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FISH and FISHERIES

A cross-taxa assessment of pelagic longline by-catch mitigation measures: conflicts and mutual benefits to elasmobranchs

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Abstract

Elasmobranch mortality in pelagic longline fisheries poses a risk to some populations, alters the distribution of abundance between sympatric competitors, changing ecosystem structure, processes and stability. Individual and synergistic effects on elasmobranch catch and survival from pelagic longline gear factors, including methods prescribed to mitigate bycatch of other vulnerable taxa, were determined. Overall relative risk of higher circle vs. J-shaped hook shark catch rates conditioned on potentially informative moderators, from 30 studies, was estimated using an inverse-precision weighted mixed-effects meta-regression modelling approach. Sharks had a 1.20 times (95% CI: 1.03–1.39) significantly higher pooled relative risk of capture on circle hooks, with two significant moderators. The pooled relative risk estimate of ray circle hook catch from 15 studies was not significant (RR = 1.22, 95% CI: 0.89–1.66) with no significant moderators. From a literature review, wire leaders had higher shark catch and haulback mortality than monofilament. Interacting effects of hook, bait and leader affect shark catch rates: hook shape and width and bait type determine hooking position and ability to sever monofilament leaders. Circle hooks increased elasmobranch catch, but reduced haulback mortality and deep hooking relative to J-shaped hooks of the same or narrower width. Using fish vs. squid for bait increased shark catch and deep hooking. Pelagic stingray (*Pteroplatytrygon violacea*) catch and mortality were lower on wider hooks. Using circle instead of J-shaped hooks and fish instead of squid for bait, while benefitting sea turtles, odontocetes and possibly seabirds, exacerbates elasmobranch catch and injury, therefore warranting fishery-specific assessments to determine relative risks.

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Introduction

Fisheries have direct impacts on target species, but also can have large effects on incidentally caught market and non-market species, and broad, community- and ecosystem-level effects through direct and indirect linkages that change structure, processes and stability (Goñi 1998; Frank *et al.* 2005; Kaiser *et al.* 2006; Baum and Worm 2009; Gilman *et al.* 2013a,b). Pelagic longline and other fisheries that target relatively fecund species with r-selected life-history characteristics like tuna and tuna-like species (Scombroidei) can have large impacts on incidentally caught species with K-selected life-history strategies, including seabirds, sea turtles, marine mammals, elasmobranchs (sharks and rays) and some bony fishes. As a result of their life-history characteristics, and due to behaviours such as forming aggregations for mating and pupping, and at nursery grounds, they have low resistance and resilience to even low levels of anthropogenic sources of mortality. Their populations can decline over short temporal scales (decades and shorter) and are slow to recover from large declines (Musick 1999a,b; Hall *et al.* 2000; Stevens *et al.* 2000; Dulvy *et al.* 2008; Gilman *et al.* 2008a).

A method that mitigates problematic catch of one taxonomic group or species may exacerbate the catch of other vulnerable species of the same or different taxa (Griffiths *et al.* 2006; Gilman 2011; Gilman *et al.* 2007b, 2013c). It is critical to identify known conflicts as well as mutual benefits of by-catch mitigation methods amongst and within species groups. Potential conflicts resulting from the uptake of alternative by-catch mitigation methods have received limited consideration. International guidelines, ecological risk assessments and binding measures defining gear and fishing methods to mitigate problematic pelagic longline by-catch have had a single-species or species group focus and have not holistically assessed relative effects across taxa (FAO 1999a,b, 2010; Gilman *et al.* 2013a).

There has been increasing concern in recent decades over the sustainability of elasmobranch mortality rates in pelagic longline fisheries, the broad, community- and ecosystem-level effects from declines in abundance of species and sizes of elasmobranchs selectively caught by pelagic longline fisheries, as well as the adverse socioeconomic effects on longline fisheries from shark interactions (Stevens *et al.* 2000; Ward and Myers 2005a;

Dulvy *et al.* 2008; Ferretti *et al.* 2010; Clarke 2011; Gilman *et al.* 2008b, 2012; Worm *et al.* 2013; Clarke *et al.* 2006). Global reported shark landings declined by about 15% since peaking in 2000. This might have been an effect of national and regional shark management measures. More likely, it was due to reductions in abundance and possibly increased under-reporting (Clarke 2013; Clarke *et al.* 2013, 2014; FAO 2014).

Depending on the fishery, season, fishing grounds, and practices of individual vessels within a fleet, sharks can be a target catch, retained incidental catch or discarded catch. Sharks can make up over half of the total catch in shallow-set pelagic longline tuna and billfish fisheries (Clarke *et al.* 2006; Gilman *et al.* 2008b). Longline fishing mortality of some elasmobranch species has the capacity to be sustainably managed if robust harvest strategies were implemented (e.g. Walker 1998; Musick *et al.* 2000). However, there are deficits in fundamental biological information for most elasmobranch stocks (Walker 1998; Shotton 1999; Musick *et al.* 2000). There is also high uncertainty in estimates of fishing mortality levels of rare as well as common elasmobranch stocks caught in pelagic longline fisheries (Clarke 2011, 2013; Gilman *et al.* 2008b, 2013b; Worm *et al.* 2013; Clarke *et al.* 2006, 2014). Combined, these information gaps prevent management systems from developing harvest strategies with high certainty of achieving sustainable exploitation.

Fishing mortality may alter elasmobranchs' density-dependent life history parameters, increasing some species' ability to rebound from large declines, such as by increasing their fecundity, reducing natural mortality or increasing growth rates as density declines (Stevens *et al.* 2000). The selective removal of large individuals within an elasmobranch population could be a driver favoring genotypes for maturation at an earlier age, smaller size and slower growth. This could alter the length frequency distributions (size structure) and evolutionary characteristics of affected populations (Stevens *et al.* 2000; Ward and Myers 2005a; Zhou *et al.* 2010).

Longline fishing mortality affects the abundance of pelagic sharks much more strongly than most of the other fish species of the pelagic apex predator trophic guild. Even moderate fishing mortality rates can trigger large population declines for some shark species (Musick *et al.* 2000; Kitchell *et al.* 2002). Of 1004 assessed elasmobranchs species, due largely to fishing mortality from incidental catch, 18% were categorized as Critically Endangered, Endangered and Vulnerable under the IUCN Red List. This is a conservative estimate, however, as over 46% were categorized as data deficient (Dulvy *et al.* 2014). For example, blue shark (*Prionace glauca*), the dominant elasmobranch species caught in many open ocean pelagic longline fisheries, is Near Threatened (Nakano and Stevens 2008; SPC 2008; Gilman 2011; IUCN 2014). And, epipelagic oceanic whitetip (*Carcharhinus longimanus*) and silky sharks (*C. falciformis*), predominant components of the shark catch in some tropical pelagic longline fisheries, are Vulnerable and Near Threatened respectively (Bromhead *et al.* 2012; Clarke *et al.* 2013; Gilman *et al.* 2013c; IUCN 2014). Despite documentation of few contemporary marine extinctions or population extirpations (Dulvy *et al.* 2003; Dulvy 2006; Gilman *et al.* 2011), fishing mortality might risk eliminating some elasmobranch populations and species. This is especially true for those with restricted ranges and with life-history characteristics that give them a relatively low ability to recover from large reductions (Stevens *et al.* 2000).

There is increasing but incomplete understanding of community- and ecosystem-level effects of longline selective removals of pelagic apex predators, including of some elasmobranchs, largely from species- and size-based ecosystem trophic interaction models and some empirical studies. In some systems, selective longline removals of some elasmobranch species may alter the relative abundance of species within the pelagic ecosystem apex predator trophic guild with nominal changes to ecosystem structure, functioning and stability. When fishing mortality reduces a shark species' biomass to a point where it is no longer filling its ecosystem role, other marine predators, including sympatric competitors that are less susceptible to capture and mortality by longline gear, may increase in abundance and functionally replace them, so that a trophic cascade does not occur, and little effect on ecosystem regulation (Cox *et al.* 2002; Kitchell *et al.* 2002; Hinke *et al.* 2004; Ward and Myers 2005a; Polovina *et al.* 2009; Polovina and Woodworth-Jefcoats 2013). In other systems, however, fisheries removals of large pelagic sharks and other large apex predators have been observed or predicted in models to alter ecosystem functioning, structure and stability, possibly because the shark species' sympatric competitors have a limited role in ecosystem regulation, such that sharks and the other apex predators taken in pelagic longline fisheries might function collectively as a keystone species guild (Stevens *et al.* 2000). In these latter systems, declines in abundance of large pelagic and coastal predators probably contributed to top-down trophic cascades, at least for upper trophic levels, by releasing pressure via reduced natural mortality. This altered ecosystem size-structure, increasing the abundance and altering the habitat use and distributions of some of the prey of the large shark and other apex predator species subject to longline fishing removal, including some midtrophic-level, smaller sized species, in some cases including smaller sharks and rays, and resulted in reduced abundance of large species and increased abundance of small species (Stevens *et al.* 2000; Cox *et al.* 2002; Hinke *et al.* 2004; Ward and Myers 2005a; Polovina *et al.* 2009; Ferretti *et al.* 2010; Polovina and Woodworth-Jefcoats 2013). This change in ecosystem size-structure in turn probably alters ecosystem function and stability. For both of these types of systems ('species replacement' systems where sharks removed by fishing are functionally replaced by sympatric predators, and systems with an 'apex predator keystone species guild'), and systems falling somewhere in between these extremes, reductions in large pelagic and coastal shark species in some systems might have reduced pressure on some species that have few other predators, including some marine mammal, sea turtle, pelagic seabird and smaller elasmobranch species, resulting in cascading effects (e.g. Ferretti *et al.* 2010).

This study aimed to improve the knowledge of individual and synergistic effects of four 'focal' pelagic longline fishing gear factors on elasmobranch catch rates, haulback disposition (alive vs. dead at the vessel before handling by the crew) and anatomical position of hooking. Of the large suite of variables demonstrated to significantly affect catch rates and the species- and size- selectivity of pelagic longline fisheries, four focal gear factors have been the focus of research and management measures to mitigate unwanted by-catch of sea turtles, seabirds, marine mammals, elasmobranchs and some teleosts. These are hook shape (circle vs. J-shaped), hook narrowest (minimum) width, bait type and leader material. See Gilman (2011), Clarke *et al.* (2014) and Gilman and Hall (2015) for reviews of the effects of pelagic longline gear and methods on vulnerable taxa. See Beverly *et al.* (2003) for a description of pelagic longline fishing gear and methods, and Curran and Bigelow (2011), Swimmer *et al.* (2011) and Serafy *et al.* (2012a) for definitions of hook narrowest width. It is not well understood how hook and bait types prescribed in some pelagic longline fisheries to mitigate the by-catch of sea turtles and cetaceans affect catch, injury and mortality of elasmobranchs (Clarke *et al.* 2014; Gilman and Hall 2015; Gilman *et al.* 2013a, 2015). A few studies found that leader material significantly affected elasmobranch catch rates, and wire leaders (steel traces) have been banned in some longline fisheries (e.g. Australia, Cook Islands, Fiji, Marshall Islands, Palau, Samoa, South Africa) with an explicit or implicit aim of reducing shark fishing mortality (Branstetter and Musick 1993; Yokota *et al.* 2006; Ward *et al.* 2008; Afonso *et al.* 2012; Clarke 2013; Gilman *et al.* 2013c, 2015). It is unclear, however, what effect leader material has on catch rates of other vulnerable taxa, and under what circumstances using monofilament instead of more durable leader materials (wire, multifilament nylon [polyamide]) results in lower elasmobranch fishing mortality (Ward *et al.* 2008; Gilman *et al.* 2008b, 2013b; Clarke *et al.* 2014). In addition to the limited understanding of the single effects of these four factors on elasmobranchs, there is likewise limited understanding of possible interacting effects (Gilman 2011; Gilman *et al.* 2008b, 2012; Afonso *et al.* 2012; Epperly *et al.* 2012; Hannan *et al.* 2013; Clarke *et al.* 2014).

We conducted a literature review and a meta-analysis, synthesizing findings from related studies, to improve the understanding of individual and interacting effects of these focal factors on pelagic longline elasmobranch catch rates, hooking position and haulback mortality. Hooking location provides an indicator of the degree of injury and concomitant probability of pre-catch, haulback and post-release survival. Externally hooked organisms have a lower haulback mortality rate and likely have a higher probability of pre-catch and post-release survival relative to those that are deeply hooked (Cooke and Suski 2004; Horodysky and Graves 2005; Campana *et al.* 2009; Pacheco *et al.* 2011; Swimmer and Gilman 2012; Gilman *et al.* 2013b). Haulback disposition enables an assessment of the effect of combinations of gear components on mortality rates and an indication of pre-catch and post-release probability of mortality. Due to the larger sample size plus the number of studies, correctly designed meta-analyses can provide estimates with increased precision and accuracy over estimates from individual studies, with increased statistical power to detect an effect (e.g. Borenstein *et al.* 2009; Musyl *et al.* 2011). The meta-analysis undertaken here extended substantially upon two previous relevant meta-analyses (Godin *et al.* 2012; Favaro and Cote 2013). This study expanded the amalgamated studies. And this study: employed a mixed-effects meta-regression approach to account for informative covariates and non-linear functional form, used a hierarchical mixed-effects meta-regression approach to account for more complex random-effect structures, employed a multimodel selection approach to screen models based on weight of evidence, conducted extensive assessment of publication bias, conducted comprehensive assessment of outlier and influential study diagnostics, and included an assessment of data censoring and potential bias due to excluding studies. Findings improve the knowledge of methods to reduce unwanted elasmobranch catch, morbidity and mortality, and contribute to assessing the relative risks, conflicts as well as mutual benefits within and across taxonomic groups of conservation concern, of alternative pelagic longline gear designs.

Methods

The following definitions were employed for the terms ‘finding’, ‘record’, ‘study’ and ‘publication’. A ‘finding’ is one result of a significant difference of one focal factor category on the catch rate, haulback survival rate or proportion of catch that was deeply hooked on a single elasmobranch species. A ‘record’ is a set of significant findings and non-significant results of the effects of a single focal factor category resulting from one discrete study where one record may include multiple findings. A ‘study’ is a single controlled or comparative at-sea experiment or analysis of observer programme data that assessed the effect of one or more of the focal factors, where one study may have produced multiple records. And, a ‘publication’ is a single publication or grey literature document, where one publication or document may report multiple records and findings from one or more studies.

