycatch, compared to the other two baits (mackerel: RR=0.38, 95% CI=0.30 to 0.48). Regional variations within the same ocean appeared to influence leatherback turtle capture rates (Figure 8). Both tests indicated that publication bias did not occur (Arcsine-Begg test: p -value=0.3223; Arcsine-Egger test: p -value=0.8218).

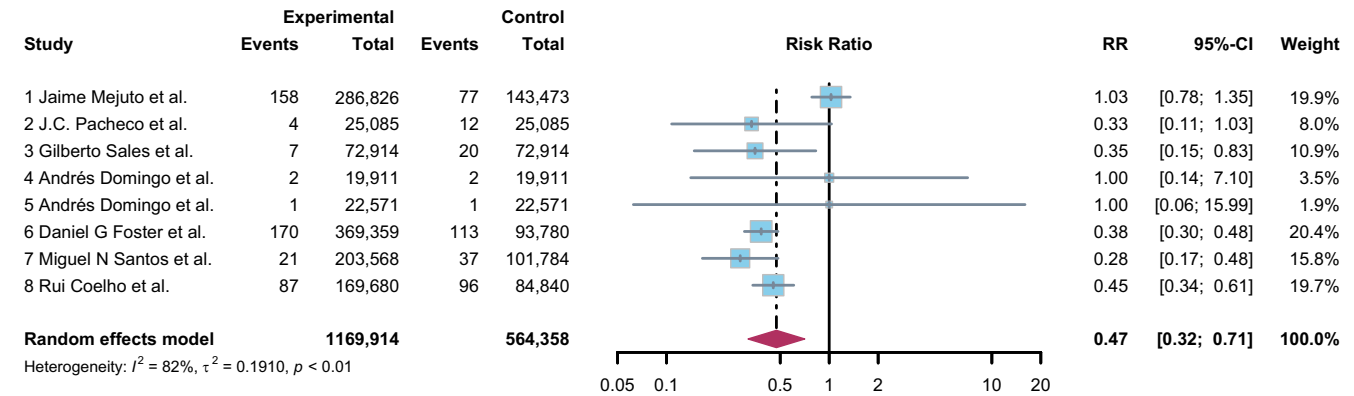


FIGURE 6 | Effect of replacing J-hooks with circle hooks on the risk of capturing leatherbacks. RR>1 or RR<1 indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights of each study and random-effects model are shown. The experiments in the references are ordered from top to bottom by publication date and are distinguished by numerical identifiers.

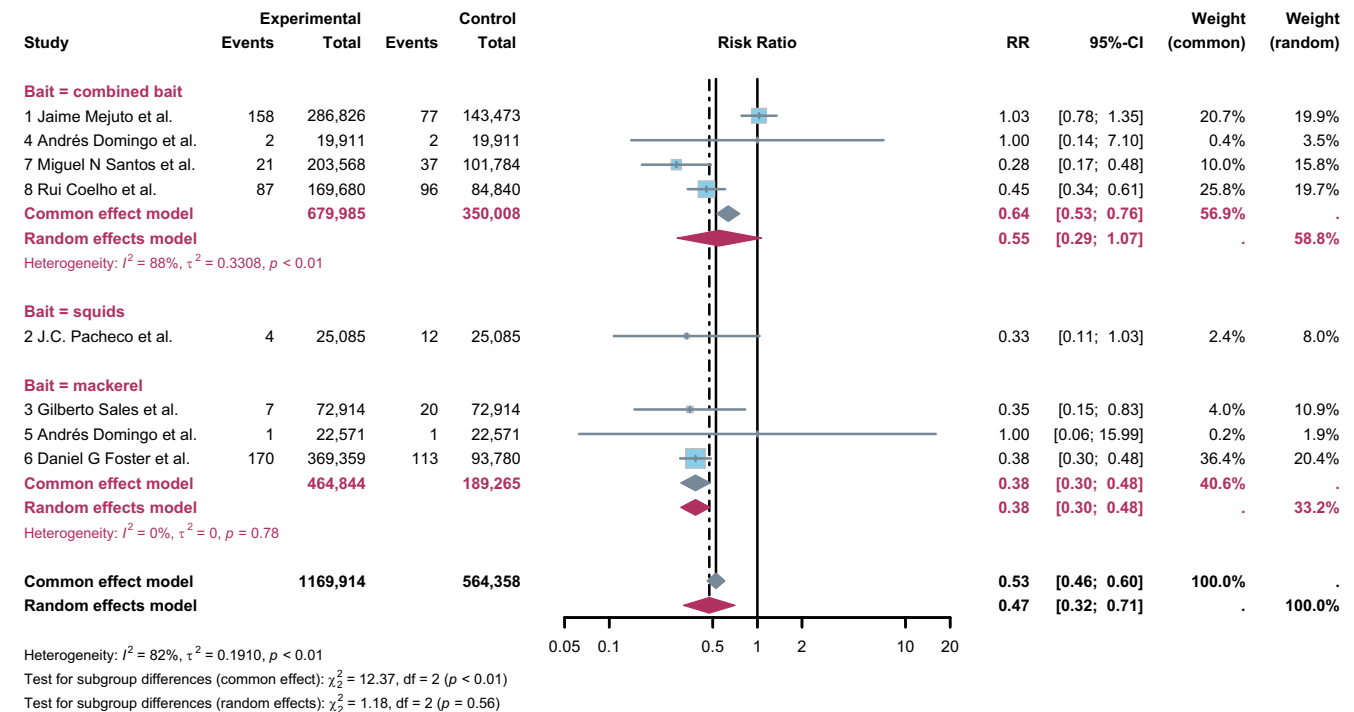


FIGURE 7 | Subgroup analysis of eight studies on leatherbacks (bait), RR>1 or RR<1 indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

