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A meta-synthesis of marine turtle post-release mortality to support evidence-informed bycatch mitigation policy

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A meta-synthesis of marine turtle post-release mortality to support evidence-informed bycatch mitigation policy

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————— Linkage to MSRA Section 318 Priority Areas —————

This meta-synthesis addresses the following cooperative research priority for the PIFSC Cooperative Research program identified under the appropriate sections of the MSRA:

“2. assessing the amount and type of bycatch or post-release mortality occurring in a fishery (Section 318(c)(ii))”

Deriving robust post-release mortality estimates for marine turtle species captured incidentally in pelagic fisheries operating in the Pacific Islands Region has also been identified as a priority research project by the Western Pacific Regional Management Council (WPRFMC) and by that Council’s Science and Statistics Committee. The specific WPRFMC 5-year research priorities addressed by this meta-synthesis are:

“PS1.2.2 Improve species-specific estimates of post-hooking mortality rates”

“PS2.3.1 Conduct research to improve post-hooking mortality rates (e.g., understanding effects of trailing gear on post-hooking mortality rates)”

Summary

A single study can never provide definitive insights into an ecological or conservation problem. Hence an accumulation or synthesis of knowledge from many studies is required to support evidence-informed conservation decision-making. Such knowledge synthesis is the foundation for principled, transparent and evidence-informed fisheries bycatch mitigation policies.

Marine turtles are caught incidentally in commercial pelagic longline fisheries that operate in most oceanic regions. Many marine turtles bycaught in these fisheries are released alive from the gear but can die subsequently, known as post-release or delayed mortality. While estimates of natural mortality are becoming increasingly available for various marine turtle species, this is not the case for reliable estimates of the cryptic sources of fishery bycatch related mortality such as post-release mortality. So, assessing study-specific estimates of marine turtle bycatch related mortality would help to support informed bycatch mitigation policy.

We present here the first comprehensive meta-synthesis of post-release mortality for 5 marine turtle species bycaught in various fishing gears. However, we specifically focussed on a meta-analytic based synthesis of the post-release mortality for loggerhead marine turtles bycaught in pelagic longline fisheries since most compiled study-specific summaries were for this species and gear type. So, our meta-synthesis revealed a knowledge gap concerning reliable information on fishery discard rates for other marine turtle species beside the loggerhead and for other gear-types beside pelagic longline gear.

We then used a Bayesian meta-regression modelling approach to draw robust and generalisable inference from our compiled study-specific summaries of loggerhead post-release mortality. The benefits of using a model based meta-synthesis to support evidence-informed fisheries bycatch mitigation policy are: (1) combines all known relevant data into a single coherent modelling framework, (2) increases precision by combining effect sizes for many (often underpowered) studies, (3) uses robust and reproducible statistical procedures to combine those data, (4) helps to evaluate the uncertainty of a conclusion based on the accumulated evidence and (5) communicates clearly any conclusion that can validly be drawn from the accumulated evidence.

We found that the most informative predictors of loggerhead marine turtle post-release mortality in our meta-synthesis were ocean basin (Mediterranean vs elsewhere) and the anatomical hooking position (shallow-hooked vs deep-hooked). Our findings suggest that management of fishing gear components that can affect anatomical hooking position such as bait type or hook size could present an opportunity to limit loggerhead bycatch and reduce post-release mortality.

It was estimated that deep-hooked loggerheads irrespective of geographic region were 2.6 times (95% HDI¹: 0.7-6.1) more likely to die when bycaught in pelagic longline fisheries than shallow-hooked loggerheads. The estimated post-release mortality rate for shallow-hooked loggerheads was 0.079 (95% HDI: 0.02-0.15) and 0.213 (95% HDI: 0.09-0.35) for deep-hooked loggerheads. It was further estimated that deep-hooked loggerheads bycaught in Pacific Ocean pelagic longline fisheries were ca 5.6 times (95% HDI: 0.7-19.4) more likely to die when than shallow-hooked

¹ HDI = highest posterior density interval

loggerheads. The estimated Pacific Ocean only PRM for shallow-hooked loggerheads was 0.041 (95% HDI: 0.02-0.12) and 0.228 (95% HDI: 0.01-0.41) for deep-hooked loggerheads.

Reliable post-release mortality estimates are necessary but not sufficient to determine the cause-specific mortality rates needed for assessing the population-level consequences for marine turtle population exposure to anthropogenic hazards. Cause-specific mortality for a loggerhead marine turtle population given an estimate of fishery-specific bycatch can be derived using for instance: (1) the pooled or aggregated post-release mortality rates presented here for say deep-hooked loggerheads coupled with (2) a natural annual mortality rate for loggerheads that are now also readily available.

The meta-analytic derived post-release mortality rates and the posterior predictive summaries presented here not only support evidence-informed bycatch mitigation policy but could also be used directly as informative priors for (1) future and updated meta-analytic syntheses and (2) for modelling the potential impact of cryptic mortality on the long-term population dynamics of loggerhead marine turtles exposed to various fishery hazards.

Introduction

Marine turtles are caught incidentally in commercial pelagic longline fisheries that operate in most oceanic regions (Chaloupka et al 2004, Wallace et al 2010, Gilman et al 2016a, Swimmer et al 2017, Báez et al 2019). Many marine turtles bycaught in these fisheries are released alive from the gear but can die subsequently, known as post-release mortality (Chaloupka et al 2004, Swimmer et al 2014). Cryptic sources of fishery discard or bycatch mortality such as post-release mortality (Gilman et al 2013) are considered a serious risk world-wide to the long-term viability of endangered marine turtle populations (Chaloupka 2003, Lewison et al 2004, Wallace et al 2013).

This issue was considered sufficiently serious for the US National Marine Fisheries Service (NMFS or NOAA Fisheries) to convene a working group to provide best estimates on post-interaction mortality rates based on the severity of the injury to the turtle and the amount of gear removed for hard-shell and leatherback turtles (Ryder et al 2006). The findings from that working group are used in helping to determine jeopardy as part of a US Biological Opinion assessing the risk of exposure of a protected marine species to a specific fishery hazard such as pelagic longline gear (see for example National Marine Fisheries Service 2012).

However, the process used by Ryder et al (2006) for deriving those estimates was not consistent with the transparency principles proposed for developing “evidence-informed” conservation management policy (Dicks et al 2014). One fundamental transparency principle includes the need for a prior independent synthesis of the best scientific information available (Gurevitch et al 2018, Nichols et al 2019). That evidence synthesis would then be used by content-experts to evaluate the likelihood of long-term population-level consequences of exposure to anthropogenic hazards such as pelagic longline gear (Chaloupka 2003).

Evidence or meta-syntheses are widely considered the foundation for informed conservation policymaking (Woodcock et al 2014, Nakagawa et al 2015, Gurevitch et al 2018) and used recently

to compile robust estimates of bait-specific catch rates in pelagic longline fisheries to support evidence-informed bycatch mitigation strategies (Gilman et al 2020).

The post-release mortality estimates proposed by Ryder et al (2006) were based on a very limited empirical foundation that is now out-of-date (Chaloupka et al 2004, Swimmer et al 2014). There have been several empirical studies of post-release mortality (PRM) since Ryder et al (2006) that could provide a stronger foundation for deriving species- and gear-specific post-release mortality estimates for marine turtles — not only for the Pacific Islands Region but also globally to support a far broader perspective of the bycatch risks to marine turtle populations in general and for the endangered loggerhead (*Caretta caretta*) marine turtle in particular (Chaloupka 2003).

Therefore, we present here a meta-synthesis (Vetter et al 2013, Gurevitch et al 2018) of all known marine turtle post-release mortality estimates with a focus not only on the Pacific Islands Region but also within a global context. Such a global synthesis based here on a meta-analytic modelling approach (van Houwelingen et al 2002) provides (1) an independent empirically based foundation for the assessment of marine turtle population viability exposed to pelagic fishery hazards and (2) the basis for evidence-informed revision of the policy prescriptions in Ryder et al (2006) that are used in NOAA Fisheries Biological Opinions affecting the continued operation of pelagic longline fisheries in the Pacific Islands Region.

Data

We followed the PRISMA guidelines to assemble a dataset suitable for our meta-analytic based synthesis (Liberati et al 2009). Specifically, we used a two-step citation search procedure to compile peer-reviewed and grey literature relevant to marine turtle post-release mortality. Firstly, a structured bibliographic search was undertaken using the Web of Science bibliographic databases (Sevinc 2004) and bycatch-specific databases such as the WCPFMC Bycatch Management Information System (<https://www.bmis-bycatch.org/references>) and the Consortium for Wildlife Bycatch Reduction (<https://www.bycatch.org/>). Our Web of Science search string for TOPIC comprised:

(post-release OR post-hook OR post-capture) AND (mortality OR survival OR survivor*) AND ((marine AND turtle*) OR (sea AND turtle*)) NOT ((freshwat* AND turtle*))*

We then followed on with an unstructured literature search by reviewing the reference lists of relevant publications and reports from the structured search, posting a query on ResearchGate.net, and through enquiries with an informal network of fisheries and marine turtle specialists. We then screened the compiled literature to determine which publications could be selected for inclusion in our meta-synthesis of marine turtle post-release mortality.

The study or publication inclusion criteria included (1) whether there was an empirical estimate of post-release mortality (PRM) for a marine turtle species, (2) whether the PRM estimate was for any marine turtle species bycaught in a pelagic longline fishery and (3) subsequently whether the PRM estimate was only for loggerhead marine turtles bycaught in a pelagic longline fishery.

The two-step citation search identified 35 unique PRM estimates of which 25 met eligibility criterion (1) for inclusion in the meta-synthesis (Appendix 1: PRISMA flowchart). The full citation source for those 25 estimates derived from 17 studies is shown in Appendix 2 with those 25 effect sizes (or PRM estimates) summarized in Appendix 3. Five of those 25 estimates were multiple species PRM estimates for entanglement interactions rather than longline fisheries bycatch, while one of those 25 estimates was for olive ridley turtles caught in a pelagic longline fishery — but a single species-specific case is not suitable for quantitative analysis.

Hence six of the 25 PRM estimates (for 5 species) were excluded from quantitative PRM meta-analysis but are summarized in Table 1 for further qualitative consideration in our meta-synthesis. Nonetheless, we derived PRM estimates for those studies based on the recorded mortalities and the number at risk in the sample using a Bayesian binomial likelihood estimator that accounts for zero recorded mortalities (Tuyl et al 2008). So, here the mean posterior PRM rate and a 95% highest posterior density interval (HDI) was summarised by sampling from a binomial likelihood with a Bayes-Laplace prior (Tuyl et al 2008) using the `binom` R package (Dorai-Raj 2014) — rather than using the raw summaries. Nonetheless, we included for completeness the maximum likelihood estimates that do not account for zero recorded mortalities (here zero mortalities results in a zero MLE).

Only 19 estimates met all selection eligibility criteria and those PRM estimates (or effect sizes) were then used for the global meta-analysis of loggerhead marine turtles bycaught in pelagic longline fisheries (Appendix 1: PRISMA flowchart). Three of the 19 retained PRM estimates were for deep-hooked loggerhead marine turtles caught in Mediterranean pelagic longline gear but maintained in land-based rehabilitation facilities prior to release to the wild and so were modelled separately.

The remaining 16 PRM estimates were for loggerheads released at-sea following capture and comprised 9 shallow-hooked and 7 deep-hooked loggerheads (see Chaloupka et al 2004 for definitions of shallow- and deep-hooked loggerhead turtles bycaught in pelagic longline fisheries). The gear interaction or anatomical hooking position is a known PRM risk factor for loggerhead turtles bycaught in pelagic longline fisheries (Chaloupka et al 2004, Gilman & Huang 2017, Swimmer et al 2014).

Methods

Predictor screening

We recorded several PRM covariates or predictors for each study (Appendix 4), but our small sample of effect sizes ($n=25$ PRM estimates) precluded using all the predictors in our meta-analysis modelling workflow without risking model overfitting. So, we used the `metaforest` package for R (van Lissa 2020) to fit a random-effects weighted metaforest model with clustered bootstrap sampling to screen for potentially informative predictors using a variable importance metric (see Curry et al 2018 for an informative and recent application of this screening approach). Briefly, `metaforest` implements a machine-learning based exploratory approach adapted from random forest algorithms (Wright & Ziegler 2017) to identify any relevant linear or nonlinear

predictors, and perhaps higher-order interactions, from a wide selection of predictors (or risk factors). Random forests are a commonly used machine-learning tool for classification and for ranking of candidate predictors based on variable importance measures (Janitza et al 2018). We used those covariates or predictors identified using the variable importance metric in our subsequent Bayesian meta-regression modelling workflow outlined below.