Records and findings included in the literature review and meta-analysis

Studies were compiled and records and findings from these studies included in a sample for a literature review if they reported findings on the significance of the effect of one or more of four pelagic longline gear ‘focal’ factors of hook shape, hook narrowest width, leader material, and bait type comparing squid species (*Illex sp.*) vs. small mackerel-like fish species, and two combinations of these focal factors, on species-specific elasmobranch catch rates, haulback disposition, and/or hooking location. The two combinations of factors were wider circle hooks vs. narrower J-shaped tuna or J hooks, and wider circle hooks and fish bait vs. narrower J-shaped hooks and squid bait. Collectively, these four factors and two combinations of factors are referred to as ‘focal factor categories’.

Studies were compiled for the meta-analysis that reported the number of sharks and/or rays that were caught, and/or alive and dead at haulback, and/or that were deeply and not-deeply hooked (internally hooked vs. hooked externally or in the mouth, Gilman *et al.* [2007a] and Kerstetter and Graves [2006]). The studies had to additionally report this previous information by: hook shape (circle vs. J-shaped), leader material (wire vs. monofilament nylon), bait type (small fish species vs. squid species), and/or hook narrowest width.

Some pelagic longline vessels will use large pieces of meat cut from tuna, sharks, rays or other catch, in some cases used on ‘shark lines’ (branchlines attached directly to floats) (Gilman *et al.* 2015; Gilman and Hall 2015). Findings on the effect of this type of fish bait (Gilman and Hall 2015) were not included in the literature review or meta-analysis due to small sample sizes. Instead, only studies that compared effects of bait type between squid species and relatively small species of fish, including those that used pelagic ‘forage’ fishes for bait, such as mackerels and species with mackerel-like characteristics (Collette and Nauen 1983), were included for this component of the analysis.

To compile relevant peer-reviewed and grey literature for both the review and meta-analysis, both structured and unstructured literature searches were conducted. The structured search was conducted using the following Boolean search terms in Google Scholar: elasmobranch, shark, ray, by-catch, longline, hook, leader, bait. These search terms were also employed to search the Western and Central Pacific Fisheries Commission's By-catch Mitigation Information System database of references, http://www.wcpfc.int/bmis/references, filtered for species group of sharks and rays, and for fishing gear of longline. The Bycatch.org database was searched for studies on elasmobranch by-catch reduction methods in hook-and-line fisheries for both field and non-field studies. An unstructured literature search was conducted by reviewing reference lists of relevant publications and reports, posting a query on ResearchGate.net, and via an informal network of fisheries professionals requesting suggestions of relevant publications. Literature compilation was conducted from July to October 2014.

Literature review analyses

Compiled studies were analysed to determine the degree of consistency/dispersion in findings of the effect of individual and combinations of the four focal factors on individual elasmobranch species' catch rates, haulback survival rates and proportion that was deeply hooked. Compiled studies were reviewed to identify those with designs that enabled an assessment of single focal factor effects vs. those that were simultaneously confounded by two or more focal factors.

The following metadata fields were compiled for each study: category (at-sea experiment, analyses of observer data, experiment of captive elasmobranchs); number of vessels; number of hooks; time-series length; years covered by the study time series; number of caught sharks and rays; epoch (time period) covered by the study time series; seasons included in the time series; region where the study occurred; time of day of the gear soak; gear soak depth; light attractor use; whether there was simultaneous variability in only one vs. two or more focal factors; main retained species; main caught shark and ray species; and journal impact factor. The number of the following suite of 19 variables, documented to have a significant and relatively large effect size on elasmobranch catch rates, haulback survival rates, and/or hooking position (Gilman and Hall 2015), that was either controlled or explicitly accounted for was also identified for each study:

1. fishing effort (number of hooks, sets, and/or trips);
2. spatial location of fishing effort;
3. use of shark lines;
4. soak duration;
5. leader material;
6. hook shape;
7. hook smallest width;
8. hook gape;
9. bait species group (fish vs. squid);
10. year;
11. month or season;
12. time of day of fishing operations;
13. gear soak depth;
14. sea surface temperature;
15. sets on shallow submerged features or open ocean;
16. effect of unique vessel;
17. effect of unique trip;
18. length of caught elasmobranch;
19. sex of caught elasmobranch.

Gaps in research on the effects of the focal factor categories on rates of catch, morbidity and mortality, by region, and by elasmobranch species, were also identified.

Meta-analysis statistical modelling approach

For 41 compiled studies, the number of branchlines was recorded for each of the four focal factors. And, for each study, the number of sharks and number of rays that were: (i) caught, and/or (ii) alive and dead upon haulback, and/or (iii) deeply vs. not-deeply hooked by each focal factor was compiled.

The summary or effect size measure used here was the study-specific log relative risk (Nakagawa and Santos 2012) of a shark being caught on a circle hook as opposed to a J-shaped hook, weighted by the inverse-precision of each estimate. This summary measure could be calculated for 30 of the 41 compiled studies for which information on both the number of hooks deployed by hook shape and the number of caught sharks by hook shape was available. To determine whether those 11 studies without a relative risk measure could be a biased subsample of the 41 studies if excluded from subsequent analyses, we explored if presence/absence of a relative risk measure was a function of potentially informative covariates by using a generalized linear mixed modelling (GLMM) approach (Bolker *et al.* 2009). This logistic regression model comprised the three additional focal factors (hook narrowest width, bait type, leader type) plus study category (described below) as covariates with the individual study as a random intercepts-only effect. If data censoring were found to be informative, then this would be helpful in interpreting any subsequent meta-analysis based on the 30 of 41 studies for which the relative risk measure could be calculated. All the GLMMs were fitted here using the *lme4* package for R (Bates *et al.* 2014). Model fit was assessed using a modified Anova( ) function and the Type II Wald chi-square test measures implemented in the *car* package for R that is appropriate for linear mixed-effects models (Fox and Weisberg 2011). It was not possible to fit GLMMs with interaction terms, as the data were too sparse with few full sets of combinations to derive orthogonal terms.

The shark catch rate data set comprised various potentially informative categorical covariates or moderators and several continuous moderators (or covariates). So we explored the functional form of the continuous covariates for inclusion in the subsequent meta-analysis by using a linear mixed model (LMM) approach with the inverse-precision weighted log relative risk as the response variable and a random-effects structure using 'research group' based on lead author of each study. Some limited inclusion of interaction terms was feasible here. All the LMMs were fitted here using the *lme4* package for R (Bates *et al.* 2014) and covariate significance was assessed using the Type II Wald chi-square test measures (Fox and Weisberg 2011). Any non-linear functional form was modelled using B-splines via the R *splines* package (R Core Team 2014) and post-model processing and visualization was undertaken using the *effects* package for R (Fox 2003). Any covariate functional form determined was then used to guide the specification of covariate functional form in the subsequent meta-regressions.

Then, a mixed-effects meta-regression modelling approach (van Houwelingen *et al.* 2002; Sutton and Higgins 2008) was used to estimate the overall relative risk of circle hook shark catch rates for the 30 studies conditioned on potentially informative covariates. The 10 covariates or moderators that were considered in the meta-regression analysis were:

1. Study category: Studies were categorized as being either a: (i) controlled or comparative at-sea experiment; or (ii) analysis of observer program data. No relevant controlled or comparative experiments of captive elasmobranchs were identified.
2. Leader: (i) wire leaders, or (ii) monofilament nylon leaders.
3. Bait: (i) small fish species for bait, or (ii) squid species for bait.
4. Hook width: (i) hooks with a narrowest width ≥ 4.5 cm, or (ii) hooks with a narrowest width <4.5 cm.
5. Main retained species: The species that made up the largest proportion of the retained catch, using the categories: (i) bigeye, yellowfin or albacore tuna, (ii) swordfish, or (iii) other.
6. Time of day of the gear soak: The primary time of day that the gear soaked: (i) primarily daytime, (ii) primarily nighttime, (iii) roughly equal soak time during day and nighttime, or (iv) other (variable mix of the three previous categories or not reported).
7. Suite of 19 variables: The number of a suite of 19 potentially significant explanatory variables (defined in the previous section) that was controlled or explicitly accounted for.
8. Time-series length: The number of years in the study data series.
9. Journal impact factor: The impact factor of the journal in which the study was published, in the year that it was published. Impact factors were obtained from BioxBio (2014), IIASA (2014) or from journal and publisher websites. Grey literature materials were assigned a zero value for impact factor.
10. Publication year: Year of study publication.

The last two covariates were used specifically to account for various forms of publication bias (Murtaugh 2002; Nakagawa and Santos 2012). A total of 1024 models were explored for every combination of the ten moderators.

As for the GLMMs, it was not possible to fit mixed-effects meta-regression models with interaction terms due to data limitations. Each mixed-effects meta-regression model was fitted using the *metafor* package for R (Viechtbauer 2010) based on the multivariate parameterization to accommodate more complex forms of random-effect structures (Gasparrini *et al.* 2012). We then explored combinations of the suite of 10 covariates for the mixed-effects meta-regression models using multi-model selection with weights based on the sample size-corrected Akaike Information Criterion (AICc, see Burnham and Anderson 2002;). These were implemented using the *glmulti* package for R (Calcagno 2013). Some covariates, such as impact factor and publication year, were also modelled in the mixed-effects meta-regressions using B-splines to account for potential non-linear functional form (Gasparrini *et al.* 2012). This was implemented within *metafor* and *glmulti* using the R *splines* package (R Core Team 2014). The study-specific inverse-variance weighted relative risk estimates and the overall pooled (or random-effects) estimate for all 30 studies were displayed in a forest plot that was augmented with key mixed-effects meta-regression results.

The restricted maximum likelihood (REML) heterogeneity variance estimator was used for fitting the mixed-effects models to derive unbiased parameter estimates, but the maximum likelihood (ML) estimator was used for likelihood ratio-based model comparisons when the random-effects structure was the same but models differed in the fixed effects (Viechtbauer *et al.* 2015). The I^2 statistic (Higgins and Thompson 2002) was used to assess the level of unexplained heterogeneity estimated in each mixed-effects meta-regression model fit to the 30 studies and the difference in the amount of explained residual heterogeneity between models was used to derive a simple R^2 measure of overall model fit. For the best-fit models, a formal test of residual heterogeneity was carried out using the Cochrane Q_E test (Viechtbauer and Cheung 2010) and an omnibus *F*-test was used to test for significance of the set of all covariates included in those models (Viechtbauer *et al.* 2015). Other model fit diagnostics included Q-Q normal plots of residuals and both outlier and influential study diagnostics (Viechtbauer and Cheung 2010).

Some of the studies in the meta-regressions were undertaken by the same author(s), possibly resulting in correlated effects between studies by the same authors or research group. If so, then this would violate the important meta-analysis assumption of independent studies or observations (Nakagawa and Santos 2012). Therefore, we tested for non-independence of the 30 studies by using multilevel or hierarchical mixed-effects meta-regression with study nested within research group (based on lead author) now used as a multilevel random-effects structure, which is a three-level hierarchical mixed-effects model (Konstantopoulos 2011; Tuck *et al.* 2014). We compared a two-level meta-regression model (random = ~1| study) with the three-level hierarchical model (random = ~factor(study)|research group) using the same set of fixed effects determined for the best-fit two-level model. A compound symmetry variance–covariance structure was used and REML estimation was now appropriate, as likelihood ratio-based comparison was between models with the same fixed effects but differing random effects structure.

We explored potential publication bias in several ways: cumulative effect or time lag bias forest plot for the random-effects model (Nakagawa and Santos 2012), Egger regression-based estimates of funnel plot symmetry for random or mixed-effects models (Nakagawa and Santos 2012), non-parametric monotone weighted probability function approach (Rufibach 2011), and inclusion of specific covariates in the mixed meta-regression models that might account explicitly for some types of publication bias (Murtaugh 2002; Nakagawa and Santos 2012). Time lag bias plot and Egger regression estimates of some forms of publication bias were implemented using the *metafor* package for R (Viechtbauer 2010). The weighted probability approach was implemented using the *selectMeta* package for R (Rufibach 2014). If publication bias was evident, then bias-corrected relative risk (variance) estimates derived from the weighted probability function approach could be used in a meta-regression, which could reduce complexity in modelling compared with the approach of explicit inclusion of informative covariates in the meta-regression.

We also conducted similar mixed-effect meta-regression analyses where possible for rays, where the relative risk summary measure could be calculated for 15 of the 41 compiled studies that contained information on both the number of hooks deployed by hook shape and the number of caught rays by hook shape. The same suite of 10 covariates used for the shark meta-analysis was used in the ray catch rate meta-analysis. However, no GLMM-based assessment of data censoring by exclusion of 26 studies from the ray data set was feasible, given data limitations.

All 15 studies included in the ray meta-analysis were also included in the sample used in the shark meta-regressions (i.e. 15 of the 30 studies included in the shark meta-regressions were also used for the ray meta-analysis).

Several additional variables were considered for inclusion as potentially informative covariates in the meta-analysis models, but were excluded because their inclusion would have required excluding many of the compiled studies, resulting in too sparse a data set. Variables that were explored in this way and not included as model terms were: temporal distribution of effort by epoch, spatial distribution of effort by region, main shark species caught, main ray species caught, gear soak depth, use of light attractors and number of vessels in the study.

While there was a sufficient sample size to conduct meta-analyses of the effect of hook shape on the relative risk of shark and ray capture, the other three focal factors, however, were not used as the response variable, and haulback survival rate and hooking position were not used as the effect size measure, as doing so would have resulted in too sparse a data set to perform a meaningful meta-analysis. We did, however, consider these other three focal factors in the shark and ray meta-analysis models of effect of hook shape on shark and ray relative risk of capture.

Results

Metadata for literature review data set

A total of 100 findings and 57 records from 40 studies reported in 37 publications and reports were compiled for the literature review (Table 1). For the compiled studies, Table 1 reports the study category, number of hooks in study samples, number of caught sharks and rays in study samples, epoch, region, whether findings were on single focal factor effects or had simultaneously variability in two or more focal factors, and the number of 19 potentially significant explanatory variables that were controlled or accounted for.

