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Phylogeny explains capture mortality of sharks and rays in pelagic longline fisheries: a global meta-analytic synthesis

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Apex and mesopredators such as elasmobranchs are important for maintaining ocean health and are the focus of conservation efforts to mitigate exposure to fishing and other anthropogenic hazards. Quantifying fishing mortality components such as at-vessel mortality (AVM) is necessary for effective bycatch management. We assembled a database for 61 elasmobranch species and conducted a global meta-synthesis to estimate pelagic longline AVM rates. Evolutionary history was a significant predictor of AVM, accounting for up to 13% of variance in Bayesian phylogenetic meta-regression models for Lamniformes and Carcharhiniformes clades. Phylogenetically related species may have a high degree of shared traits that explain AVM. Model-estimated posterior mean AVM rates ranged from 5% (95% HDI 0.1%–16%) for pelagic stingrays and 76% (95% HDI 49%–90%) for salmon sharks. Measures that reduce catch, and hence AVM levels, such as input controls, bycatch quotas and gear technology to increase selectivity are appropriate for species with higher AVM rates. In addition to reducing catchability, handling-and-release practices and interventions such as retention bans in shark sanctuaries and bans on shark finning and trade hold promise for species with lower AVM rates. Robust, and where applicable, phylogenetically-adjusted elasmobranch AVM rates are essential for evidence-informed bycatch policy.

Elasmobranchs (sharks and rays) belong to one of the most diverse marine taxonomic groups and include apex and mesopredators essential for maintaining ecosystem structure, functions and stability^{1–3}. Overexploitation is the primary cause of declines of marine species. It can cause protracted or irreparable harm and permanent loss of populations, with changes and loss in marine biodiversity and ecosystem services^{4,5}. Bycatch in pelagic longline fisheries is a global threat to the conservation of some elasmobranchs⁶. Pelagic sharks experienced a 71% decline in abundance over the past 50 years⁷. Depending on a fishery's management framework and markets, catch composition and practices of individual vessels, sharks and rays may be discarded or retained as either incidental or target catch^{8,9}. Retention may entail the entire fish or only shark fins or ray gill rakers.

There has been increasing concern in recent decades over the sustainability of elasmobranch mortality in pelagic fisheries given elasmobranchs' vulnerability to exploitation, ecosystem-level cascading effects from declines in elasmobranch abundance, and fisheries-induced evolution and reduced population fitness that results from selective removals based on heritable traits^{2,3,10–12}. There has also been increasing attention to the socioeconomic costs to fisheries from shark interactions such as from the depredation of catch and bait^{8,13} and risks to food, nutrition and livelihood security of coastal fishing communities from declining elasmobranch abundance^{14,15}.

Accurate estimates of all sources of mortality are needed for robust assessments of the ecological effects of fishing, including through quantitative stock assessments, population viability models and multispecies ecosystem models^{16,17}. For non-retained catch, a key component of total fishing mortality is at-vessel mortality (AVM), also referred to as haulback or capture mortality, which is the proportion of the catch that is dead upon retrieval of

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the fishing gear before being handled by crew. Because small changes in mortality can result in large changes in mature biomass and therefore population growth, uncertainty in AVM rates is a major impediment to effective management and sustainable fisheries, in particular for elasmobranchs¹⁸. Robust estimates of species-specific AVM rates enable performance assessments of conservation and management measures, such as retention bans—including within Shark Sanctuaries, bans on international trade, bycatch quotas, shark finning bans, gear design requirements and handling-and-release practices. Identifying informative predictors of AVM risk, including phylogeny, physiological attributes, fishing methods and gear designs, facilitates estimation of AVM rates for data-limited species and identification of effective methods to mitigate AVM.

There is limited information available on AVM rates for most elasmobranchs, and quantitative meta-analytic synthesis studies of AVM rates in longline fisheries have been conducted for few elasmobranch species^{18–21}. Independent and unbiased synthesis of all accumulated scientific information is a fundamental transparency principle for developing evidence-informed conservation management decisions^{22,23}. Meta-analytic based synthesis approaches typically produce the strongest evidence with generalizable results that are optimal for global and regional decision-making^{24,25}.

This study fills this priority research gap on elasmobranch AVM rates. We assembled an extensive database and conducted a global meta-synthesis to aggregate, test and summarize species-specific AVM rates for elasmobranchs captured in pelagic longline fisheries. The study significantly extends previous meta-analyses^{26–30} through: (1) the inclusion of a much larger number of studies and species; (2) applying Bayesian multilevel or hierarchical meta-regression models to account for informative covariates; and (3) phylogenetically adjusting the AVM rate estimates for the evolutionary history for two major shark clades with either relatively high (Carcharhiniformes) or low (Lamniformes) extant species diversity³¹. The study objectives were to:

1. Derive robust species-specific estimates and measures of uncertainty of AVM rates for elasmobranchs captured in pelagic longline fisheries;
2. Determine if phylogeny, operational longline fishing methods and gear designs, ventilation mode, morphology and ocean region are informative predictors of AVM rates; and
3. Identify gaps in information on priority potentially informative predictors and in taxonomic groups and regions for which additional primary studies are required for robust meta-syntheses of AVM rates.

The AVM rates derived for 61 elasmobranch species, estimated using robust statistical procedures for synthesizing evidence from multiple studies, supports evidence-informed conservation and fisheries management for sharks and rays.

Results

Predictor screening. The random forest derived variable importance plot identified several potentially informative predictors of elasmobranch AVM for the entire sample of 1,438 effect sizes summarized in Fig. S1. Only six predictors (genus, family, body type, number of hooks between floats, order, ocean) were deemed sufficiently informative with variable importance > 10%, which was used as the cut-off threshold. Several of those six predictors (genus, family, order) are taxonomic specific and accounted for most of the expected predictor importance but can be explicitly modelled using a single phylogenetic tree structure instead. We also included in our modelling workflow two less informative predictors shown in the variable importance plot (hook type, soak duration) as they are of general interest to fisheries managers because they are operational parameters that can be managed. Hence, all subsequent meta-analytic regression models considered this set of predictors in the Bayesian GAMMs.

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 $Rhat < 1.01$ ³², reflected convergence of the Bayesian GAMMs with binomial-Normal likelihood. The best-fit GAMMs identified by the LOOcv and Bayesian stacking metrics fitted the clade-specific AVM datasets well as shown for example by the graphical posterior predictive check tests summarized in Fig. S2.1 for the model fitted to the 466 AVM study-specific effect sizes for 13 Lamniform species caught in pelagic longline fisheries operating in two ocean basins (Atlantic, Pacific).

Clade-specific AVM estimates adjusting for phylogenetic structure. The pooled mean AVM estimates for the Carcharhiniform species (Fig. 1A) and Lamniform species (Fig. 2A) were 0.376 [95% highest posterior density interval (HDI) 0.13–0.63] and 0.383 (95% HDI 0.15–0.65), respectively. In both models, only ocean basin (Figs. 1C, 2C) was a significant predictor of species-specific AVM rates in addition to the phylogenetic structure—hook type and number of hooks between floats were not significant predictors in either model (Figs. 1B,D, 2B,D).

Phylogenetic signal. The mean phylogenetic signal or constraint estimated for Carcharhiniform species was estimated to be 0.06 (95% HDI 0.01–0.23) and 0.13 (95% HDI 0.01–0.42) for Lamniform species. These are significant but moderate phylogenetic signals, implying that evolutionary history played an important but relatively minor role in explaining the AVM rate differences among the 26 Carcharhiniform species and the 13 Lamniform species.

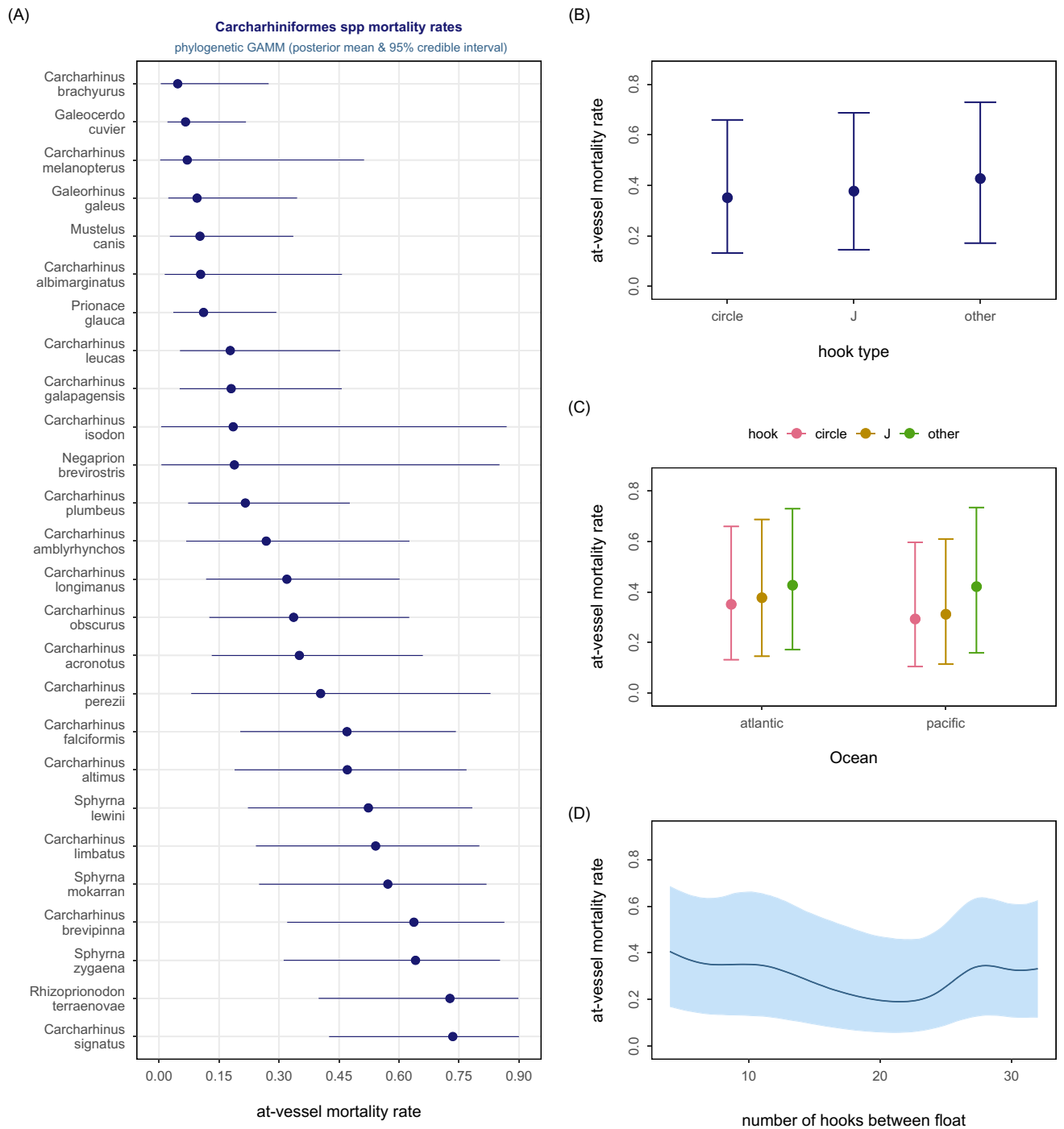


Figure 1. CARCHARHINIFORMES. Graphical summary of the Bayesian phylogenetic meta-regression model (binomial-Normal GAMM) fitted to 706 AVM effect sizes compiled for this 26 shark species clade. Panel (A) shows the estimated conditional species-specific AVM rate arranged from lowest to highest rate. Panel (B) shows the estimated conditional hook type effect on AVM. Panel (C) shows the estimated conditional effect of hook shape within ocean basin effect on AVM. Panel (D) shows the estimated conditional effect of number of hooks between floats on AVM. Solid dot = posterior mean, horizontal or vertical bar = 95% credible interval, solid curve = mean nonlinear trend, shaded polygon = 95% pointwise credible interval.

Estimated ocean basin effect in phylogenetic models. Carcharhiniform species had a >0.95 probability of lower AVM rates in the Pacific Ocean than the Atlantic Ocean. Carcharhiniform species in the Atlantic were 2.9 times (95% HDI 1.6–4.8) more likely to be dead at haulback than in the Pacific. The ocean-specific effect was significant for sharks caught on either circle or J-shaped hooks (Fig. 1C). A similar ocean-specific effect was evident for the Lamniformes (Fig. 2C) with the estimated mean marginal effect suggesting that Lamniform