Statistical modelling approach

Meta-analysis is a robust statistical procedure for synthesising evidence from multiple studies to support, for instance, evidence-informed conservation and fisheries management (Gilman et al 2016, Gilman et al 2020). Specifically, we used a random-effects meta-analytic modelling approach (van Houwelingen et al 2002, Higgins et al 2009, Seide et al 2019) to aggregate and summarise post-release mortality rates for loggerhead marine turtles bycaught in pelagic longline fishing gear. We implemented these meta-analytic or data synthesis models within a fully Bayesian inference framework (Sutton & Abrams 2001, Du et al 2020, Pappalardo et al 2020) and applied those models to the 19 PRM estimates for loggerhead turtles bycaught in pelagic longline fisheries (see Appendix 3).

Specifically, we fitted multilevel Bayesian random-effects regression models to the proportion of loggerhead turtles recorded in each of the 19 summaries that were found dead on the gear. The specific random-effects meta-regression structure used here is known as a binomial-Normal hierarchical meta-analytic model (Seide et al 2019, Günhan et al 2020: or Model 4 in Jackson et al 2018) but was fit here within a Bayesian inference framework (Pappalardo et al 2020) using weakly informative regularising priors (Lemoine 2019, Ott et al 2021, Röver et al 2021). Bayesian inference is particularly useful for small sample situations and especially so for small sample meta-syntheses as was the case here (Rhodes et al 2015, McNeish 2016, Seide et al 2019, Pappalardo et al 2020).

It is a binomial-Normal GLMM regression model because the model likelihood is binomial to account for the proportion response data while the random effects are sampled from a multivariate Gaussian distribution (Günhan et al 2020) — other more flexible distributional forms for the random-effects such as heavy-tailed multivariate Student-t distributed effects (McCulloch & Neuhaus 2011, Noma et al 2022) were also explored using leave-one-out cross-validation (LOOcv) metrics and Bayesian stacking to estimate any comparative difference in expected predictive accuracy between the various models fitted (Vehtari et al 2017, Yao et al 2018). We also explored using LOOcv metrics whether a regression model with Beta-binomial likelihood that accounts for over-dispersion or correlated effects (Mathes & Kuss 2018) might be a better fit to the proportion data compared to the models with binomial likelihood.

Some PRM estimates used in our models were undertaken by the same author(s), possibly resulting in correlated effects between studies by the same authors or research group (see Konstantopoulos 2011 for a thorough discussion of this issue). Gilman et al (2016) addressed this issue using a 3-level hierarchical mixed-effects model in their multi-species meta-regression modelling of pelagic longline catch rates for sharks. We adopted a similar multilevel random effects structure to account for study-specific or citation effects and apparent research-group-specific effects for those studies

comprising similar study authors. This hierarchical or multilevel modelling approach accounts for both the within-study and the between-study variance (Zhou et al 1999).

We then fitted separate GLMMs with various predictors for the following datasets: (1) all 19 PRM estimates for the loggerheads caught in pelagic longline fisheries operating in 3 ocean basins (Mediterranean, Atlantic, Pacific) to review geographic-specific effects, (2) the 3 PRM estimates for deep-hooked loggerheads released post-recovery from the Mediterranean rehabilitation centres and then (3) the 16 PRM estimates for the shallow- and deep-hooked loggerheads released at-sea following capture in either the Atlantic or Pacific Oceans.

We fitted these 3 GLMMs with binomial likelihood appropriate for proportion data (Stijnen et al 2010, Lin & Chu 2020) using the Stan computation backend (Carpenter et al 2017) via the `brms` interface for R (Bürkner 2017). All models were fit with 4 chains with 10,000 iterations per chain after a warm-up of 2000 iterations. Model convergence was assessed using parameter-specific diagnostics such as multiple chain rank plots, bulk and tail effective sample size metrics and a rank-based *Rhat* statistic (Vehtari et al 2021). Further evaluation of the best-fit-model was then assessed using graphical posterior predictive checks (Gelman et al 2000, Gabry et al 2019). All inference was then made using the best-fit model and the posterior predictive samples (Higgins et al 2009, Rhodes et al 2015, Lazic et al 2020).

We also included potentially informative predictors in these meta-regression structured GLMMs to evaluate whether the post-release mortality rate was a function of those predictors. We had previously screened a range of potential predictors to determine a minimal set of risk factors in the predictor screening stage above — predictors or risk factors such as ocean, anatomical hooking position and hook type. A probability statement about the existence of predictor-specific effects in each model was determined with the 40,000 model-specific posterior draws using the probability of direction metric in the `BayestestR` package for R (Makowski et al 2019).

The best-fit GLMM for each of the three PRM estimate sets (or effect sizes) were then used to derive an overall or pooled post-release mortality rate for each dataset based on the posterior predictions for each estimate comprising 40,000 samples or draws that were also used to derive the uncertainty estimates. We summarized the estimated PRMs in a forest plot of the study-specific posterior densities to display the model-predicted posterior estimates (Schild & Voracek 2015, Parola et al 2020).

Here we use the highest posterior density interval (HDI) as our measure of uncertainty, which is the shortest credible interval (Kruschke & Liddell 2018) and promoted by Pappalardo et al (2020) to support robust meta-analyses. The HDIs were summarized from the posterior predictive samples for each best-fit model using the `tidybayes` package for R (Kay 2020a) and the `stat_halfeye()` function from the `ggdist` package for R (Kay 2020b).

This summary display or forest plot showing both the full posterior predictive distribution of the parameter coupled with the summary metrics (median, 95% HDI) helps to (1) support a more precise form of communicating parameter uncertainty (van der Bles et al 2019) and (2) rigorously accounts for between-study heterogeneity (Wang & Lee 2019). We also included the observed effect sizes in these bespoke forest plots for comparison to illustrate why the model-based

estimates are used to account for PRM estimates of varying precision (see also Parola et al 2020) — PRM estimates with low precision are shrunk towards the pooled estimate while the estimates with high precision show little if any shrinkage. Parameter shrinkage within Bayesian modelling frameworks is analogous to the best linear unbiased predictors or BLUPs in a frequentist modelling framework (Röver & Friede 2020). The observed effect sizes (± 1 standard deviation) were derived using the `escalc()` function in the `metafor` package for R (Viechtbauer 2010) and the data summarised in Appendix 3.

Finally, the estimated effects summaries based on the best-fit conditional regression GLMMs were then adjusted for variable sample size using the estimated marginal means approach (Searle et al 1980, Lenth 2016) and implemented using the `emmeans` package for R (Lenth 2020) — here however, we specifically use the median rather than the mean as the preferred meta-analysis estimator (Hartwig et al 2020). Muff et al (2016) provide an informative overview of the important difference between conditional and marginal effects regression models. We then summarised the marginal effect posterior densities to assess any apparent difference for instance between the estimated marginal PRMs for deep-hooked and shallow-hooked loggerheads. The posterior ratio summary was also included in the summary plot for this effect. The `ggplot2` (Wickham 2016) and `colorspace` (Zeileis et al 2020) packages for R were used for all summary graphics.

Accounting for heterogeneity

Irrespective of meta-analytic model fit, any remaining between-study heterogeneity can still be an issue affecting parameter estimation and inference in mean-response meta-analysis (Senior et al 2016). Such heterogeneity is assessed using metrics such as the estimated between-study variance (τ^2) and a relative index of that variance (I^2). These metrics are readily derived in a frequentist (Higgins & Thompson 2002, Senior et al 2016) or a Bayesian modelling framework that also provides uncertainty estimates of the metric and not just the point-estimate (Röver et al 2021).

The between-study variance, parameterised here as (τ) rather than (τ^2), was then directly estimated by our GLMM-based meta-regressions with the point-estimate summarised as the mean of the posterior predictive samples for that parameter and a 95% HDI also derived from those samples using the `tidybayes` package for R (Kay 2020a). The relative index metric (I^2) is a parameter derived from the τ posterior predictive samples and was summarised using the procedure used to summarise τ .

Publication bias

We explored potential publication bias (Page et al 2021) for the best-fit GLMMs using a standard error-based contour-enhanced funnel plot (Sterne & Egger 2001, Peters et al 2008), which was more readily implemented here within a frequentist rather than a Bayesian modelling framework. Specifically, we used model predicted post-release mortality rates estimated using the `metafor` package for R (Viechtbauer 2010) but with the `GLMMadaptive` package for R (Rizopoulos 2020) as the backend for fitting a frequentist-based binomial-Normal meta-analytic model.

But as stated above, Bayesian inference is better suited for small sample meta-syntheses and so was the main inference framework used here to derive the post-release mortality estimates and

measures of uncertainty. Moreover, our Bayesian GLMMs can be easily modified to account for nonlinear predictor functional form as Bayesian GAMMs (see Gilman et al 2021), which is not readily implemented in a frequentist meta-analytic setting.

Results

Miscellaneous rates

The six PRM estimates that were excluded from any quantitative meta-analysis are summarized in Table 1. The binomial likelihood derived PRM estimates ranged from ca 0.08 to 0.50 for the 5 marine turtle species and the 4 fishing gears — most were caught in that gear by entanglement with only one estimate for a gear using hooks. These estimates based on the data provided in Appendix 3 are included here for completeness but are too limited and heterogeneous to warrant further statistical analysis other than for potential predictor screening. So, the 6 miscellaneous effect sizes for 5 marine turtle species summarised in Table 1 represents the qualitative component of our meta-synthesis — a synthesis that then also comprised a formal meta-analytic statistical modelling or quantitative component for the loggerheads bycaught in pelagic longline fisheries.

Predictor screening

The random forest derived variable importance plot identified several potentially informative risk factors or predictors of post-release mortality for the 25 PRM effect sizes summarised in Appendix 3. The out-of-bag ($R^2(oob)$) and cross-validation ($R^2(cv)$) predictive performance metrics suggest that the random effects weighted metaforest model was an adequate fit to the 25 PRM effects sizes and so including the set of predictors improved model fit (Appendix 5: SF1).

However, only 2 predictors (ocean basin, gear interaction) were deemed sufficiently informative for the PRMs with a variable importance metric $> ca\ 0.40$ (Appendix 5: SF1) — a threshold proposed for exploratory predictor selection using the metaforest approach (van Lissa 2020). The 2 predictors were **ocean basin** (Mediterranean, Atlantic, Pacific) and **gear interaction** (entangled, shallow-hooked, deep-hooked). Hence all subsequent meta-analytic regression modelling included those predictors in the Bayesian GLMMs fitted to the 19 PRM estimates (the 6 studies in Table 1 are now excluded and so no entanglement records used).

Model evaluation diagnostics

Convergence diagnostics such as multiple chain rank plots, and the effective posterior sample size (ESS) metrics coupled with the rank-based diagnostic statistic $Rhat < 1.01$ (Vehtari et al 2021), all reflected convergence of the 3 Bayesian GLMMs with binomial-Normal likelihood used here for statistical inference. The best-fit GLMMs identified by the LOOcv and Bayesian stacking metrics fitted all 3 data sets well as shown for example by the graphical posterior predictive check tests summarised in Appendix 5: SF2 for the model fitted to the 19 PRM effect sizes for loggerhead turtles bycaught in pelagic longline fisheries operating in 3 ocean basins (Mediterranean, Atlantic, Pacific).

All best-fit models were GLMMs with binomial-Normal likelihood with no support for models with Beta-binomial likelihood nor for models with Student-t distributional forms for the random-effects (or GLMMs with binomial-Student likelihood). All inference was based on these binomial-Normal GLMMs conditional on the fixed effects or predictors (ocean, gear interaction for instance) and the study-specific and research-group-specific random effects included in the models.

Existence and significance of anatomical hooking-position and geographic effects

Figure 1 shows for example the existence of the modelled conditional effects based on the posterior draws from the best-fit GLMM for the 19 loggerhead PRMs. Specifically, it shows that the gear interaction predictor had a > 0.97 probability of significantly lower post-release mortality for shallow-hooked loggerheads compared to deep-hooked loggerheads. While loggerheads in either the Atlantic or Pacific Ocean studies had a > 0.92 probability of significantly lower post-release mortality than loggerheads bycaught in the Mediterranean.