The 37 studies with information on the number of years in the time series had a mean of 4.3 years (±0.7 years standard error of the mean [SEM], range 1–19 years). The years from which data were collected had a mean of year 2004.0 (±0.4 SEM, range 1981 to 2012, $n = 159$), with 85% from 2000 or later. For 36 studies with information enabling categorization by season, there was one study each with a time series only from quarter 1, 2, 3 and 4, and 32 studies had time series occurring during two or more quarters. Of 23 studies with information on the time of day of gear soak, four were from primarily daytime gear soaks, 16 nighttime, and three a mix of day and night. For 19 studies that reported gear soak depth, six had hooks that soaked shallower than 50 m depth, seven where hooks soaked shallower than 100 m and with some hooks soaking between 50 and 100 m, five where some hooks soak shallower than and some soak deeper than 100 m, and one where all hooks soak deeper than 100 m. There were 18 studies where light attractors were used in the gear, four where light attractors were not used, and 18 where information on light attractor use was not reported. The mean journal impact factor of the 40 studies was 1.5 (±0.2 SEM, range 0–4.036).

Bigeye and yellowfin tunas made up the largest proportion of the retained catch for six of the studies, albacore for two studies, swordfish for 18 studies, other teleosts for one study, sharks for three studies, other species groups or a mix of the previous categories for eight studies, and there were two studies where the retained catch composition was not reported. Blue shark was the main caught shark species for 25 of the studies, other pelagic shark species found in either just oceanic habitats or both oceanic and coastal habitats for eight studies, pelagic and other sharks that are found only in coastal and reef habitats for three studies, and there were four studies where information on the shark species catch composition was not reported. Pelagic stingrays (*Pteroplatytrygon violacea*) were the main caught ray species in 17 studies, and ray species catch composition was not reported for 23 studies.

Literature review records and findings

The 40 literature review studies reported 100 findings where a focal factor category had a significant effect on a single elasmobranch species' catch rate, haulback survival rate or hooking position. Fig. 1 summarizes the number of findings of significant increases and decreases in individual elasmobranch species' catch rates, haulback survival rates and proportion of catch that was deeply hooked by focal factor category. The number of findings in each category that enabled an assessment of single focal factor effects is also identified. All findings in Fig. 1 panels e and f had simultaneous differences in at least two and three focal factors respectively: findings in Fig. 1e differed by both hook shape and width, while findings in Fig. 1f differed in hook shape, hook width and bait type. The 100 findings were for 16 elasmobranch species (Fig. 1).

Table 2 summarizes the results displayed in Fig. 1 by identifying the ratio of the number of

Table 1 Experiments, and selected categorizations, from studies that were compiled and analysed in a meta-analysis and literature review of study findings on the significance of individual and interacting effects of pelagic longline hook shape, hook narrowest width, bait type and leader material on elasmobranch catch rates, haulback disposition and hooking location.

Citation	Study com-ponent[14]	Study cat-egory[15]	No. hooks	No. sharks	No. rays	Epoch[16]	Region[17]	Findings on single focal factor effect[18]	No. potentially significant explanatory variables addressed[19]
Afonso *et al.* (2011)	1,3	1	7800	134	NR	3	SAO	3	5
Afonso *et al.* (2012)[1]	1,2,3	1	17 000	142	40	3	SAO	2	7
Amorim *et al.* (2014)	1,2,3	1	446 400	298	144	3	SAO	2	5
Andraka *et al.* (2013)[2]	1,3	1	151 673	245	0	3	NPO	3	1
Andraka *et al.* (2013)[3]	1,3	1	209 684	2305	0	3	NPO	3	1
Andraka *et al.* (2013)[4]	1,2	1	36 420	39	42	3	NSPO	3	1
Andraka *et al.* (2013)[5]	1,2,3	1	356 674	2423	88	3	NSPO	3	1
Andraka *et al.* (2013)[6]	1	1	75 509	327	0	3	NPO	3	1
Ariz *et al.* (2006)	1,2	1	782 876	147	2432	2	IO	3	3
Berkeley and Campos (1988)	3,4	1	1604	85	0	1	NAO	3	0
Bolten and Bjorndal (2006)[7]	1	1	138 121	2129	NR	2	NAO	3	5
Bolten and Bjorndal (2006)[8]	1	1	88 150	3990	NR	2	NAO	2	6
Bolten and Bjorndal (2006)[9]	1	1	40 838	1326	NR	2	NAO	2	6
Branstetter and Musick (1993)	3,4	1	10 641	640	NR	1	NAO	1	5
Bromhead *et al.* (2013)	3	2	NR	NR	NR	3	NSPO	3	1
Campana *et al.* (2009)	3	2	NR	NR	NR	3	NAO	3	6
Caneco *et al.* (2014)	3	2	NR	NR	NR	NR	NSPO	3	12
Carruthers *et al.* (2009)	3,4	2	950 000	11 549	942	2	NAO	3	5
Coelho *et al.* (2012a)	1,2,3	1	305 352	278	547	3	NSAO	2	4
Curran and Beverly (2012)	3,4	1	145 982	137	51	NR	SPO	1	7
Curran and Bigelow (2011)	1,2,3	1	2 777 427	9280	350	2	NPO	3	7
Domingo *et al.* (2012)[10]	1,2,3	1	39 822	1996	17	3	SAO	3	3
Domingo *et al.* (2012)[11]	1,2,3	1	45 142	844	48	3	SAO	3	2

Table 1 Continued.

Citation	Study com-ponent[14]	Study cat-egory[15]	No. hooks	No. sharks	No. rays	Epoch[16]	Region[17]	Findings on single focal factor effect[18]	No. potentially significant explanatory variables addressed[19]
Epperly *et al.* (2012)	3	1	813 157	NR	NR	2	NAO	2	7
Ferrari and Kotas (2013)	3,4	1	24 452	NR	126	3	SAO	3	4
Foster *et al.* (2012)	3	1	973 734	NR	NR	2	NAO	2	6
Galeana-Villasenor *et al.* (2008)	3,4	1	15 200	383	11	2	NPO	3	7
Garcia-Cortes *et al.* (2009)	3	1	356 600	NR	NR	3	SPO	3	4
Gilman *et al.* (2007a)	1,3	2	3 433 422	58 201	NR	3	NPO	3	1
Gilman *et al.* (2012)	1,3	2	71 740 263	168 778	NR	3	NSPO	3	9
Gilman *et al.* (2015)	4	2	314 246	471	336	3	NPO	3	2
Kerstetter and Graves (2006)[12]	1,2,3	1	14 070	62	119	2	NAO	3	5
Kerstetter *et al.* (2007)	1,3	1	16 624	147	NA	2	SAO	3	3
Kim *et al.* (2006)	1,2	1	44 100	147	8	2	NSPO	3	5
Kim *et al.* (2007)	1,2	1	62 720	292	24	2	NSPO	3	5
Kumar *et al.* (2013)	1,3	1	123	14	0	NR	IO	3	7
Mejuto *et al.* (2008)	1,3	1	430 299	11 842	NR	2	NSAO	2	3
Pacheco *et al.* (2011)	1,2,3	1	50 170	124	182	3	NSAO	3	4
Piovano *et al.* (2009)	1,2,3	1	30 000	10	75	3	MS	3	4
Piovano *et al.* (2010)	3,4	1	86 116	NR	222	3	MS	2	6
Sales *et al.* (2010)	1,3	1	145 828	3889	NR	3	SAO	3	3
Serafy *et al.* (2012b)	3	2	7 661 319	NR	NR	3	NAO	3	7
Vandeperre *et al.* (2014)[13]	3	1	NR	NR	NR	2	NAO	3	5
Vega and Licandeo (2009)	3,4	1	72 090	269	3	2	SPO	3	7
Ward *et al.* (2008)	3,4	1	75 101	147	0	2	SPO	3	7
Ward *et al.* (2009)	1,2,3	1	95 150	125	12	3	SPO	3	2
Watson *et al.* (2005)	1,3	1	427 382	12 755	0	2	NAO	2	6

Table 1 Continued.

Citation	Study com-ponent[14]	Study cat-egory[15]	No. hooks	No. sharks	No. rays	Epoch[16]	Region[17]	Findings on single focal factor effect[18]	No. potentially significant explanatory variables addressed[19]
Yokota *et al.* (2006)	1,3	1	48 600	3405	NR	2	NPO	2	6
Yokota *et al.* (2009)	3,4	1	36 480	1745	20	2	NPO	1	8

[1] An error in a results summary table in Afonso *et al.* (2012, Table 1, CPUEs by four treatments were out of order by elasmobranch species, A. Afonso, pers. comm., 5 December 2014) was corrected for the meta-analysis.

[2] Costa Rica mahi-mahi fishery.

[3] Costa Rica tuna, billfish and shark fishery.

[4] Ecuador mahi-mahi fishery.

[5] Ecuador tuna, billfish and shark fishery.

[6] Panama tuna, billfish and shark fishery.

[7] Experiment from 2000 that included two types of 9/0 J hooks and 16/0 circle hooks; also see Bolten and Bjorndal (2002).

[8] Experiment from 2001 that included a 9/0 J hook, 16/0 circle hook and 18/0 circle hook; also see Bolten and Bjorndal (2003).

[9] Experiment from 2003 (Phase 4a) that included 16/0 circle hook, 18/0 circle hook and 2.6 mm tuna hook; also see Bolten and Bjorndal (2005).

[10] 'American' style gear experiment.

[11] 'Spanish' style gear experiment.

[12] Data from fall study component only.

[13] Data from hook and leader experiment only. Literature review findings and records covered those from Bolten and Bjorndal (2006).

[14] 1 = hook shape shark catch relative risk meta-regression model, 2 = hook shape ray catch relative risk meta-regression model, 3 = literature review, 4 = considered for meta-analysis components that were excluded due to too small sample sizes, and/or excluded from the meta-analyses on effect of hook shape on relative risk of shark or ray capture due to lack of information on the number of circle or J-shaped hooks and the number of caught sharks or rays by hook shape.

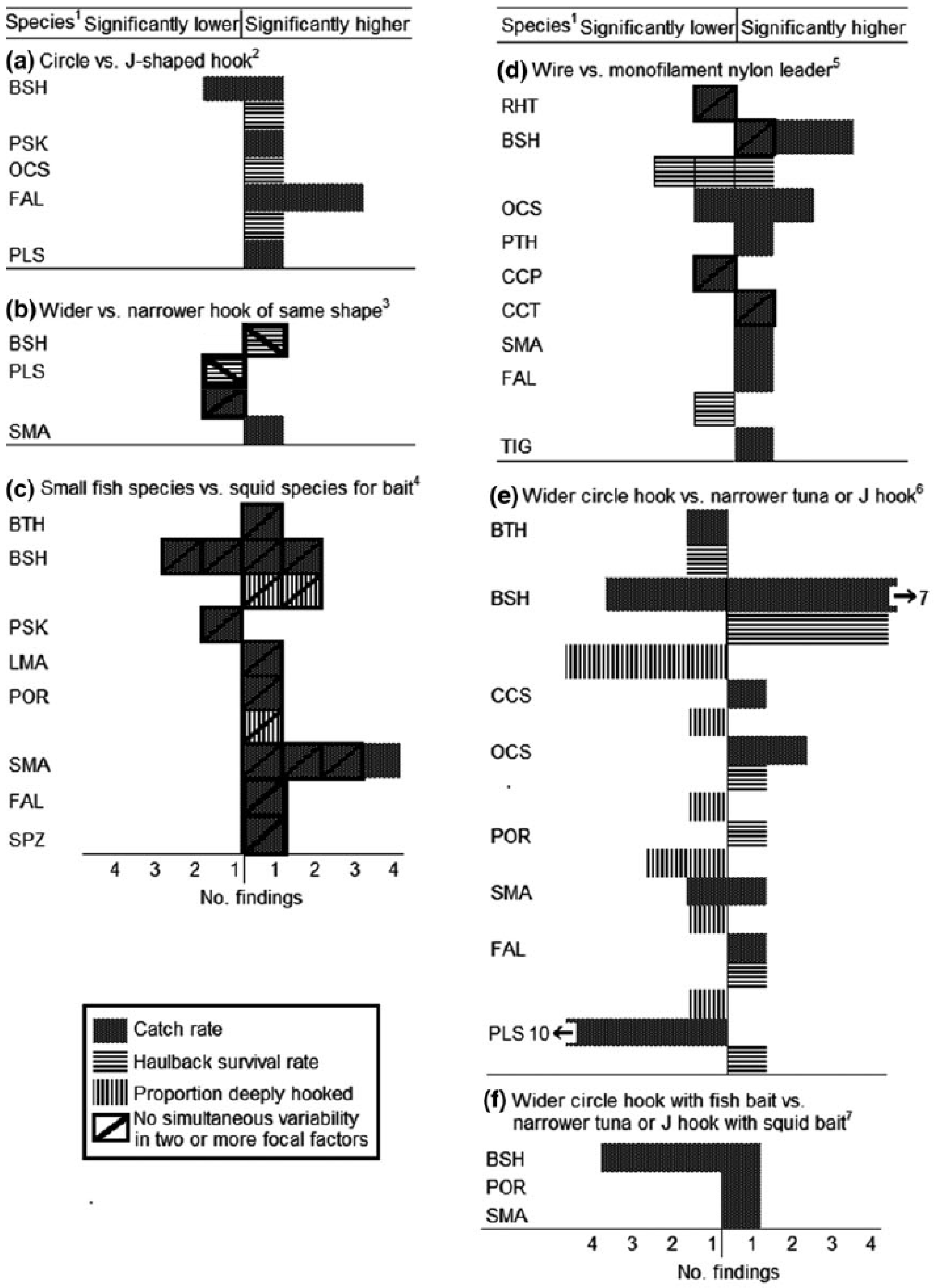
[15] 1 = controlled or comparative at-sea experiment; 2 = observer data analyses.

[16] 1 = 1999 and older; 2 = 2006 and older with 1 year >1999; 3 = 2014 and older with 1 year >2006; NR = not reported.