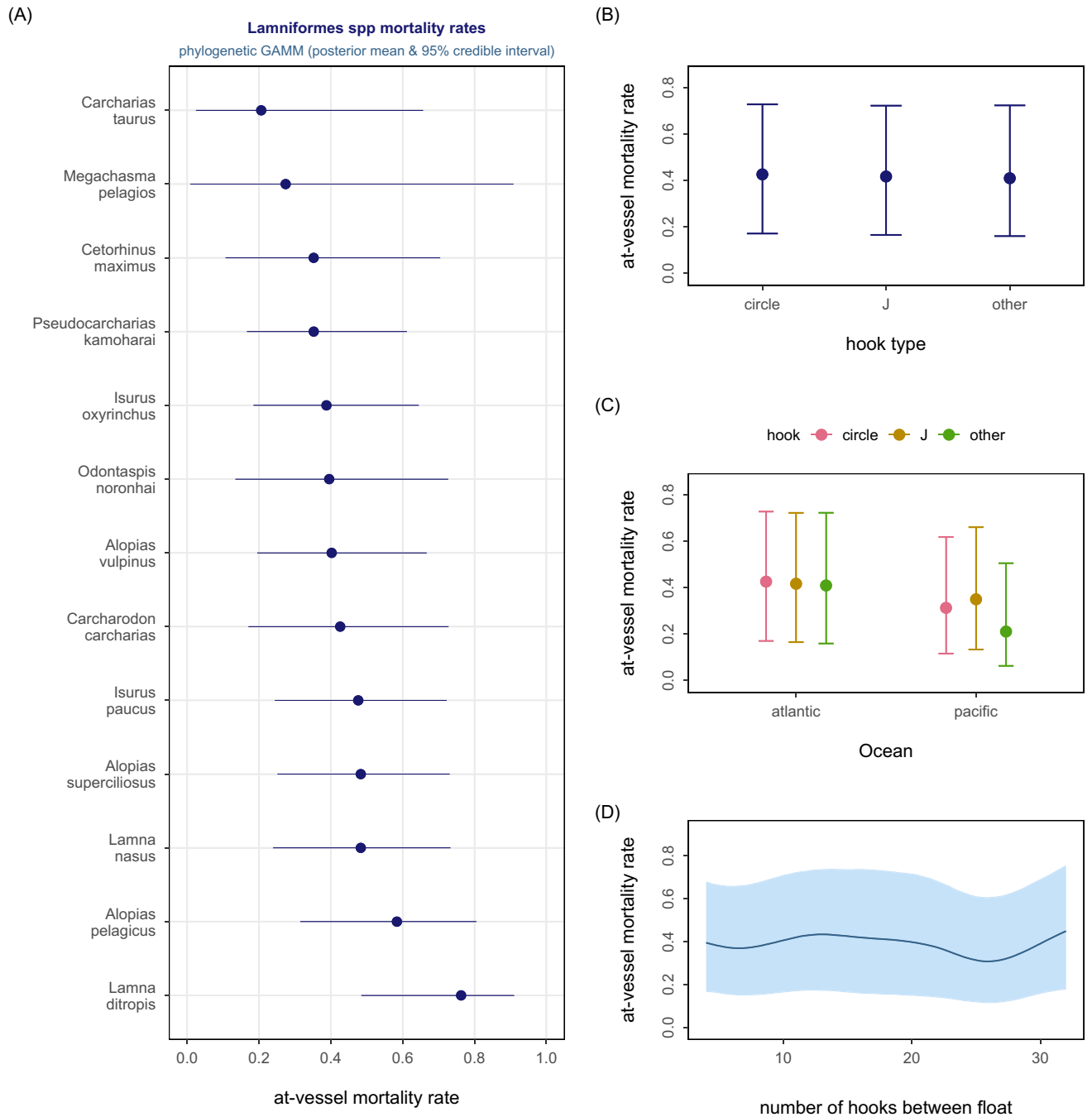


Figure 2. LAMNIFORMES. Graphical summary of the Bayesian phylogenetic meta-regression model (binomial-Normal GAMM) fitted to 466 AVM effect sizes compiled for this 13 shark species clade. Panel (A) shows the estimated conditional species-specific AVM rate arranged from lowest to highest rate. Panel (B) shows the estimated conditional hook shape effect on AVM. Panel (C) shows the estimated conditional effect of hook type within ocean basin effect on AVM. Panel (D) shows the estimated conditional effect of number of hooks between floats on AVM. Solid dot = posterior mean, horizontal or vertical bar = 95% credible interval, solid curve = mean nonlinear trend, shaded polygon = 95% pointwise credible interval.

species caught in the Atlantic were 1.4 times (95% HDI 1.1–1.8) more likely to be dead at haulback than in the Pacific (Fig. S2.2).

Publication bias. We found no evidence of potential publication bias for our phylogenetically adjusted meta-regression models that could be identified by funnel plot asymmetry based on a random-effects meta-regression model estimated within a frequentist inference framework. For instance, Fig. S3 shows a standard

Pteroplatytrygon violacea
binomial-normal GAMM

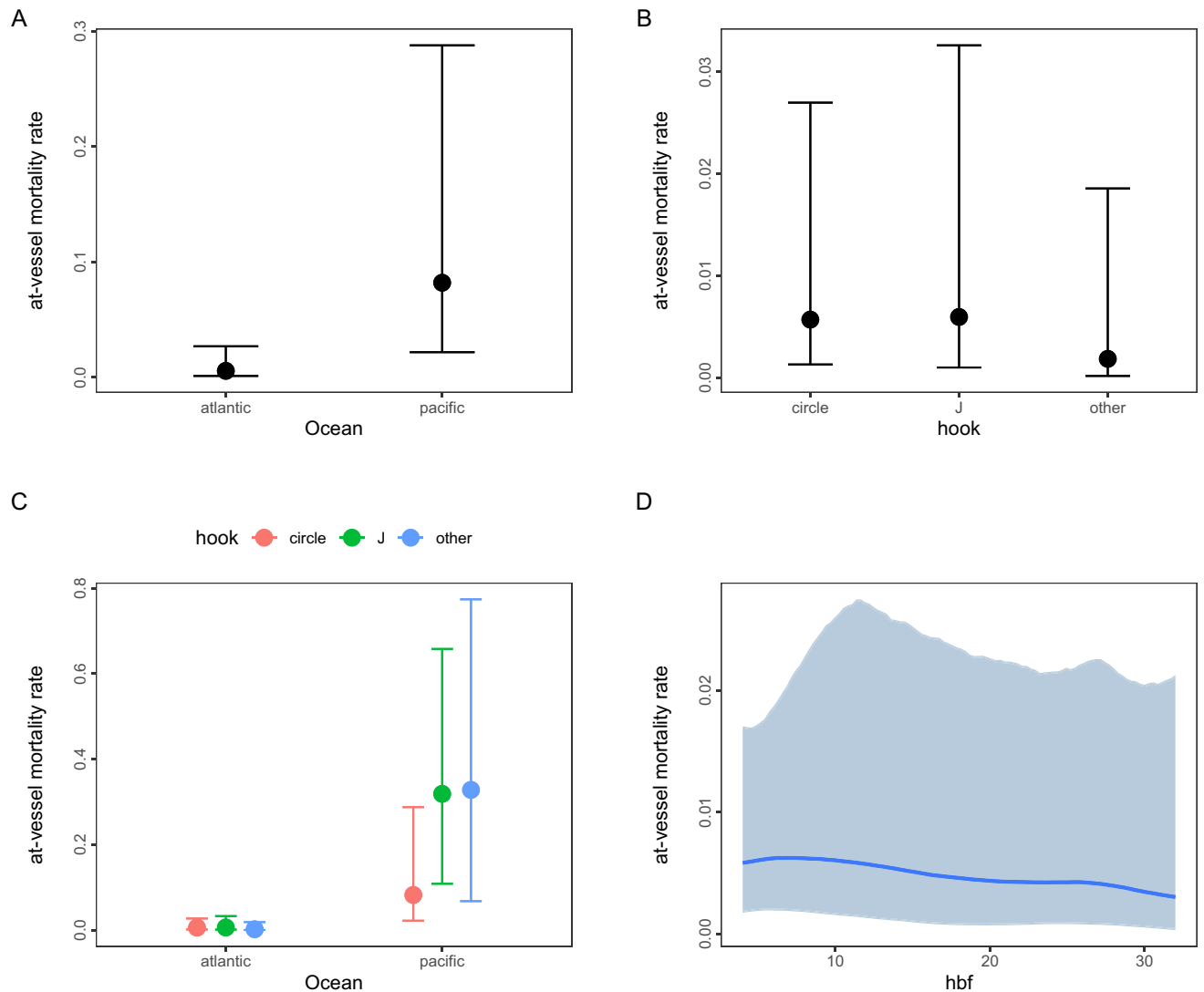


Figure 3. PELAGIC STINGRAY. Graphical summary of the Bayesian meta-regression model (binomial-Normal GAMM) fitted to 90 AVM effect sizes compiled for the pelagic stingray. Panel (A) shows the estimated conditional ocean-specific AVM rate. Panel (B) shows the estimated conditional hook shape effect on AVM. Panel (C) shows the estimated conditional effect of hook shape within ocean basin effect on AVM. Panel (D) shows the estimated conditional effect of number of hooks between floats on AVM. Solid dot = posterior mean, vertical bar = 95% credible interval, solid curve = mean nonlinear trend, shaded polygon = 95% pointwise credible interval.

error-based contour-enhanced funnel plot for the Carcharhiniform species with little evidence for potential publication bias for this large data set of 706 study-specific effect sizes.

AVM rate estimates from species-specific GAMMs. The pelagic stingray *Pteroplatytrygon violacea* contained the largest number of records of the seven ray species in the assembled database (101 of 114). The overall AVM rate from a binomial-Normal GAMM was mean of 0.047 (95% HDI 0.001–0.157) (Table S1). Ocean basin (Fig. 3A) and hook shape in the Pacific Ocean (Fig. 3C) were significant predictors of pelagic stingray AVM. In combined ocean basins, hook shape (Fig. 3B) and number of hooks between floats (Fig. 3D) were not significant predictors. With >99% certainty, the estimated AVM rate was significantly higher for the Pacific than the Atlantic Ocean effect sizes. The predicted marginal mean ocean-specific AVM rates, weighted proportionally according to sample size, for the pelagic stingray were 0.005 (95% HDI 0.001–0.02) for the Atlantic and 0.18 (95% HDI 0.04–0.41) for the Pacific Ocean effect sizes. In the Pacific, the pelagic stingray predicted marginal mean AVM rate for circle hooks was 0.08 (95% HDI 0.001–0.23) and 0.31 (95% HDI 0.001–0.61) for J-shaped hooks.

For giant manta ray *Mobula birostris*, cookie cutter shark *Isistius brasiliensis* and velvet dogfish *Zameus squamulosus*, overall AVM rates from binomial-Normal GAMMs were a mean of 0.332 (95% HDI 0.015–0.707), 0.295 (95% HDI 0.055–0.564), and 0.226 (95% HDI 0.071–0.368), respectively (Table S1). Only hook shape was a significant predictor of giant manta ray AVM rate. We can be >96% sure that the estimated giant manta ray AVM rate was significantly higher on J-shaped than on circle hooks—the predicted marginal mean AVM rate for circle hooks was 0.19 (95% HDI 0.001–0.52) and 0.56 (95% HDI 0.01–0.99) for J-shaped hooks.

Summary of species-specific AVM estimates. AVM rates were estimated for 54 shark species ($n = 1322$ records), and for 7 ray species ($n = 116$ records) (Table S1). Of these 61 species, 39 are in the two phylogenetic GAMMs. For sharks, AVM rates ranged from a low of a mean of 0.039 (95% HDI 0.01–0.07) for the picked dogfish *Squalus acanthias* to a high of a mean of 0.76 (95% HDI 0.49–0.90) for the night shark *Carcharhinus signatus*. For rays, mean AVM rates ranged from a low for the pelagic stingray (“AVM rate estimates from species-specific GAMMs” section) to a high of 0.5 (95% HDI 0.18–0.82) for the blackchin guitarfish *Glaucostegus cemiculus*.

Figure S4 is an example of a forest plot summarizing the model-predicted log relative risk ratios and the estimated random or Pooled Effects for the Atlantic sharpnose shark *Rhizoprionodon terraenovae*, with separate forest plots from records using only squid bait shown in Panel A and records using only fish, a mix of fish and squid, or unknown bait type in Panel B. Weighted relative risk estimates are ordered by effect size, and an estimated overall Pooled Effect log relative risk ratio is shown at the bottom of the forest plot and by the dashed vertical line. The overall AVM rate with only squid bait of 0.878 (95% HDI 0.75–0.99) was significantly higher than a mix of bait types of 0.427 (95% HDI 0.26–0.61).

Discussion

Phylogenetic signal. This is the first study to comprehensively assess the relationship between phylogeny and AVM risk for elasmobranch species exposed to pelagic longline fisheries. The finding of a moderate but significant relationship highlights the importance of accounting for phylogenetic dependence in elasmobranch multispecies meta-analytic syntheses on AVM rate^{25,33,34}. Not accounting for phylogeny potentially risks estimating biased species-specific AVM rates, reduces the robustness of stock assessments, perhaps drawing incorrect conclusions and adopting misinformed policy. This finding is consistent with conclusions of previous studies that not accounting for phylogenetic non-independence of taxa in ecological meta-analyses produces biased results^{33–35}.

More accurate estimates of shark species-specific AVM rates are obtained when meta-analytic syntheses are designed to account for phylogeny—the degree of shared evolutionary histories between species. Accounting for phylogeny in meta-analytic syntheses produces more robust species-specific AVM estimates for Lamniform and Carcharhiniform clades. The significant phylogenetic signal does not mean that species within these two clades have similar AVM rates; conversely, there is a broad range in species-specific AVM within these clades (Figs. 1, 2; Table S1). Instead, as with other significant explanatory predictors of AVM rates, accounting for phylogeny produces more accurate pooled estimates of species-specific AVM rates. Stock assessments, population models, multispecies ecosystem models, bycatch management strategy evaluations and other models that include AVM rates as a data input will in turn have more accurate findings, providing stronger evidence to guide decision-making.

The phylogenetic signal estimated by the Bayesian multilevel meta-regression models accounted for the dependence among elasmobranch species due to shared evolutionary histories. Closely related taxa share a phylogenetic history and would be expected to be ecologically similar³⁶. They may have a high degree of shared non-heritable as well as heritable traits—if traits were conserved during evolution leading to descendent lineages, which occurs when traits are under strong selection (phylogenetic niche conservatism)^{34,36–38}. For example, while there is some co-occurrence, most extant Lamniformes and Carcharhiniformes are ecologically differentiated by diet, morphology and in some cases habitat type³⁹. Some shared physiological, morphological and behavioral traits may be informative predictors of AVM risk. For example, the lamnid sharks and common thresher shark (*Alopias vulpinus*) are the only elasmobranchs with regional red aerobic myotomal muscle endothermy^{40,41}. They can occupy deeper and cooler habitats on an ephemeral basis. Not being dependent on ambient temperature for thermoregulation may contribute to their AVM rate being less affected by the duration hooked and ocean temperature relative to ectothermic elasmobranchs⁴². Endothermic sharks, which may have had a single origin in the Cretaceous, also tend to have larger body sizes than ectothermic sharks, which previous studies have found to be an informative predictor of AVM risk—larger fishes have larger energy stores relative to smaller individuals, making them more resilient to stressors, including a fight response to capture^{43–46}. However, not all traits may be conserved during evolution. Trait divergence can occur during adaptive radiation, when species quickly diverge to avoid competition and fill different ecological niches³⁷. Fisheries are also altering populations' evolution through selective removals based on heritable traits¹², possibly including through selective AVM within populations based on traits such as for fitness⁴⁷.

Furthermore, it is likely that vulnerability to AVM is a function of both evolutionarily conserved and labile traits⁴⁸. While conserved traits, such as thermal tolerance and niche tracking, will be expressed consistently by individuals of a population, flexible, labile traits such as stress response, shyness/boldness and timing of reproduction may have high variability in their expression both by an individual and between individuals of a population^{48,49}. The strength of any phylogenetic signal may be decreased by this complex mixture of conserved and labile traits that affect AVM rates⁴⁹.