There was no meaningful difference between the estimated PRMs for the Pacific or Atlantic studies (posterior probability < 0.73). No other predictors such as telemetry platform used (PSAT, PTT) or hook type were found to have a significant existence effect — as expected from the metaforest predictor screening procedure.

Estimated marginal hooked-position effect

The predicted GLMM-adjusted marginal hooked-position effect for the loggerhead PRM rates is summarised in Figure 2 for shallow-hooked and deep-hooked loggerhead marine turtles. It was estimated that deep-hooked loggerheads were 2.6 times (95% HDI: 0.7-6.1) more likely to die when bycaught in pelagic longline fisheries than shallow-hooked loggerheads. The estimated PRM for shallow-hooked loggerheads was 0.079 (95% HDI: 0.02-0.15) and 0.213 (95% HDI: 0.09-0.35) for deep-hooked loggerheads.

Estimated marginal geographic effect

The predicted GLMM-adjusted marginal geographic effect for the loggerhead PRM rates is summarised in Figure 3 for loggerhead marine turtles bycaught in pelagic longline fisheries in the Atlantic [0.064 (95% HDI: 0.01-0.19)], Pacific [0.111 (95% HDI: 0.01-0.31)] and Mediterranean [0.294 (95% HDI: 0.02-0.69)]. It is apparent that loggerheads in the Mediterranean are more likely to die when bycaught in pelagic longline fisheries than loggerheads in either the Atlantic or Pacific Oceans — a finding consistent with the posterior directional probabilities shown in Figure 1.

Study-specific post-release mortality rates for Atlantic and Pacific loggerhead marine turtles

A bespoke forest plot summarizing the study-specific model-predicted post-release mortality rates for the 7 deep-hooked loggerhead studies and the estimated overall or pooled effect is shown in Figure 4. The observed study-specific effects sizes are also shown to reveal the degree of shrinkage for those studies with smaller sample sizes and so less precision in the observed effect size. Figure 5 shows a similar forest plot for the 9 shallow-hooked loggerhead studies that were also summarised for the pooled effect in Figure 2.

Estimated marginal hooked-position effect for the Pacific Ocean

The predicted GLMM-adjusted marginal hooked-position effect for the loggerhead PRM rates in Pacific Ocean is summarised in Figure 6 for shallow-hooked and deep-hooked loggerhead marine turtles. It was estimated that deep-hooked loggerheads were 5.6 times (95% HDI: 0.7-19.4) more likely to die when bycaught in Pacific Ocean pelagic longline fisheries than shallow-hooked loggerheads. The estimated Pacific Ocean only PRM for shallow-hooked loggerheads was 0.041 (95% HDI: 0.02-0.12) and 0.228 (95% HDI: 0.01-0.41) for deep-hooked loggerheads.

Study-specific post-release mortality rates for Mediterranean loggerheads

Figure 7 shows a forest plot summarizing the model-predicted conditional post-release mortality rates derived for the deep-hooked loggerheads released back to the Mediterranean following recovery in rehabilitation centres. The observed effect sizes are also shown along with the estimated pooled PRM effect for the 3 studies, which was 0.53 (95% HDI: 0.17-0.87).

Heterogeneity

We found little between-study heterogeneity in our meta-regression estimated loggerhead PRMs as shown for instance by the heterogeneity metrics estimated for the dataset comprising the 19 shallow- and deep-hooked loggerhead effect sizes summarised in Figures 4, 5 and 7: $\tau = 0.61$ (95% HDI: 0.50-0.73) and $I^2 = 23.9\%$ (95% HDI: 0-57.4%). Metric rules-of-thumb suggest that $\tau < 0.65$ [or $\tau^2 < 0.40$] or $I^2 < 50\%$ indicate low-to-moderate between-study heterogeneity and hence of little concern for model inference (Higgins & Thompson 2002).

Publication bias

We found no evidence of potential publication bias for either shallow- or deep-hooked loggerheads that could be identified by funnel plot asymmetry based on a random-effects meta-analytic model fitted within a frequentist inference framework. For instance, Appendix 5 SF3 shows a standard error-based contour-enhanced funnel plot for the 7 deep-hooked loggerhead studies with the between-study heterogeneity included — the corresponding and bespoke forest plot for the 7 deep-hooked loggerhead study effect sizes estimated using a frequentist binomial-Normal GLMM is shown in Appendix 5 SF4.

Discussion and Conclusion

Reliable estimates of natural and anthropogenic sources of mortality are important for modelling marine turtle population dynamics exposed to various anthropogenic hazards and for developing hazard mitigation strategies (Chaloupka 2003, Bjørndal et al 2011). While estimates of natural mortality are becoming increasingly available for various marine turtle ontogenetic stages (Pfalter et al 2018), this is not the case for reliable estimates of the cryptic sources of fishery bycatch related mortality such as post-release mortality (Chaloupka et al. 2004, Sasso & Epperly 2007, Swimmer et al 2014). Even less is known of potential sublethal post-release effects such as impaired somatic growth and reproductive capacity (Williard et al 2015) — and not just for marine turtles but for

most threatened marine species incidentally caught in coastal and pelagic fisheries (Wilson et al 2014, Mohan et al 2020).

So, assessing study-specific estimates of marine turtle cryptic sources of bycatch related mortality would help to better support informed US bycatch mitigation policy (Ryder et al 2006, Stacy et al 2016). However, the utility of a conservation policy intervention or the validity of a scientific hypothesis cannot be determined by a single study. An accumulation or synthesis of evidence is needed to support strong inference about intervention efficacy or for uncovering demographic generalizations (Woodcock et al 2014, Gurevitch et al 2018, Nichols et al 2019). There are 3 statistical approaches used for conducting a comprehensive, transparent and reproducible evidence synthesis (Sung et al 2014, Du et al 2020):

- meta-analysis (including meta-regression) of the aggregated or summary results from each study [see Gilman et al (2016) and O’Dea et al (2019) for fisheries relevant examples using frequentist inference and Gilman et al (2020) using Bayesian inference]
- mega-analysis of the original data sets used in each study — also known as integrative data models or “individual participant data” models [see Musyl & Gilman (2019) for a mega-analysis of silky shark post-release mortality rates using frequentist inference]
- Bayesian data fusion using augmented or aggregated data-dependent priors [an uncommon approach and while no fisheries-specific study is immediately apparent, the prior-proposal-recursive Bayesian inference procedures applied by Hooten et al (2021) to Steller sea lion pup survey data is possibly an example]

We present here the first comprehensive meta-synthesis of post-release mortality for 5 marine turtle species bycaught in various fishing gears. All studies provided aggregated or summary estimates of post-release mortality that were suitable for meta-analysis rather than mega-analysis, which would have required sourcing the original data from all data custodians and is one of the major challenges for mega-analyses (Sung et al 2014). Moreover, it has been shown that meta-analysis of summary data usually provides similar inference (or conclusions) to evidence syntheses based on mega-analysis of the original raw data (Mathew & Nordstrom 1999, Sung et al 2014).

While we used a meta-analytic approach, the main benefits of using meta-synthesis based on any of the 3 statistical approaches to support evidence-informed fisheries management or conservation policy are: (1) combines all known relevant data into a single coherent modelling framework, (2) increases precision by combining effect sizes for many (often underpowered) studies, (3) uses robust and reproducible statistical procedures to combine those data, (4) helps to evaluate the uncertainty of a conclusion based on the accumulated evidence and (5) communicates clearly any conclusion that can validly be drawn from the accumulated evidence.

Loggerhead post-release mortality

Most of our 25 compiled studies provided summary post-release mortality data for loggerheads incidentally caught in pelagic longline fisheries (Appendix 3). Clearly, there is a concerning lack

of post-release mortality estimates for other marine turtle species and gear types. So, our statistical modelling based meta-synthesis focussed mainly on drawing generalisable inference about post-release mortality for loggerhead marine turtles bycaught in pelagic longline fisheries (Figures 2-7). We specifically used a Bayesian meta-regression modelling approach to draw robust and generalisable inference from the modest sample set of 19 loggerhead post-release mortality summaries.

Reliable estimates of loggerhead post-release mortality are urgently needed to better inform US fisheries management authorities about the risk of incidental capture in pelagic longline fisheries (Ryder et al 2006, Swimmer & Gilman 2012). Our meta-synthesis based on a robust assessment of many studies provides the first reliable post-release loggerhead mortality estimates suitable for supporting informed bycatch policy making and hazard mitigation. The pooled or overall global mean PRM for shallow-hooked loggerheads was 0.079 (95% HDI: 0.02-0.15) and 0.213 (95% HDI: 0.09-0.35) for deep-hooked loggerheads. The pooled mean PRM for Pacific Ocean shallow-hooked loggerheads was 0.041 (95% HDI: 0.02-0.12) and 0.228 (95% HDI: 0.01-0.41) for Pacific Ocean deep-hooked loggerheads. Our meta-synthesis also reveals a knowledge gap concerning reliable information on fishery discard rates for other marine turtle species beside the loggerhead and for other gear-types beside pelagic longline gear.

Loggerhead post-release mortality risk factors

The most informative predictors of loggerhead post-release mortality in our meta-synthesis (Figure 1, Appendix 5 SF1) were ocean basin (Mediterranean vs elsewhere) and the anatomical hooking position (shallow-hooked vs deep-hooked). Anatomical hooking position is a known risk factor for the post-release mortality of marine turtles bycaught in longline gear (Chaloupka et al 2004, Epperly et al 2012). Hook size was not recorded for the studies used in our meta-analysis but is a known risk factor itself for the anatomical hooking position where the larger the hook the lower the proportion of deep-hooked bycatch (Yokota et al 2012, Gilman et al 2018). Anatomical hooking position is also a post-release mortality risk factor for other marine species such as coastal sharks caught and released from recreational fisheries (Mohan et al 2020).

Anatomical hooking position is also a function of hook type where circle hooks tend to catch hard-shelled turtles like loggerheads in the mouth resulting in a shallow-hooked interaction while J-shaped hooks tend to catch turtles internally resulting in a deep-hooked interaction (Cooke & Suski 2004, Epperly et al 2012). Bait type can also be a factor since shallow-hooked turtles are often caught on squid baited hooks and deep-hooked turtles on fish baited hooks (Epperly et al 2012, Gilman & Huang 2017). So, hook and bait type are two possible bycatch hazard mitigation options to reduce cryptic mortality sources such as post-release mortality for marine turtles — although hook type was not an informative predictor in our study (see Appendix 5 SF1).

We found little unexplained between-study heterogeneity in our model-derived loggerhead PRMs given those informative predictors (ocean basin, anatomical hooking position). And the predictive performance of our meta-analytic Bayesian GLMMs with binomial-Normal likelihood was sufficient to support strong inference (Appendix 5 SF2). Moreover, statistical modelling using Bayesian inference is particularly robust for small sample meta-syntheses as was the case here (Pappalardo et al 2020). So, it is unlikely that our meta-analytic models were mis-specified due to

unrecorded potential risk factors affecting PRMs that could not be sourced from the compiled summary effect sizes (Appendix 3).

Nonetheless, it is possible that the higher pooled PRM estimate for the Mediterranean Sea (Figure 7) was due to ocean basin-specific differences in the duration that a deep-hooked loggerhead was submerged prior to retrieval, the ensuing exercise (struggling) intensity prior to retrieval during longline gear haulback or hook removal practices. Exercise intensity has been shown to affect retrieval condition of bycaught species such as sharks prior to release from the gear (Bouyoucos et al 2018), and this might be important for predicting marine turtle post-release mortality (Epperly et al 2012). It is also possible that there are significant differences in the bycaught marine turtle handling and release methods used in Mediterranean pelagic longline fisheries compared to elsewhere (Álvarez de Quevedo et al 2013). So, there could be other informative predictors that were not considered here since they were unrecorded in the original studies but might be useful for inclusion where possible in further PRM meta-synthesis updates.