[17] IO, Indian Ocean; MS, Mediterranean Sea; NAO, north Atlantic Ocean; SAO, south Atlantic Ocean; NSAO, north and south Atlantic Ocean; NPO, north Pacific Ocean; SPO, south Pacific Ocean; NSPO, north and south Pacific Ocean.

[18] 1 = all findings on effects of focal factors were not confounded simultaneously by other focal factors; 2 = one or more finding on the effect of a focal factor was not confounded simultaneously by other focal factors, and one or more finding on the effect of a focal factor was confounded simultaneously by one or more additional focal factor; 3 = findings on the effect of focal factors were all simultaneously confounded by one or more additional focal factor. Not reported in the article methods, only monofilament leaders were used in records included in data sets analysed by Watson *et al.* (2005), Epperly *et al.* (2012) and Foster *et al.* (2012), and therefore assessments of effects of bait type were not simultaneously confounded by another focal factor, D. Foster, US National Marine Fisheries Service, pers. comm., 28 October 2014; assessments of combinations of hook shape, width and bait type, however, were simultaneously confounded by multiple focal factors.

[19] Suite of 19 potentially significant explanatory variables defined in Methods section 'Literature review analyses'.



[1] RHT=Atlantic sharpnose shark, BTH=bigeye thresher shark, BSH=blue shark, PSK=crocodile shark, LMA=longfin mako shark, CCS=night shark, OCS=oceanic whitetip shark, PTH=pelagic thresher shark, PLS=pelagic stingray, POR=porbeagle shark, CCT=sand tiger shark, CCP=sandbar shark, SMA=shortfin mako shark, FAL=silky shark, SPZ=smooth hammerhead shark, TIG=tiger shark

[2] Ward et al., 2009; Serafy et al., 2012b; Andraka et al., 2013; Caneco et al., 2014

[3] Vega and Licandeo, 2009; Piovano et al., 2010; Curran and Beverly, 2012

[4] Watson et al., 2005; Mejuto et al., 2008; Vega and Licandeo, 2009; Coelho et al., 2012a; Epperly et al., 2012; Foster et al., 2012; Amorin et al., 2014

[5] Branstetter and Musick, 1993; Ward et al., 2008; Vega and Licanadeo, 2009; Afonso et al., 2012; Bromhead et al., 2013; Caneco et al., 2014

[6] Domingo et al., 2002; Watson et al., 2005; Kerstetter and Graves, 2006; Mejuto et al., 2008; Campana et al., 2009; Carruthers et al., 2009; Piovano et al., 2009, 2010; Sales et al., 2010; Afonso et al., 2011; Curran and Bigelow, 2011; Pacheco et al., 2011; Coelho et al., 2012a; Domingo et al., 2012; Epperly et al., 2012; Foster et al., 2012; Gilman et al., 2012; Ferrari and Kotas, 2013; Amorin et al., 2014; Caneco et al., 2014; Vandeperre et al., 2014

[7] Watson et al., 2005; Gilman et al., 2007a; Foster et al., 2012; Amorin et al., 2014

Figure 1 Number of findings of significant increases and decreases in individual elasmobranch species' catch rates, haulback survival rates and proportion of catch that was deeply hooked, by individual and combinations of pelagic longline gear factors. A black border and forward slash indicates findings that were from experiments with designs that did not have simultaneous variability in two or more of the focal gear factors hook shape, hook narrowest width, bait type and leader material.

findings with a significant increase to number with a significant decrease, and ratio of the number of species with ≥1 record of a significant increase to number with a significant decrease, by factor and by catch rate, haulback survival rate and hooking position. Table 3 summarizes the number of records and the number of findings by focal factor category, observing significant differ-

Table 2 The number of findings with a significant increase and decrease, and number of elasmobranch species with ≥1 finding of a significant increase and decrease, in elasmobranch catch rates, haulback survival rates and proportion deeply hooked, by six pelagic longline terminal tackle factors. References from Fig. 1.

	No. findings significant increase: decrease			No. species significant increase: decrease		
Factor category	Catch rate	Haulback survival rate	Proportion deep hooked	Catch rate	Haulback survival rate	Proportion deep hooked
C vs. J-shaped hook	6:1	3:0	0:0	4:1	3:0	0:0
Wider vs. narrower hook	1:1	1:1	0:0	1:1	1:1	0:0
Fish vs. squid for bait	11:3	0:0	3:0	7:2	0:0	1:0
Wire vs. monofilament leader	10:3	1:3	0:0	7:3	1:2	0:0
Wider C vs. narrower J-shaped hook	12:15	8:1	0:10	5:4	5:1	0:6
Wider C and fish bait vs. narrower J-shaped and squid bait	3:3	0:0	0:0	3:1	0:0	0:0

Table 3 (a) Number of records by focal factor category by region, and (b) number of findings of significant differences of the effects of hook, bait or leader material on individual elasmobranch species' catch rates, haulback survival rates or hooking position, by region. In (b), values in parentheses are the subset of findings with designs that did not have simultaneous variability in two or more of the gear factors hook shape, hook narrowest width, bait type and leader material. References from Fig. 1.

	(a) No. records by region[1]							
Factor category	NAO	SAO	NSAO	NPO	SPO	NSPO	IO	MS
Hook shape	1			3	1	1		
Hook narrowest width				1	2			1
Bait type	3	1	2	1	2			
Leader material	2	1			2	2		
Wider circle hook vs. narrower tuna or J hook	7	7	3	3	1	2	1	2
Wider circle hook with fish bait vs. narrower tuna or J hook with squid bait	2	1		1	1			
	(b) No. findings of significant effect by region							
Hook shape	1			3	1	5		
Hook narrowest width					3(2)			1(1)
Bait type	7(7)	2(2)	7(7)		1			
Leader material	3(3)	1(1)			4	9		
Wider circle hook vs. narrower tuna or J hook	15	18	3	5		3		2
Wider circle hook with fish bait vs. narrower tuna or J hook with squid bait	4	1		1				

[1] NAO, north Atlantic Ocean; SAO, south Atlantic Ocean; NSAO, north and south Atlantic Ocean; NPO, north Pacific Ocean; SPO, south Pacific Ocean; NSPO, north and south Pacific Ocean; IO, Indian Ocean; MS, Mediterranean Sea.

ences of the effects of hook, bait and leader material on species-specific elasmobranch catch rates, haulback survival rates and hooking position, by region. As in Fig. 1 and Table 1, the number of findings in each category that enabled a determination of single focal factor effects is also identified in Table 3b.

Of the significant findings on the effect of hook shape, 86% had significantly higher catch rates and all three findings had significantly higher haulback survival rates on circle than J-shaped hooks of the same narrowest width. All findings had simultaneous variability in at least one additional focal factor (Fig. 1a, Table 2). The four findings on the single-factor effect of hook narrowest width showed variable effects on catch rates of shortfin mako sharks (*Isurus oxyrinchus)* and pelagic stingrays, and on haulback survival rates of blue sharks and pelagic stingrays (Fig. 1b, Table 2). There were higher shark catch rates on fish vs. squid for bait for 79% of significant findings and a larger proportion of caught sharks were deeply hooked on fish bait for all three findings. All but one of the 17 findings were from studies designed so that there was no simultaneous variability in other focal factors (Fig. 1c, Table 2). Findings on the effect of leader material on catch rates observed two shark species had only findings of significantly lower catch rates on wire leaders, and six shark species had only findings of significantly higher catch rates on wire leaders. Three of four findings on the effect of leader material found significantly lower shark haulback survival on wire leaders. There were no findings on hooking position by leader type. There were also no findings on leader material effects on ray species. All but four compiled findings had simultaneous variability in at least one additional focal factor (Fig. 1d, Table 2).

Findings on the effect of wider circle vs. narrower J-shaped hooks on haulback survival rates and hooking position were relatively consistent across elasmobranch species. Of the significant findings, 89% found higher haulback survival rates on wider circle vs. narrower J-shaped hooks, and 100% observed a lower proportion of deep hooking on wider circle hooks. Of the findings, 71% observed a significantly higher shark catch rate on wider circle than on narrower J-shaped hooks. All 10 pelagic stingray findings observed a significantly higher catch rate on wider circle hooks. There was some variability across shark species, and in two cases there was variability within single species (blue and shortfin mako sharks) (Fig. 1e, Table 2). For the findings on the effect of wider circle hooks with fish bait vs. narrower J-shaped hooks with squid bait, porbeagle (*Lamna nasus*) and shortfin mako sharks had one finding each of significantly higher catch rates on wider circle hooks with fish bait, and blue shark had three findings showing significantly lower and one finding of significantly higher catch rates on wider circle hooks with fish bait. There were no significant findings identified for ray species (Fig. 1f, Table 2).

Of the 40 studies, 33 had one or more finding of no significant effect of a focal factor on an individual elasmobranch species' catch rate, haulback disposition or hooking location. Seven studies included in the literature review had no findings of a significant effect of a focal factor or the two combinations of focal factors on an individual elasmobranch species' catch rate, haulback survival rate or hooking position (Berkeley and Campos 1988; Kerstetter *et al.* 2007; Galeana-Villasenor *et al.* 2008; Garcia-Cortes *et al.* 2009; Yokota *et al.* 2006, 2009; Kumar *et al.* 2013). Ten of the 57 records identified in Table 3a were results observing no significant effect of a focal factor category on a single elasmobranch species.

Meta-analysis data censoring

Table 1 provides summary information on the 41 studies from 34 publications and reports that were compiled for possible inclusion in the meta-regression analyses, of which 30 and 15 studies were included in shark and ray meta-analyses models, respectively, for effect of hook shape on the relative risk of capture. There were no significant main effects in the random-effects logistic regression based on the Type II Wald summary statistic (Fox and Weisberg 2011): study type (Type II Wald $\chi^2_{\mathrm{df}=1} = 0.187$, $P = 0.67$), bait type (Type II Wald $\chi^2_{\mathrm{df}=3} = 0.019$, $P = 0.99$), leader material (Type II Wald $\chi^2_{\mathrm{df}=3} = 0.195$, $P = 0.98$), and hook narrowest width (Type II Wald $\chi^2_{\mathrm{df}=3} = 1.156$, $P = 0.76$). We conclude that data censoring comprising exclusion of the 11 studies that provided no summary measure (relative risk) had little effect at least on these four variables as explanatory covariates in the subsequent meta-analysis of shark catch rates.

Meta-analysis exploring covariate functional form and interaction terms

An effect display is shown in Fig. 2 for the fit of the inverse-precision weighted random intercepts-only LMM fitted to 30 shark relative risk estimates, given various potentially informative covariates. It is not possible to fit a study-specific random-effect structure using this approach as it would be over-specified with a parameter for each study, so the random-effect component of the LLM comprised the 30 studies aggregated within 19 research groups. It was possible to include a two-way interaction term for bait type X publication year, but this term was not a significant contributor to model fit. The only significant effects determined using Type II Wald chi-square tests were the categorical factors study category and time of day of gear soak. Non-linear functional form was evident for some covariates such as the number of 19 potentially significant explanatory variables addressed by each study (Fig. 2c), but these covariates were not found to be limited contributors to model fit. Nonetheless, it was evident that including low-order splines to model the possible non-linear functional form of some of the continuous covariates would be useful in the subsequent meta-analysis.

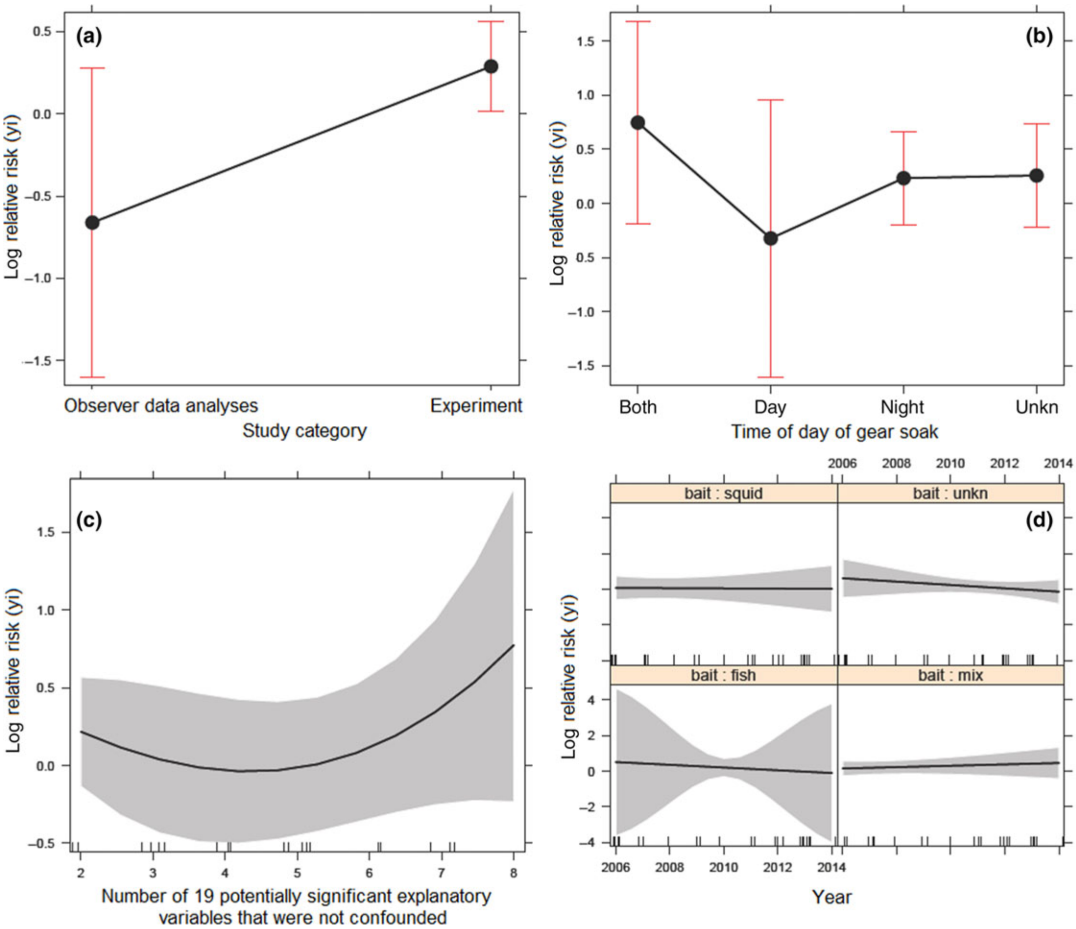


Figure 2 Effect display for the outcome of shark meta-regressions, which used inverse-precision weighted LMMs with only random-intercepts, which were fitted to relative risk estimates for potentially informative covariates. Plot (a) study category, (b) time of day of gear soak, (c) number of 19 potentially significant explanatory variables (defined in Methods section 'Literature review analyses') addressed by each study, (d) interaction between bait type and publication year. Solid dot = estimated parameter mean, vertical bar = 95% confidence interval around the mean, solid curves = term fitted using low-order spline such as bs(19.vars, 3) to account for any non-linear functional form, shaded polygon = 95% confidence region around curve, with two-way interaction term for bait type X publication year shown in the multipanel display in (d).