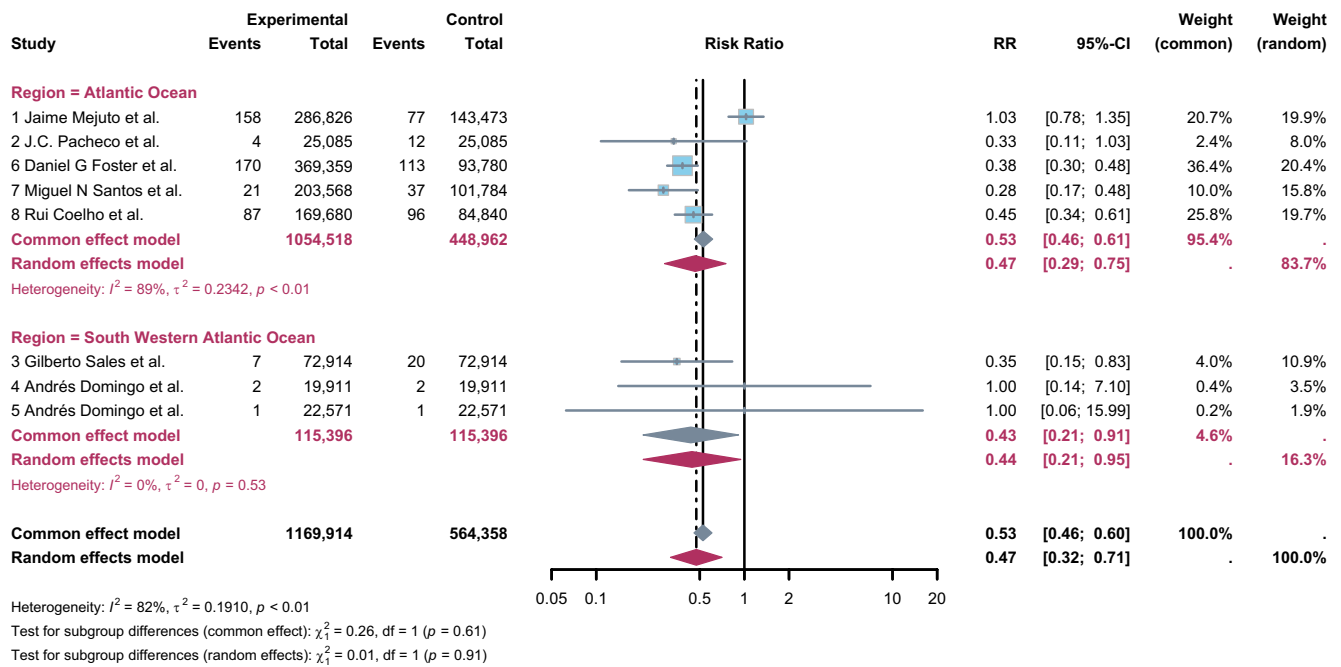


FIGURE 8 | Subgroup analysis of eight studies on leatherbacks (region), $RR > 1$ or $RR < 1$ indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

3.1.4 | Olive Ridley (*Lepidochelys olivacea*)

The heterogeneity test showed high heterogeneity ($I^2 = 76\%$, 95% CI = 49.1% to 88.6%; $\tau^2 = 0.1287$, 95% CI = 0.0245 to 1.8779; $H = 2.04$, 95% CI = 1.40 to 2.96; $Q = 24.87$, $df = 6$, $p < 0.01$). The random effects model indicated that circle hooks effectively reduced the bycatch of olive ridley ($RR = 0.56$, 95% CI = 0.40 to 0.78; Figure 9). Robust variance estimation using the CR2 method confirmed these results: RR (CR2) = 0.56, 95% CI (CR2) = 0.36 to 0.87. Study 6 significantly impacted heterogeneity (Figure S5). Sensitivity analysis showed no result reversal and study 6 met the inclusion criteria. Subgroup analysis on bait and region indicated that neither factor significantly impacts heterogeneity (Figures 10 and 11). An intriguing finding was that circle hooks had a greater mitigation effect in the Pacific region compared to the Atlantic region (Atlantic: $RR = 1.00$, 95% CI = 0.49 to 2.06; Pacific: $RR = 0.54$, 95% CI = 0.35 to 0.85). There was no publication bias in our analysis (Arcsine-Begg test: p -value = 0.6523; Arcsine-Egger test: p -value = 0.8756).

3.2 | Meta-Analysis of Turtle Bycatch Mitigation Using Fish Bait

Data from seven studies using fish bait to mitigate sea turtle bycatch were included in the meta-analysis (Table S5). Significant heterogeneity was detected ($I^2 = 79\%$, 95% CI = 57.9% to 90.0%; $\tau^2 = 0.1290$, 95% CI = 0.0281 to 1.7529; $H = 2.21$, 95% CI = 1.54 to 3.16; $Q = 29.19$, $df = 6$, $p < 0.01$), necessitating a random effects model. The analysis showed a significant mitigation effect ($RR = 0.57$, 95% CI = 0.41 to 0.79; Figure 12), supported by robust variance estimation (RR (CR2) = 0.57, 95% CI (CR2) = 0.37 to 0.88). Sensitivity analysis with random effects

models confirmed the robustness of these results. No outliers were identified when each study was individually removed, as the 95% confidence interval remained below 1 (Figure S6). Considering that the number of studies was less than 10, we did not conduct a meta-regression. Instead, we performed subgroup analysis based on hook type, species and region. The results indicated that none of these factors were major sources of heterogeneity. However, the J-style hook combined with fish bait demonstrated a superior mitigation effect compared to the other types (Figure 13). The subgroup analysis by species revealed that different species responded differently to bait, with loggerhead turtles showing a significantly better-mitigating effect than combined species (Figure 14). Regional differences were also observed, with fish bait proving more effective in the Pacific than in the Atlantic (Figure 15). A single source of heterogeneity could not be pinpointed, as it may be multifaceted. The Arcsine-Begg test and Arcsine-Egger test applied to the seven studies showed no evidence of publication bias (Arcsine-Begg test: p -value = 0.1765; Arcsine-Egger test: p -value = 0.0629).

3.3 | The Results of Using Circle Hooks on Target Fish Species and Sharks

Most comparative experiments replacing J-style hooks with circle hooks have recorded the catch for the target fish species. An initial meta-analysis of these data using random effects models revealed high heterogeneity (Table 1). Specifically, the catch quantity of tuna and sharks did not significantly decrease, while the catch quantity of swordfish reduced by approximately 17% (Table 1). However, robust variance estimation showed that the 95% confidence interval for the swordfish effect size included

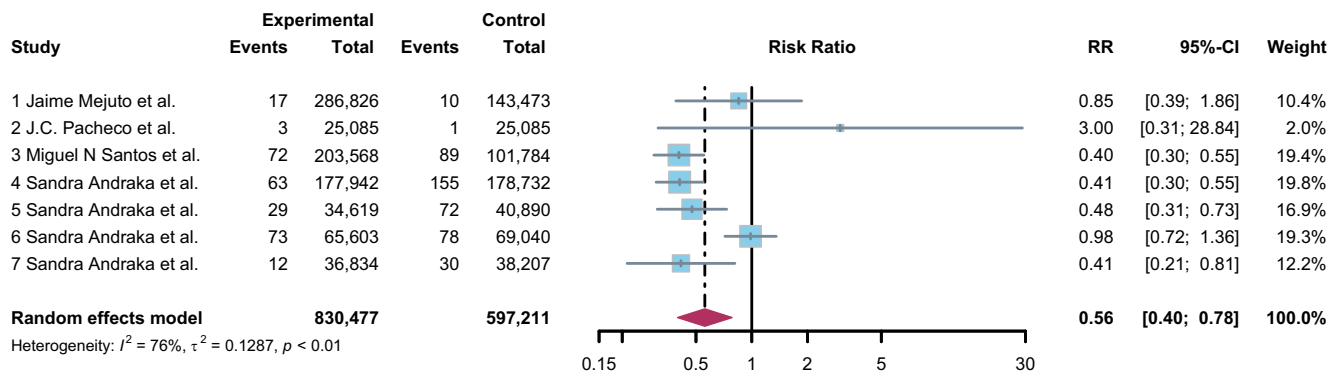


FIGURE 9 | Effect of replacing J-hooks with circle hooks on the risk of capturing olive ridley turtles. RR > 1 or RR < 1 indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights of each study and random-effects model are shown. The experiments in the references are ordered from top to bottom by publication date and are distinguished by numerical identifiers.