Marine megafauna cryptic mortality

Coggins et al (2007) suggest that cryptic mortality sources such as discard mortality can lead to recruitment overfishing with major ecological and economic consequences, especially for long-lived low productivity marine species such as apex predators. Despite this concern there is limited understanding of the extent of gear-specific fishery discard or post-release mortality for the marine megafauna such as seabirds (Phillips & Wood 2020), pelagic tunas (Sepulveda et al 2020), sharks (Mohan et al 2020, Sulikowski et al 2020, Whitney et al 2021), marine turtles (Chaloupka et al 2004, Swimmer et al 2014) and marine mammals such as dolphins (McHugh et al 2021) and pinnipeds (Punt et al 2021). Comprehensive meta-syntheses of cryptic mortality sources such as post-release mortality are only available for several species of pelagic shark (Musyl & Gilman 2019) and the loggerhead marine turtle (current study).

Cause-specific mortality

Estimating cause-specific mortality is important for developing reliable risk assessment models for marine turtle populations exposed to various anthropogenic hazards such as coastal and pelagic fisheries (Chaloupka 2003, Bjorndal et al 2011). Reliable estimates of annual survival rates (or natural mortality) are increasingly available for most marine turtle species (Pfaller et al 2018), but this is not the case for fishery-related mortality estimates derived using archival satellite tagging studies (Chaloupka et al 2004, Sasso & Epperly 2007, Swimmer et al 2014). Bowlby et al (2021) use a nonlinear regression model with Weibull-type parametric form to derive estimates of post-release as well as natural mortality for 2 discarded lamnid shark species, which were bycaught in pelagic longline fisheries and tracked post-release using archival satellite tags. This could be a promising approach to estimate mortality for marine turtles bycaught in pelagic longline gear, but it requires substantial long-term archival satellite tagging data to estimate both post-release and natural mortality — no marine turtle studies using archival satellite telemetry have achieved sufficient tracking duration or sample sizes to support this approach for the moment.

However, post-release mortality estimates are not sufficient to determine cause-specific mortality rates needed for assessing the population-level consequences for marine turtle population exposure

to anthropogenic hazards. Cause-specific mortality for a marine turtle population given an estimate of fishery-specific bycatch can be derived using a method-of-moments estimator presented by Joly et al (2009; see also Heisey & Patterson 2006), which is suitable for a competing risks assessment based on the following mortality rates: (1) a pooled or aggregated PRM summarised for instance in Figure 4 for deep-hooked loggerheads coupled with (2) a natural annual mortality rate for loggerheads sourced for instance from Pfaller et al (2018 – Figure 1).

Estimated marine turtle PRM rates need to be evaluated in a competing risks context with annual natural mortality to derive the all-cause or total mortality to assess population-level consequences of incidental capture in a pelagic longline fishery (Chaloupka 2003; see Byrne et al 2017 for an example for estimating shortfin mako shark bycatch mortality risk given a known natural mortality estimate). Otherwise, estimated PRMs can only be used as a relative but informative risk metric suitable for comparing for example the expected post-release mortality rates for deep- and shallow-hooked loggerheads (see Figure 2).

Post-release mortality is not the only source of mortality related to fishery bycatch. Some turtles can also drown on the submerged fishing gear and are then retrieved dead on gear haulback, which is known as at-vessel mortality (Gilman & Huang 2017). Reliable estimates of marine turtle at-vessel mortality are limited but could be of concern depending on the fishery and species (Camiñas et al 2006) — for instance, an apparent at-vessel mortality rate ca 17% was estimated for olive ridley turtles bycaught in a pelagic longline tuna fishery (Gilman et al 2016a) and an estimate ca 13% for olive ridley bycatch in a bottom trawl penaeid prawn fishery that accounted for capture rate (Poiner & Harris 1996).

Accounting for both at-vessel and post-release mortality (Álvarez de Quevedo et al 2013) is an important focus for future assessments of marine turtle cause-specific fishery related mortality as also shown for other marine species exposed to commercial longline fisheries such as large coastal sharks (Whitney et al 2021). A better understanding is also needed of the risk to marine turtle population viability exposed to other cryptic sources of fishery discard or bycatch mortality such as ghost-fishing caused by abandoned, lost or discarded gear (Gilman et al 2013).

Modelling beyond the mean

Sánchez-Tójar et al (2020) point out that most meta-analytic approaches to evidence synthesis are based on modelling the mean response rather than the variation in the expected response — which could help uncover previously overlooked effects. The modelling approach adopted in our study accounts for the sampling variance since it is based explicitly on the data generating process for proportion data (binomial likelihood). In fact, the procedure advocated by Sánchez-Tójar et al (2020)² based on separate models for study-specific mean and variance (coefficient of variation) effect sizes is not applicable for binomial data. Nonetheless, accounting explicitly within a single integrated statistical model for the mean effect sizes and variability of the data generating process is readily undertaken using the distributional regression modelling framework, which can model all distributional family-specific parameters including parameter-specific covariates (Kneib et al 2021).

² O'Dea et al (2019) used this procedure for a meta-analysis of the developmental temperature effects for fish

This distributional regression approach, applied within a Bayesian inference framework, was used recently to model Caribbean green turtle somatic growth dynamics (Bjorndal et al 2019). This approach is not applicable for the single family-parameter binomial likelihood used in our meta-synthesis but would have been applicable if we had used, for instance, the Beta-binomial meta-regression model that was discounted in our model selection procedures based on cross-validation and Bayesian stacking. Moreover, a multivariate or multiple response meta-analytic modelling approach (see Ogle et al 2021) that accounts simultaneously for both at-vessel and post-release mortality effect sizes is readily implemented using a Bayesian distributional regression modelling framework (Kneib et al 2021).

Future application

The meta-analytic derived post-release mortality rates and posterior predictive summaries (Figures 4-5) not only support evidence-informed bycatch mitigation policy but could be used directly as informative priors for (1) future and updated meta-analytic syntheses (Rhodes et al 2015) and (2) for modelling the potential impact of cryptic mortality on the long-term population dynamics of loggerhead marine turtles exposed to various fishery hazards (Chaloupka 2003). The prediction interval estimates for species-specific marine turtle annual survival rates provided by Pfaller et al (2018) could also be used for constructing informative priors for modelling of loggerhead marine turtle exposure to anthropogenic hazards such as pelagic fisheries and for providing an empirically informed natural mortality context for our cause-specific post-release mortality rates.

Future directions

Most of the 25 marine turtle post-release mortality studies explored here (Appendix 3) used a ratio-based estimator to derive an apparent PRM rate that has several known shortcomings (see Murray 2006), while 2 studies used a binomial-type estimator and bootstrap sampling to derive uncertainty estimates (Álvarez de Quevedo et al 2013, Swimmer et al 2014). Only two studies accounted explicitly for the `time-to-failure` of the telemetry device using statistical modelling approaches that also accounted for the censored data issues evident in the data — Chaloupka et al (2004) used a Kaplan-Meier-Turnbull estimator accounting for left, right and interval censored time-to-event data while Swimmer et al (2008) used a Bayesian georeferenced Cox-type semi-parametric hazard regression modelling approach for time-to-failure data that also accounted for left, right and interval censored mechanisms as well as left truncation (staggered entry). Sasso & Epperly (2007) used a known-fate estimator (Kaplan-Meier type product of binomial likelihoods) that accounted only for right censored data.

No other studies accounted for any data censoring mechanisms where applicable — see Chaloupka et al (2004) for a thorough discussion of the important issue of data censoring mechanisms for telemetry studies used to estimate marine turtle post-release mortality. So, a range of estimation methods of varying robustness were then used in the 25 studies to derive the PRM effect sizes considered here. Nonetheless, estimation method was not identified here as an informative risk factor or predictor of the apparent PRM estimates or effect sizes (Appendix 3) using a metaforest-based predictor screening approach (see Appendix 5 SF1).

Nevertheless, future marine turtle PRM telemetry-based studies could use more robust statistical modelling approaches that are applicable for `time-to-failure` data, such as hazard regression models that account explicitly for informative predictors and any study-specific data censoring mechanisms (Swimmer et al 2008). The Bayesian geoaddivitive hazard regression modelling approach used in Swimmer et al (2008) is a flexible means for modelling satellite telemetry data that involves a nonparametric baseline hazard function, nonproportional hazards, complex data censoring, nonlinear risk factor or predictor functional form and multiple sources of heterogeneity including georeferenced spatial effects and turtle-specific random effects. This Bayesian hazard regression modelling approach is particularly suitable for a mega-analysis of fishery discard or post-release mortality accounting for each individually tagged turtle and turtle-specific covariates sourced from each study included in the synthesis.

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Table 1: Miscellaneous post-release mortality rate estimates

| gear | ocean (habitat) | species | gear interaction | source | MLE ¹ | posterior mean | 95% highest posterior density interval | reference |
|---------------------------------|--------------------|---------------|------------------|---------|------------------|----------------|--|--------------------------|
| bottom trawl | Atlantic (coastal) | loggerhead | entangled | psat | 0.214 | 0.251 | 0.06 - 0.46 | Parga et al (2020) |
| | | olive ridley | entangled | psat | 0.000 | 0.200 | 0.00 - 0.53 | Maxwell et al (2018) |
| gillnets | Atlantic (coastal) | green | entangled | ptt | 0.200 | 0.251 | 0.04 - 0.48 | Snoddy & Williard (2010) |
| | | Kemp's ridley | entangled | ptt | 0.500 | 0.496 | 0.15 - 0.85 | Snoddy & Williard (2010) |
| fixed-gear (pot, trap, gillnet) | Atlantic (coastal) | leatherback | entangled | carcass | 0.151 | 0.155 | 0.11 - 0.20 | Hamelin et al (2017) |
| longlines | Pacific (pelagic) | olive ridley | shallow-hooked | psat | 0.000 | 0.077 | 0.00 - 0.22 | Swimmer et al (2006) |

1. MLE = maximum likelihood estimate

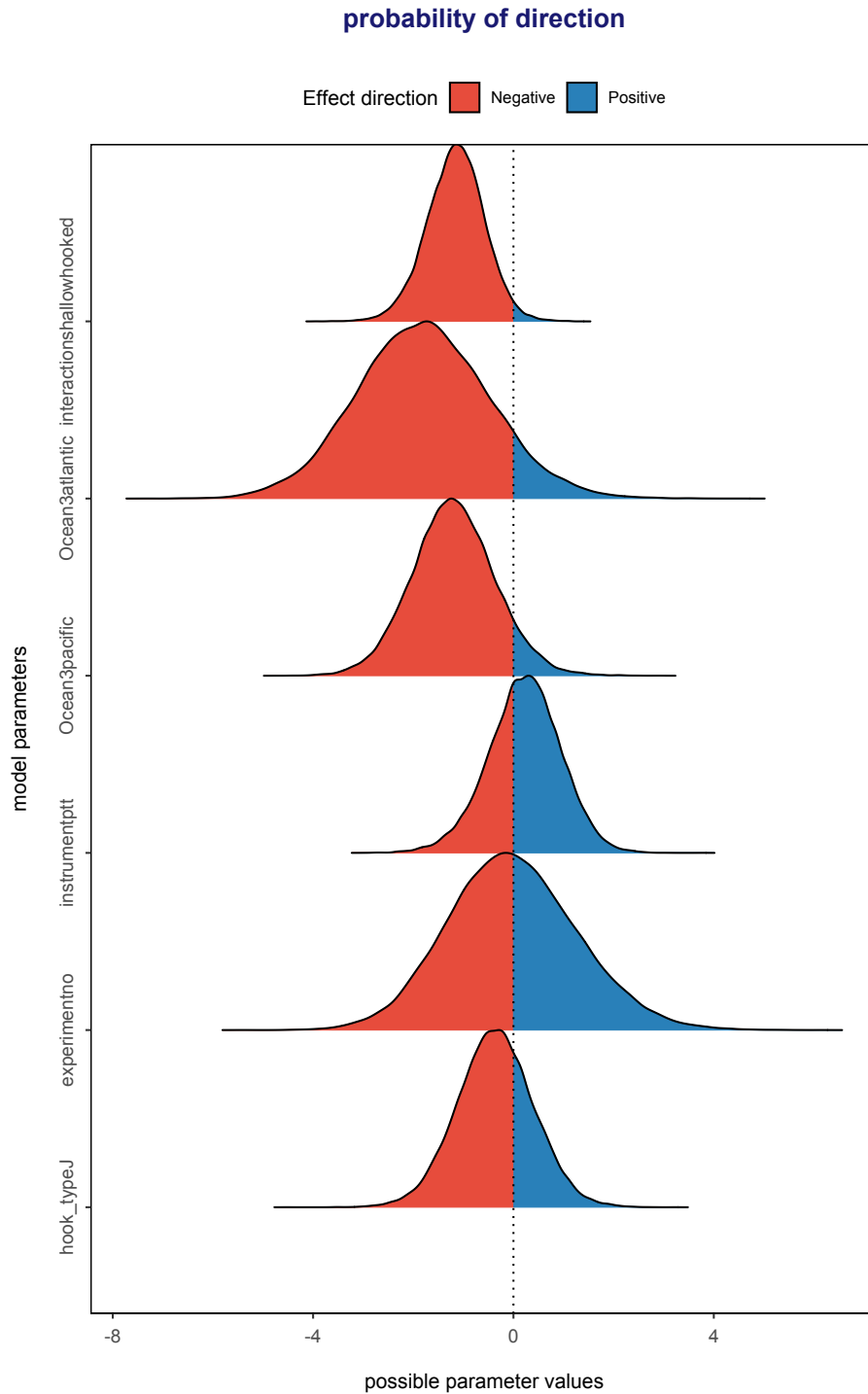


Figure 1 Probability of direction plot for selected parameters estimated from the binomial-Normal GLMM fit for the loggerhead post-release mortality rates. Polygons show the density summary of the 10,000 posterior draws and coloured given the estimated direction (positive or negative) of the effect or parameter. The proportion of the polygon that does not include zero is a statement about the probability of the proposed direction of the effect.