Shark catch rate meta-regression models

The inverse-precision weight summary measures (relative risk) for the 30 shark catch rate studies are summarized in the forest plot shown in Fig. 3. The pooled or random-effects log relative risk estimate is 0.18 (95% CI: 0.03, 0.33), suggesting that combined shark species (predominantly blue sharks) had a 1.20 (95% CI: 1.03–1.39) times or 20% significantly higher risk of capture on circle hooks than on J-shaped hooks. The top 12 mixed- or random-effects meta-regression models fitted to the relative risk summary measures (effect size) for the 30 shark studies are shown in Table 4. Model 4 is the random-effects or RE model and is the reference model for assessing improvement in model when various moderators were included. These 12 models account for ca. 95% of the weight of evidence for the large assemble of random- or mixed-effects models fitted. Model-specific tests were included for the top three best-fitting models (Table 4). The pooled or RE estimate (REML) = 0.155 (95% CI: = −0.03 to 0.34, $P = 0.09$). No aberrant residual behaviour relative to the normal distribution was apparent using review of Q-Q plots for the top three models, although further model diagnostics (see below) revealed two outliers. The best-fit model (model 1) was a mixed-effects model comprising one significant covariate or moderator (time of day of gear soak), and this model accounted for ca. 32% of the weight of evidence for the modelled set. The best-fit model 1 had a $R^2 = 41.6\%$ improvement in model fit compared to the random-effects model. The top three models accounted for 62% of the weight of evidence and they were all significantly better model fits than the random-effects model 4 (Table 4).

Model averaging the top three models led to very similar estimates, so we included the parameter estimates for model 3 in the forest plot (Fig. 3), which includes both the random-effects (pooled) estimate and the mixed-effects estimates for the various levels of the two included covariates, time of day of gear soak and study category. The omnibus test for inclusion of both moderators was significant (Table 4, moderator test for model 3). There was a significantly higher pooled relative risk of catch of sharks on circle hooks than J-shaped hooks in controlled and comparative experiments and during certain times of day of gear soak (Fig. 3). A fitted meta-regression effects polygon, not shown on study-specific effect size in Fig. 3 to avoid visual clutter, revealed that it fit well, with only two significant outliers: Coelho *et al.* (2012a) (significantly lower relative risk of capture on circle hooks than expected from the other studies) and Ariz *et al.* (2006) (significantly high relative risk of capture on circle hooks than expected from the other studies) and three additional influential studies were Gilman *et al.* (2007a, 2012) and Kim *et al.* (2007).

Irrespective of model fit, considerable heterogeneity still remained in all models indicated using either the I^2 statistic where >75 signifies considerable heterogeneity (Higgins and Thompson 2002) or the more formal Q_E test for residual heterogeneity. So for instance, while model 1 is a significantly better fit than the random-effects model 4, there was still considerable unexplained heterogeneity between the 30 studies that was not fully accounted for by study-specific random effects and the covariates.

The hierarchical or three-level mixed-effects meta-regression model with the same fixed effects (or covariates) was not a better fit compared with any of the top two-level mixed-effects models listed in Table 4. For instance, a loglikelihood ratio (LLR) test comparing Model 3 with the corresponding three-level or hierarchical model was not significant (LLR statistic = 1.15, df = 1, $P = 0.28$). So, including more complex levels of random-effects structures in the mixed-effects meta-regression models did not provide for better model fit nor provide any additional insight into these 30 shark catch rates.

Of the 30 studies used for the shark model, two (Gilman *et al.* 2007a, 2012) were based on analyses of observer program data (Table 1), which were two of seven studies finding a lower relative risk of shark capture on circle hooks (Fig. 3). Discussed in the following section, these two studies had a significant influence on meta-regression model outcomes, calling into question the robustness of the observed effect of the covariate study category.

There was a significantly higher relative risk of shark capture on circle hooks in studies with soaks that occurred partially during both day and night than with daytime-only soaks. There was a significantly higher relative risk of shark capture on circle hooks for both mixed day/night soaks and the 'unknown' soak time category. Studies with gear soak time occurring only during the night showed no effect of hook shape on the relative risk of capture, while studies with day-only

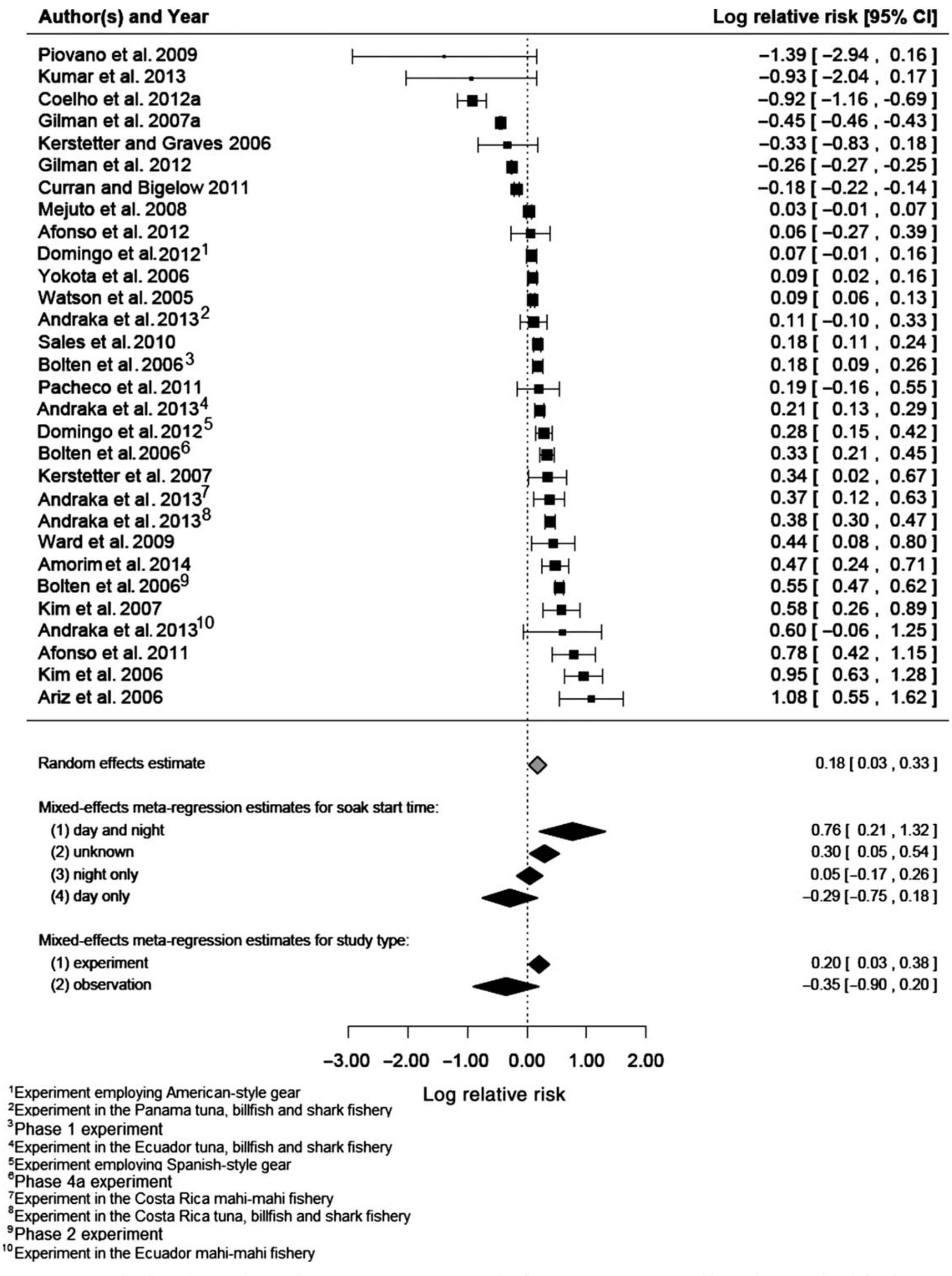


Figure 3 Mixed-effects forest plot of the inverse-precision weighted summary measure of log relative risk of shark capture on circle vs. J-shaped hooks for 30 studies. A log relative risk >0 indicates a higher relative risk of capture on circle hooks. The pooled or random-effects estimate (RE) of the relative risk metric is shown in addition to mixed-effects meta-regression estimates for two informative covariates of best-fit models (time of day of gear soak and study category). Plot ordered by effect size. Solid square = relative risk metric and size of the square reflects relative weighting. Horizontal bars = 95% confidence interval of the relative risk metric.

Table 4 Summary statistics for the top 12 best-fitting meta-regression models of the effect of pelagic longline hook shape on relative risk of catching sharks, from 30 studies. 'yi' = log relative risk of capture of sharks by hook shape summary measure. bs() = B-spline with three degrees of freedom.

Meta-regression model formula	AICc	AICc weight	Cumulative weights	I^2	R^2
yi ~ 1 + time.of.day.soak	37.491	0.3158	0.3158	98.7	41.6
yi ~ 1 + study.category	38.885	0.1572	0.4730	99.3	21.5
yi ~ 1 + study.category + time.of.day.soak	39.085	0.1423	0.6153	97.8	49.8
yi ~ 1	40.389	0.0741	0.6894	99.6	0.0
yi ~ 1 + time.of.day.soak + 19.variables	40.834	0.0593	0.7487	98.2	41.6
yi ~ 1 + study.category + 19.variables	40.964	0.0556	0.8043	98.4	22.5
yi ~ 1 + 19.variables	41.694	0.0386	0.8429	99.1	3.6
yi ~ 1 + study.category + bs(impact.factor)	42.172	0.0304	0.8733	97.4	37.5
yi ~ 1 + study.category + time.of.day.soak + 19.variables	42.741	0.0228	0.8961	96.8	49.6
yi ~ 1 + study.category + main.retained.species	43.028	0.0198	0.9159	98.3	33.6
yi ~ 1 + main.retained.species	43.675	0.0143	0.9302	99.1	15.3
yi ~ 1 + bs(impact.factor)	43.716	0.0140	0.9442	98.9	21.7

Model-specific test for first three models:

(a) Residual heterogeneity	(b) Moderators
Q_E (23) = 1709.9, $P < 0.0001$	F (3,23) = 3.43, $P = 0.03$
Q_E (25) = 757.8, $P < 0.0001$	F (1,25) = 3.57, $P = 0.07$
Q_E (22) = 469.1, $P < 0.0001$	F (4,22) = 2.96, $P = 0.04$

soak times had a non-significant lower relative risk of capture on circle hooks (Fig. 3).

Meta-analysis model diagnostics

Two studies were identified as major outliers (Ariz *et al.* 2006; Coelho *et al.* 2012a) based on review of studentized deleted residual plots of any of the top three models listed in Table 4. However, based on review of influence measures such as Cook's distance, DFBETAs, Q_E delete or the covariance ratio metrics (Viechtbauer and Cheung 2010), neither study had any significant effect on the mixed-effects meta-regression model outcomes, although deletion of the studies and refitting the models would slightly improve the precision of parameter estimates.

Three additional studies (Gilman *et al.* 2007a, 2012; Kim *et al.* 2007) were not outliers, but had a significant influence on meta-regression model outcomes. In particular, Gilman *et al.* (2007a) distorted the parameter estimates for study type so that inference based on this covariate that depends on inclusion of one particular study is weak. Removal of these three highly influential studies improved precision and significance of the soak time variable, but resulted only in marginal improvement in reduction in the residual heterogeneity. The findings on soak time effect on the relative risk of shark capture rates are therefore robust, but this may not be so for study type. This affirms the finding that Model 1 in Table 4 is the best-fit model for the shark catch rates. Excluding those three studies results in a pooled or random-effects estimate = 0.21 (95% CI: 0.04–0.38), further increasing the strength of the finding that pelagic sharks had a significantly higher relative risk of capture on circle than J-shaped hooks (see RE estimate for all 30 studies in Fig. 3).

Meta-analysis publication bias

The various meta-regression models summarized in Tables 4 and 5 show that neither publication year nor publication impact factor was a moderator that contributed to any of the best-fitting models. The functional form used for these two covariates (either linear or non-linear) did not have a bearing on shark catch rate model fit and there was no temporal trend evident in the estimated relative risk metric (Fig. 4). No temporal trend is evident in either panel of Fig. 4, suggest-

Table 5 Summary statistics for the top five best-fitting meta-analysis models of the effect of pelagic longline hook shape on relative risk of catching rays, from 15 studies. 'yi' = log relative risk of capture of rays by hook shape summary measure.