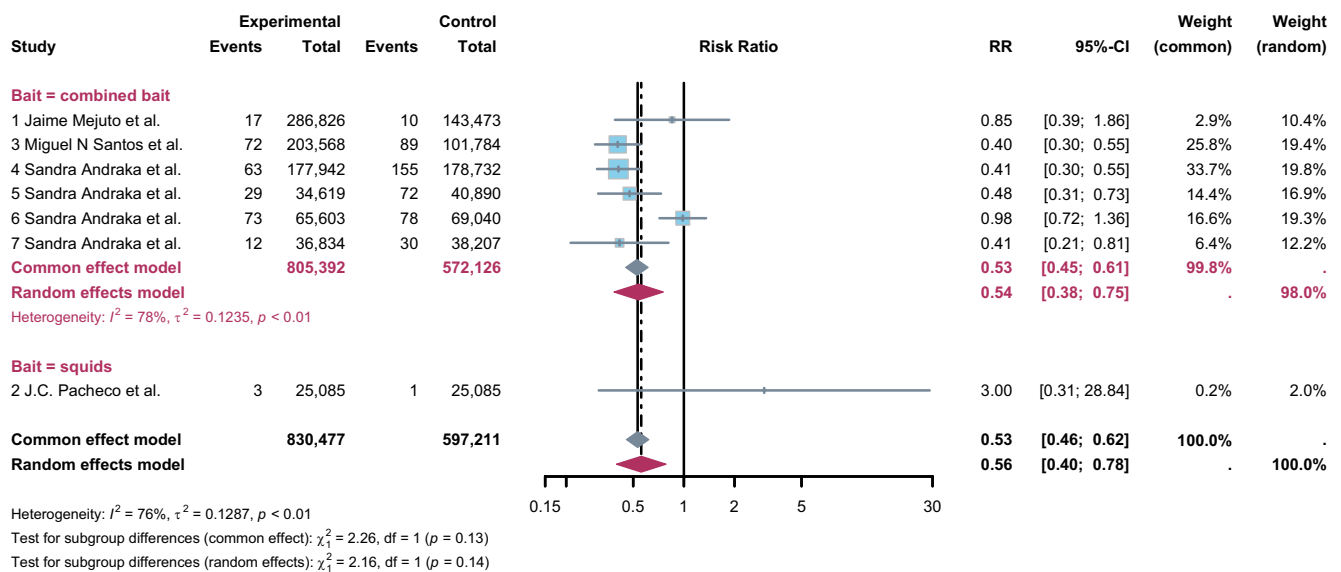


FIGURE 10 | Subgroup analysis of seven studies on olive ridley turtles (bait), RR > 1 or RR < 1 indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

1, indicating no significant association between circle hooks and capture rates (Table 1). Publication bias tests revealed no significant bias for tunas (Arcsine-Begg test: p -value = 0.6547; Arcsine-Egger test: p -value = 0.2200), sharks (Arcsine-Begg test: p -value = 0.1394; Arcsine-Egger test: p -value = 0.5241) and swordfish (Arcsine-Begg test: p -value = 0.4106; Arcsine-Egger test: p -value = 0.2422).

4 | Discussion

The present study refined bycatch mitigation strategies by demonstrating that while circle hooks and fish bait significantly reduce bycatch for loggerhead and olive ridley turtles, their effectiveness varies by species and highlights the need for tailored approaches in bycatch reduction. The use of a

single mitigation method, such as circle hooks, effectively reduces bycatch in specific sea turtle species, but the combined use of bait may influence this mitigation effect. We revealed species-specific variations in the effectiveness of circle hooks, particularly noting that they were not as effective for green turtles. Interestingly, our findings for leatherback turtles diverged from previous studies which did not find a significant mitigation effect of circle hooks (RR = 0.64, 95% CI = 0.38 to 1.08; Reinhardt et al. 2018), possibly due to differences in default calculation settings and literature scope. This underscored the need for caution when generalising the effectiveness of mitigation measures. Overall, despite the widespread and effective use of both fish bait and circle hooks in longline fisheries (Gilman et al. 2007), our results provided nuanced insights into their species-specific impacts and highlighted the enhanced mitigation techniques.

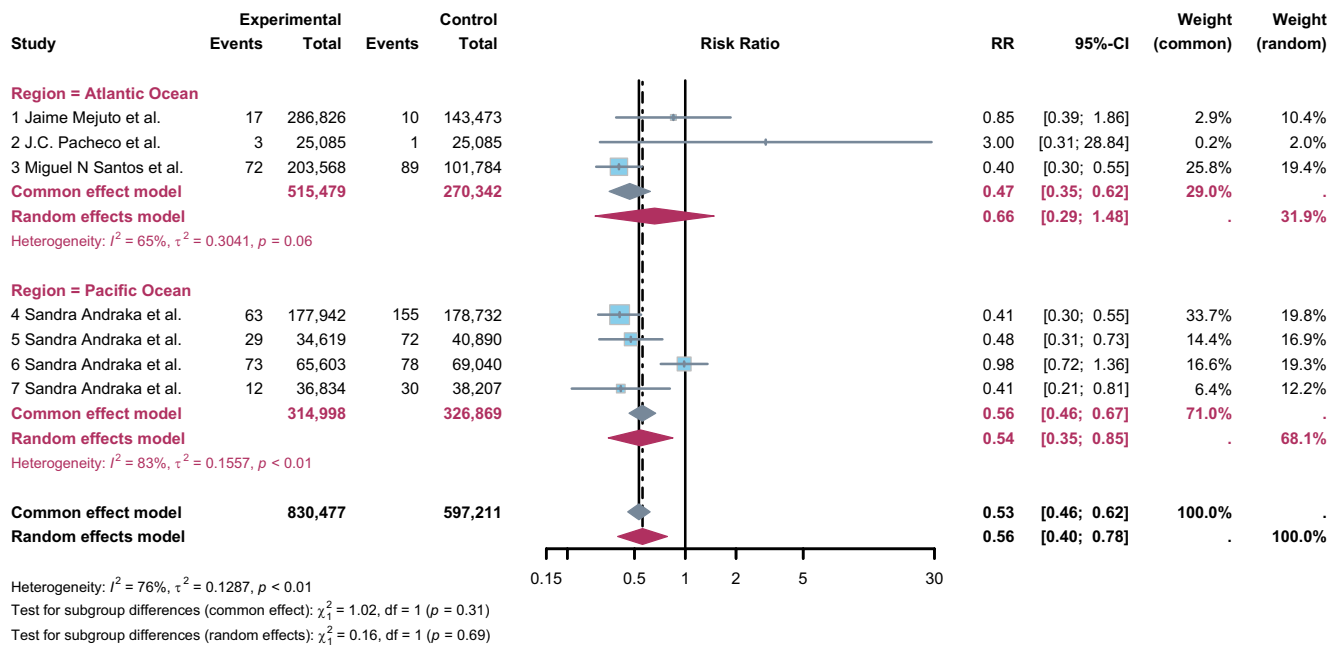


FIGURE 11 | Subgroup analysis of seven studies on olive ridley turtles (region), $RR > 1$ or $RR < 1$ indicates that the capture rate with circle hooks is higher or lower compared to J-hooks. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