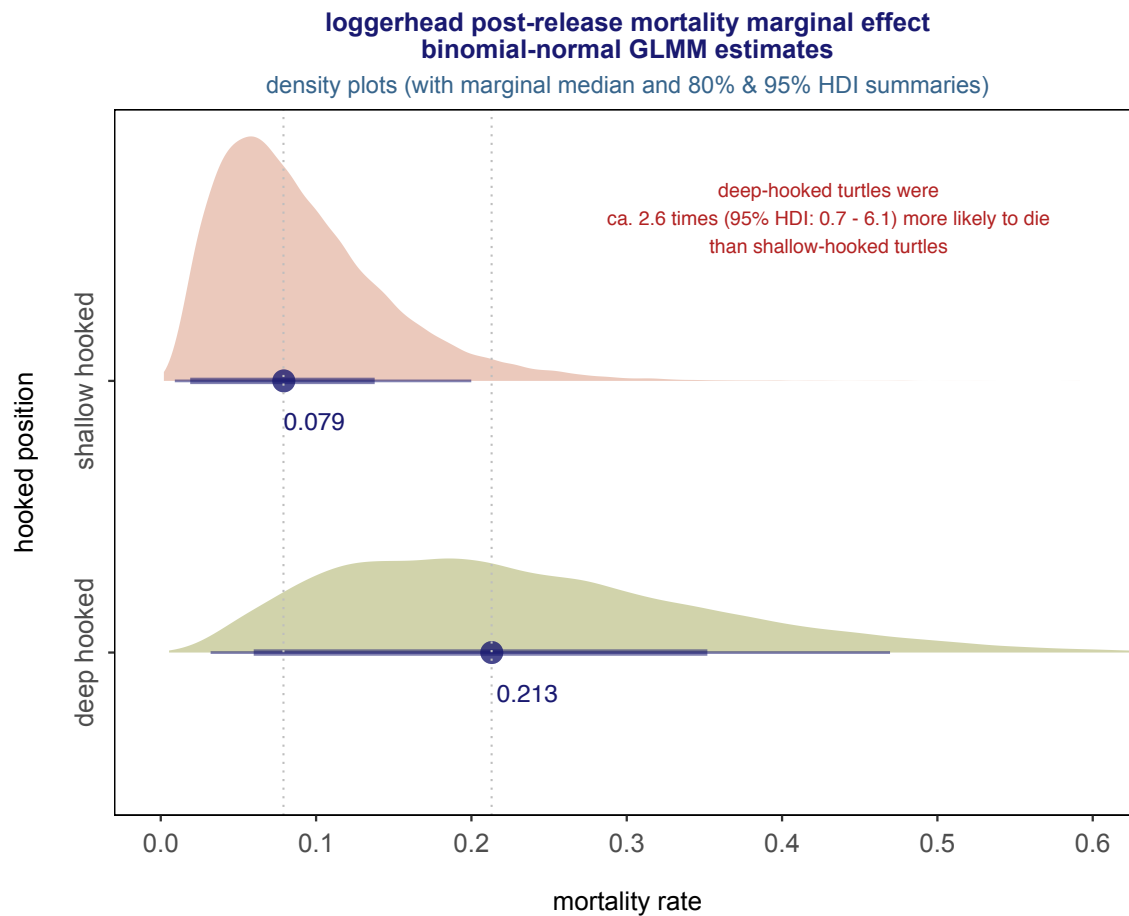


Figure 2 Summary of the estimated marginal median hooked-position effect (shallow- vs deep-hooked) sourced from a binomial-Normal GLMM conditional model fit for loggerhead post-release mortality rates. Coloured polygon shows the density distribution summary of the 10,000 posterior draws, solid dot (+ numeric label) = median estimated of the density polygon, thick horizontal line below each polygon shows the 80% highest posterior density interval for the density polygon while the thin horizontal line is the 95% HDI.

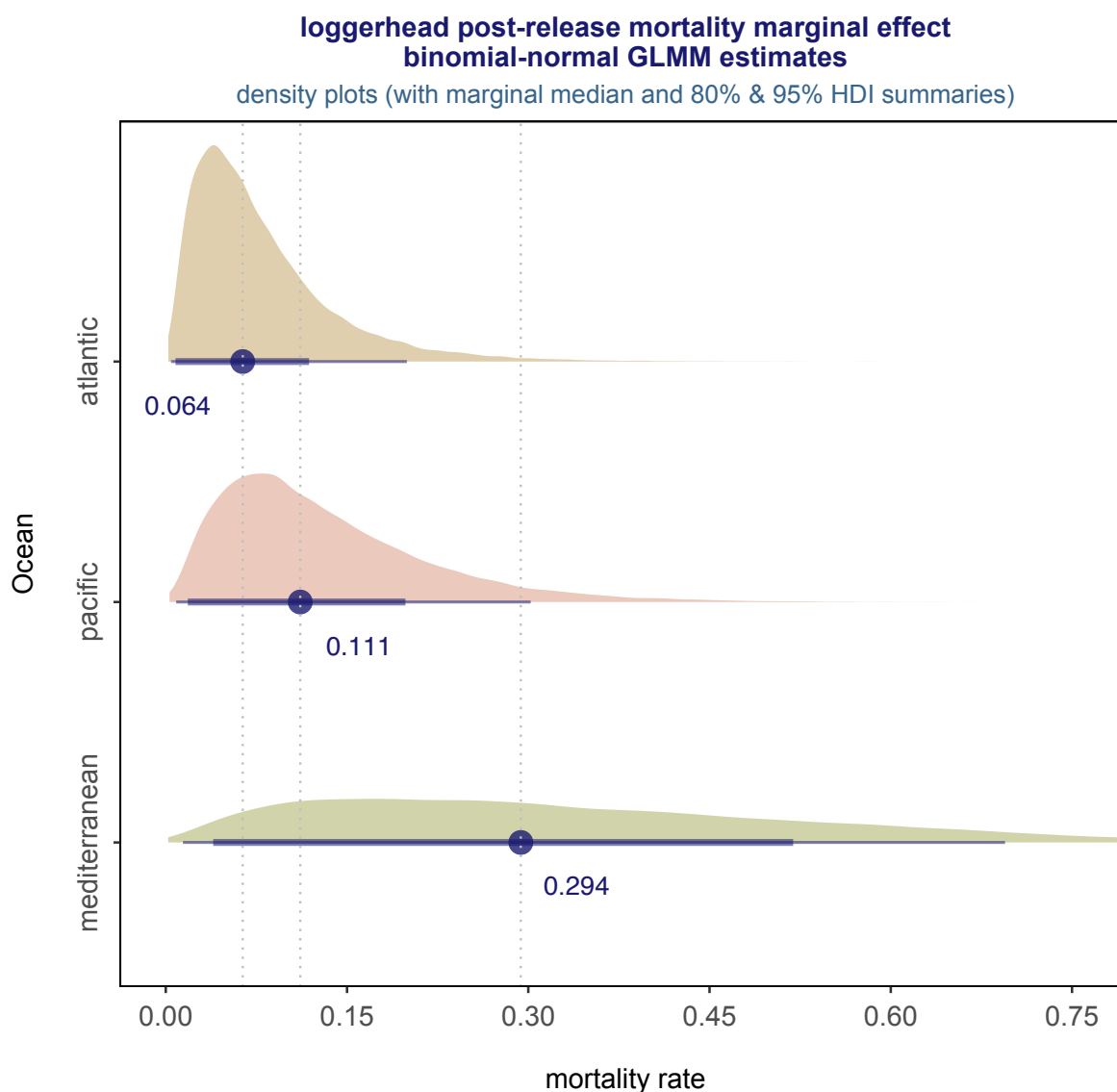


Figure 3 Summary of the estimated marginal median ocean-specific effect sourced from a binomial-Normal GLMM conditional model fit for loggerhead post-release mortality rates. Coloured polygon shows the density distribution summary of the 10,000 posterior draws, solid dot (+ numeric label) = median estimated of the density polygon, thick horizontal line below each polygon shows the 80% highest posterior density interval for the density polygon while the thin horizontal line is the 95% HDI.

**deep-hooked loggerheads:
forest plot with study-specific posterior distribution**
(with posterior mean & 95% HDI summary)

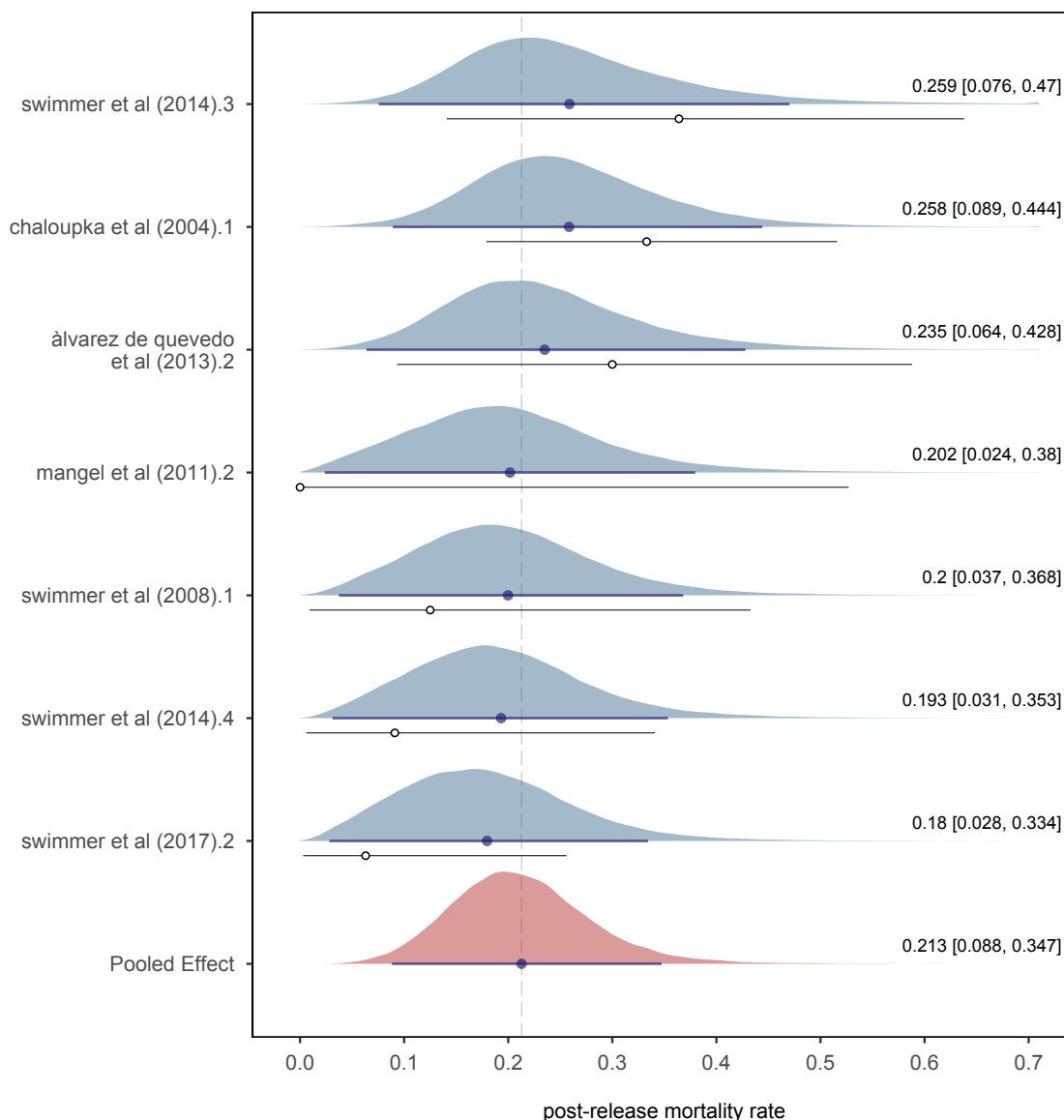


Figure 4 Model-predicted post-release mortality rates derived from 7 study-specific effect sizes for deep-hooked loggerhead turtles. The shrinkage estimates were derived using a Bayesian random-effects meta-analytic model with binomial-Normal likelihood. Polygon = density of the posterior draws (the effective sample size = 10,000) and the horizontal line underneath each polygon = 95% highest posterior density interval (HDI) of the posterior draws, solid dot = mean of the posterior draws shrunk towards the Pooled Effect (dashed vertical line), which is the mean or overall expected deep-hooked post-release mortality rate for all 7 studies (right-side labels = the posterior mean and HDI summaries). For each study, below the density polygon is an open dot = observed effect size and thin horizontal line = observed effect size \pm 1 standard deviation derived using the `metafor::escalc()` function. The difference between solid and open dots reflects the degree of shrinkage that is dependent on sample size — where Bayesian shrinkage is the equivalent concept to BLUPs in a frequentist setting.