Population-level consequences and potential risk of extinction. Some sharks with high AVM rates have relatively high extinction risks due to pelagic longline fisheries. This includes the pelagic thresher shark

(*Alopias pelagicus*), with a relatively high mean AVM rate of 58%, which is categorized as Endangered by IUCN⁵⁰, with a relatively low phylogenetically adjusted r_{\max} (maximum intrinsic rate of population increase, a standard measurement of population productivity and extinction risk) of 0.15⁵¹ and low mean r_{\max} of 0.06⁵². Based on phylogenetically adjusted estimates of r_{\max} , Lamniformes have a high extinction risk and have moderate to high AVM rates. Carcarhiniformes had highest AVM rates but a lower extinction risk relative to Lamniformes⁵¹.

For individual fisheries with species-specific AVM rates that are substantially higher than the overall or pooled estimate for that species from the meta-analysis, modifications to operational explanatory predictors may reduce the AVM rate closer to the global pooled estimate. However, context-specific biological (e.g., size, sex) and environmental factors (e.g., thermocline depth, sea surface temperature, dissolved oxygen) may be more important predictors of AVM than manageable, operational fishing parameters. Similarly, there may be fisheries where a species tends to be retrieved alive but are subsequently discarded dead. For elasmobranch species with low AVM rates, in fisheries where these species have low retention, comparing at-vessel and release conditions would help determine if improved handling and release practices could increase the proportion of released catch that are alive, as well as reduce the post-release mortality rate. Furthermore, in fisheries where elasmobranch species with low AVM rates are retained, output controls that limit or ban their retention or trade have the potential to substantially reduce fishing mortality.

For elasmobranchs with relatively high AVM rates, methods that avoid and reduce their catch risk hold promise to reduce total fishing mortality. For these species, retention bans, shark finning restrictions and other output controls may be inappropriate approaches, unless they indirectly lead to the use of methods that reduce catch rates. Instead, measures that avoid and minimize shark and ray catch in pelagic longline fisheries are needed, either by: (1) reducing effort; or reducing one or more capture susceptibility attributes of: (2) spatial and temporal overlap through static and dynamic area-based management tools; (3) vertical overlap by managing fishing depth and the time of day of fishing; and (4) selectivity such as by adjusting leader material, hook and bait type and restricting the use of light attractors (Section S4). For species with relatively low AVM rates, in addition to catch avoidance and minimization approaches, prescribed handling and release practices (Section S5) may substantially reduce their total fishing mortality.

In addition, managing operational fishing methods and gear designs such as soak duration, fishing depth, branchline length, hook shape and size, bait type, leader material, time-of-day and fishing location can reduce elasmobranch AVM risk^{18,53,54}. Supplemental Information Section S2 discusses the implications of findings for predictors of ocean basin, hook shape and the number of hooks between floats. Previous studies found that AVM rates for some individual elasmobranch species were a function of some of these operational predictors^{27,53–56}. We found little support for such predictors affecting estimated AVM rates for our two clades of 39 shark species. Species-specific interactions with all operational predictors could not be explored for most of these 39 species because the publications compiled to assemble our dataset provided insufficient coverage of all predictors included in the models. However, the sample forest plot presented for the Atlantic sharpnose shark (Fig. S4) indicates that fisheries using only squid bait had a higher AVM rate than those not using only squid bait. This observed difference in AVM rates may have been caused by bait type. This observed effect conflicts with the prevailing understanding that, due to the prevalent hooking location, using squid, which results in a higher incidence of jaw hooking, instead of forage fish species for bait, which results in a higher incidence of gut hooking, might result in lower AVM rates⁵⁷. Section S2.1 discusses a possible interacting effect of bait and hook type on anatomical hooking position. Bait type also affects size selectivity, an additional explanatory predictor of AVM^{58,59}. Or it may have been due to various other differences between the two groups of fisheries. As with ocean basin (Section S2.1) and with hook shape (Section S2.2), there may have been simultaneous variability in other potentially significant predictors of AVM. However, for our single species GAMMs, we did have sufficient study-specific coverage of operational characteristics and could test whether such predictors were informative, with hook shape being a significant predictor in two of these models (Section S2.2).

Retention bans and limits, and prohibitions on shark finning and international trade might reduce shark and ray retention. This could substantially reduce the total fishing mortality of elasmobranchs with relatively low AVM rates and hence a relatively high capacity to be released alive. These measures, as well as bycatch quotas (a limit on the catch level of a bycatch species), may also cause fishers to discontinue using fishing methods and gear designs used to target sharks, such as shark lines, wire leaders, and using pieces of incidental catch for bait. If both a bycatch quota and consequences of reaching the threshold are sufficient, then quotas may incentivize fishers to adjust fishing gear and methods to increase selectivity^{60–62}. Individual transferable bycatch quotas incentivize fishers to minimize their bycatch so that they can sell unused quota⁶¹. Fleetwide quotas, however, can incentivize a race for fish and can be inequitable as some vessels may be responsible for a disproportionate share of the quota-limited bycatch⁶³. Robust monitoring systems are needed to produce accurate catch estimates of species subject to bycatch quotas. Because bycatch quotas increase the sensitivity of reporting bycatch data, observers are increasingly vulnerable to coercion, corruption and safety risks, which could be addressed by employing electronic monitoring systems^{64,65}.

Bans on shark finning, where fins are retained and the remaining carcass is discarded, might reduce retention of sharks with little or no market value other than for the fins, and might discontinue fishing methods and gear designs used to target sharks. If shark carcasses have low market value, then shark finning bans will be a disincentive for targeting sharks, as fishers will want to use space in the fish hold for more valuable catch. However, for shark species that are retained for their meat and various other products, finning bans are unlikely to affect fishing mortality rates^{9,66}. Furthermore, relative to species with low AVM rates, for shark species with high AVM rates, finning bans will be less effective at reducing fishing mortality.

Banning elasmobranch retention and international trade might cause pelagic longline fisheries to change targeting practices, discontinue retention and prevent sharks from becoming targets⁶⁷. While most pelagic longline elasmobranch catch is from incidental capture by fisheries targeting tuna and tuna-like species (Scombroidei)

and billfishes (Xiphoidei)^{8,11}, these fisheries may also use gear designs to target sharks on shallower branchlines. This shark targeting would be discontinued if shark retention or trade were banned⁶⁸ and subject to robust surveillance and enforcement. Several elasmobranch species are listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, which establishes close control of their international trade, but none are currently listed on Appendix I, which would ban their international trade⁶⁹. Retention bans, such as through measures adopted by regional fisheries management organizations (RFMOs) and under national Shark Sanctuaries, have been documented to decrease shark fishing mortality rates in some fisheries⁶⁸ but may be ineffective under certain management frameworks^{67,70}.

Reducing discards is prescribed in international guidelines and required by a growing number of fisheries management frameworks^{71,72}. While discard bans may incentivize fishers to implement more selective fishing gear designs and methods to reduce catch rates of unwanted species and sizes of catch subject to the policy, this may be counterproductive, in particular for species with low AVM and post-release mortality rates⁵³.

The five tuna RFMOs tap a very small subset of elasmobranch bycatch mitigation methods. They all ban shark finning and have retention bans in place for certain elasmobranch species. One has catch limits for two shark stocks, some restrict the use of wire leaders and shark lines, and some have voluntary guidelines on handling and release practices^{73–77}. This leaves substantial opportunities to improve regional conservation and management measures for elasmobranch longline bycatch.

Research priorities and conclusions

Completely resolving elasmobranch phylogeny may enable more robust accounting of phylogenetic dependence in multispecies meta-syntheses of AVM rates. Several species had insufficient sample sizes for robust meta-regression models. Additional haulback condition records are needed for these species, in particular for threatened, rare and phylogenetically distinct species which may play relatively large roles in shaping evolutionary processes and ecosystem resilience^{2,78}. We found a paucity of elasmobranch haulback condition records from the Indian Ocean and Mediterranean Sea, and no records from the Black Sea. Addressing these regional gaps is an additional priority.

Richer datasets would enable the inclusion of additional potentially informative predictors of AVM. Numerous predictors could not be explored here due to limitations of the assembled database. This includes, for example, duration spent hooked (fight time), dissolved oxygen, sea surface temperature, depth of the thermocline/mixed layer, salinity, body size and sex of the catch, hook number of the catch (which hook between two floats and hence relative fishing depth), whether the catch was on a shark line, anatomical hooking position, hook size, hook degree of offset, and time-of-day of the gear soak^{18,20,53,54,56}. Unfortunately, most of these variables are rarely or never measured.

Furthermore, many of the potentially informative predictors that were extracted from the compiled publications had low variability, including soak duration, hooks between floats and branchline length, the latter being particularly important for obligate ram-ventilating elasmobranchs¹⁸. Compiling records from a broader range of pelagic longline fisheries employing diverse fishing methods and gear designs, including from artisanal, small-scale longline fisheries, would enable a more robust assessment of the significance of these variables.

Phylogeny was a moderate but significant predictor of pelagic longline AVM rate. This was the first comprehensive study to assess the influence of elasmobranch phylogeny on AVM. Contrary to some hypotheses^{30,53}, ventilation mode and body form (morphology) were not informative predictors of haulback condition for pelagic elasmobranchs in our study. Body form categories based on gill slit morphology and ventilation mode used here may be correlated with phylogeny^{79,80}, so when models are phylogenetically adjusted, these variables become redundant.

The most promising approach to reduce total fishing mortality of species with high AVM rates is to employ methods that reduce catch risk. To reduce total fishing mortality of species with low AVM rates, in addition to reducing catchability, handling-and-release practices and policy interventions that, under certain enabling environments, reduce retention, including retention bans in blue water shark sanctuaries, and shark finning and trade bans, are appropriate. The elasmobranch AVM rates, estimated here through Bayesian meta-regression analysis, a robust statistical procedure for synthesizing evidence from multiple studies, support evidence-informed elasmobranch conservation and fisheries bycatch management. When combined with robust estimates of natural and other anthropogenic hazards, including other components of fishing mortality, these AVM rates can improve the reliability of models of elasmobranch population dynamics and support developing strategies to mitigate risks.

Methods

Data compilation. A two-tiered literature search was employed to compile relevant peer-reviewed published and grey literature and assemble a dataset suitable for meta-analytic evaluation. A link to the assembled dataset, which includes references for retained publications, is provided in the Data Availability section. The methods for the systematic literature review were adapted from the Reporting Standards for Systematic Evidence Syntheses⁸¹, Collaboration for Environmental Evidence^{82,83} and Preferred Reporting Items for Systematic reviews and Meta-Analyses⁸⁴. An unstructured literature search was implemented by reviewing reference lists of the compiled publications from the systematic search. Supplemental Information Section S3.1 contains details on approaches employed for the literature review searches. The number of articles retrieved and screened and retained/discarded were recorded in a flow diagram (Supplemental Information Fig. S5).

Statistical modelling approach. *Datasets and model overview.* Our dataset comprised 1438 study-specific summary or aggregate AVM rates for 61 elasmobranch species from 33 genera, 22 families and 9 orders. Two shark clades or taxonomic orders (Carcharhiniformes, Lamniformes) accounted for 39 of those species

(ca 64%) and phylogenetic Bayesian meta-regression models were fitted to those data. Separate Bayesian meta-regression models without phylogenetic adjustment were fitted to the AVM data for 4 other species (2 Myliobatiformes spp, 2 Squaliformes spp)—far too few species to explicitly account for any phylogenetic resolution. Overall, we used some form of Bayesian meta-regression model to summarize the AVM rates for 43 of the 61 elasmobranch species (ca. 70%). We excluded from meta-regression modelling the remaining 18 species with limited data records, including zero dead for 1 or more of the records but, nonetheless, derived AVM rates for further qualitative consideration in our meta-synthesis. The AVM rate for each of those 18 species (15 genera, 14 families, 8 orders) was estimated using a Bayesian binomial likelihood estimator that accounts for zero recorded mortalities⁸⁵. The mean posterior rate and a 95% highest posterior density interval (HDI) was summarized by sampling from a binomial likelihood with a Bayes-Laplace prior⁸⁵ using the `binom` package for R⁸⁶—rather than just using the raw study-specific summaries.

Predictor screening and missing predictor imputation. We extracted several AVM covariates or predictors for each study but including all predictors in our meta-synthesis workflow would increase the risk of model overfitting. So, we used the `metaforest` package for R⁸⁷ to fit a random-effects weighted metaforest model with clustered bootstrap sampling to screen for potentially informative predictors using a variable importance metric. Briefly, `metaforest` implements a machine-learning based exploratory approach adapted from random forest algorithms⁸⁸ to identify relevant linear or nonlinear predictors, and perhaps higher-order interactions, from a wide selection of predictors. Random forests are a commonly used machine-learning tool for classification and for ranking of candidate predictors based on variable importance measures⁸⁹. We used those predictors identified using the variable importance metric for all 1438 effect sizes in our subsequent Bayesian meta-regression modelling workflow that was based on a subset of those effect sizes. Some of the predictors such as soak duration of the gear and number-of-hooks-between-floats were incomplete with missing values ranging from 4% for hooks between floats and 14% for soak duration. So, we used the `missRanger` package for R⁹⁰, which itself uses the `ranger` package for R⁸⁸, to do fast missing value imputation by chained random forests. Here we also used predictive mean matching to avoid any imputation with values that were not present in the original data. This data set with imputed missing predictor values was then used for predictor screening for the entire data set of 1438 effect sizes.

Elasmobranch phylogenetic structure. The multilevel or hierarchical meta-regression modelling approach⁹¹ that we used accounted for elasmobranch species-level variance by including a phylogenetic correlation matrix derived from a phylogenetic tree. This matrix allowed us to account explicitly for correlated species-level random effects³³. However, Chondrichthyan (shark, ray and chimaera) phylogeny remains unresolved^{37,46,92–94}, so we derived the phylogenetic correlation matrix for all the 61 elasmobranch (shark and ray) species in our study by using the phylogenetic tree construction proposed by Stein et al.⁹⁵ for 1192 Chondrichthyan species. Credible sets of the species-level phylogenetic history are available for subsetting and downloading at <http://vertlife.org/phylosubsets>. We recovered 100 random Chondrichthyan phylogenetic trees in NEXUS file format⁹⁶ from a posterior of distribution of 10,000 phylogenetic trees using the “[fully resolved 1 fossil (set of 10 k trees)]” source—Upham et al.⁹⁷ provide details on how these phylogenetic tree posterior distributions have been constructed using a Bayesian 2-level “backbone-and-patch” approach. We then randomly selected one tree from that 100-tree selection, which was used as the phylogenetic hypothesis or template for our meta-synthesis. Similar results were found using other randomly selected trees. With that phylogenetic tree we were then able to derive variance and correlation matrices using the `ape` package for R⁹⁸ and tree visualisations using the `ggtree` package for R⁹⁹—see Fig. S6 for a radial tree plot showing the proposed phylogenetic structure for the 61 elasmobranch species evaluated in our study. Clade-specific subsets of that tree (Carcharhiniformes, Lamniformes) and the derived correlation matrices were used for the phylogenetically adjusted Bayesian GAMM models fitted to the species-specific AVM rates for each clade.