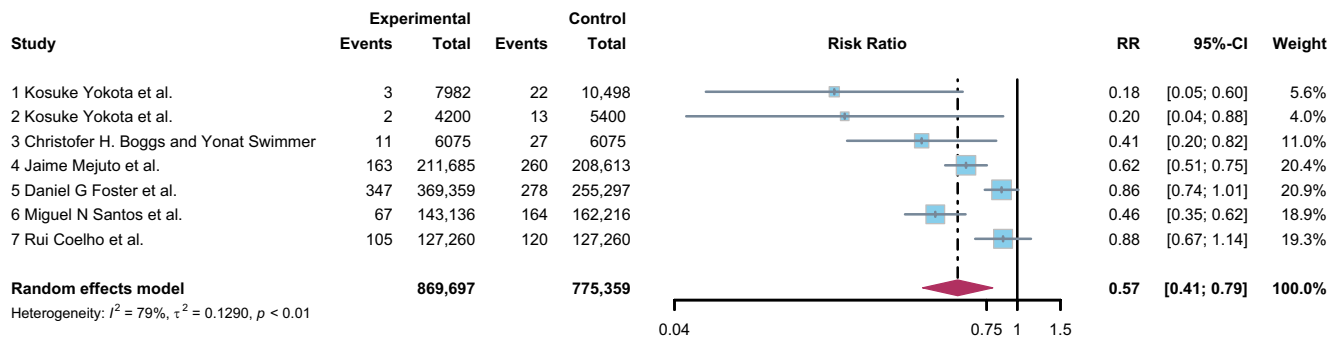


FIGURE 12 | Effect of replacing squid bait with fish bait on the risk of capturing sea turtles. $RR > 1$ or $RR < 1$ indicates that the capture rate of fish bait is higher or lower compared to squid bait. The 'Events' in the meta-analysis plot represent the number of turtles captured, while 'total' refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights of each study and random-effects model are shown. The experiments in the references are ordered from top to bottom by publication date and are distinguished by numerical identifiers.

The significance of using meta-analysis in our study lies in its robust statistical approach (Balduzzi, Rücker, and Schwarzer 2019), enabling the synthesis of research findings from various publications. However, our meta-analysis had certain limitations. It included only studies with control data on sea turtle bycatch mitigation, potentially overlooking more effective methods not yet field-tested or subjected to controlled experiments. Some mitigation strategies may have been excluded due to classification issues or insufficient sample sizes, which, despite their potential effectiveness, rendered them unsuitable for meta-analysis. This pointed to a gap in the current research landscape, necessitating extensive field testing of a wider array of mitigation techniques to better understand their effectiveness and applicability.

We applied the robust variance estimation method (CR2) to assess the robustness of our results against heteroscedasticity and within-cluster correlation. Changes in standard errors and

confidence intervals were minimal, indicating insensitivity to heteroscedasticity. All analyses passed the publication bias test (p -values > 0.05). It should be noted that although all the research methods using circle hooks for mitigation were based on field experiments involving longline fishing, variations in the sizes of the circle and J-style hooks used might affect the results of the heterogeneity test in our study. If heterogeneity persists within a subgroup, the variation in the results of the meta-analysis may be attributed to the diverse range of fishing techniques, captured species and catch environments, thus influencing heterogeneity (Seraphy et al. 2012).

Additionally, categorisation remains challenging due to significant disparities in latitude and longitude across experimental locations, compounded by inconsistencies or the absence of recorded soaking time (the distribution of the field tests is shown in Figure 16). Due to the limited number of studies and the lack

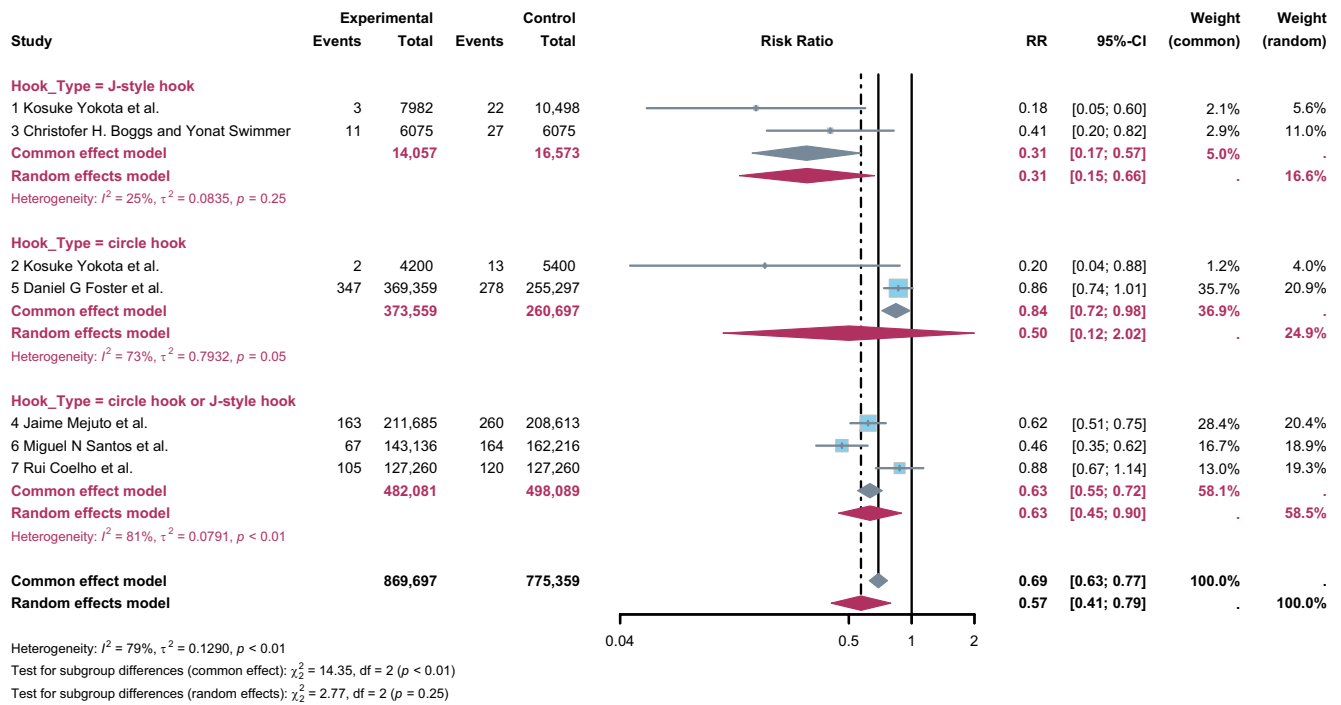


FIGURE 13 | Subgroup analysis of seven studies on bait (hook type), $RR > 1$ or $RR < 1$ indicates that the capture rate of fish bait is higher or lower compared to squid bait. The ‘Events’ in the meta-analysis plot represent the number of turtles captured, while ‘total’ refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