**shallow-hooked loggerheads:
forest plot with study-specific posterior distribution**
(with posterior mean & 95% HDI summary)

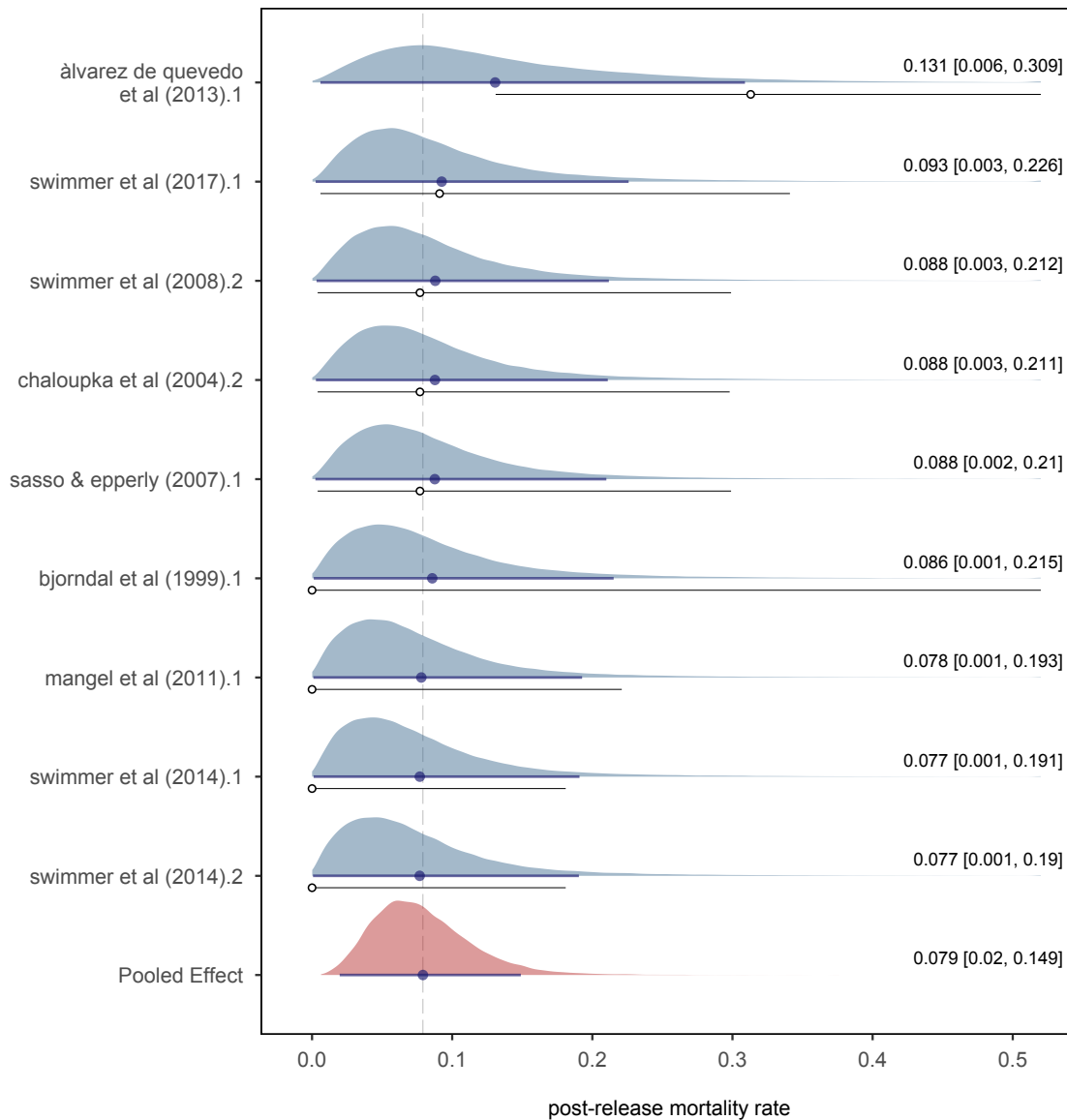


Figure 5 Model-predicted post-release mortality rates derived from 9 study-specific effect sizes for shallow-hooked loggerhead turtles. The shrinkage estimates were derived using a Bayesian random-effects meta-analytic model with binomial-Normal likelihood. Polygon = density of the posterior draws (effective sample size = 10,000), horizontal line = 95% highest posterior density interval (HDI) of the posterior draws, solid dot = mean of the posterior draws shrunk towards the Pooled Effect (dashed vertical line), which is the mean shallow-hooked post-release mortality rate for all 9 studies, open dot = observed effect size and thin horizontal line = observed effect size \pm 1 standard deviation derived using the `metafor::escalc()` function.

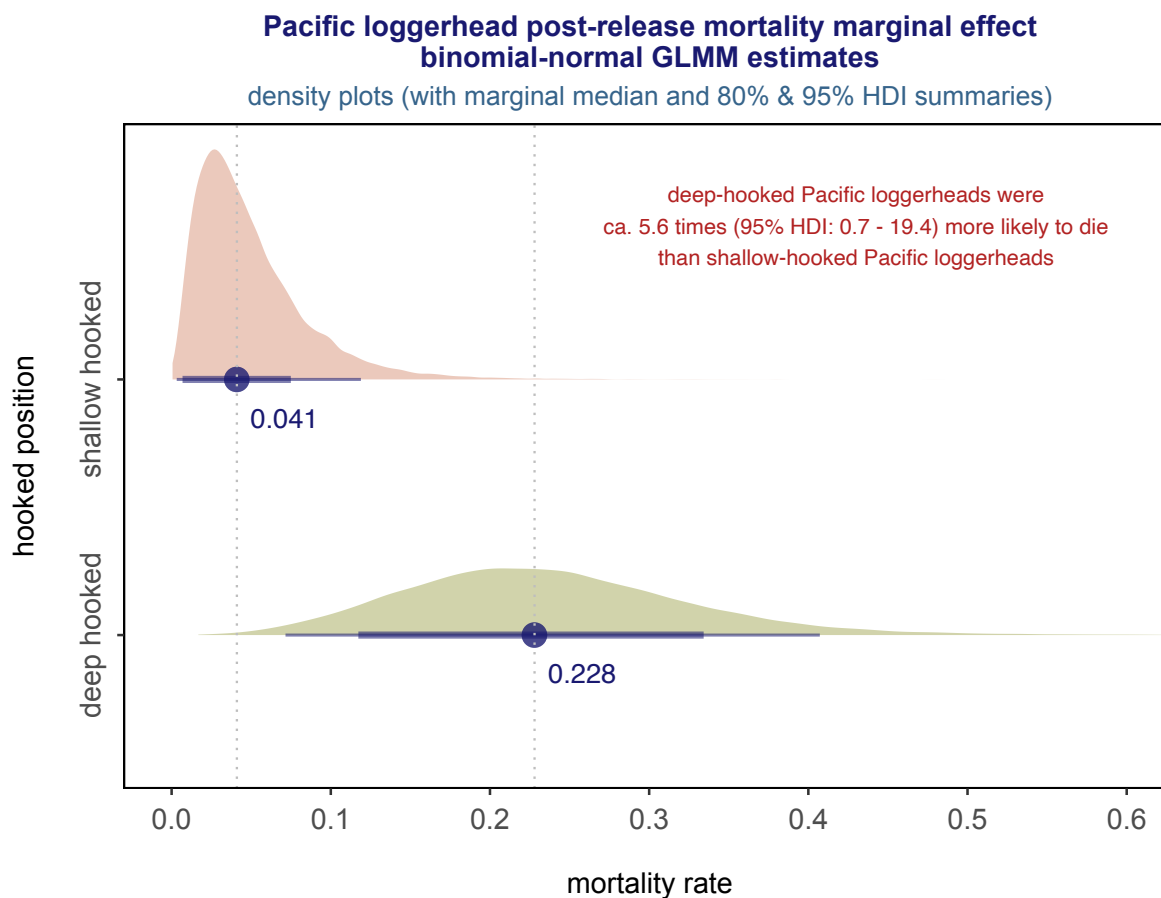


Figure 6 Summary of the estimated marginal median hooked-position effect (shallow- v deep-hooked) for Pacific Ocean loggerhead studies sourced from the binomial-Normal GLMM conditional model fit for loggerhead post-release mortality rates. Coloured polygon shows the density distribution summary of the 10,000 posterior draws, solid dot (+ numeric label) = median estimated of the density polygon, thick horizontal line below each polygon shows the 80% highest posterior density interval for the density polygon while the thin horizontal line is the 95% HDI.

**deep-hooked loggerheads (Mediterranean rehab studies):
forest plot with study-specific posterior distribution**
(with posterior mean & 95% HDI summary)