Bayesian phylogenetic regression models. We modelled the effect of potentially informative predictors on elasmobranch species-specific AVM rates using a Bayesian multilevel or hierarchical regression modelling approach, which included a species-level phylogenetic structure as a group-level or random effect to adjust for any phylogenetic dependence¹⁰⁰. We fitted this model to each of the two clades: the Carcharhiniformes (26 species, 8 genera, 3 families) and the Lamniformes (13 species, 9 genera, 6 families). These data comprised 706 study-specific effect sizes for the Carcharhiniformes and 466 effect sizes for the Lamniformes, covering both the Atlantic and Pacific Oceans for both clades—records from the Mediterranean and Indian Ocean were excluded from this meta-analysis due to small sample sizes. We fitted these meta-analytic models to the study-specific proportion for each species recorded dead at haulback in pelagic longline gear. The multilevel structure for each model comprised the individual study identification, multiple records nested within some studies and the research group cluster for the various studies (see Konstantopoulos⁹¹ for a discussion of multilevel meta-analytic models). We included the potentially informative covariates or predictors in the meta-regression structured models to evaluate whether AVM rate was a function of those predictors. We had previously screened a range of potential predictors to determine a minimal set of informative predictors using machine learning approaches discussed above.

We fitted these random-effects meta-regression models with binomial likelihood appropriate for proportion data¹⁰¹ using the Stan computation back-end¹⁰² via the `brms` interface for R¹⁰³. This is also known as a binomial-Normal hierarchical meta-analytic model¹⁰⁴ but was fit within a Bayesian inference framework¹⁰⁵ using weakly informative priors¹⁰⁶. It is a binomial-Normal GAMM regression model because: (1) the model likelihood is binomial to account for the proportion response data, (2) the group-level or random effects including the

phylogenetic structure are sampled from a multivariate Gaussian distribution¹⁰⁴, and (3) any nonlinear covariate functional form was accounted for using a thin plate regression spline basis commonly applied to fit generalized additive mixed models or GAMMs¹⁰⁷. The fitted binomial-Normal model to the study-specific estimates for each species were then used to derive the overall or pooled mean AVM rate based on the posterior for each estimate comprising 10,000 samples or draws that were also used to derive the uncertainty estimates.

We used HDI as our measure of uncertainty, which is the shortest credible interval¹⁰⁸. The HDIs were summarized from the posterior samples for each species meta-analytic model fit using the `tidybayes` package for R¹⁰⁹. A probability statement about the existence of a particular predictor-specific effect can also be determined with those 10,000 draws using the probability of direction metric proposed recently using the `BayestestR` package for R¹¹⁰.

The estimated effect summaries based on the best-fit conditional regression GAMMs were then adjusted for variable sample size using the predicted estimated marginal means approach¹¹¹ and implemented using the `emmeans` package for R¹¹². We then summarized the marginal effect posterior densities to assess any apparent difference for instance between the estimated marginal AVM rates for the Atlantic and Pacific estimates. The posterior ratio summary was included in the summary plot for this effect.

We estimated the model-specific phylogenetic signal as the mean posterior proportion (with 95% HDI) of the summed group-level variances attributable to the phylogenetic group-level component—this approach assumes a Brownian diffusion or genetic drift process of character evolution for a continuous species-specific trait¹¹³. The phylogenetic signal or constraint is a simple metric that reflects the apparent effect of shared evolutionary history or ancestry on the specific trait or attribute state being evaluated¹¹⁴.

All models were fit with 4 Markov 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* statistic³². We also used leave-one-out cross-validation (LOOcv) metrics and Bayesian stacking^{115,116} to explore any comparative difference in expected predictive accuracy between models fitted with or without a specific predictor such as for instance body form, ventilation mode or phylogenetic correlation structure. Further evaluation of the best-fit-model was then assessed using graphical posterior predictive checks¹¹⁷. All inference was then made using the best-fit model and the posterior predictive samples¹¹⁸.

Bayesian species-specific regression models. We modelled the effect of potential informative predictors on AVM rates for each of the following four species using a similar Bayesian GAMM modelling approach but without phylogenetic adjustment as no phylogenetic structure was relevant for this small subset of species—two Myliobatiformes species (*Manta (Mobula) birostris*, *Pteroplatytrygon violacea*) and two Squaliformes species (*Isistius brasiliensis*, *Zameus squamulosus*).

Publication bias. We explored potential publication bias¹¹⁹ for the best-fit clade-specific models using a standard error-based contour-enhanced funnel plot¹²⁰, which was more readily implemented here within a frequentist rather than a Bayesian modelling framework. Specifically, we used predicted AVM rates for the Carcharhiniformes and Lamniformes clades estimated using the `metafor` package for R¹²¹ for fitting a clade-specific frequentist-based meta-analytic type model with the same species-level phylogenetic structure and the other group-level (or random) effects used in the Bayesian GAMMs. `Metafor` cannot directly fit a binomial-Normal GAMM (or GLMM) with phylogenetic structure, so we used the multivariate parameterization form of a meta-regression model in `metafor`¹²² with logit transformed AVM response to mimic a GLMM and specifically accommodate in `metafor` the more complex forms of random-effect structures used here including the phylogenetic tree structure³³.

Data availability

The assembled database used for the meta-analyses is openly available from <https://tinyurl.com/elasmobran-ch-mortality>.

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Author contributions

E.G. and M.C. conceived and designed the study; E.G. lead project management; E.G., L.B., H.B. and M.F. compiled publications/collected the data; E.G. assembled the database; M.C. performed statistical analyses; E.G. and M.C. wrote the draft manuscript; all authors edited and contributed to writing the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Supporting Information

Phylogeny explains capture mortality of sharks and rays in pelagic longline fisheries: A global meta-analytic synthesis

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S1. RESULTS

S1.1. Predictor Screening

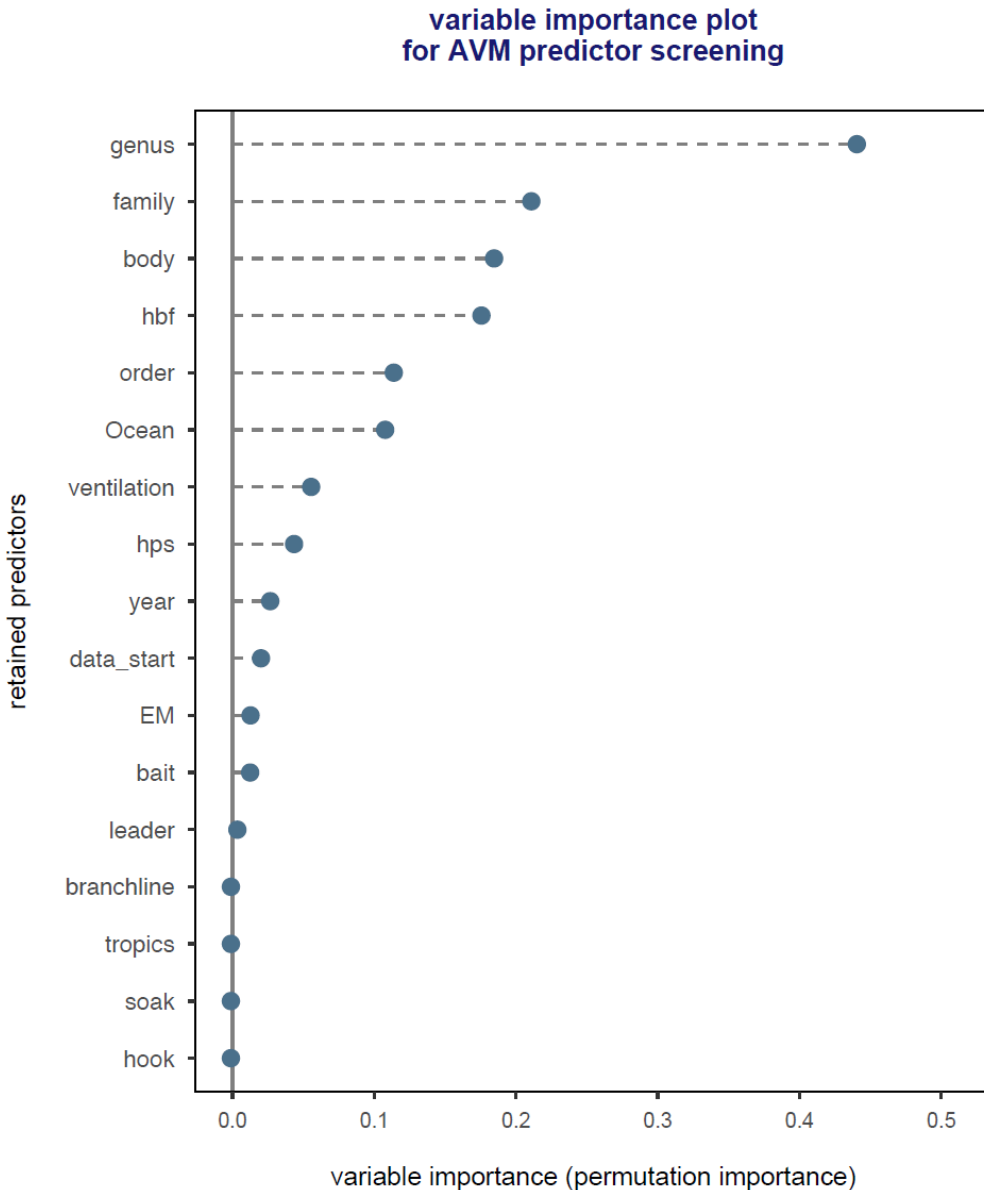


Fig. S1. Metaforest derived variable importance plot using chained random forests, identifying potentially informative moderator (or covariate) effects on at-vessel mortality (AVM) for the full dataset comprising 1,438 records for 61 elasmobranch species. [$R^2(oob) = 0.034$, $R^2(cv) = 0.25$, $\tau^2 = 1.29 =$ residual heterogeneity].

body = body type (morphology), 5 categories for sharks from Dolce and Wilga (2013), and all rays; **hbf** = number of hooks between two floats; **Ocean** = Ocean basin; **ventilation** = respiratory mode of either obligate ram ventilator or buccal pump; **hps** = number of hooks deployed per set; **year** = year of publication; **data_start** = the first year of the time series; **EM** = data source (experiment, observer or electronic monitoring program, logbook program); **bait** = bait type (forage fish, squid, other); **leader** = leader material (wire, monofilament, other); **branchline** = branchline length; **tropics** = majority of fishing effort occurred in the tropics - between 23.4N and 23.4S (yes, no, other – mix or unknown); **soak** = maximum soak duration; **hook** = hook shape (circle, J-shaped J, tuna or teracima, other).

S1.2. Heterogeneity

Both Bayesian phylogenetic meta-regression models were good fits to the AVM data for either the Carcharhiniform or Lamniform species (Fig. S2.1). Nonetheless, there was significant between-study heterogeneity indicated by the following heterogeneity metrics (Higgins and Thompson, 2002) estimated for the Carcharhiniformes [median $\tau = 0.93$ (95% HDI: 0.89-0.97); median $I^2 = 99.8\%$ (95% HDI: 99.7-99.9%)] and for the Lamniformes [median $\tau = 0.84$ (95% HDI: 0.76-0.92); median $I^2 = 98.2\%$ (95% HDI: 96.1-99.3%)].

S1.3. Lamniformes Phylogenetic Meta-Regression Model

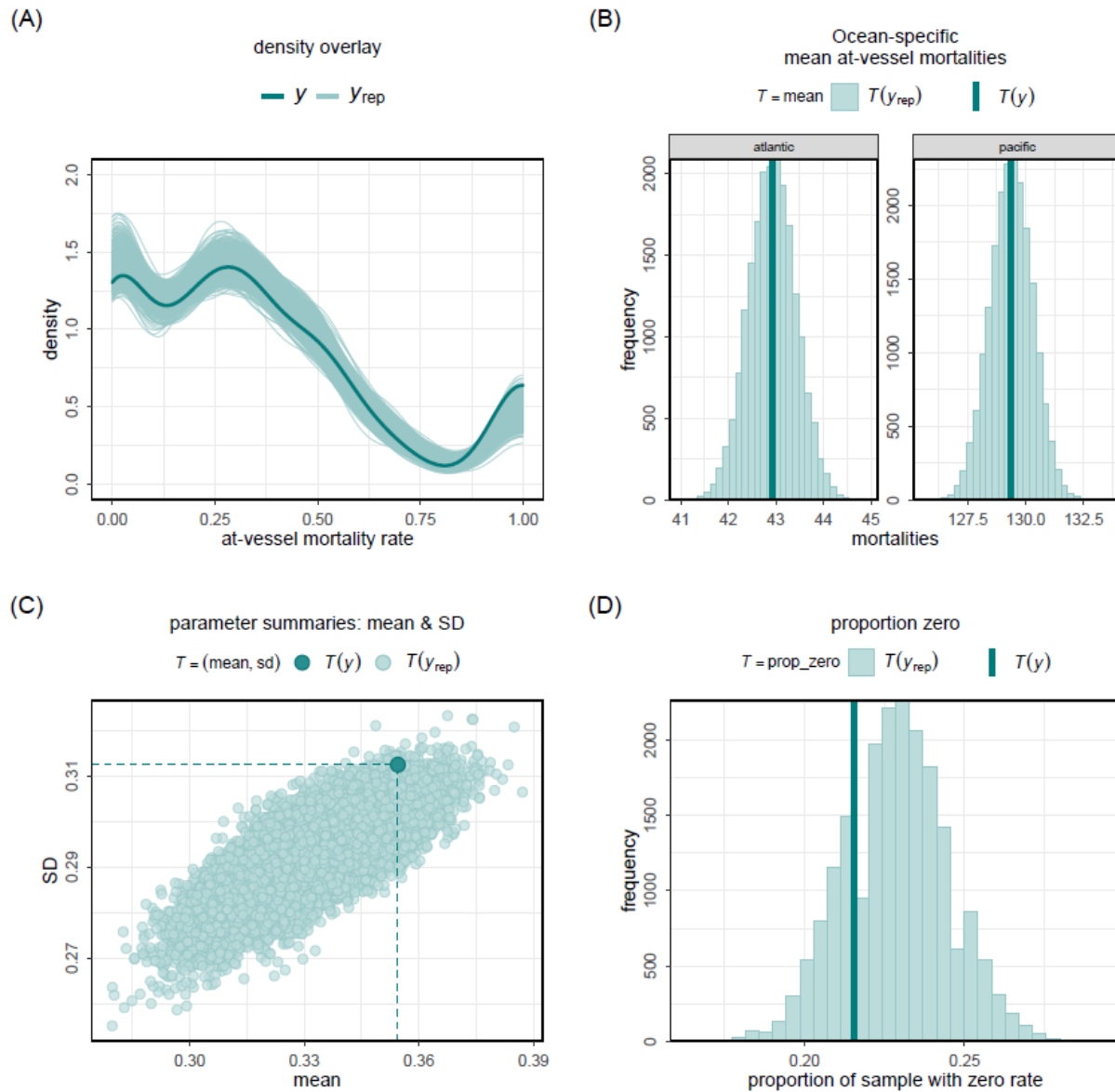


Fig. S2.1. Posterior predictive check tests for 1000 randomly selected draws from the best-fit phylogenetic binomial-Normal GAMM fitted to the AVM rates for the Lamniiformes species. (Panel A) shows the posterior predictive check for the response variable where the solid curve (y) is the density curve summarizing 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.