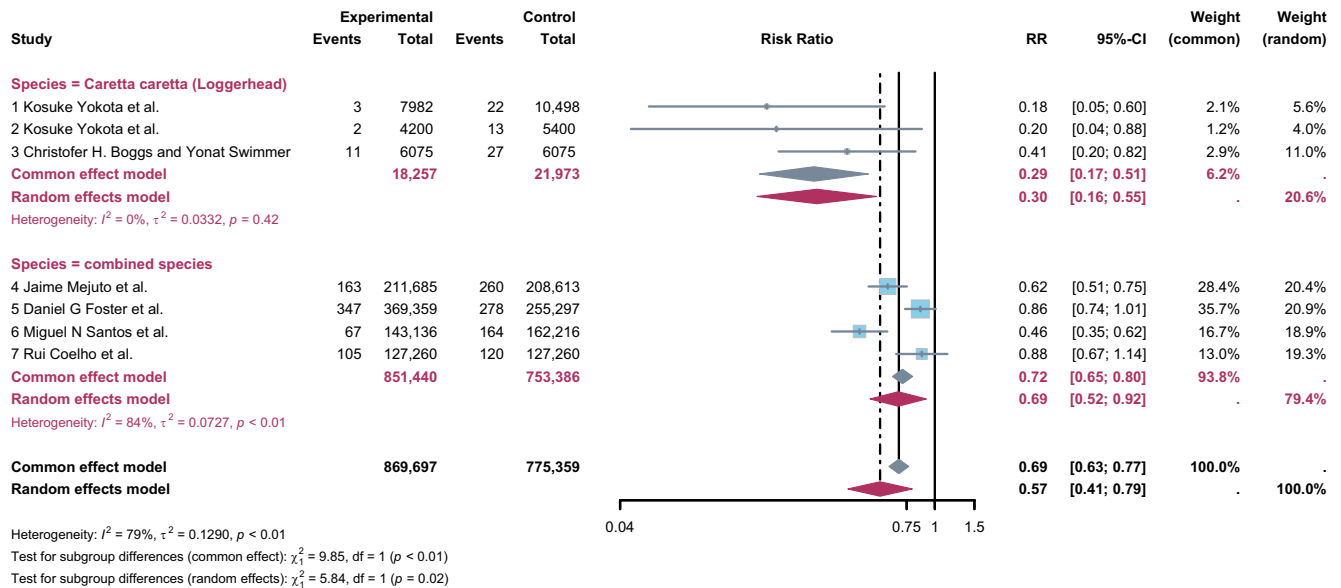


FIGURE 14 | Subgroup analysis of seven studies on bait (species), $RR > 1$ or $RR < 1$ indicates that the capture rate of fish bait is higher or lower compared to squid bait. The ‘Events’ in the meta-analysis plot represent the number of turtles captured, while ‘total’ refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

of precise geographical coordinates, we did not perform subgroup analysis or meta-regression on these factors. Nonetheless, their potential impact on heterogeneity remained evident. There are variations in mitigation effects across different areas, with significantly higher or lower effects in some regions. For instance, the experimental mitigation effect on loggerhead turtles

in the Mediterranean Sea was superior to that in the Azores waters (Figure 16), suggesting that geographical differences, local environmental conditions or marine ecosystem characteristics may influence the effectiveness of mitigation methods, necessitating optimisation for specific regions to apply mitigation measures effectively.

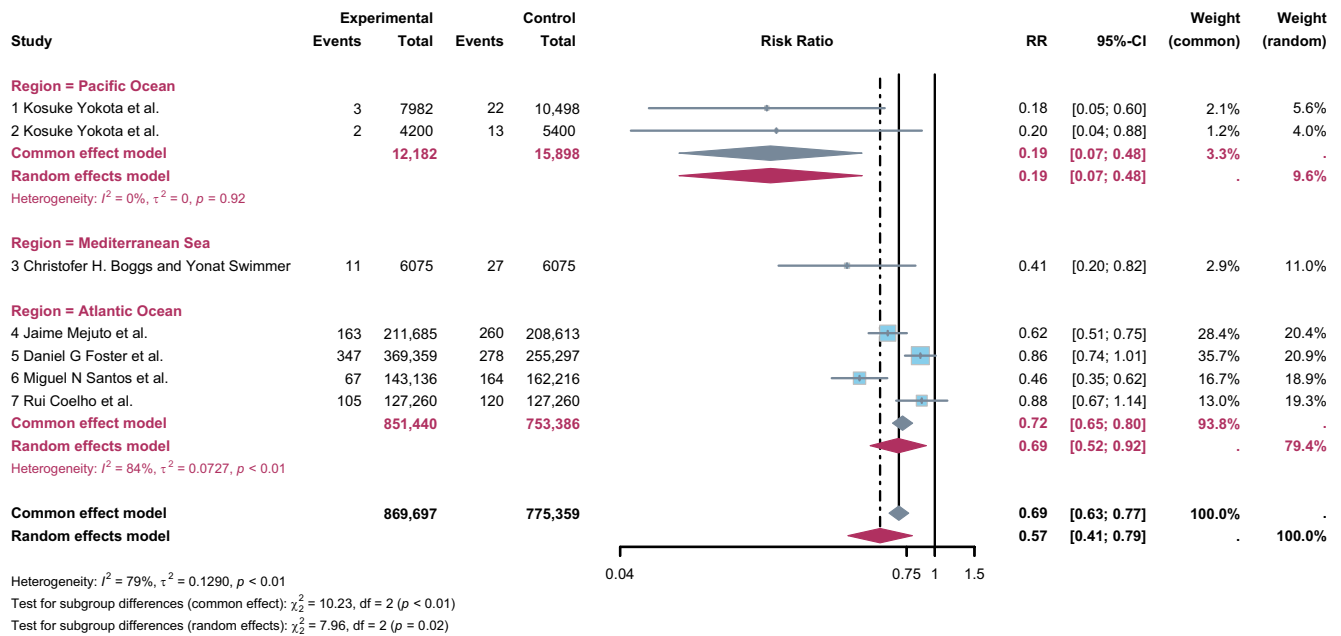


FIGURE 15 | Subgroup analysis of seven studies on bait (region), $RR > 1$ or $RR < 1$ indicates that the capture rate of fish bait is higher or lower compared to squid bait. The ‘Events’ in the meta-analysis plot represent the number of turtles captured, while ‘total’ refers to the number of hooks observed. The effect sizes (relative risk—RR), 95% confidence intervals (CI) and weights for both the common effects model and random effects model are shown.

4.1 | Using Circle Hooks to Mitigate Sea Turtle Bycatch

In the analysis of loggerhead turtles, we found that the use of circle hooks was effective in reducing the bycatch of loggerhead turtles. However, different bait types significantly impacted the heterogeneity of the analysis. This heterogeneity was likely to arise from variations in the bait composition during operations—in the combined bait group, study 6 (Mejuto, García-Cortés, and Ramos-Cardelle 2008) used average bait composition (i.e., fish bait and squid bait each account for approximately 50%, along with a small portion of other types of bait), while study 9 (Domingo et al. 2012) predominantly used squid (87%) and a smaller proportion of mackerel (13%). Interestingly, using squid bait did not result in any mitigation for loggerhead turtles and in fact, it performed even worse than the combination bait or fish bait (Figure 4), consistent with the findings of Watson et al. (2005). It may be reasonably inferred that modifying the bait is a more effective approach than altering the hook design in terms of mitigating the bycatch of loggerhead. And our meta-analysis of loggerhead turtles aligns with Reinhardt et al. (2018)—the 95% confidence interval < 1 ($RR = 0.58$, 95% CI = 0.36 to 0.92).