Meta-analysis model formula	AICc	AICc weight	Cumulative weights	I^2	R^2
yi ~ 1	29.681	0.3355	0.3355	97.5	0.00
yi ~ 1 + study.category	29.681	0.3355	0.6711	97.5	0.00
yi ~ 1 + impact.factor	32.279	0.0916	0.7629	96.8	0.05
yi ~ 1 + study.category + impact.factor	32.279	0.0916	0.8542	96.8	0.05
yi ~ 1 + bait	35.167	0.0216	0.8758	94.1	0.31

Model-specific test for models 1, 3 and 5:

(a) Residual heterogeneity	(b) Moderators
Q_E (14) = 265.5, $P < 0.0001$	No moderators
Q_E (13) = 249.5, $P < 0.0001$	QM (1) = 0.59, $P = 0.44$
Q_E (11) = 125.1, $P < 0.0001$	QM (3) = 6.92, $P = 0.08$

ing little evidence of temporal publication bias. Thus, the relative risk of capture on circle hooks for pelagic sharks has remained stable and consistent over the 10 years or so spanning the studies considered here. This finding was also apparent using a cumulative effect or time lag bias forest plot for the random-effects model (without moderators). There was also no evidence of any publication year temporal trend for the ray catch rates using a cumulative effect forest plot. There was no evidence of funnel plot asymmetry for either shark catch rates (Egger regression test for Model 1, Table 4, funnel plot symmetry: $z = -1.12$, $P = 0.28$) or ray catch rates (Model 1, Table 5, funnel plot symmetry: $z = -0.42$, $P = 0.68$). There was no evidence found using a non-parametric monotone weight function modelling approach (Rufibach 2011) for any bias towards publication of only significant results. In fact >30% of the 30 estimated P-values for the relative risk summary measures for the 30 shark studies were larger than $P = 0.05$ with a maximum P-value = 0.73. So overall, there was no evidence for any form of publication bias in either the shark or ray catch rates for which we could test for using a range of different approaches.

Ray catch rate meta-analysis models

The inverse-precision weighted summary measures (relative risk) for the 15 ray (predominantly pelagic stingrays) catch rate studies are summarized in Fig. 5. The pooled or random-effects log relative risk estimate of 0.20 (95% CI: −0.11, 0.51) was not significant. The top five mixed- or random-effects meta-regression models fitted to the relative risk summary measures (effect size) for the 15 ray studies are shown in Table 5. Model 1 is the RE model and is the reference model for assessing improvement in model when various moderators were included. The RE model is the best-fit model because there were no significant moderators. The top five models accounted for ca. 88% of the weight of evidence. Model-specific test results are presented for the first, third and fifth models (Table 5). Data limitations precluded exploring more complex random-effects structures such as a hierarchical or three-level model. As with the shark meta-regressions, there was considerable unexplained heterogeneity of the 15 relative risk estimates not accounted for by the study-specific mixed effects, as indicated by the I^2 statistic and Q_E test (Table 5).

Discussion

Hook shape

The meta-analyses findings of significantly higher combined sharks (predominantly blues) and higher but non-significant combined rays (predominantly pelagic stingrays) pooled relative risk of capture on circle hooks than on J-shaped hooks, where most compiled studies compared wider circle with narrower J-shaped hooks, were consistent with the

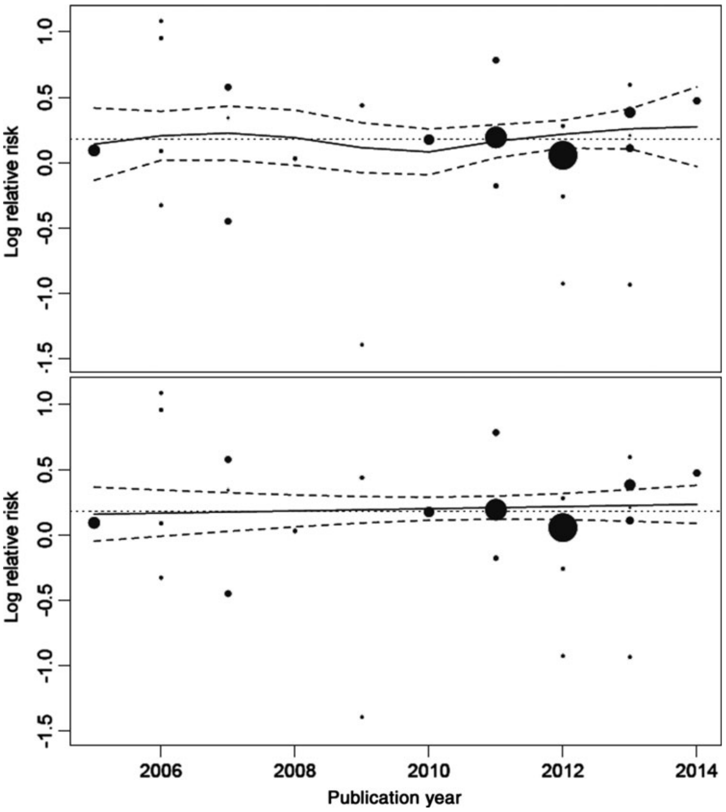


Figure 4 The relative risk metric derived for the 30 shark catch rate studies as a function of study publication year. Solid dots show the relative risk estimate and dot size is proportional to the precision of the estimate. Solid curve shows expected functional form, while dashed curves show 95% confidence curve around the expected curve. Top panel based on a loess smoother weighted by inverse of the precision of the effect size estimate to highlight any non-linear functional form. Bottom panel based on a weighted linear regression fit to highlight a linear trend. The horizontal dotted line in each panel is the estimated pooled or random-effects estimate from Fig. 3.

literature review findings on the single-factor effect of hook shape. Based on a small number of findings and species, and recognizing that the observed effect may have been confounded by other significant focal factor variables, the literature review findings suggest that, for some elasmobranch species, circle hooks significantly increased catch rates, but reduced haulback mortality rates relative to tuna and J hooks of the same narrowest width.

In the shark and ray meta-analyses, there are several possible explanations for the two studies that were outliers and three studies that had a significant influence on the meta-regression model outcomes. Ariz *et al.* (2006) was one of only two studies from the Indian Ocean, where the broad spatial-scale distribution of fishing effort can significantly affect catch and survival rates (Gilman and Hall 2015;). It was also only one of two studies determined to not compare only wider circle and narrower J-shaped hooks. Five studies in the shark meta-regression did not provide sufficient information to compare circle and J-shaped hook widths, and 23 compared wider circle with narrower J-shaped hooks. For the ray meta-analysis, 11 studies compared wider circle with narrower J-shaped hooks, two lacked sufficient information to determine the differences in widths of the circle and J-shaped hooks, and the remaining two, Ward *et al.* (2009) and Ariz *et al.* (2006), included multiple widths of each hook shape. Ariz *et al.* (2006) compared a J hook with two sizes of circle hooks, one that was the same narrowest width and one that was narrower than the J hook. Ward *et al.* (2009) compared multiple circle and tuna hooks, where some of the circle hooks were wider and some narrower than the tuna hooks. Gilman *et al.* (2007a, 2012) were the only two studies analysing obser-

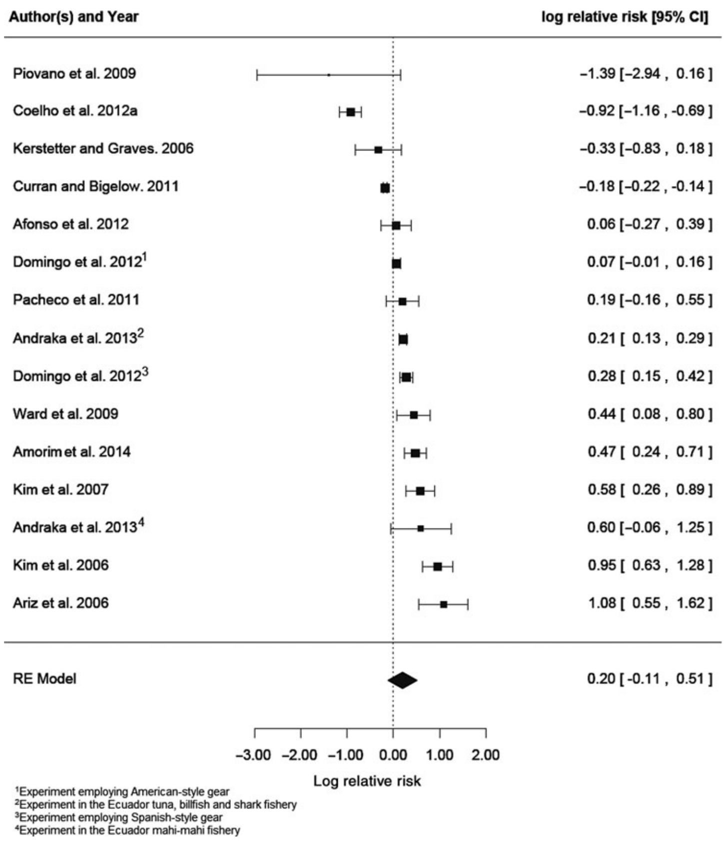


Figure 5 Random-effects forest plot of the inverse-precision weighted summary measure of log relative risk of ray capture on circle vs. J-shaped hooks for 15 studies. A log relative risk >0 indicates a higher relative risk of capture on circle hooks. The pooled or random-effects estimate (RE) of the relative risk metric is also shown. Plot ordered by effect size. Solid square = relative risk metric and size of the square reflects relative weighting. Horizontal bars = 95% confidence interval of the relative risk metric.

ver data; the other 28 studies were controlled or comparative experiments, discussed below (Table 1). Kim *et al.* (2007) and Gilman *et al.* (2012) were atypical in having relatively deep gear soaks. Information on soak depth was available for 18 of the studies; of these, only three (Gilman *et al.* 2012; Kim *et al.* 2006, 2007) reported hooks soaking predominantly or exclusively >100 m. Gilman *et al.* (2012) analysed data from a fishery where most hooks soak at depths >100 m, and Kim *et al.* (2007) reported that hooks soaked between 100 m and 300 m (see Gilman and Hall [2015] for a review of the effect of soak depth on catch and survival rates). The main caught shark species in Kim *et al.* (2007) (crocodile shark, *Pseudocarcharias kamoharai*) and Coelho *et al.* (2012a) (bigeye thresher, *Alopias superciliosus*) were atypical. Pelagic shark species found in either just oceanic habitats or both oceanic and coastal habitats other than blue shark were the main caught shark species for 9 of the 30 studies. Crocodile and bigeye thresher sharks were the main caught shark species for only two studies each: crocodile shark was also the main caught shark in Amorim *et al.* (2014) and bigeye thresher shark was also the main caught shark in Kim *et al.* (2006). Blue shark was the main caught shark species in 17 of the 30 studies; catch composition affects catch and survival rates and hooking position (Gilman and Hall 2015).

The meta-analysis undertaken here extended substantially upon two previous relevant meta-analyses (Godin *et al.* 2012; Favaro and Cote 2013) by: expanding the amalgamated studies; employing a mixed-effects meta-regression approach to account for informative covariates including accounting for non-linear functional form, also employing a hierarchical mixed-effects meta-regression approach to account for more complex random-effect structures, using a multi-model selection approach to screen models based on weight of evidence, conducting extensive assessment of publication bias, performing comprehensive assessment of outlier and influential study diagnostics, and conducting extensive assessment of data censoring and potential bias due to excluding studies.

Favaro and Cote (2013) conducted a meta-analysis of compiled controlled at-sea experiments of pelagic and demersal longline fisheries on the effect of nine gear designs, including hook shape, on elasmobranch catch rates. There was a 7.6% non-significant higher elasmobranch catch risk on circle hooks relative to catch risk on hooks with a non-circle design (Favaro and Cote 2013), consistent with the findings from the meta-analysis undertaken here (Figs 3 and 5).

Godin *et al.* (2012) conducted a meta-analysis on shark catch and haulback mortality rates in both pelagic and demersal longline fisheries. They found no significant difference between circle and J-shaped hooks on shark catch rates (all combined shark species, and individually for blue shark, shortfin mako shark, crocodile shark, Lamnidae [mackerel sharks], and Alopiidae [thresher sharks]) based on records combined from 18 studies. Godin *et al.* (2012) found that haulback mortality rates of combined shark species and individually for blue sharks were significantly lower on circle than J-shaped hooks based on records combined from eight studies, consistent with literature review findings of the current study (Fig. 1a). Godin *et al.* (2012) observed that six of the eight studies found that a larger proportion of sharks caught on circle hooks were hooked in the mouth or jaw vs. hooked internally, consistent with the literature review finding here for wider circle hooks vs. narrower J-shaped hooks (Fig. 1e). There were no studies identified in the literature review here that assessed the single-factor effect of hook shape on hooking position that did not also have simultaneous variability in hook width.

J hooks are shaped as the name implies, with the point positioned parallel to the hook shaft. Tuna hooks have a slightly curved shaft, and like J hooks, the point is not protected by the shaft, and as a result, tuna hooks have been categorized as a type of J-shaped hook (Serafy *et al.* 2009). Unlike J-shaped J and tuna hooks, which tend to result in deep hooking, circle hooks (circular or oval in shape, the point is turned perpendicularly back towards the shank, making the point less exposed relative to J-shaped J and tuna hooks) with little or no offset, when swallowed, tend not to initially hook an organism, but instead, as the organism pulls and turns away from the leader, this pulls on and rotates the circle hook and the hook slides over soft tissue as the eye of the hook exits the mouth, causing the hook's point to typically catch in the corner of the organism's mouth (Cooke and Suski 2004; Curran and Beverly 2012; Epperly *et al.* 2012; Clarke *et al.* 2014). Due to the prevalent hooking location, relative to using J-shaped hooks, using circle hooks might result in a higher incidence of catch being alive upon haulback and result in less trauma, increasing the probability of post-release survival of organisms released alive (Horodysky and Graves 2005; Kerstetter and Graves 2006; Carruthers *et al.* 2009; Serafy *et al.* 2009, 2012a; Gilman and Hall 2015).

Furthermore, hook shape can affect the difficulty of hook removal, which in turn can affect the probability of post-release survival. Due to their predominant hooking location, organisms captured on circle hooks that will be released require less handling time and therefore experience less stress, such as due to the duration of air exposure (Cooke and Suski 2004).

No studies were identified that assessed the effect of the single-factor hook shape on elasmobranch hooking position (Fig. 1a). Pelagic stingrays tend to be hooked in the mouth regardless of hook shape or narrowest width (e.g. Kerstetter and Graves 2006; Piovano *et al.* 2010; Pacheco *et al.* 2011).

Hook narrowest width

There were only four literature review findings on the single-factor effect of hook narrowest width, which showed variable effects on catch rates and haulback survival rates. For some species, hook narrowest width affects size selectivity between and within species. Larger hooks reduce the relative catchability of species and sizes of organisms with relatively small mouths and that tend to be caught by ingesting a baited hook, where the larger the hook, the lower the probability that these smaller mouthed organisms can fit it in their mouths (Piovano *et al.* 2009, 2010; Curran and Beverly 2012; Yokota *et al.* 2012; Gilman and

Hall 2015). Variability in the length frequency of a species that overlaps with a fishery's grounds, the difference between the width of the two hooks being compared, and the difference in the hook widths relative to the species' range of mouth sizes will determine the size of the effect on catch rates of two hooks of different widths.