**Lamniformes spp: at-vessel mortality marginal effect
binomial-normal phylogenetic GAMM estimates**
density plots (with marginal median and 80% & 95% HDI summaries)

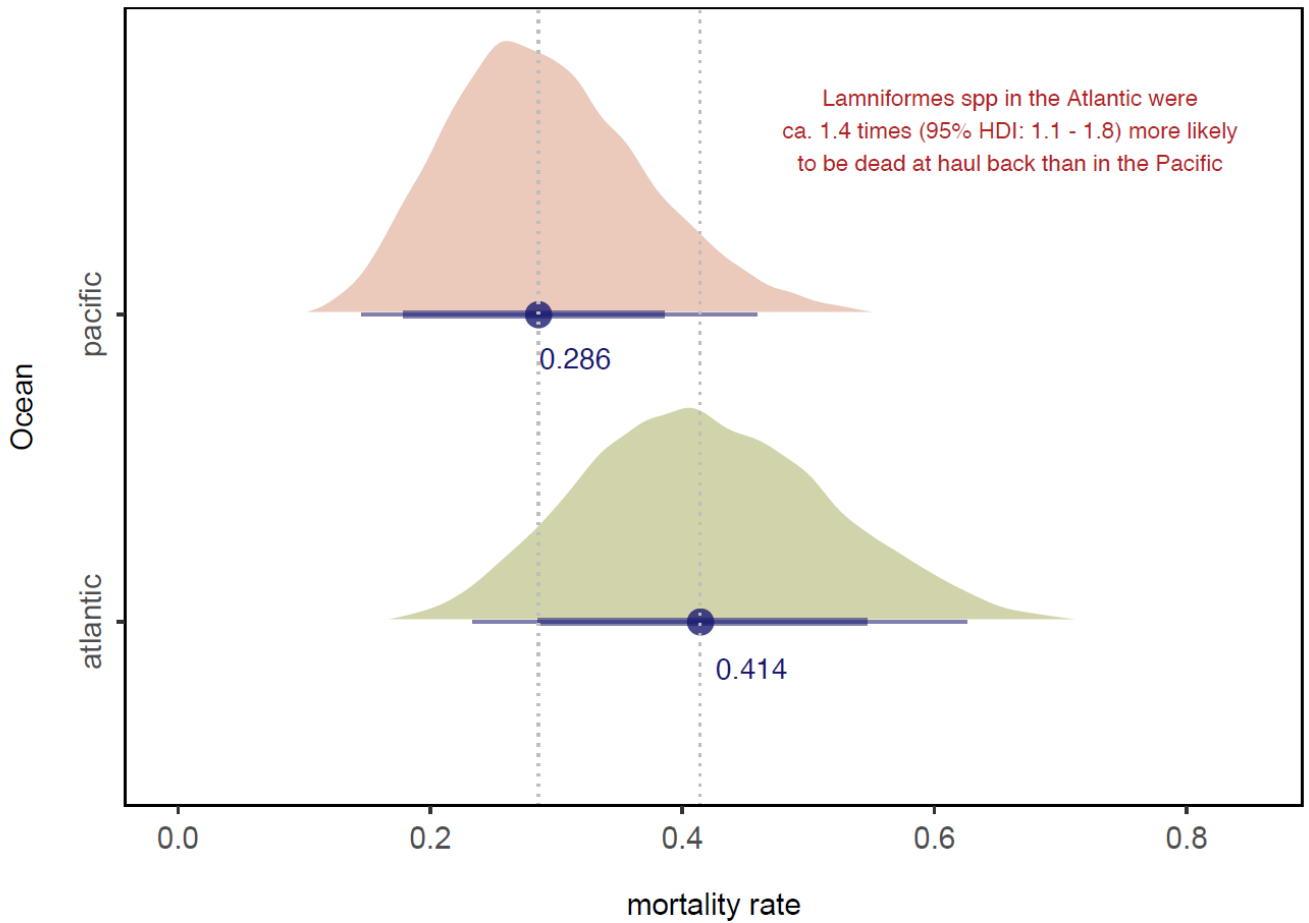


Fig. S2.2. Summary of the estimated marginal mean ocean-specific effect derived from the phylogenetic GAMM meta-regression model fitted to the Lamniformes AVM rates. Colored polygon shows the density distribution summary, solid dot (+ numeric label) = mean estimated of the density polygon, thick horizontal line below each polygon shows the 80% highest posterior density interval for the density polygon while the thin horizontal line is the 95% HDI.

S1.4. Publication Bias

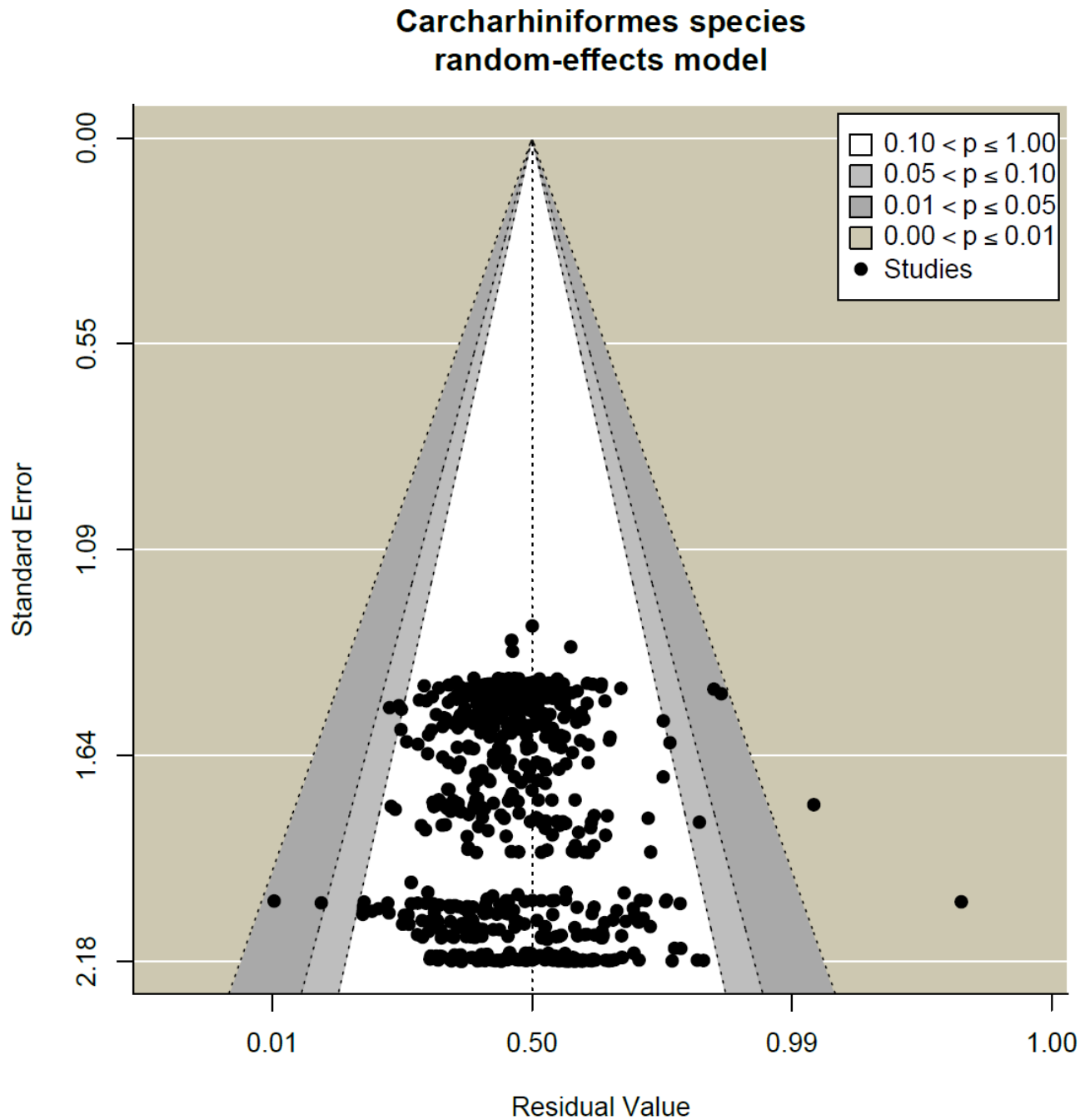


Fig. S3. Contour-enhanced funnel plot of the phylogenetically adjusted multivariate meta-regression model derived AVM estimates for the Carcharhiniformes study-specific effect sizes (N=706, 26 species).

S1.5. Summary of Elasmobranch Species-specific AVM Rate Estimates

Table S1. AVM rates for 61 elasmobranch species, identifying the modeling method used for each species-specific estimate. Records are arranged from highest to lowest posterior mean values.

Order	Family	Species			Method	posterior		95 % HDI	
		Scientific name	Common name			median	mean	lower	upper
Lamniformes	Lamnidae	<i>Lamna ditropis</i>	Salmon shark	phylogenetic GMM	0.722	0.761	0.491	0.902	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus signatus</i>	Night shark	phylogenetic GMM	0.749	0.735	0.508	0.924	
Carcharhiniformes	Carcharhinidae	<i>Rhizoprionodon terraenovae</i>	Atlantic sharpnose shark	phylogenetic GMM	0.742	0.727	0.486	0.922	
Carcharhiniformes	Sphyrnidae	<i>Sphyrna zygaena</i>	Smooth hammerhead shark	phylogenetic GMM	0.659	0.641	0.380	0.864	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus brevipinna</i>	Spinner shark	phylogenetic GMM	0.654	0.637	0.388	0.881	
Lamniformes	Alopiidae	<i>Alopias pelagicus</i>	Pelagic thresher shark	phylogenetic GMM	0.530	0.584	0.304	0.754	
Carcharhiniformes	Sphyrnidae	<i>Sphyrna mokarran</i>	Great hammerhead shark	phylogenetic GMM	0.591	0.572	0.311	0.842	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus limbatus</i>	Blacktip shark	phylogenetic GMM	0.559	0.542	0.295	0.813	
Carcharhiniformes	Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead shark	phylogenetic GMM	0.542	0.524	0.270	0.789	
Rhinobatiformes	Rhinobatidae	<i>Glaucostegus cemiculus</i>	Blackchin guitarfish	binomial (Bayes-Laplace prior)	0.500	0.500	0.180	0.820	
Squaliformes	Centrophoridae	<i>Centrophorus granulosus</i>	Gulper shark	binomial (Bayes-Laplace prior)	0.500	0.500	0.150	0.850	
Lamniformes	Lamnidae	<i>Lamna nasus</i>	Porbeagle shark	phylogenetic GMM	0.432	0.485	0.208	0.654	
Lamniformes	Alopiidae	<i>Alopias superciliosus</i>	Bigeye thresher shark	phylogenetic GMM	0.430	0.484	0.214	0.650	
Lamniformes	Lamnidae	<i>Isurus paucus</i>	Longfin mako shark	phylogenetic GMM	0.425	0.477	0.215	0.650	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus altimus</i>	Bignose shark	phylogenetic GMM	0.489	0.471	0.224	0.764	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus falciformis</i>	Silky shark	phylogenetic GMM	0.487	0.470	0.230	0.734	
Lamniformes	Lamnidae	<i>Carcharodon carcharias</i>	Great white shark	phylogenetic GMM	0.375	0.428	0.142	0.648	
Lamniformes	Alopiidae	<i>Alopias vulpinus</i>	Thresher shark	phylogenetic GMM	0.354	0.406	0.168	0.578	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus perezii</i>	Caribbean reef shark	phylogenetic GMM	0.419	0.404	0.069	0.798	
Lamniformes	Odontaspidae	<i>Odontaspis noronhai</i>	Bigeye sand tiger shark	phylogenetic GMM	0.345	0.394	0.099	0.636	
Lamniformes	Lamnidae	<i>Isurus oxyrinchus</i>	Shortfin mako shark	phylogenetic GMM	0.340	0.390	0.151	0.557	
Lamniformes	Cetorhinidae	<i>Cetorhinus maximus</i>	Basking shark	phylogenetic GMM	0.307	0.356	0.072	0.608	
Lamniformes	Pseudocarchariidae	<i>Pseudocarcharias kamoharai</i>	Crocodile shark	phylogenetic GMM	0.305	0.354	0.130	0.511	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus acronotus</i>	Blacknose shark	phylogenetic GMM	0.367	0.351	0.133	0.628	