Our findings on green turtles suggest a conservative interpretation, particularly in light of the random effects model results. The meta-analysis indicated that only study 6 showed a significant reduction in green turtle bycatch with circle hooks and this study also emerged as a source of heterogeneity (Figure S3). In contrast, the other five studies using size 18/0 or size 16/0 circle hooks did not demonstrate any reduction in bycatch (Table S2; Figure 5). The reasons for the inconsistent results with size 18/0 circle hooks in green turtles remain unclear and future research should explore these species-specific responses to hook size and design. However, we did not dismiss the possibility that variations

in fishing methods, bait types or the size and abundance of sea turtles across different oceans could influence the effectiveness of circle hooks in reducing green turtle bycatch. These differences might obscure the true impact of circle hooks. The reference data revealed inconsistencies in soaking times and J-hook sizes used in control experiments (Table S2; Andraaka et al. 2013), which could lead to variability in results. Such factors might explain why some studies, such as study 6, showed a significant mitigating effect that could be due to chance and not representative of other findings. Moreover, while circle hooks might indeed be ineffective for green turtles, the most probable explanation for the non-significant results is the limited number of studies and insufficient statistical power to detect a true effect. This suggests that further field experiments and research are essential to accurately assess the effectiveness of circle hooks in reducing green turtle bycatch (Table S2; Figure 5; Figure S3; Andraaka et al. 2013; Reinhardt et al. 2018).

The heterogeneity within the leatherback group stemmed from study 1: study 1 (Mejuto, García-Cortés, and Ramos-Cardelle 2008) used size 16/0 J-style hooks, while study 5 (Domingo et al. 2012) also used a larger J-hook of size 17/0, but with a smaller sample size, resulting in less impact on the model's heterogeneity compared to study 1. In other experiments, size 9/0 J-style hooks were used uniformly (Table S3). This variation suggests that differences in hook size may contribute to variability in results. Furthermore, both the leatherback and loggerhead turtle groups demonstrated that using mackerel bait with circle hooks was more effective for mitigation than squid bait or mixed bait (Figures 4 and 7). Our findings for leatherback turtles differed from those of Reinhardt et al. (2018), likely due to differences in inclusion criteria and literature selection. Nevertheless, our results indicate that circle hooks have significant potential to reduce the bycatch of leatherback turtles.

TABLE 1 | Meta-analysis results of target fish species after replacing J-style hooks with circle hooks.

Species	RR	RR (CR2)	95% CI	95% CI (CR2)	p	p (CR2)	I ² (%)	H	Q	τ^2
Tunas (<i>Thunnus</i> spp.)	1.30	1.30	0.93–1.81	0.88–1.91	0.1209	0.1570	98.8	9.09	743.16	0.2591
Sharks (Mostly blue sharks)	1.15	1.15	0.96–1.37	0.93–1.40	0.1416	0.1705	99.6	16.36	2945.24	0.0978
Swordfish (<i>Xiphias gladius</i>)	0.83	0.83	0.70–0.99	0.69–1.00	0.0346	0.0559	98.5	8.14	861.71	0.0854

In our research on olive ridley, study 6 had a significant impact on heterogeneity, as illustrated in Figure S5. Although studies 5, 6, 7 and 8 were all conducted by the same author, the results still exhibited heterogeneity (Andraka et al. 2013). Subgroup analysis revealed that bait type and region did not significantly affect heterogeneity and not all subgroup analyses resolved the heterogeneity issue (Figures 10 and 11). The reasons for heterogeneity remain unclear, but potential factors include variations in fishing methods, hook materials, bait types, fishing locations, turtle nesting seasons coinciding with fishing activities or differences in turtle size or abundance across regions (Andraka et al. 2013; Serafy et al. 2012).

4.2 | Using Fish Bait to Mitigate Sea Turtle Bycatch

Our results and existing studies indicated that fish bait significantly reduced the number of loggerhead turtles remaining on hooks but did not significantly affect the hook retention of swordfish or blue sharks (*Prionace glauca*) (Santos et al. 2012; Figure 14). However, Gilman et al. (2020) presented a contrasting view, suggesting that bait affects catches of blue sharks and that tuna and istiophorid billfishes may be more likely to be caught on squid bait compared to fish bait. The overall effect of bait on pelagic sharks remains unclear. Laboratory experiments and field tests in the Mediterranean showed that when squid and mackerel were used as bait simultaneously, loggerhead turtles were more likely to feed on squid rather than mackerel (Echwikhi et al. 2010). A study found that loggerhead turtles were more likely to tear and consume fish meat fragments or completely detach the fish from the hook for consumption (Stokes et al. 2011). In contrast, the flesh of squid is harder to tear or detach from the hook and most hard-shelled turtle species tend to eat the squid completely. This results in squid bait usually covering the hook until the turtle swallows the hook, when using fish as bait, hard-shelled turtle species may better observe or perceive the presence of the hook and sometimes actively avoid the hook when in contact with metal (Stokes et al. 2011). Based on this, it is reasonable to hypothesise that the impact of bait on loggerhead may outweigh the choice of hook type, as our meta-analysis findings support this—it was not exclusively the combination of circle hooks and fish bait that mitigated loggerhead bycatch; similarly, J-style hooks paired with fish bait also demonstrated a reduction in loggerhead bycatch (Figures 4 and 13). Additionally, research by Huang et al. (2016) suggested that fish bait had a similar impact on leatherbacks, speculating that it might be due to fish bait obstructing the point of the Japanese tuna hook—a reasonable hypothesis suggests that fish bait might have a mitigating effect on all sea turtles.

However, discernible variations in the overall effects of bait on different turtle species were evident (Figure 14). These results suggest that fish bait impacts various sea turtle species differently—hard-shelled turtles tend to bite the hooks, while leatherbacks often get hooked in other parts of their bodies, such as fins (Watson et al. 2005). This interaction could contribute to the heterogeneity observed in our meta-analysis. Moreover, the heterogeneity might be attributed to the distinct characteristics of the marine ecosystems in the Pacific and Atlantic, coupled with