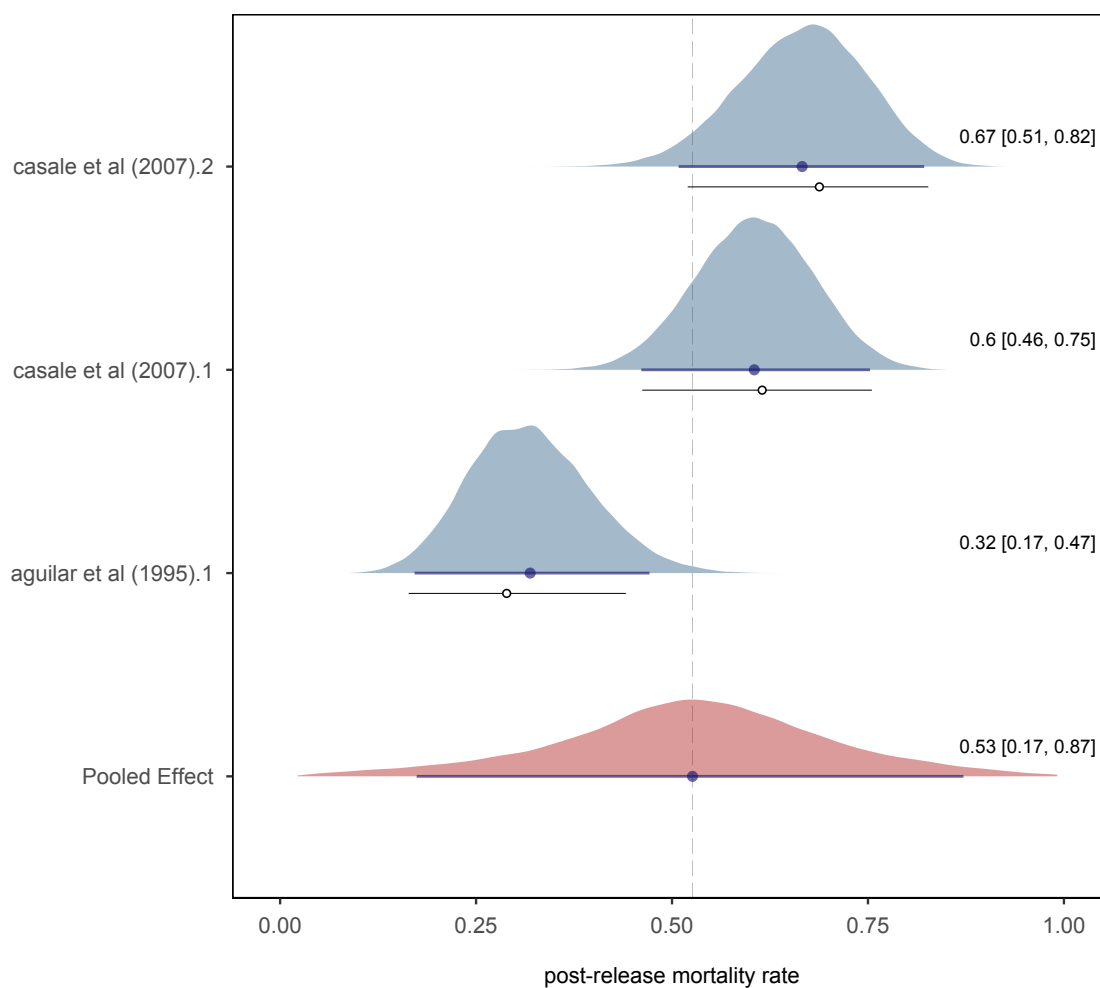
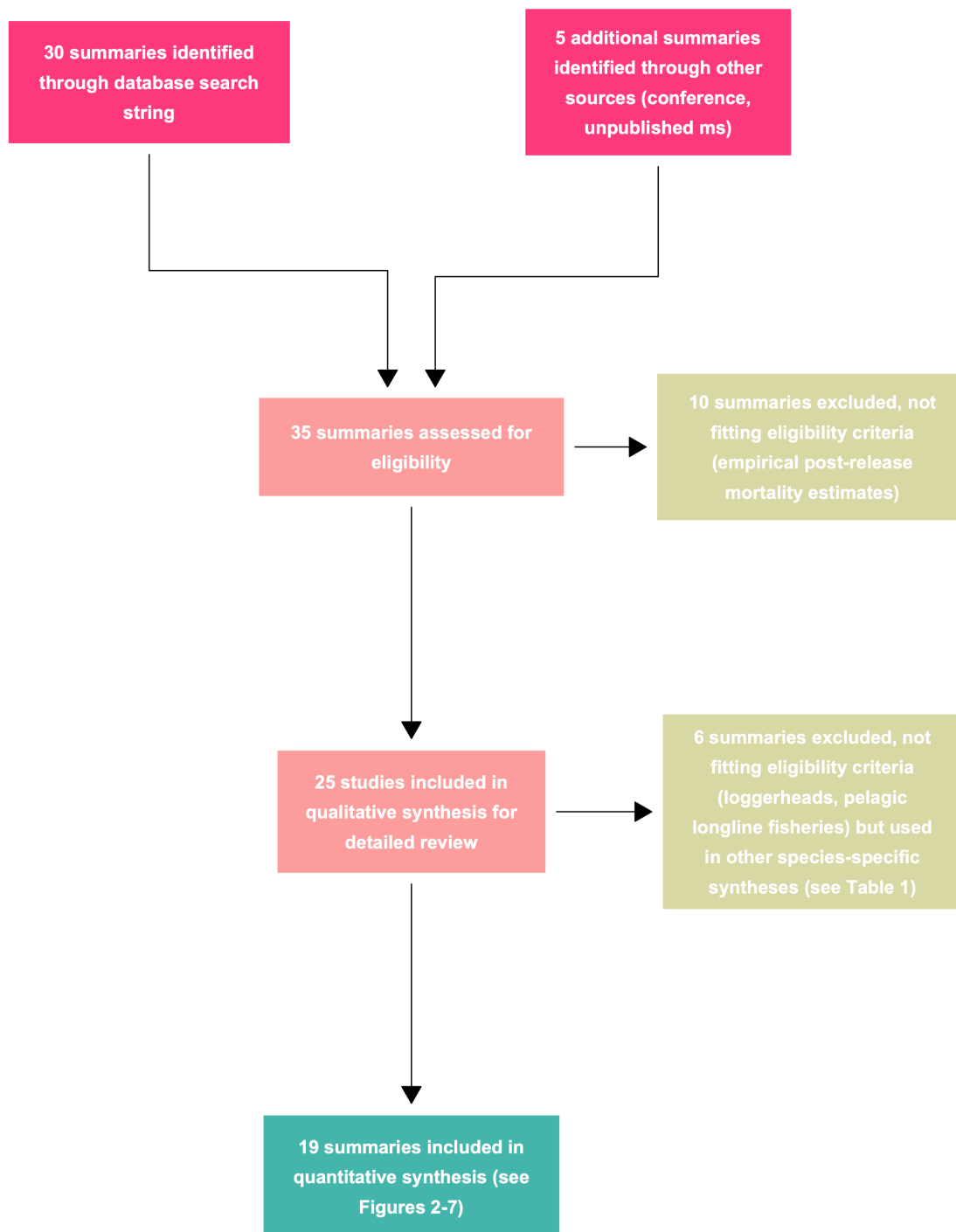


Figure 7 Model-predicted post-release mortality rates derived from 3 study-specific effect sizes for deep-hooked loggerhead turtles released after recovery from various Mediterranean rehabilitation centres. The shrinkage estimates were derived using a Bayesian random-effects meta-analytic model with binomial-Normal likelihood. Polygon = density of the posterior draws (the effective sample size = 10,000), horizontal line = 95% highest posterior density interval (HDI) of the posterior draws, solid dot = mean of the posterior draws shrunk towards the Pooled Effect estimate (dashed vertical line), which is the mean deep-hooked post-release mortality rate for all 3 studies, open dot = observed effect size and thin horizontal line = observed effect size \pm 1 standard deviation derived using the `metafor::escalc()` function.

Appendix 1: PRISMA plot (marine turtle post-release mortality studies).

Process and results of a 2-step citation search conducted to compile publications for an assessment of marine turtle post-release mortality rates from interactions with various fishing gears. PRISMA flowchart constructed using the metagear R package (Lajeunesse 2016).



Appendix 2: References for the 19 effect sizes used in the synthesis

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Swimmer Y, Gilman E (2012) Report of the Sea Turtle Longline Fishery Post-Release Mortality Workshop, November 15–16, 2011. US Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-PIFSC-34. 31 pp

Appendix 3: Source summaries (x = dead, N = sample size)

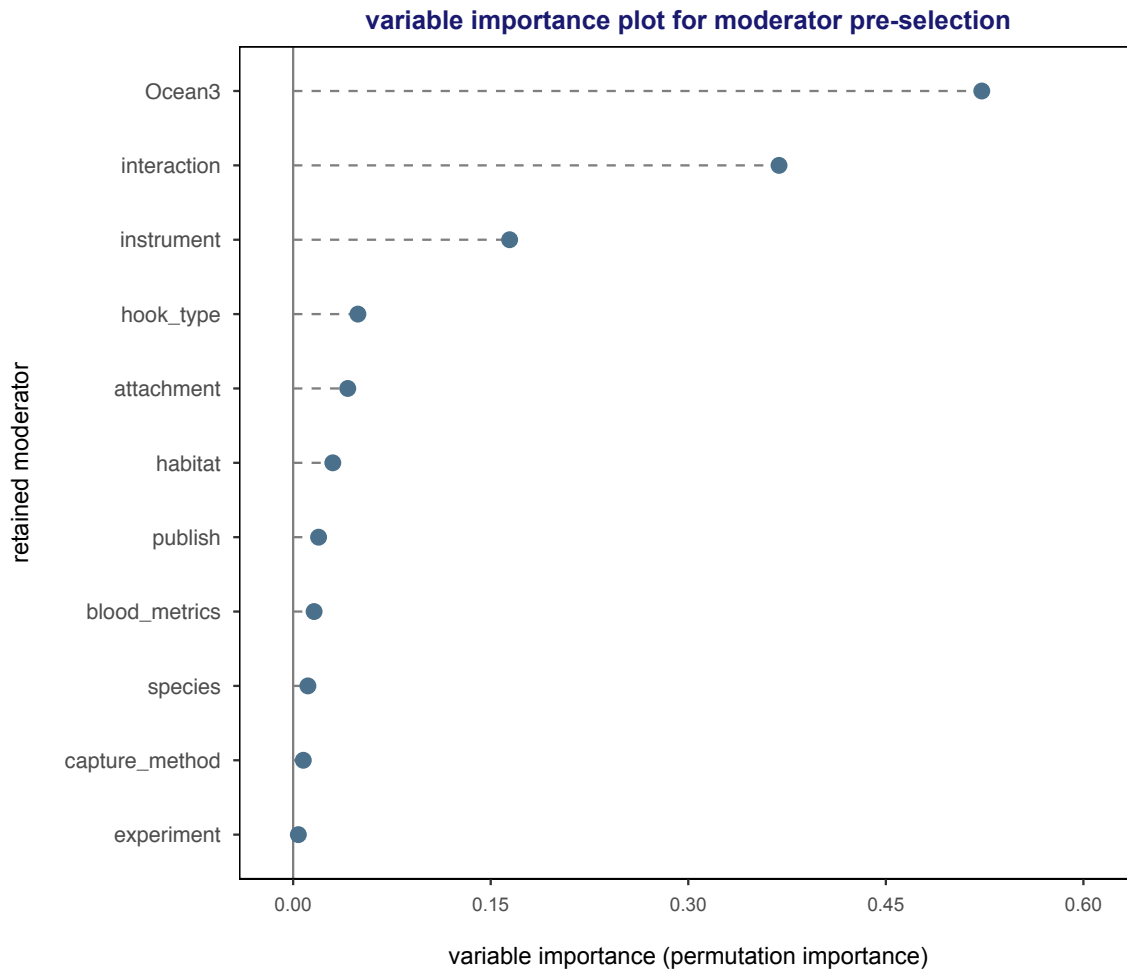
| gear | species | gear interaction | source | x | N | citation |
|--------------|---------------|------------------|----------|----|-----|-----------------------------------|
| longline | loggerhead | deep-hooked | rehab | 11 | 38 | aguilar et al (1995).1 |
| longline | loggerhead | shallow-hooked | psat | 5 | 16 | àlvarez de quevedo et al (2013).1 |
| longline | loggerhead | deep-hooked | psat | 3 | 10 | àlvarez de quevedo et al (2013).2 |
| longline | loggerhead | shallow-hooked | ptt | 0 | 3 | bjorndal et al (1999).1 |
| longline | loggerhead | deep-hooked | rehab | 24 | 39 | casale et al (2007).1 |
| longline | loggerhead | deep-hooked | rehab | 22 | 32 | casale et al (2007).2 |
| longline | loggerhead | deep-hooked | ptt | 9 | 27 | chaloupka et al (2004).1 |
| longline | loggerhead | shallow-hooked | ptt | 1 | 13 | chaloupka et al (2004).2 |
| pot/trap | leatherback | entangled | pot/trap | 31 | 205 | hamelin et al (2017).1 |
| longline | loggerhead | shallow-hooked | ptt | 0 | 11 | mangel et al (2011).1 |
| longline | loggerhead | deep-hooked | ptt | 0 | 3 | mangel et al (2011).2 |
| bottom trawl | olive ridley | entangled | psat | 0 | 3 | maxwell et al (2018).1 |
| bottom trawl | loggerhead | entangled | psat | 3 | 14 | parga et al (2020).1 |
| longline | loggerhead | shallow-hooked | psat | 1 | 13 | sasso & epperly (2007).1 |
| gillnet | green | entangled | ptt | 2 | 10 | snoddy & williard (2010).1 |
| gillnet | Kemp's ridley | entangled | ptt | 2 | 4 | snoddy & williard (2010).2 |
| longline | olive ridley | shallow-hooked | psat | 0 | 11 | swimmer et al (2006).1 |
| longline | loggerhead | deep-hooked | psat | 1 | 8 | swimmer et al (2008).1 |
| longline | loggerhead | shallow-hooked | psat | 1 | 13 | swimmer et al (2008).2 |
| longline | loggerhead | shallow-hooked | psat | 0 | 14 | swimmer et al (2014).1 |
| longline | loggerhead | shallow-hooked | psat | 0 | 14 | swimmer et al (2014).2 |
| longline | loggerhead | deep-hooked | psat | 4 | 11 | swimmer et al (2014).3 |
| longline | loggerhead | deep-hooked | psat | 1 | 11 | swimmer et al (2014).4 |
| longline | loggerhead | shallow-hooked | ptt | 1 | 11 | swimmer et al (2017).1 |
| longline | loggerhead | deep-hooked | ptt | 1 | 16 | swimmer et al (2017).2 |