Order	Family	Species		Method	posterior		95 % HDI	
		Scientific name	Common name		median	mean	lower	upper
Carcharhiniformes	Carcharhinidae	Carcharhinus obscurus	Dusky shark	phylogenetic GAMM	0.354	0.337	0.132	0.594
Carcharhiniformes	Carcharhinidae	Negaprion acutidens	Sicklefin lemon shark	binomial (Bayes-Laplace prior)	0.333	0.333	0.000	0.780
Hexanchiformes	Hexanchidae	Heptranchias perlo	Sharpnose sevengill shark	binomial (Bayes-Laplace prior)	0.333	0.333	0.030	0.670
Myliobatiformes	Mobulidae	Mobula japonica	Spinetail mobula	binomial (Bayes-Laplace prior)	0.333	0.333	0.000	0.780
Orectolobiformes	Rhincodontidae	Rhincodon typus	Whale shark	binomial (Bayes-Laplace prior)	0.333	0.333	0.000	0.780
Squatiformes	Squatinae	Squatina tergocellatoides	Ocellated angelshark	binomial (Bayes-Laplace prior)	0.333	0.333	0.000	0.780
Myliobatiformes	Mobulidae	Mobula birostris	Giant manta ray	GAMM	0.332	0.332	0.015	0.707
Carcharhiniformes	Carcharhinidae	Carcharhinus longimanus	Oceanic whitetip shark	phylogenetic GAMM	0.336	0.320	0.121	0.571
Squaliformes	Dalatiidae	Isistius brasiliensis	Cookie cutter shark	GAMM	0.278	0.294	0.055	0.564
Lamniformes	Megachasmidae	Megachasma pelagios	Megamouth shark	phylogenetic GAMM	0.232	0.273	0.000	0.818
Carcharhiniformes	Triakidae	Mustelus mustelus ¹	Smooth-hound shark	binomial (Bayes-Laplace prior)	0.268	0.268	0.156	0.384
Carcharhiniformes	Carcharhinidae	Carcharhinus amblyrhynchos	Grey reef shark	phylogenetic GAMM	0.281	0.268	0.058	0.586
Squaliformes	Centrophoridae	Centrophorus zeehaani	Southern dogfish	binomial (Bayes-Laplace prior)	0.250	0.250	0.000	0.630
Squaliformes	Somniosidae	Zameus squamulosus	Velvet dogfish shark	GAMM	0.225	0.226	0.071	0.368
Carcharhiniformes	Carcharhinidae	Carcharhinus plumbeus	Sandbar shark	phylogenetic GAMM	0.229	0.216	0.068	0.433
Lamniformes	Odontaspidae	Carcharias taurus	Sand tiger shark	phylogenetic GAMM	0.175	0.208	0.004	0.516
Hexanchiformes	Hexanchidae	Hexanchus griseus	Bluntnose sixgill shark	binomial (Bayes-Laplace prior)	0.200	0.200	0.000	0.530
Carcharhiniformes	Carcharhinidae	Negaprion brevirostris	Lemon shark	phylogenetic GAMM	0.198	0.188	0.000	0.783
Carcharhiniformes	Carcharhinidae	Carcharhinus isodon	Finetooth shark	phylogenetic GAMM	0.196	0.185	0.000	0.798
Carcharhiniformes	Carcharhinidae	Carcharhinus galapagensis	Galapagos shark	phylogenetic GAMM	0.191	0.180	0.038	0.398
Carcharhiniformes	Carcharhinidae	Carcharhinus leucas	Bull shark	phylogenetic GAMM	0.189	0.178	0.045	0.406
Squaliformes	Somniosidae	Centroscymnus owstonii ²	Roughskin dogfish shark	binomial (Bayes-Laplace prior)	0.124	0.124	0.120	0.130
Carcharhiniformes	Carcharhinidae	Prionace glauca	Blue shark	phylogenetic GAMM	0.119	0.111	0.028	0.251
Carcharhiniformes	Carcharhinidae	Carcharhinus albimarginatus	Silvertip shark	phylogenetic GAMM	0.110	0.104	0.003	0.392
Carcharhiniformes	Triakidae	Mustelus canis	Dusky smooth-hound shark	phylogenetic GAMM	0.109	0.102	0.019	0.284
Rajiformes	Rajidae	Raja clavata	Thornback ray	binomial (Bayes-Laplace prior)	0.100	0.100	0.000	0.280
Carcharhiniformes	Triakidae	Galeorhinus galeus	Tope shark	phylogenetic GAMM	0.101	0.095	0.014	0.285

Order	Family	Species			Method	posterior		95 % HDI	
		Scientific name	Common name			median	mean	lower	upper
Myliobatiformes	Dasyatidae	Taeniura grabata	Round stingray		binomial (Bayes-Laplace prior)	0.083	0.083	0.000	0.240
Carcharhiniformes	Carcharhinidae	Carcharhinus melanopterus	Blacktip reef shark		phylogenetic GAMM	0.075	0.071	0.000	0.421
Carcharhiniformes	Carcharhinidae	Galeocerdo cuvier	Tiger shark		phylogenetic GAMM	0.071	0.066	0.016	0.175
Myliobatiformes	Mobulidae	Mobula mobular	Devil fish		binomial (Bayes-Laplace prior)	0.059	0.059	0.000	0.170
Myliobatiformes	Mobulidae	Mobula tarapacana	Chilean devil ray		binomial (Bayes-Laplace prior)	0.059	0.059	0.000	0.170
Myliobatiformes	Myliobatidae	Pteromylaeus bovinus	Bull ray		binomial (Bayes-Laplace prior)	0.056	0.056	0.000	0.160
Orectolobiformes	Ginglymostomatidae	Ginglymostoma cirratum	Nurse shark		binomial (Bayes-Laplace prior)	0.056	0.056	0.000	0.160
Carcharhiniformes	Carcharhinidae	Carcharhinus brachyurus	Copper shark		phylogenetic GAMM	0.050	0.047	0.001	0.215
Myliobatiformes	Dasyatidae	Pteroplatytrygon violacea ³	Pelagic stingray		GAMM	0.019	0.047	0.001	0.157
Squaliformes	Squalidae	Squalus acanthias	Picked dogfish		binomial (Bayes-Laplace prior)	0.039	0.039	0.010	0.070

¹ The 7 compiled records for the common smooth-hound shark *Mustelus mustelus* were all from the Mediterranean Sea.

² The 2 compiled records for the roughskin dogfish shark (Owston's dogfish shark) *Centroscymnus owstonii* were both from the Pacific Ocean.

³ The predicted marginal mean ocean-specific AVM rates, weighted proportionally according to sample size, for the pelagic stingray *Pteroplatytrygon violacea* were 0.005 (95% HDI: 0.001–0.02) for the Atlantic and 0.18 (95% HDI: 0.04–0.41) for the Pacific Ocean effect sizes. In the Pacific, the pelagic stingray predicted marginal mean AVM rate for circle hooks was 0.08 (95% HDI: 0.001-0.23) and 0.31 (95% HDI: 0.001-0.61) for J-shaped hooks.

S1.6. Sample Forest Plot

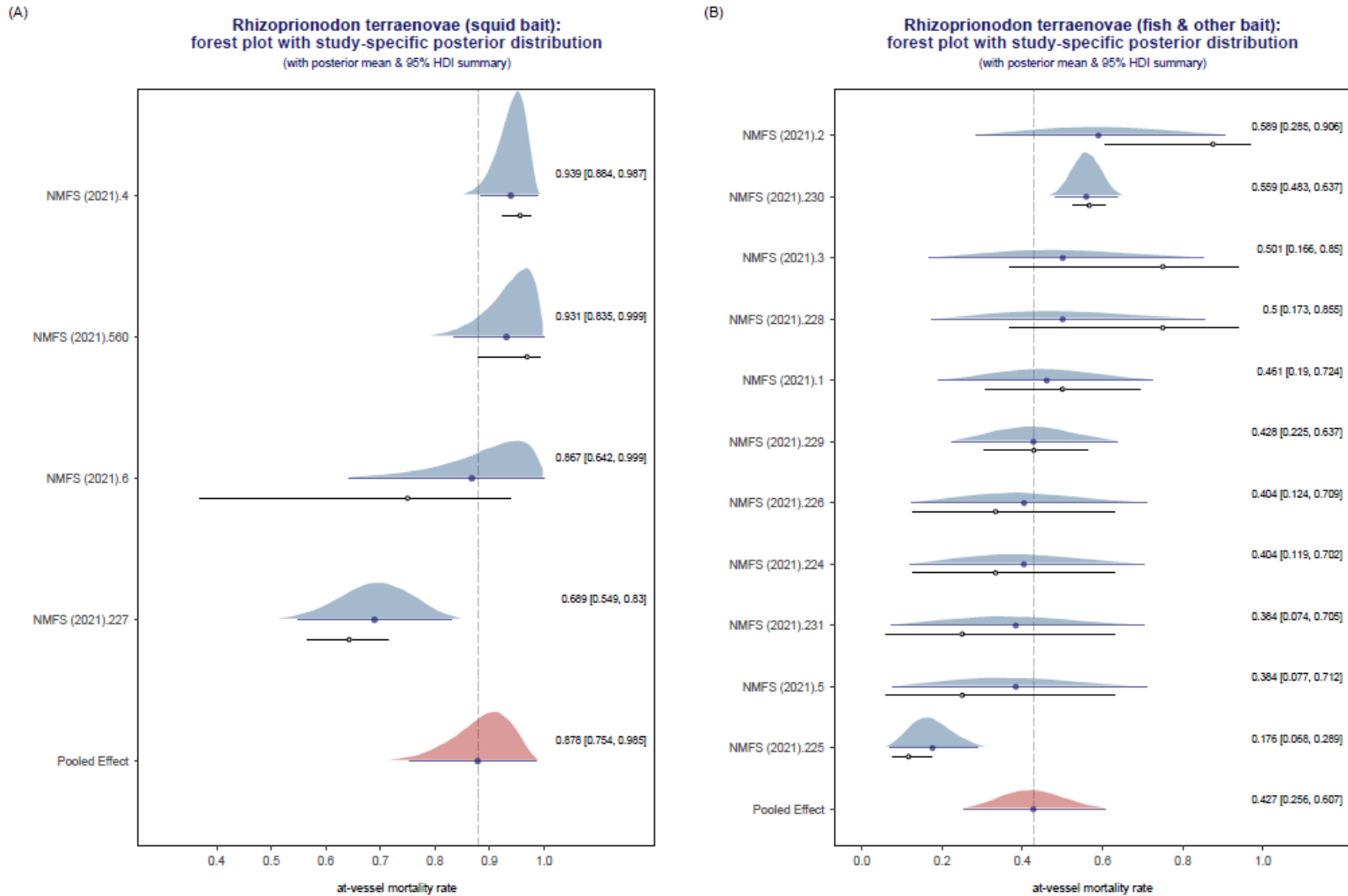


Fig. S4. Model-predicted log relative risk ratio derived for Atlantic sharpnose shark *Rhizoprionodon terraenovae* for 4 effect sizes for records using only squid for bait (Panel A) and 11 effect sizes for records using only fish, a mix of fish and squid, or unknown bait

type (Panel B). Shrinkage estimates were derived using a precision weighted Bayesian random-effects meta-analytic model with Gaussian likelihood. Polygon = density of the posterior draws (the effective sample size = 10,000) and reflects the distribution of each estimate, where a wide and thin polygon indicates low precision from a small sample size, and narrow and tall indicates there was high precision and large sample size. The horizontal line underneath each polygon = 95% HDI of the posterior draws, solid dot = mean of the posterior draws shrunk towards the random or Pooled Effect, which is the mean or overall expected log relative risk ratio (right-side labels = the posterior mean and HDI summaries). 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.

S2. DISCUSSION OF EXPLANATORY PREDICTORS AND INTERACTING EFFECTS OF COMPONENTS OF FISHING MORTALITY

S2.1. Ocean Basin

There was a significant ocean basin effect on elasmobranch AVM rates. For the assembled database, shark AVM rates were generally higher in the Atlantic than the Pacific. The opposite effect occurred for pelagic stingray, the main ray species represented in the assembled database and captured in global pelagic longline fisheries (Clarke et al., 2014).

This observed ocean basin effect could be due to biological (e.g., body size) or behavioral (e.g., fight response to capture) differences between populations of a species in different oceans, or because thermocline depth, temperature, dissolved oxygen, salinity and other environmental parameters that affect at-vessel condition vary over broad spatial and temporal scales (Stramma et al., 2012; Ellis et al., 2017; Hyatt et al., 2018; Musyl and Gilman, 2019). The basin effect could also have been due to correlations between ocean basin and various informative predictors of AVM. For example, Pfaller et al. (2018) determined that an ocean effect on adult marine turtle survival rates was correlated with study methodology, including tag type, habitat type from which turtles were sampled, as well as statistical modeling approaches. In the current study, several environmental and operational (gear design and fishing method) informative predictors, and regional differences in species composition of the catch were likely correlated with ocean basin.

The species composition in the two regions was substantially different for the Carcharhiniformes model. The species with the five highest overall global AVM rates made up only 7.5% of the Pacific Ocean records but 21.5% of Atlantic Ocean records. In the Pacific Ocean, over 26% of Carcharhiniformes records were for the blue shark, which had the seventh lowest overall global AVM rate of the 26 species in the order included in the assembled database (Table S1). The distribution of Lamniformes records by species and global pooled AVM rates in the two regions was less variable than for the Carcharhiniformes. There were large differences in the latitudinal distribution of records by region, with ca. 75% of Pacific Ocean and ca. 25% of Atlantic Ocean Carcharhiniformes, Lamniformes and pelagic stingray records occurring in the tropics. A latitude effect may explain why regions within the Atlantic was found in a previous study to be an important predictor of species-specific AVM risk (Coelho et al., 2012; Dapp et al., 2017). Latitude is a proxy for ocean temperature and dissolved oxygen, which are informative predictors of at-vessel condition due to species- and size-specific physiological stress responses and tolerance thresholds (Gallagher et al., 2014; Schlaff et al., 2014; Hyatt et al., 2018; Massey et al., 2019; Musyl and Gilman, 2018, 2019; Ochi et al., 2021). A latitude effect may also be due to the spatial segregation by size and sex within elasmobranch species (Mucientes et al., 2009; Schlaff et al., 2014). Differences in survival probability have been observed by size and sex within species for some elasmobranchs (Musyl *et al.* 2011; Gallagher *et al.* 2014; Butcher et al., 2015; Ellis et al., 2017; Saidi et al., 2019). A lower probability of AVM occurs with an increase in body size for some species (Musyl et al., 2009; Musyl and Gilman, 2018; Massey et al., 2019; Nunes et al., 2019). Higher AVM rates for males than females have also been observed for some elasmobranch species (Coelho et al., 2011, 2012; Butcher et al., 2015). This may be due to differences in body size by sex for species that exhibit sexual size dimorphism (differences in size by sex of the same age class, i.e., differential growth by sex). The effect of sex on AVM risk may also be due to differences in depth distributions by sex and concomitant differences in environmental explanatory predictors, and to physiological differences, such as different energy demands, and different skin thickness when females are reproductively active (Schlaff et al., 2014; Ellis et al., 2017).