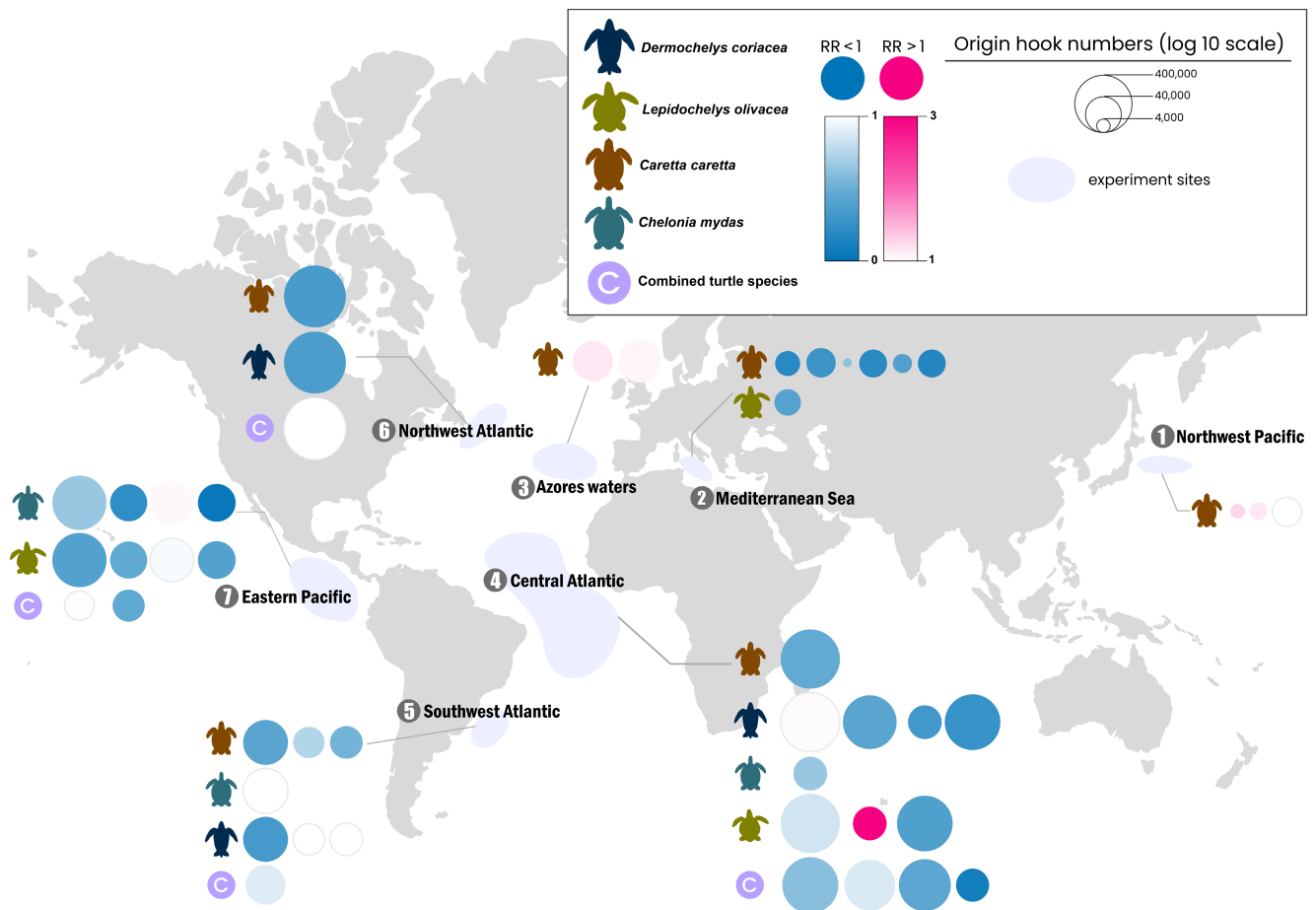


FIGURE 16 | Approximate geographical distribution of field tests (represented by circles of varying colours and shades indicating different results of the experiments, with circle size proportional to the number of hooks used). [Correction added on 5 December 2024, after first online publication: In Figure 16, the scientific name ‘*Eretmochelys imbricata*’ is replaced as ‘*Dermochelys coriacea*’ in this version.]

differences in fisheries management and conservation practices, which could explain the substantial variations seen in regional subgroup analyses (Figure 15).

4.3 | Target Fish Species and Sharks

Our analysis of circle hooks revealed no significant adverse effects on tuna and shark catch rates and even suggested a slight increase in catches, aligning with findings from Reinhardt et al. (2018). For swordfish, the results of robust variance estimation included 1, indicating that circle hooks may not substantially alter swordfish catch rates; observed variations are likely due to random error or sample variability (Table S8). Regarding the economic impact of circle hooks, reports indicated that replacing J-style hooks with circle hooks and switching bait from squid to mackerel significantly reduced swordfish catches (Santos et al. 2012). However, the potential economic losses for fishermen remain uncertain, as the change in hooks or bait might also affect the capture rates of other commercially valuable species (Santos et al. 2012). A recent study might have shed some light on the issue—a meta-analysis suggested that using fish bait might mitigate shark catches compared to squid bait and a qualitative literature review implied that tunas and billfishes may have had higher capture rates when using squid bait, contradicting the goal of reducing sea turtle and blue shark

catches (Gilman et al. 2020). While circle hooks and fish bait show promise in reducing bycatch for certain species, their varying effects on target species and other bycatch must be carefully considered. Future research should continue to explore these dynamics, aiming to develop strategies that address complex trade-offs involved in bycatch mitigation.

4.4 | Other Mitigation Methods

There were methods aimed at mitigating or reducing sea turtle bycatch (the current sample size is insufficient for a meta-analysis to evaluate)—stingray baits were found to be more effective than mackerel baits, but their impact on targeted fish species remains a concern (Echwikhi et al. 2010). Studies examining the effect of bait colour (blue versus non-blue) concluded that blue bait did not reduce turtle bycatch (Swimmer et al. 2005; Yokota, Kiyota, and Okamura 2009). Hooks with and without offset showed no significant difference in the number of turtles captured (Swimmer et al. 2010). These methods, while explored, appear ineffective in significantly mitigating sea turtle bycatch, requiring continued research and innovation in this area.

The Hookpod-mini device (Gianuca et al. 2021) at the branch end of longline fishing showed no significant impact on

sea turtle bycatch but effectively mitigated seabird bycatch. Experimental data from southern Brazilian waters indicated that both Hookpod-mini equipped vessels and untreated vessels experienced higher bycatch rates during the warm seasons (spring and summer) compared to cold seasons (autumn and winter). Conversely, another referenced study found higher sea turtle bycatch numbers in spring and autumn during offshore experiments in the southwestern Atlantic, with lower bycatch observed in summer and winter (Sales et al. 2010). Despite these discrepancies, both results suggest a correlation between sea turtle bycatch and seawater temperature, indicating temporal variation. This seasonal aspect could inform future policymaking to regulate the fishing seasons for longline fishing vessels.

Current research suggests that sea turtles can perceive light within the blue-green range, potentially attracting them towards longline fishing gear—mitigating sea turtle bycatch may be possible by prohibiting green vessel lights in Hawaii's waters (Witzell 1999; Pradhan and Leung 2006; Wang et al. 2007; Southwood et al. 2008). However, this reduction could also impact the catch rates of targeted fish species (Afonso et al. 2021). Environmental factors like lunar illumination may interact with species' colour sensitivity, affecting both incidental turtle catches and targeted fish species differently (Afonso et al. 2021). Identifying a light wavelength that is invisible to most target fish throughout the lunar cycle but affects sea turtles could offer significant potential, given that green and loggerhead turtles have a broader colour perception range than pelagic fish (Yokota, Kiyota, and Okamura 2009). Circle hooks with a wire appendage (Boggs and Swimmer 2007; Swimmer et al. 2011) have shown promise in reducing sea turtle bycatch. Increasing hook size further decreases the likelihood of catching hard-shelled sea turtles, although more field experiments are needed to confirm effectiveness for leatherback turtles, as there have been reports of detrimental effects on the catch rates of tunas and billfishes (Boggs and Swimmer 2007; Swimmer et al. 2011). Despite these challenges, these strategies warrant further investigation for their potential to mitigate sea turtle bycatch.

4.5 | Prospects and Limitations

Future methods to mitigate sea turtle bycatch could focus on understanding and leveraging sea turtle senses, such as olfaction

or audition. Research has shown that sea turtles consume bait treated with natural defensive compounds (like *Aplysia* ink and *Loligo* spp. ink) or pungent and bitter substances (Southwood et al. 2008). Yellowfin and skipjack tuna, the target fish species, also consumed squid bait treated with these chemicals (Southwood et al. 2008). While these treated baits did not produce the desired results, green turtles and loggerheads can detect and identify various chemicals in bait underwater (Manton, Karr, and Ehrenfeld 1972; Southwood et al. 2007). This suggests that olfactory interventions in bait remain a promising research avenue. However, the complex field conditions at sea necessitate further research to validate the effectiveness of these treated baits in practical applications.