Hook size may also affect hooking location. Larger hooks may be less likely to be ingested and instead be more likely to foul hook (Stokes *et al.* 2011). No significant findings, however, were identified on the effect of the single-factor hook narrowest width on hooking location of elasmobranchs (Fig. 1b) or other species (Gilman and Hall 2015). Hook width, however, has been observed to significantly affect haulback disposition of some pelagic fishes (Curran and Beverly 2012) (Fig. 1b). This effect may be due to hook width effect on size selectivity within and between species, where differences in survival probability have been observed by species and by size (and sex for species that exhibit sexual size dimorphism) within species (Campana *et al.* 2009; Musyl *et al.* 2011; Coelho *et al.* 2012b; Gallagher *et al.* 2014). And it might be due to the effect of hook width on hooking location (Cooke and Suski 2004; Epperly *et al.* 2012; Gilman *et al.* 2013b).

Bait type

Based on a small number of findings and species, the literature review findings suggest that using small fish species for bait instead of squid species increases both catch rates and deep hooking for some shark species. Bait effect on catch rates and hooking position had relatively consistent effects across shark species.

Different species and sizes of predatory fish have different prey preferences. These preferences are due to differences in prey chemical components, visual stimuli, and differences in the duration of retention of different bait species on hooks during the gear setting, soaking and retrieval operations. These are possible factors explaining differences in catch rates on fish vs. squid for bait between pelagic fish species and between sizes within species (Lokkeborg and Bjordal 1992; Broadhurst and Hazin 2001; Ward and Myers 2007; Yokota *et al.* 2009).

While no findings were identified for elasmobranchs (Fig. 1c), bait type has been observed to affect haulback disposition of some pelagic teleosts, probably due to the prevalent hooking position (Broadhurst and Hazin 2001; Epperly *et al.* 2012), but also possibly due to size selectivity by bait type. Bait type has been observed to affect size selectivity within some pelagic teleost and elasmobranch species (Amorim *et al.* 2014).

Leader material

Based on a small number of findings and species, and recognizing that the observed effect may have been confounded by other significant focal factor variables, findings from the literature review suggest that wire leaders resulted in higher catch rates and possibly lower haulback survival for most shark species susceptible to capture in pelagic longline fisheries. The literature review found relatively consistent effects across shark species of higher catch rates on wire than monofilament leaders. Given the small number of findings and species, the effect of leader material on haulback survival is unclear. There were no findings on hooking position by leader type or on leader material effects on ray species. A meta-analysis by Favaro and Cote (2013) did not find a significant effect on elasmobranch capture risk between monofilament nylon and wire leaders, based on findings from a single study by Ward *et al.* (2008).

Wire leaders are used in some longline fisheries to reduce the risk of having large tunas escape, including in fisheries that infrequently retain caught sharks. Durable leader material, however, including wire and multifilament leaders, may be used in some longline fisheries to increase shark catches (Gilman *et al.* 2008b).

Species with sharp teeth, including sharks and some teleosts such as snake mackerel (*Gempylus serpens*), can sever by biting through or abrading monofilament leaders and escape, but cannot sever more durable leader materials (Ward *et al.* 2008; Afonso *et al.* 2012). Species with serrated teeth, like tiger sharks (*Galeocerdo cuvier*), are more likely to be able to bite through nylon leaders than those with needle-like teeth, like bigeye threshers (Ward *et al.* 2008). Species that tend to thrash violently when hooked, such as longtailed (common) threshers (*A. vulpinus*) and blue marlins (*Makaira nigricans*), are more likely to abrade and sever a monofilament leader than those with relatively less energetic reactions to being caught, such as black marlins (Gilman *et al.* 2008b; Ward *et al.* 2008).

Furthermore, species with relatively good vision may have lower susceptibility to capture on branchlines with wire or multifilament leaders relative to monofilament leaders because they can more readily see wire and multifilament leaders and avoid preying on adjacent baited hooks (Ward *et al.* 2008; Berkeley and Campos 1988; Afonso *et al.* 2012; Gilman and Hall 2015). For some of these species, the relatively lower susceptibility to capture on wire leaders might be offset to a degree by a higher escapement rate on monofilament leaders (Ward *et al.* 2008).

For species of sharks with teeth that can sever monofilament line, and/or thrash violently when hooked, and that are deeply hooked, individuals caught on monofilament leaders may have a higher probability of being dead upon haulback relative to individuals caught on wire leaders (Afonso *et al.* 2012). This is because, while wire leaders tend to indiscriminately retain all deeply hooked sharks, for sharks caught on monofilament leaders, larger, stronger, more vigorous individuals may have a higher probability of escaping than smaller, weaker, seriously injured individuals. These individuals that do not escape from monofilament leaders may have low resistance to surviving the gear soak.

The difference between pre-catch mortality rates of sharks that escape from monofilament leaders, possibly with a hook and trailing line attached, and mortality rates of sharks caught on wire leaders is not well understood (Ward *et al.* 2008; Gilman *et al.* 2008b, 2013b, 2015; Clarke *et al.* 2014). The effect is probably species and size specific and will also vary by fishery and by vessel within a fishery. Soak duration, depth of capture, ambient conditions, length, sex, hooking location, handling and release methods employed, duration out of the water, physical conditions onboard such as air temperature, and tackle remaining attached upon release can all have significant effects on the probability of post-release survival (Davis 2002; Suuronen 2005; Benoît *et al.* 2013; Gilman *et al.* 2013b). For species/sizes/sexes that have a high haulback survival rate, in fisheries that do not retain sharks and employ handling and release methods that support post-release survival (e.g. Gilman 2014), use of wire leaders might result in lower fishing mortality relative to using monofilament leaders, where sharks that escape by biting through the leader might have a high pre-catch mortality rate due to retaining terminal tackle. However, in some fisheries, caught sharks are routinely killed, or poor handling or release practices are regularly used (e.g. fishers employ methods to recover terminal tackle that injure or kill the elasmobranch, such as body-gaffing, yanking the hook out, or killing caught sharks to reduce subsequent unwanted interactions) (Gilman *et al.* 2008b; Campana *et al.* 2009; Ward *et al.* 2008). In these latter fisheries, and for species/sizes/sexes that have low haulback survival, monofilament leaders in combination with hook and bait types that enable the shark to bite through the leader might result in lower fishing mortality.

For example, in fisheries where all live caught sharks are released alive, and best-practice handling and release practices are employed, if blue and common thresher shark survival rates after escaping by swallowing a hook and then biting through a monofilament leader are <76% and 30%, respectively, then, it might be a larger benefit to these species, in this fishery, to use wire leaders. Table 6 summarizes compiled estimates of elasmobranch haulback mortality rates. Few estimates of shark and ray post-release mortality were identified (6 records for blue sharks, 1 for common thresher sharks). These available estimates suggest that blue sharks have a low probability of post-release mortality (mean of 9.1% ± 5.3% 95% CI, Stevens *et al.* 2000; Weng *et al.* 2005; Moyes *et al.* 2006; Campana *et al.* 2009; Musyl *et al.* 2011), while the estimate for common threshers is a bit higher (26%, recreational fishery, Heberer *et al.* 2010). Based on this sparse number of haulback and post-release mortality rate estimates, roughly 76% (based on a mean of 15.9% dead at haulback [Table 6], and 9.1% of those released alive subsequently die) of blue sharks and 30% of common thresher sharks would survive capture and release. These estimates, however, do not account for indirect sources of fishing mortality, such as pre-catch losses, which have not been estimated for longline-elasmobranch interactions (Gilman *et al.* 2013b).

Wider circle hooks vs. narrower J-shaped hooks

The meta-analyses findings were consistent with the literature review findings on the effect of wider circle vs. narrower J-shaped hooks on shark catch rates. Overall, the literature review found a higher shark catch rate on wider circle than narrower J-shaped hooks, but with some variability between and within species. Findings on the effect of wider circle vs. narrower J-shaped hooks on haulback

Table 6 Mean elasmobranch haulback mortality rates (Beerkircher *et al.* 2002; Kerstetter and Graves 2006; Yokota *et al.* 2006; Kerstetter *et al.* 2007; Campana *et al.* 2009; Carruthers *et al.* 2009; Walsh *et al.* 2009; Curran and Bigelow 2011; Musyl *et al.* 2011; Afonso *et al.* 2011, 2012; Bromhead *et al.* 2012; Coelho *et al.* 2012a,b; Curran and Beverly 2012; Epperly *et al.* 2012; Serafy *et al.* 2012b; Amorim *et al.* 2014; Gallagher *et al.* 2014).

	% dead at haulback		
Family or species	Mean of means	±95% CI	*n* (number of findings)
Mobulidae	2.39	3.82	4
Pelagic stingray	15.06	14.52	16
Blue shark	15.91	5.22	27
Tiger shark	23.78	22.34	6
Crocodile shark	26.24	22.56	7
Porbeagle shark	27.99	4.31	4
Shortfin mako shark	33.41	14.58	11
Oceanic whitetip shark	35.21	15.50	9
Silky shark	46.62	13.08	11
Bigeye thresher shark	46.67	18.65	12
Dusky shark *Carcharhinus obscurus*	51.28	33.21	4
Scalloped hammerhead shark *Sphyrna lewini*	58.60	16.99	5
Night shark *Carcharhinus signatus*	81.02	11.23	5

survival rates and hooking position were relatively consistent across elasmobranch species of higher haulback survival rates on wider circle vs. narrower J-shaped hooks and lower proportion of deep hooking on wider circle hooks. Based on the findings from the literature review and the meta-analyses, for most shark species, hook shape may have a larger effect size than hook narrowest width (Fig. 1a,b,e).

While the meta-analysis found a higher but non-significant difference in relative risk of ray capture on circle than J-shaped hooks, where most studies compared wider circle with narrower J-shaped hooks, literature review findings suggest that catch rates of pelagic stingrays were lower on wider hooks (Fig. 1b), lower on wider circle vs. narrower J-shaped hooks (Fig. 1e), and higher on circle than J-shaped hooks of the same width (Fig. 1a). Based on these findings, it is unclear whether narrowest width or shape has a larger effect on pelagic stingray catch (Figs 1a,b,e and 5, Table 2). The effect of hook width is likely due to pelagic stingrays' relatively small-sized mouths, causing them to almost always get hooked in the mouth regardless of hook shape (Piovano *et al.* 2010; Curran and Bigelow 2011; Yokota *et al.* 2012). However, if two hooks of different narrowest widths were either both too large for stingrays to ingest, both were sufficiently narrow to enable ingestion, or if the two hooks had only small differences in width, then no significant effect on catch risk would be expected.

Wider circle hooks and fish bait vs. narrower J-shaped hooks and squid bait

It is unclear from the small sample size of compiled significant findings on the effect of wider circle hooks with fish bait vs. narrower J-shaped hooks with squid bait how this combination of longline gear affects shark catch rates. Combined findings suggest that there is a relatively consistent effect of hook shape and bait type on shark catch rates (Fig. 1a,c,e). It is unclear, however, what the catch rate effect size of bait type is relative to hook shape and narrowest width based on a comparison of findings from the records compiled for the literature review. No findings were identified for ray species. Also, no findings were identified on the effect of combinations of hook shape, hook width and bait type on hooking position or haulback survival rates for elasmobranchs (Fig. 1f) or other taxa when leader material was not a confounding factor.

Heterogeneity and variability in focal factor effects

A possible cause of the considerable unexplained heterogeneity between the studies that was not fully accounted for by either random effects or potentially informative covariates was the effect of pooling data across species, sizes and sex. This is due to species-, size- and sex-specific variability in the effect of hook shape on shark and ray catch rates (reviewed in Gilman and Hall [2015]). Variability in confounding effects from simultaneous differences in significant explanatory variables other than hook shape between the studies (Table 1, number of 19 potentially significant explanatory variables addressed by each study, and whether there was simultaneous variability in other focal factors) is another possible cause.

Literature review findings suggest that the single-factor hook shape effect on catch and haulback survival rates, bait species effect on catch rates and hooking position, leader material effect on catch rates, and wider circle vs. narrower J-shaped hook effect on catch and haulback survival rates and hooking position had relatively consistent effects across shark species. Wider hooks reduced catch and haulback mortality rates of pelagic stingrays. Hook narrowest width effect on catch and haulback survival rates, and wider circle hook with fish bait vs. narrower J-shaped hook with squid bait effect on catch rates were relatively variable across elasmobranch species, and in some cases were also variable for a single species. This observed variability may be due to species-, size- and sex-specific differences in resilience to stress (Table 6), mouth size and morphology (Piovano *et al.* 2010; Curran and Bigelow 2011; Pacheco *et al.* 2011; Yokota *et al.* 2012), prey preferences (Lokkeborg and Bjordal 1992; Broadhurst and Hazin 2001; Ward and Myers 2007; Yokota *et al.* 2009), teeth morphology and concomitant ability to sever monofilament leaders (Ward *et al.* 2008; Afonso *et al.* 2012), whether they thrash violently when hooked and likelihood of abrading the branchline (Gilman *et al.* 2008b; Ward *et al.* 2008), and visual acuity (Ward *et al.* 2008). The observed variability may also have been due to different gear designs and fishing methods employed in the different studies, and differences in lengths and sex ratios of shark species in each study (Gilman and Hall 2015). There was some evidence of variable effects of hook shape, interacting effect of hook shape and width, and bait type on blue shark catch rates (Fig. 1a,c,e), which may have been due to differences in age classes and sexes between studies included in the literature review (Gilman and Hall 2015). Given the variability in focal factor effects by shark species apparent in Fig. 1, which was largest for hook narrowest width effect on catch and haulback survival rates, and wider circle hook with fish bait vs. narrower J-shaped hook with squid bait effect on catch rates, pooling data for the numerous shark species for the meta-analyses may have contributed to the considerable unexplained heterogeneity between the included studies, and the wide estimates of error in individual study findings.