The ocean basin effect in the two phylogenetic and the pelagic stingray models may have also been due to large operational differences between the Atlantic and Pacific Ocean fleets. The use of different pelagic longline gear designs and fishing methods to target different species can significantly explain elasmobranch AVM rates (Gallagher et al., 2014). Atlantic Ocean records in the three models were predominantly from shallow-set fisheries with about 5 hooks between floats, squid used for bait in about 30% of records, and wire leaders used in about 4% of records. Elasmobranchs captured on shallow gear may be trapped in the uniform mix-layer and not be able to dive deeper to cool off and repay oxygen debts. Pacific Ocean records in the three models were largely from deep-set fisheries with about 19 hooks between floats, squid used for bait in about 12% of records, and wire leaders used in about 35% of records. A larger proportion of some sharks has been observed to be alive on wire than monofilament leaders (Afonso et al., 2012; Gilman et al., 2016). Leader material may affect within-species selectivity by relative strength and vigor. While wire leaders tend to indiscriminately retain all sharks that ingest baited hooks, for sharks caught on monofilament leaders, stronger and more vigorous individuals may have a higher probability of escaping than weaker and more seriously injured individuals. Individuals retained on monofilament leaders may therefore have a higher probability of being dead upon haulback than sharks that are able to sever the monofilament leader and escape (Afonso et al., 2012; Gilman et al., 2016). However, there may be synergistic effects of hook, bait and leader types on shark AVM rates. If hook and bait types are used that result in mouth hooking, then this may diminish or eliminate any effect of leader material on at-vessel condition (Gilman et al., 2016). As with hook shape (discussed below), bait type affects anatomical hooking position, which is an explanatory predictor of haulback condition, and can also affect size selectivity (Coelho et al., 2012; Amorim et al., 2014). Due to the prevalent hooking location, using squid instead of forage fish species for bait might result in lower AVM rates (Epperly et al., 2012). This bait effect on anatomical hooking position may occur only when used in combination with J-shaped hooks (Watson et al., 2005). Fishing depth is also an important predictor of haulback condition, discussed below. Hook type and mean maximum soak duration were similar in the two regions.

S2.2. Hook Shape

Pelagic stingrays had a 74% lower mean AVM rate on circle than J-shaped hooks from records in the Pacific Ocean. Similarly, giant manta rays had a 66% lower mean AVM rate on circle than on J-shaped hooks. Hook shape was not an informative predictor in the phylogenetic GAMMs (Figs. 1 and 2) nor in the predictor screening for the full dataset (Fig. S1). For most organisms that tend to be captured by ingesting a hook, circle hooks tend to lodge in the corner of the mouth while J-shaped hooks tend to result in deep hooking, lodging internally in the esophagus and gut (Curran and Beverly 2012; Epperly *et al.* 2012; Serafy et al., 2012; Dapp et al., 2017). Mouth and externally-hooked organisms have lower AVM rates relative to deeply hooked catch (Campana et al. 2009; Pacheco et al. 2011; Epperly et al., 2012).

However, neither pelagic stingrays nor manta rays tend to be captured by ingesting a hook. Pelagic stingrays tend to be hooked in the mouth regardless of hook type (Piovano *et al.* 2010; Pacheco *et al.* 2011; Gilman et al., 2016), while filter-feeding mobulid rays may be captured predominantly by foul hooking in the body and entanglement in line (Mas et al., 2015). The cause of the substantially lower pelagic stingray and giant manta ray AVM rates on circle relative to J-shaped hooks is therefore unclear. As with ocean basin, this could have been due to correlations between hook shape and other explanatory predictors of haulback condition. For example, pelagic stingray Pacific Ocean records using circle hooks used longer branchlines (mean of 13.9 m) than records using J-shaped hooks (mean of 12.5 m). For this obligate ram ventilator, the shorter branchlines may have been more likely to impair their movement during the gear soak, contributing to the higher AVM rate on J-shaped hooks (Smith et al., 2004; Musyl

and Gilman, 2019). Also, because some captured pelagic stingrays do ingest hooks deeply, if circle hooks had a wider minimum width than J-shaped hooks, because wider circle hooks are expected to result in a lower rate of deep-hooking relative to narrower J-shaped hooks (Gilman et al., 2016), this correlation between hook shape and width may have contributed to the higher AVM rate on J-shaped hooks.

S2.3. Hooks between Floats – Index for Relative Fishing Depth

The number of pelagic longline hooks that are attached between two floats is an approximate index for relative fishing depth. The more hooks that are deployed between two floats, the deeper the depth range of the hooks along a catenary curve will be if all other variables are constant. Differences in other factors that affect fishing depth, including shoaling from ocean currents and wind, and variability in other gear designs (e.g., length of mainline between floats, mainline diameter, distance between floats, distance between the point of attachment to the mainline of the first branchline and the point of attachment of the nearest floatline, distance between branchlines, and length of branchlines and floatlines) will determine the absolute depth range of the longline hooks (Ward and Myers, 2005; Bigelow et al., 2006; Rice et al., 2007).

There is variability in the degree of barotrauma, dissolved oxygen, salinity, temperature and other environmental variables with capture depth. These environmental variables affect physiology, metabolism, movement and stress, which are important predictors of at-vessel condition (Gallagher et al., 2014; Butcher et al., 2015; Ellis et al., 2017; Musyl and Gilman, 2019). The effect of fishing depth on haulback condition will vary spatially and temporally due to variability in environmental conditions, including the depth of the mixed layer and oxygen/temperature gradients. In general, because shallower, warmer water generally has lower dissolved oxygen concentration, higher stress occurs for fish caught at shallower depths due to a combination of temperature, limited oxygen and higher metabolic rates (Moyes et al. 2006; Gallagher et al. 2014). However, the effect of capture depth on AVM risk is species-specific, and size-specific within species, as different species and sizes have different environmental tolerances (Musyl et al., 2011). For example, while carcharhinid sharks have higher AVM risk with higher water temperature and shallower capture depth (i.e., preventing vertical migration to deeper, cooler waters), epipelagic sharks exhibit the opposite response (i.e., an increased risk of AVM when captured below the mixed layer) (Gallagher et al., 2014; Butcher et al., 2015; Massey et al., 2019). Therefore, tradeoffs result from adjusting fishing depth, which will reduce AVM rates for some species, but increase rates for others (Musyl et al., 2011; Gilman et al., 2019).

S2.4. Interacting Effects of Components of Fishing Mortality

There are likely interacting effects between the components of fishing mortality. For example, relative to live catch, if dead catch is more likely to be depredated from the gear by scavengers, and thus is less likely to be retained on the gear by the haulback than live catch, then a higher pre-catch mortality rate would be associated with a lower AVM rate (Ward et al., 2004). However, in particular for species with relatively low pre-catch mortality rates, a longer gear soak and other factors may result in higher escapement rates, also contributing to higher AVM rates. Which of these has a larger effect on retention is likely species- and fishery-specific, depending on, for instance, how strenuously the species attempts to escape, the local abundance of scavengers, effects of mechanical action, and gear designs (e.g., hook shape and leader material).

S3. METHODS

S3.1. Systematic and Unstructured Literature Reviews

Web of Science and Google Scholar databases were searched for the systematic literature review. The Web of Science proprietary database contains information on peer-reviewed articles from journals in the natural sciences, social sciences, arts and humanities, selected based on their meeting high editorial standards and scientific impact, with records from 1975 (Birkle et al., 2020). While Web of Science and similar bibliographic databases mainly include only established peer-reviewed journals, Google Scholar searches a wider range of sources, including conference proceedings, theses, books and book chapters, technical reports and various grey literature. Furthermore, for narrow literature searches, Google scholar, which searches the entire text, may identify relevant publications that are missed by main bibliographic databases, which only search keywords, abstracts and titles (Bramer et al., 2017). Two specialized databases were also searched to potentially identify unique references related to their specific narrow focuses that might not identified through Wed of Science or Google Scholar searches (Bramer et al., 2017). These were the Western and Central Pacific Fisheries Commission's Bycatch Management Information System (BMIS) online database of references (www.bmis-bycatch.org/references) and the Consortium for Wildlife Bycatch Reduction's online database of references (www.bycatch.org/search).

In order to be retained, a publication had to meet screening criteria of reporting, for one or more elasmobranch species, the number that was alive and number that was dead upon haulback (before being handled by crew) in pelagic longline gear. For the Web of Science and Google Scholar searches, we explored numerous alternative search strings of combinations of keywords (search terms) and Boolean operators designed to obtain publications that meet the screening criteria, and to restrict the combined number of results (hits) to ~1,300. The retained search strings had a specificity with $\geq 45\%$ of 20 sampled titles of hits (first and last 10 titles for the combined hits from the Web of Science searches, and for the combined hits from the Google Scholar searches) being retained.

Because no publications are considered 'Gold Standard' for this research question, the sensitivity of the combined search string results was not assessed by determining inclusion of specific publications. Furthermore, relying on highly recognized publications to assess sensitivity, as recommended by CEE and ROSES (Haddaway et al., 2017a, 2018; Pullin et al., 2021), risks introducing prevailing paradigm and publication bias (Sutton, 2009; Bayliss and Beyer, 2015), where, for example, individual studies finding conflicting or non-significant results may not be highly cited, published or easily discoverable. The inclusion of grey literature and inclusion of all hits from database searches (and not for instance limiting results to the subset of the first 100 hits, which may be sorted by number of citations) contributed to reducing the risk of introducing these sources of bias.

The following four search strings were used for the Web of Science: (1) pelagic AND longline AND mortality; (2) "pelagic longline" AND (haulback OR at-vessel) AND mortality; (3) "pelagic longline" AND (haulback OR at-vessel) AND (mortality OR survival) AND shark - demersal; and (4) allintitle: "pelagic longline" AND (mortality OR survival). Four search strings using Google Scholar were: (1) "at-vessel" mortality shark "pelagic longline" fisheries; (2) haulback mortality shark "pelagic longline" fisheries -demersal -bottom; (3) mortality "blue shark" "pelagic longline" alive dead ray soak hook -demersal; and (4) allintitle: "pelagic longline" mortality OR survival -demersal -bottom. Searches without "allintitle" term searched for keywords anywhere in the text. The Google Scholar search was conducted without being affected by the browsing history, IP address and other personalization factors. The BMIS search was conducted for longline fishing gear and elasmobranchs, and keyword 'mortality', with no restrictions on year or collection category. The Consortium for Wildlife Bycatch Reduction

database search was conducted for hooks-and-lines fishing gear and elasmobranchs, including both field and non-field studies, with no restrictions on mitigation technique. Searches of the four databases were conducted on 2 October 2021. To reduce language bias and avoid temporal bias (Bayliss and Beyer, 2015; Pullin et al., 2021), searches did not restrict the time period or language of publications, but only English search terms were used. The number of articles retrieved, screened and retained/discarded from the systematic review were recorded in a flow diagram adapted from Haddaway et al. (2017b) (Fig. S5).

We then conducted an unstructured literature search by reviewing reference lists of the compiled publications from the systematic search (snowballing, Pullin et al., 2020) and obtained primary observer program data, resulting in the retention of an additional 12 publications. We screened the compiled literature against the aforementioned eligibility criteria for retention. Both primary research and synthesis studies were considered for retention. Publications were not excluded based on a study design eligibility criterion. Published and grey literature results did not need to be peer reviewed in order to be retained. Of 64 retained publications from the systematic review, 16 were not included in an assembled database of records for use in meta-analytic models because they contained a subset of data from observer program datasets (DFO, 2021; NMFS, 2021a,b,c) that were compiled through the unstructured review. One of the retained systematic review publications is a corrigendum (containing a corrected table, Afonso et al., 2015); only the original publications (Afonso et al., 2012) is referenced in the final assembled database. A total of 59 publications were included in the final assembled database, of which 47 were derived from the systematic literature review and 12 from the unstructured review. Several variables were extracted from the compiled and retained publications, including several predictors of AVM risk defined in the caption of Fig. S1: number of hooks between floats, ocean basin, whether the majority of fishing effort occurred in the tropics, hooks per set, publication year, date of the start of the time series, data source, leader material, branchline length, maximum soak duration, and hook shape.

A Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA, Page et al. 2021a,b) checklist follows.

Title: Identify the report as a systematic review.

Checklist response: The title of the article identifies the study as a meta-analytic synthesis.

Introduction rationale: Describe the rationale for the review in the context of existing knowledge.

Checklist response: Addressed in the introduction.

Introduction objectives: Provide an explicit statement of the objective(s) or question(s) the review addresses.

Checklist response: Addressed in the introduction.

Methods eligibility criteria: Specify the inclusion and exclusion criteria for the review and how studies were grouped for the syntheses.

Checklist response: Included in the methods and supplemental information.

Methods information sources: Specify all databases, registers, websites, organizations, reference lists and other sources searched or consulted to identify studies.

Checklist response: Included in the supplemental information.

Methods search strategy: Present the full search strategies for all databases, registers and websites, including any filters and limits used.

Checklist response: Included in the supplemental information.

Methods selection process: Specify the methods used to decide whether a study met the inclusion criteria of the review, including how many reviewers screened each record and each report retrieved, whether they worked independently, and if applicable, details of automation tools used in the process.

Checklist response: Included in the supplemental information. A single reviewer screened records.

Methods data collection process: Specify the methods used to collect data from reports, including how many reviewers collected data from each report, whether they worked independently, any processes for obtaining or confirming data from study investigators, and if applicable, details of automation tools used in the process.

Checklist response: Included in the supplemental information. A single reviewer extracted information from publications.

Methods – data items: List and define all outcomes for which data were sought. Specify whether all results that were compatible with each outcome domain in each study were sought (e.g. for all measures, time points, analyses), and if not, the methods used to decide which results to collect. List and define all other variables for which data were sought (e.g. participant and intervention characteristics, funding sources). Describe any assumptions made about any missing or unclear information.