To effectively mitigate the accidental capture of sea turtles, it is crucial to promote or develop methods that prevent sea turtle capture using longline hooks without impacting the catch rate of target fish species. If these methods adversely affect target fish catches, it would be challenging to gain adoption from fishermen or fishing companies (Santos et al. 2012). Ideal mitigation methods should differ from restrictive measures like fishing closures or protected areas. Instead, they should allow fishermen or fishing companies to continue their fishing operations at lower costs while implementing sea turtle bycatch reduction strategies in swordfish and tuna longline fisheries. Accordingly, we have presented a figure illustrating the feasibility of the methods discussed in this research for practical applications, with fish baits and circle hooks identified as the most feasible approaches (Figure 17).

We did not conduct further meta-analyses on other bycatch species or target fish species, revealing a limitation in our study. The potential effects of circle hooks on these species could be either positive or negative, an area warranting future research. Other meta-analyses employing similar methodologies provide a broader understanding of the impacts on other bycatch and target fish species (Watson et al. 2005; Avery et al. 2017; Reinhardt et al. 2018; Santos et al. 2019; Gilman et al. 2020). Our reliance on publications primarily from BMIS represents another limitation, potentially restricting our study's scope and excluding certain findings from turtle-related field experiments and longline fisheries targeting dolphinfish. Secondly, our analysis does not delve into specific environmental factors, such as sea surface temperature (SST), which could have significantly enhanced our analysis.










Methods	Decrease ↓				No significant effect —		Increase ↑		No records ✕		Is it economically viable?	Is field deployment feasible?
	Loggerhead	Green turtle	Leatherback	Olive ridley	Combined species (sea turtle)	Tunas	Swordfish	Sharks				
 Circle hook replaces J-style hook	↓	—	↓	↓	✕	↑	—	↑	✓	✓	✓	✓
 Fish bait replaces squid bait	↓	✕	✕	✕	↓	?	?	?	?	?	?	✓
 Circle hook (size 16/0) with appendage	✕	✕	✕	↓	✕	✕	✕	✕	?	?	?	✓
 Blue-dyed	—	✕	✕	✕	✕	—	—	—	✓	✓	✓	✓
 Stingrays bait	↓	✕	✕	✕	✕	✕	—	↑	?	?	?	✓
 Offset 14/0 circle hooks	✕	—	✕	—	✕	—	—	—	✓	✓	✓	✓
 Circle hook (size 14/0) with appendage	✕	↓	✕	↓	✕	↓	↓	↓	?	?	?	✓
 Blue light bait/white light bait	✕	✕	✕	✕	↓	↓	↓	↓	?	?	?	✓
 Circle hook with hookpod-mini	—	✕	—	✕	✕	—	—	—	✓	✓	✓	✓

FIGURE 17 | Reference information on mitigation methods. Decrease: Reduce the capture rate of the species mentioned in the figure; increase: Increase the capture rate of the species mentioned in the figure.

While some studies report sea temperature data or other environmental variables, this is not consistent across all the research reviewed, potentially introducing heterogeneity and hindering analysis. It is crucial to establish standardised research designs and data collection procedures, including the consistent reporting of environmental factors. Such standardisation could enhance the robustness and accuracy of meta-analyses in this field.

We adopted strict screening criteria and data quality control measures to ensure the credibility of the included research. However, a notable limitation of this study is the absence of formal quality assessment tools, such as the Cochrane Risk of Bias Tool (Higgins et al. 2011), which could impact the interpretation of results. While these tools have been widely applied and standardised in clinical and public health research, their use in fisheries and ecological research is still developing. It is essential to acknowledge that applying non-standardised quality assessment tools may introduce inconsistencies in assessment outcomes. Given the varying levels of bias risk and understanding among different assessors, future studies should focus on developing and employing appropriate quality assessment tools customised for fisheries research. Another key limitation of our analysis is the assumption that bycatch reduction methods have uniform effects across different sea turtle subspecies. Evaluating interventions at the broader species level may not fully capture the nuances of these methods, potentially leading to increased heterogeneity. More focused research on specific populations or subspecies is urgently needed to yield more precise insights. Future field tests should aim to collect and analyse data at the subspecies level or incorporate regional management units (Wallace et al. 2010, 2011). Such targeted research will enhance understanding of the specific responses and management needs of sea turtle populations.

5 | Conclusion

Sea turtle bycatch is a pervasive issue in global swordfish and tuna longline fisheries, posing significant threats to turtle populations worldwide. Through the evaluation of mitigation methods to determine their effectiveness on sea turtle bycatch, our analysis has four main conclusions. First, circle hooks can effectively reduce sea turtle bycatch in swordfish and tuna longline fisheries, with varying mitigation effects across different sea turtle species. However, the use of different bait types may obscure the effectiveness of hooks and prioritising fish bait over squid bait as a bycatch reduction method might be more important than the choice of hook types. The differing outcomes observed across the Atlantic, Pacific and Mediterranean oceans emphasise the importance of tailoring bycatch mitigation measures to regional contexts. Given the intricate interactions between fishing practices and local environmental conditions, ongoing research and adaptive management are essential to protect sea turtle populations while sustaining fishing activities. Although circle hooks and fish bait are expected to reduce the incidental capture of sea turtles while not yet presenting adverse effects on target species such as tuna, swordfish and sharks, the different impacts they have on other bycatch must be carefully considered in future research to improve the complex issues involved in mitigating bycatch. Future approaches must strike a delicate balance

between conserving non-target species and maintaining the sustainability of longline fisheries. Other methods currently lack sufficient data for meta-analyses, but promising strategies, such as circle hooks with wire appendages and blue and white lights, require extensive field testing across various species and fishing conditions to confirm their effectiveness. Lastly, we highlight the importance of ongoing and expanded data collection to address current limitations and strengthen future meta-analyses. Developing comprehensive, species-specific and regionally tailored strategies is vital for the sustainable management of swordfish and tuna longline fisheries and the protection of vulnerable sea turtle populations. Overall, given the numerous uncertainties arising from field experiments at sea, coupled with the complexity of controlling variables that may not be singular, the results from our naive model can only provide a vague general direction. In the future, with more empirical data from sea measurements supporting higher-level or multi-layered meta-analyses, it may be possible to reach more precise and clear conclusions.

Author Contributions

C.Z. and R.W. conceptualisation. H.Y. and C.Z. drafted the initial version of the manuscript (methods and code written by H.Y.). E.G., F.Z., J.C., L.X., L.S., X.D. and S.T. provided critical assistance in revising the manuscript. All authors contributed to the writing of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest. The illustrations in this manuscript are partly hand-painted and partly royalty-free vector graphics.

Data Availability Statement

The data used in the meta-analysis are listed in the supplementary information. All codes included in this study are available upon request by contact with the corresponding author. If you seek further information about the Bycatch Management Information System (BMIS), please visit <https://www.bmis-bycatch.org> or refer to the link provided in our manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.