Appendix 4: Study-specific variables

| variable | description |
|-------------------------|---|
| reference (study ID) | unique reference number for each of the 25 studies (<i>see Appendix 3 for the study sources</i>) |
| replicate within study | number assigned to each replicate estimate within each study |
| citation (author.year) | shortened reference comprising first author name and the study “publication” year |
| research group | apparent research group (same authors or close collaborators) for each study |
| publication type | journal, report, conference paper |
| species | green, Kemp’s ridley, loggerhead, leatherback, olive ridley |
| sizeclass | apparent turtle sizeclass (immature, adult) |
| region (ocean) | study-specific geographic region [Mediterranean, Pacific (north, east, southeast), Atlantic (north, northeast, south, southeast)] |
| habitat | habitat type of each study (pelagic, coastal) |
| fishery | bottom trawl, gillnet, longline, pots/traps |
| observers | observers onboard for this study (no, yes) |
| gear interaction | entangled, deep-hooked, shallow-hooked |
| hook type | J-hook, circle hook or unknown (NA) |
| capture method | entangled, hooked, caught in net/pot |
| instrument (source) | mortality data source (pot/trap, PSAT, PTT, rehabilitation facility) |
| instrument (attachment) | PSAT/PTT attachment (baseplate, drilled tether, tether baseplate) |
| died | number of the dead turtles at recovery |
| N | number of the turtles at recovery (whether dead or alive) |
| fate method | time-depth profile, recovered carcass, range of subjective criteria |
| blood metrics | turtle blood metrics collected (no, yes) |
| experiment | experimental study comparing specific effects (no, yes) |
| treatment (died) | number of the dead turtles at recovery for the experimental treatment |
| treatment (N) | number of the turtles at recovery (dead or alive) for experimental control |
| control (died) | number of the dead turtles at recovery for the experimental control |
| control (N) | number of the turtles at recovery (dead or alive) for experimental control |
| failed to report | number of PSATs/PTTS for each study that failed to report |
| fate unknown | number of turtles for each study that were not assigned a fate |
| metric | metric used to determine post-release fate (time-to-report, time-at-large) |
| geolocation | georeferenced location recorded (no, yes) |
| censored right | PSAT/PTT duration data right censored (no, yes) |
| censored left | PSAT/PTT duration data left censored (no, yes) |
| data truncation | PSAT/PTT study used a staggered entry design (no, yes) |
| random effects | PSAT/PTT study used a hierarchical model with random effects (no, yes) |
| model estimator used | binomial + bootstrap, empirical Bayes, Kaplan-Meier-Turnbull, ratio, Wilcoxon rank sum |

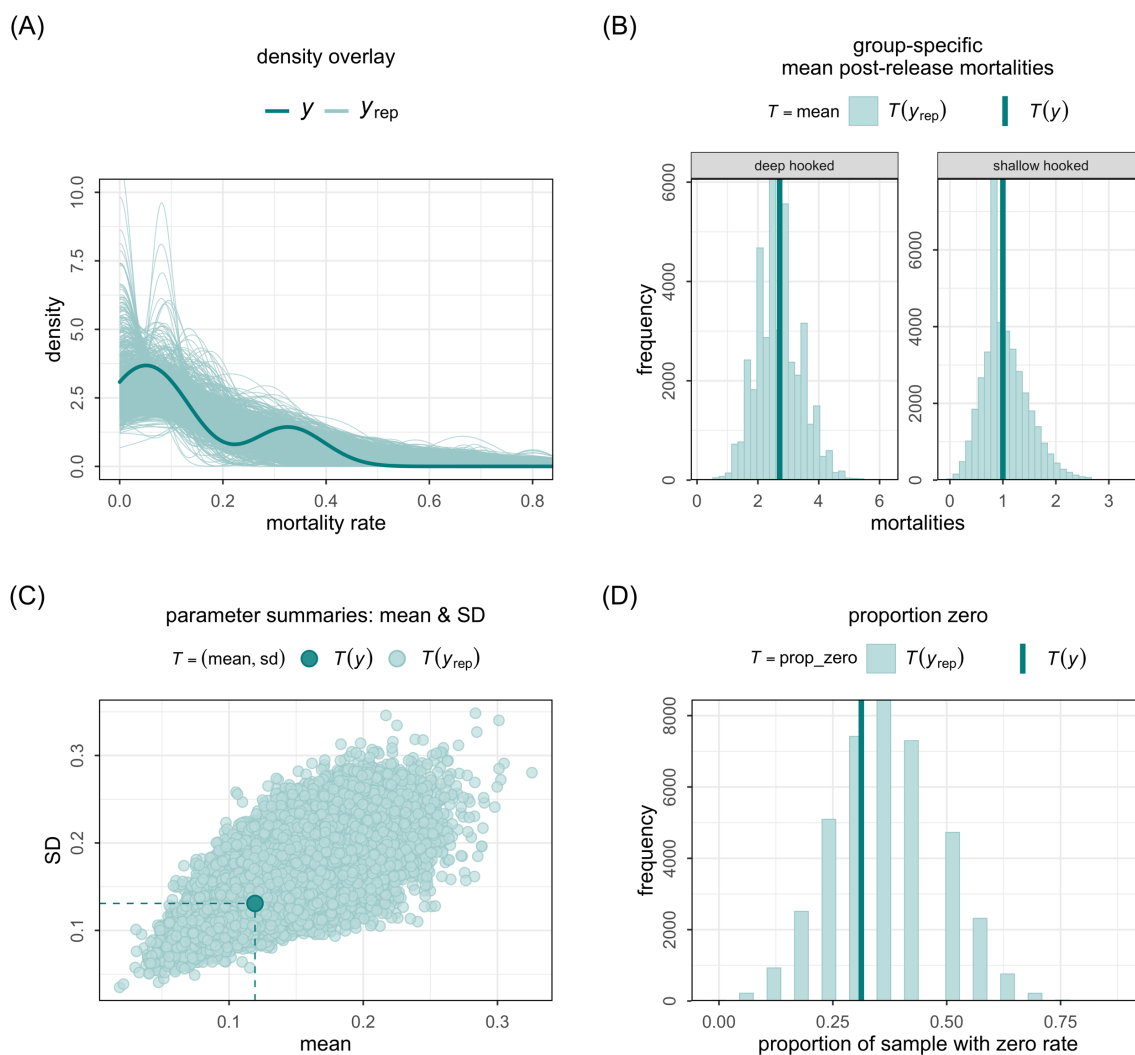
Appendix 5: Supplementary figures

SF1 Random forest derived variable importance plot identifying 11 from 25 potentially informative moderator (or covariate) effects on post-release mortality of marine turtles [$R^2(oob) = 0.43$, $R^2(cv) = 0.81$, $\tau^2 = 0.38$ = residual heterogeneity]. The complete list of screened moderators is shown in Appendix 4.



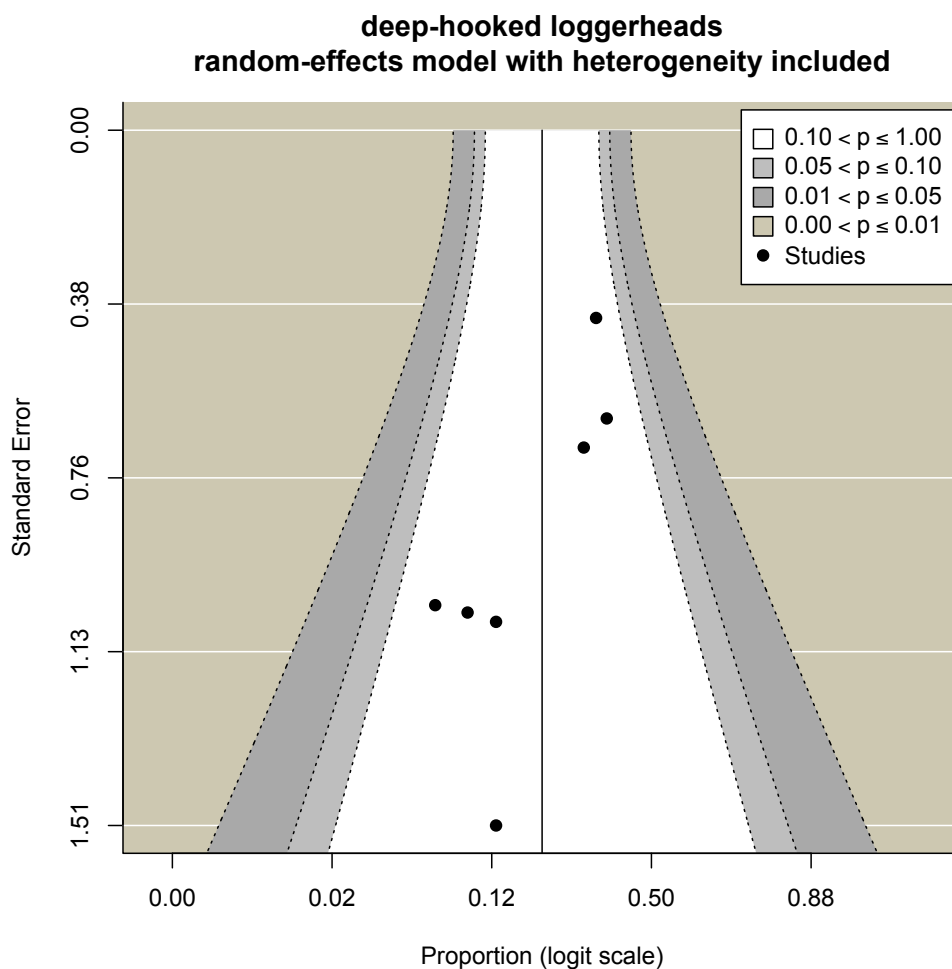
Appendix 5: Supplementary figures (continued ...)

SF2 Posterior predictive check tests for 1000 randomly selected draws from the best-fit binomial-Normal GLMM fitted to the loggerhead post-release mortality rates. (Panel A) shows the posterior predictive check for the response variable where the solid curve (y) is the density curve summarising the observed rates while the mass of curves (y_{rep}) are 1000 model-based simulations of the expected post-release mortality rate. (Panel B) shows a group-specific check for the mean observed rate (solid vertical line) and the histogram of the expected rates ($T(y)$) conditional on whether deep- or shallow-hooked. (Panel C) shows a check for 2 key summary parameters (mean and standard deviation of the observed rate) where the solid dot = observed bivariate estimate and the mass of dots ($T(y_{rep})$) are the bivariate estimates for the 1000 model-based simulations. (Panel D) shows the observed proportion of zeroes (solid vertical line, $T(y)$) and expected proportion of zeroes for 1000 model-based simulations (light shaded vertical bars, $T(y_{rep})$). All check tests show that the best-fit model was an adequate fit to these data and therefore appropriate for inference.



Appendix 5: Supplementary figures (continued ...)

SF3 Contour-enhanced funnel plot for the deep-hooked loggerhead estimates with between-study heterogeneity (τ^2) included.



Appendix 5: Supplementary figures (continued ...)

SF4 Model-predicted post-release mortality rates derived for the 7 deep-hooked loggerhead effect sizes referred to in Appendix 5 SF3 — estimates derived using a random-effects meta-analytic model with binomial-Normal likelihood fit using the `metafor` package for R (Viechtbauer 2010). solid blue dot = estimated mean and shown proportional to sample size, horizontal line = 95% confidence interval, solid dark red polygon shows the pooled effect and 95 % CI along with the 95% prediction interval (dark red line through polygon), dotted vertical line = estimated mean pooled post-release mortality (0.203). Heterogeneity summary metrics also shown ($Q_{(wald)}$, I^2).