Checklist response: Included in the supplemental information.

Methods study risk of bias assessment: Specify the methods used to assess risk of bias in the included studies, including details of the tool(s) used, how many reviewers assessed each study and whether they worked independently, and if applicable, details of automation tools used in the process.

Checklist response: The methods section includes a component on the assessment of publication bias.

Methods effect measures: Specify for each outcome the effect measure(s) (e.g. risk ratio, mean difference) used in the synthesis or presentation of results.

Checklist response: Covered in the methods section.

Methods synthesis methods: Describe the processes used to decide which studies were eligible for each synthesis. Describe any methods required to prepare the data for presentation or synthesis, such as handling of missing summary statistics, or data conversions. Describe any methods used to tabulate or visually display results of individual studies and syntheses. Describe any methods used to synthesize results and provide a rationale for the choice(s). If meta-analysis was performed, describe the model(s), method(s) to identify the presence and extent of statistical heterogeneity, and software package(s) used. Describe any methods used to explore possible causes of heterogeneity among study results (e.g. subgroup analysis, meta-regression). Describe any sensitivity analyses conducted to assess robustness of the synthesized results.

Checklist response: Covered in the methods section and supplemental information.

Methods reporting bias assessment: Describe any methods used to assess risk of bias due to missing results in a synthesis (arising from reporting biases).

Checklist response: Covered in the methods section.

Methods certainty assessment: Describe any methods used to assess certainty (or confidence) in the body of evidence for an outcome.

Checklist response: Covered in the methods section and supplemental information.

Results study selection: Describe the results of the search and selection process, from the number of records identified in the search to the number of studies included in the review, ideally using a flow diagram. Cite studies that might appear to meet the inclusion criteria, but which were excluded, and explain why they were excluded.

Checklist response: Covered in the methods section and supplemental information.

Results study characteristics: Cite each included study and present its characteristics.

Checklist response: Covered in the supplemental information and online assembled database (data availability section of the article).

Results risk of bias in studies: Present assessments of risk of bias for each included study.

Checklist response: Risk of bias of individual retained studies was explored through a candidate predictor of study category.

Results of individual studies: For all outcomes, present, for each study: (a) summary statistics for each group (where appropriate) and (b) an effect estimate and its precision (e.g. confidence/credible interval), ideally using structured tables or plots.

Checklist response: Included in the Results section and supplemental information.

Results of syntheses: For each synthesis, briefly summarize the characteristics and risk of bias among contributing studies. Present results of all statistical syntheses conducted. If meta-analysis was done, present for each the summary estimate and its precision (e.g. confidence/credible interval) and measures of statistical heterogeneity. If comparing groups, describe the direction of the effect. Present results of all investigations of possible causes of heterogeneity among study results. Present results of all sensitivity analyses conducted to assess the robustness of the synthesized results.

Checklist response: Included in the Results section and supplemental information.

Results reporting biases: Present assessments of risk of bias due to missing results (arising from reporting biases) for each synthesis assessed.

Checklist response: Included in the Results section and supplemental information.

Results certainty of evidence: Present assessments of certainty (or confidence) in the body of evidence for each outcome assessed.

Checklist response: Included in the Results section and supplemental information.

Discussion: Provide a general interpretation of the results in the context of other evidence. Discuss any limitations of the evidence included in the review. Discuss any limitations of the review processes used. Discuss implications of the results for practice, policy, and future research.

Checklist response: Covered in the discussion section and supplemental information.

Registration and protocol: Provide registration information for the review, including register name and registration number, or state that the review was not registered.

Checklist response: The review was not registered.

Support: Describe sources of financial or non-financial support for the review, and the role of the funders or sponsors in the review.

Checklist response: Disclosed in the article.

Competing interests: Declare any competing interests of review authors.

Checklist response: Disclosed in the article.

Availability of data, code and other materials: Report which of the following are publicly available and where they can be found: template data collection forms; data extracted from included studies; data used for all analyses; analytic code; any other materials used in the review.

Checklist response: The data availability statement provides directions to access the database assembled for the meta-synthesis.

Systematic Literature Search Process and Results

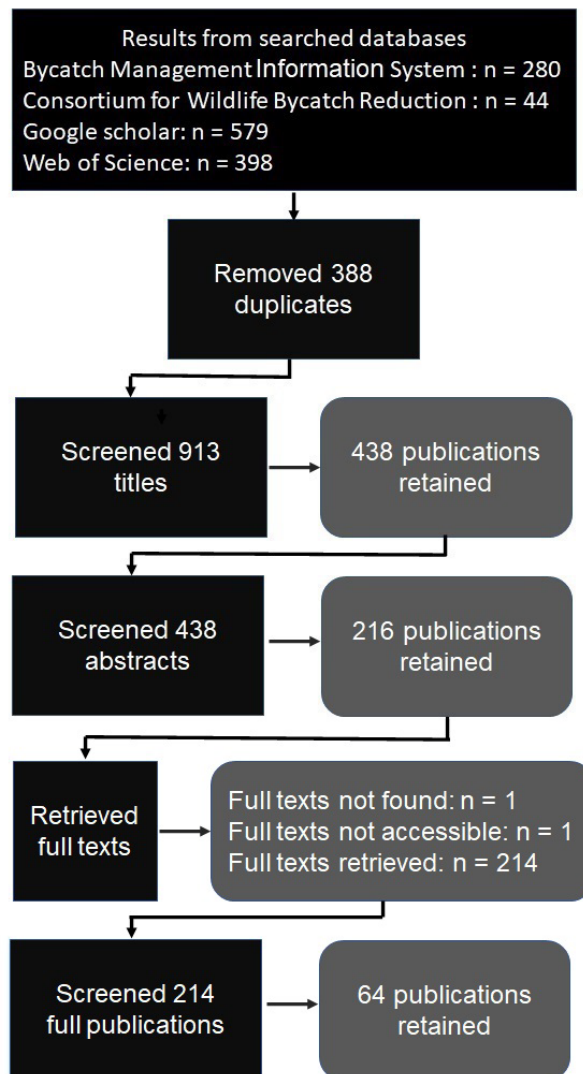


Fig. S5. Process and results of a systematic literature search conducted to compile publications on methods to mitigate bycatch and mortality of vulnerable species in pelagic longline fisheries (adapted from Haddaway et al., 2017b).

S3.2. Elasmobranch Phylogenetic Structure

Elasmobranch Phylogenetic Tree

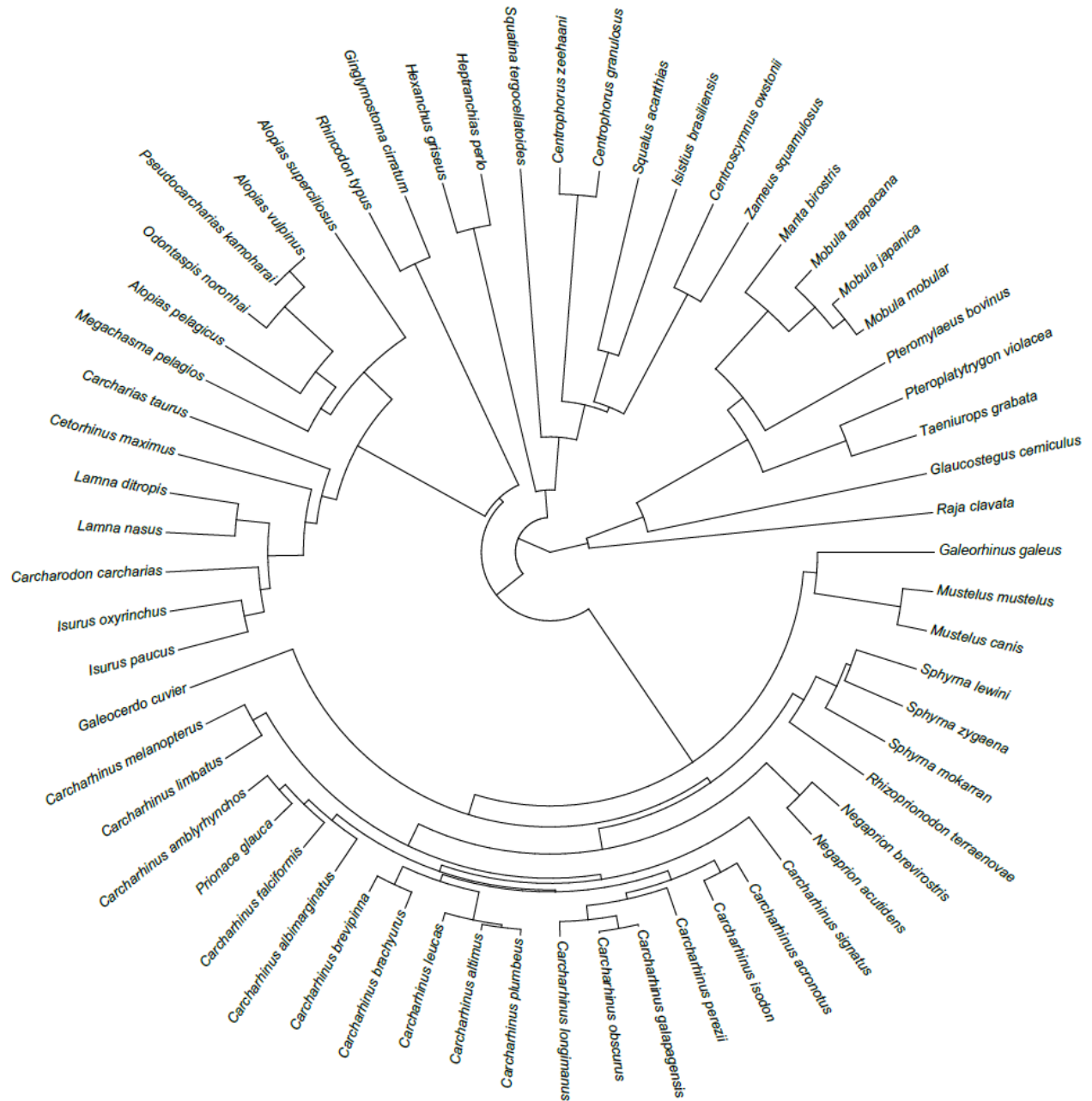


Fig. S6. Radial or circular tree plot showing the elasmobranch phylogenetic structure used for deriving the correlation matrices for the clade-specific Bayesian GAMMs. The phylogenetic tree was sourced online from <https://vertlife.org/phylosubsets> based on the phylogeny for ca. 1,200 Chondrichthyan species presented in Stein et al. (2018).

S4. METHODS TO AVOID AND REDUCE ELASMOBRANCH CATCH IN PELAGIC LONGLINE FISHERIES

Methods to avoid and minimize shark and ray catch in pelagic longline fisheries can either (1) reduce effort; (2) cap bycatch or employ other output controls that incentivize the use of methods that reduce catch rates; or reduce one or more capture susceptibility attributes of: (3) areal and temporal overlap, (4) vertical overlap, and (5) selectivity. Examples of each category of approach follow.

- **Input controls on effort.** This includes, for example, limits on: the number of vessels (limited entry), vessel size, amount of gear, fishing days, number of sets, hooks per set, and soak duration (Ward et al., 2004; Anderson et al., 2018).
- **Output controls:** Bycatch quotas result in the cessation of effort once the individual- or fleet-based threshold is reached. Retention bans (by species, sex, size), international trade bans, banning shark finning, and retention limits (individual- or fleet-based, for marketable species) do not directly affect catch levels, but might indirectly lead to fishers' use of methods that reduce catch rates.
- **Static and dynamic area-based management tools** to avoid or reduce areal or temporal overlap for spatially and temporally predictable bycatch hotspots. For instance, area-based approaches include: permanent static closures, such as longline closed areas near shallow submerged features; seasonal closures, such as at dynamic sites important for critical life history stages, including shark pupping and nursery areas; and quasi real-time measures, based on habitat suitability and species distribution models and fisheries-dependent observations implemented through move-on rules and voluntary industry fleet communication programs (Hazen et al., 2018; Maxwell et al., 2020; Hilborn et al., 2021).
- Fishing methods that **reduce depth overlap** by adjusting the time of day of fishing and the fishing depth of the gear. For example, fishing depth can be managed by adjusting the number of hooks between floats (Section S2.3), length of mainline between floats, branchline and floatline lengths, distance between the floatline and adjacent branchline, and banning the use of 'shark lines' - branchlines that fish near the surface to target epipelagic sharks (Musyl et al., 2011; Hall et al., 2017).
- **Increased selectivity** through fishing gear designs that (1) **Increase escapement** (e.g., weak leader material to enable some sharks to sever the line, Ward et al., 2008); (2) **Repel sharks** (e.g., electrical, chemical/olfactory, magnetic and rare earth electropositive metals, Hart and Collin, 2014; Mitchell et al., 2018); (3) **Create a mismatch with morphological characteristics** (e.g., hook shape and size – Section S2.2; Gilman et al., 2018; Reinhardt et al., 2018); and (4) **Reduce attractiveness** (e.g., bait species and artificial bait, not using light attractors; Poisson et al., 2016; Gilman et al., 2020).

S5. PRESCRIBED ELASMOBRANCH HANDLING AND RELEASE PRACTICES AND EQUIPMENT FOR PELAGIC LONGLINE FISHERIES

Based in part on findings on informative predictors of post-release mortality risk (e.g., McGrath et al., 2011; FAO, 2019; Musyl and Gilman, 2019), prescribed shark and ray handling and release methods for pelagic longline fisheries include (SPC et al., 2012; WCPFC, 2017, 2018; IOTC, 2020; Jorgensen et al., 2022):

- Having a lifting device, bolt cutters, dehooker and line-cutters available where they are readily accessible by crew;
- Removing as much trailing line as safely possible;

- Removing hooks that are visible in the body or mouth;
- Using hooks and/or hook rings that degrade relatively quickly;
- Handling and releasing in the water, if possible, otherwise, bringing small elasmobranchs onboard but minimizing the duration out of the water;
- Minimizing the duration restrained, including by not using 'lazy lines' where crew attach catch to a line off the stern until the end of the haulback; and
- Various proscribed practices, including not: attempting to remove deeply ingested hooks, using lifting devices that risk entanglement, inserting anything into gill slits, putting tension on branchlines especially when deeply hooked, gaffing in the body, lifting by the head or tail, and putting excessive pressure on their bodies.

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