The observed considerable heterogeneity in the meta-analyses and variability in some focal factor category effects in the literature review might be explained by most of the compiled studies having not been designed to assess single focal factor effects and having addressed a small proportion of potentially significant explanatory variables (Table 1). Most studies employed designs that introduced simultaneous variability in two or more of the focal factors. A small proportion of other potentially significant explanatory variables were controlled or explicitly accounted for (Table 1). There was also high variability in sample sizes (both fishing effort and number of observed elasmobranchs). Studies with relatively small sample sizes may have had relatively low certainty in results from statistical analyses. Also, small sample sizes were probably the cause of the observed lack of significant effects in many of these studies (Freiman *et al.* 1978). There was also high variability in time-series lengths, regions, main market species caught (suggesting that different fishing methods and gear were used), gear soak depth, number of longline vessels, and light attractor use between the studies, which are all potentially significant explanatory factors (Gilman and Hall 2015).

There were, however, a few potentially significant explanatory variables that were somewhat consistent across the studies. The main ray species caught was pelagic stingray (74 and 100% of the literature review records and ray meta-analysis studies with information on the main caught ray species respectively), the main shark species caught was blue shark (69 and 61% of the literature review records and shark meta-regression studies with information on main caught shark species respectively), time series spanning multiple seasons (89 and 90% of the literature review records and combined shark and ray meta-analysis studies with information on the seasonal distribution of the time series respectively), and gear soak occurring at night (70 and 67% of the literature review records and combined shark and ray meta-analysis studies with information on the time of day of gear soak respectively).

Synergistic effects

There may be synergistic effects of hook design and width, leader material and bait type on shark catch rates (Afonso *et al.* 2012; Epperly *et al.* 2012; Hannan *et al.* 2013; Clarke *et al.* 2014). Literature review findings suggest that interacting effects of certain gear elements may be important. Wider circle hooks had a significantly lower proportion of deeply hooked sharks than narrower J-shaped hooks for all six shark species for which findings were compiled (Fig. 1e). This is consistent with observations that circle hooks tend to catch organisms in the mouth and jaw, while J and tuna hooks tend to result in deep hookings, hooking organisms internally in the in the oesophagus and gut (Epperly *et al.* 2012; Godin *et al.* 2012; Serafy *et al.* 2012a), and that the wider the hook, the lower the probability of ingesting the hook (Stokes *et al.* 2011). The literature review findings also indicate that fish bait results in a significantly higher proportion of deeply hooked sharks than squid bait (Fig. 1c). As a result, observations of lower shark catch rates on J-shaped hooks relative to circle hooks (Fig. 1a), and lower shark catch rates on fish bait vs. on squid bait, if monofilament leaders were used, might have been due to the differences in hooking position between the hook shape and bait types. This is because mouth- and jaw-hooked sharks are less likely to be able to bite through a monofilament leader (their teeth cannot reach the monofilament leader), while deeply hooked sharks have a higher likelihood of biting through monofilament leaders and hence a lower shark catch rate. One observation supports this hypothesis: Afonso *et al.* (2012) observed a significantly higher blue shark catch rate on wire leaders than on monofilament nylon leaders on J hooks, but did not observe a significant effect of leader material on blue shark catch rate on circle hooks, perhaps because of the effect of hook shape on hooking position and the interacting effect with leader material.

There may also be an interacting effect between circle hook narrowest width and wire leader length. When wire leaders are used, there might be a higher probability that hooked organisms can sever monofilament branchlines above the wire leader and escape when small circle hooks are used: the narrower the circle hook, the higher likelihood that it will be swallowed, which enables biting through the branchline above the wire leader, depending on the leader length and size of the fish, before the hook slides back up to the mouth (pers. comm., John Peschon, National Marine Fisheries Service, 23 May 2015).

There are probably numerous additional synergistic effects between combinations of fishing gear designs, fishing methods and environmental variables on pelagic longline catch rates and haulback disposition. For example, the time of day of fishing operations in combination with gear soak depth will affect catch rates of species that exhibit diel vertical migration (Gilman and Hall 2015). And, for example, soak duration might have an interacting effect with leader material: The longer the gear soak, higher escapement rates are likely when nylon monofilament leaders are used for species that can sever the monofilament leaders, as they will have a longer time to abrade or bite through the leaders, while this effect of soak time would be smaller for vessels using wire and multifilament leaders (Ward *et al.* 2008).

Study category

The effect of the moderator study category in the shark meta-regressions may not have been robust due to the influence of one study, Gilman *et al.* (2007a). This moderator was included in the meta-analysis because of potentially large differences in certainty of results between experiments and studies based on analysis of observer data. Because analyses of observer data do not experimentally manipulate specific variables and control for others, estimated effects of individual factors are always confounded by innumerable other variables (Gilman *et al.* 2008a). Thus, in general, findings from experimental studies, when properly designed, including controlling for all significant explanatory variables and with sufficient sample sizes, are of higher certainty than studies analysing observer data. However, while controlled and comparative experiments typically support more definitive conclusions on causality, analyses using observer data typically have much larger sample sizes and longer time series.

Time of day of gear soak

The shark meta-regression model finding of a significantly different relative risk of shark catch rates on circle than J-shaped hooks during different time of day of gear soak may reflect the effect of the variability by species and size class in local abundance, depth distribution and diving and foraging behaviour by time of day on susceptibility to capture (e.g. Bigelow *et al.* 2002; Ward *et al.* 2004; Musyl *et al.* 2011; Gilman *et al.* 2008a, 2012). Given this variability in spatial distribution by time of day in combination with differences in susceptibility to capture by hook shape by species, size and sex (Gilman and Hall 2015), the relative risk of capture on circle vs. J-shaped hooks also is expected to vary by time of day. Vertical distribution varies temporally for some species due to diel vertical migration cycles, time of day of active foraging, and variability in diving depth by time of day (Schaefer and Fuller 2002; Nakano *et al.* 1997; Nakano *et al.* 2003; Weng and Block 2004; Ward and Myers 2005b; Beverly *et al.* 2009; Musyl *et al.* 2011). See Gilman and Hall (2015) for a discussion of the interacting effect of the time of day of the gear soak with gear depth and spatial distribution of effort. The 'unknown' category for soak time was probably a mix of day, night and overlapping day and night soak times, resulting in a relative risk range falling in between the day and night soaks and the day-only and night-only soaks.

This finding does not indicate whether shark catch rates on circle and J-shaped hooks will be higher or lower at different times of day when the gear soaks. Instead, the finding refers to the relative risk of shark capture on circle vs. J-shaped hooks by time of day of gear soak. For example, if a fishery using only circle hooks has gear soak only during the daytime, instead of partially during day and night, this would not necessarily minimize the circle hook shark catch rate, but instead would reduce the circle hook catch rate relative to a J hook catch rate. This is because, in some fisheries, shark catch rates on both hook shapes might be highest during daytime gear soaks.

Publication bias

Publication bias is an important issue with meta-analyses. Studies with negative or insignificant results are less likely to be published than those with positive and significant findings. This causes meta-analyses' findings to over-estimate effect sizes (Rosenthal 1979; Rothstein *et al.* 2006). However, there was no evidence of any form of publication bias in either the shark or ray catch rate meta-analyses. In the various meta-analysis models, summarized in Tables 4 and 5, neither publication year nor publication impact factor was a moderator that contributed to any of the best-fitting models.

Journal impact factor, a measure of the average number of citations to articles published in a journal, is a commonly used index for comparing relative journal quality within a discipline (Seglen 1997; Bornmann *et al.* 2012). Journal impact factor provides information on the relative quality of articles published in an individual journal on average. The quality of an individual article, however, may be poorly correlated with the relative quality of the journal in which it is published (Seglen 1997; Bornmann *et al.* 2012).

Conclusions and research needs

Using circle instead of J-shaped hooks and fish instead of squid for bait, while benefitting sea turtles, odontocetes and possibly seabirds (Clarke *et al.* 2014; Gilman and Hall 2015), may increase the catch and injury of some elasmobranchs. Fishery-specific assessments to determine relative risks are therefore warranted when prescribing hook shape and bait. Both the meta-regressions and literature review assessments found higher shark catch rates on circle than J-shaped hooks of the same or narrower width. Literature review findings suggest that circle hooks increased elasmobranch catch, but reduced haulback mortality relative to J-shaped hooks of the same width, and wider circle vs. narrower J-shaped hooks increased shark catch, but reduced haulback mortality and deep hooking. Using fish vs. squid for bait increased shark catch and deep hooking.

Most studies observed higher catch and haulback mortality on wire vs. monofilament leaders for most shark species. However, leader material effect on total shark fishing mortality is unclear. The effect of recent bans on wire leaders on shark fishing mortality rates requires improved understanding of gear factors that affect hooking position, and estimates of each component of fishing mortality (pre-catch, at-vessel, post-release, Gilman *et al.* [2013b]) for various combinations of leader, hook and bait types. Research is also needed to augment the understanding of the effect of leader material on other vulnerable taxa caught in longline fisheries. Observations of lower catch rates of some teleosts on wire vs. monofilament leaders (Gilman and Hall 2015) may be due to higher visibility of the wire that results in lower rates of predation of hooks adjacent to wire vs. monofilament lines (Ward *et al.* 2008). A similar mechanism could exist for some species of sea turtles and other taxonomic groups. Furthermore, due to safety concerns, fishers are less likely to attach branchline weights close to hooks when the leader is not made of a durable material. If a branchline breaks during hauling, which frequently occurs when sharks are caught and bite off the terminal tackle, or if the hooks pulls free from a caught fish with the line under high tension (the fish 'throws' the hook), the weight can fly at the vessel at high velocity (Gilman *et al.* 2008b; Walsh *et al.* 2009). As a result, banning wire leaders to benefit sharks could exacerbate seabird catch rates by altering the location of branchline weights, causing a decrease in baited hook sink rates (Gilman *et al.* 2005, 2008b; Gilman 2011; Graham *et al.* 2013). New branchline weight designs, however, might reduce the safety risk of placing weights close to the hook when using monofilament leaders (Sullivan *et al.* 2012).

Therefore, monofilament leaders could be one solution to elasmobranch by-catch if it is determined that there are lower shark mortality rates for escapees than for those caught on wire and other durable leader materials, and no conflicts with other vulnerable taxa. Wider hooks may also benefit elasmobranch species with relatively small mouths, documented to also reduce catch rates of hard-shelled turtles, some teleosts, and possibly seabirds (Clarke *et al.* 2014; Gilman and Hall 2015;). Other methods to reduce shark and ray catch and injury in pelagic longline fisheries that do not conflict with by-catch mitigation of other taxonomic groups of conservation concern, for most elasmobranchs susceptible to pelagic longline capture, include: deeper setting, no use of 'shark lines', ban on shark and ray retention (including retaining fins and discarding the carcass), and employment of best-practice handling and release methods (Gilman 2011; Clarke *et al.* 2014; Gilman and Hall 2015; Gilman *et al.* 2015).

Interacting effects of hook, bait and leader affect shark catch rates: hook shape, hook width and bait type affect hooking position and the concomitant ability of a shark to sever monofilament leaders. It is possible that the hook and bait type effect on shark catch rates observed here may be smaller or not occur in longline fisheries that use wire leaders. There is, however, evidence of an effect of hook shape, hook width and bait type on shark catch and survival rates in fisheries that used only wire leaders (Mejuto *et al.* 2008; Sales *et al.* 2010; Andraka *et al.* 2013). There is limited understanding of these synergistic effects, where effects on catch and survival rates may be species and size specific.

There is a need for continued investment in research studies that are designed to assess single-factor effects of fishing gear elements on catch and haulback survival rates and hooking position of market and vulnerable species in pelagic longline fisheries. Most studies had simultaneous variability in two or more focal factors. For the few records where there was variability in only one focal factor, the estimated effect of the individual focal factor might still have been confounded by other explanatory variables with large effect sizes other than the focal factors.

There are gaps by region, elasmobranch species, and focal factor in research on the effects of the focal factors on elasmobranch catch and haulback mortality rates and hooking position. Most compiled studies were from the Atlantic and Pacific Oceans, most studies were conducted in fisheries from the Americas, with very small sample sizes from the Indian Ocean and Mediterranean Sea. Because the distribution of fishing effort over broad meso- and basin scales significantly affects elasmobranch longline catch rates and haulback disposition (Gilman and Hall 2015), it is a research priority to conduct studies on the effect of longline terminal tackle in these under-represented regions.

Studies compiled for the two research components were relatively recent, almost all were published in the last decade, and had relatively short time-series lengths. As more studies are conducted, the longer time series of records compiled for future meta-analyses are more likely to span the temporal variability in dynamic environmental variables that significantly affect elasmobranch catchability and disposition (Gilman and Hall 2015). On the other hand, longer time series will more likely be affected by more confounding variables, introduced by changes in fishing gear and practices.

Most study findings were for blue sharks and pelagic stingrays, which were the main caught shark and ray species, respectively, for samples compiled for both the meta-analysis and literature review. For example, of findings of a significant effect on a shark species of a focal factor category compiled for the literature review, 44% (38 of 86) were for blue sharks. All 14 ray significant findings were for pelagic stingrays. Given evidence reviewed here of elasmobranch species-specific effects of longline gear factors on catch and survival, larger sample sizes for other species are needed.

There were insufficient sample sizes to conduct a meta-analysis to assess the effects of three of the four focal gear factors (hook narrowest width, leader material, bait type) on catch rates, or to assess the effects of any of the four focal factors on hooking position or haulback survival rates for sharks or rays, highlighting additional research priorities. Most compiled studies were on the effects of wider circle hooks vs. narrower J-shaped hooks, with relatively small sample sizes for the effects of each of the other focal factor categories. Thus, continued support for research on effects of hook narrowest width, leader material and bait type on catch and survival rates is needed.

No relevant captive survival studies were identified for inclusion in either the meta-analysis or literature review. Captive elasmobranchs could be used for an experiment to compare differences in catch rates, haulback disposition and hooking location for the focal factors and other potentially significant explanatory variables. Including control animals in experiments using captive organisms provides a basis for separating effects from a gear design factor from effects caused by stressors associated with being held in captivity (Suuronen 2005; Neilson *et al.* 2012; Swimmer and Gilman 2012). However, many of the shark species commonly caught in pelagic longline fisheries have not survived long in captivity (Dehart 2004).

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