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Catch rate and at-vessel mortality of circle hooks versus J-hooks in pelagic longline fisheries: A global meta-analysis

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Abstract

We conducted a meta-analysis of literature reporting on the use of circle hooks and J-hooks in pelagic longline fisheries. Our study included more data than previous meta-analyses of the effects of hook type, due to both a larger number of relevant studies available in recent years and a more general modelling approach. Data from 42 empirical studies were analysed using a random effects model to compare the effects of circle hooks and J-hooks on catch rate (43 species) and at-vessel mortality (31 species) of target and bycatch species. Catch rates with circle hooks were greater for 11 species, including four tuna species, six shark species and one Istiophorid billfish. Catch rates on circle hooks were lower for seven species, including two Istiophorid billfishes and two species of sea turtle. At-vessel mortality was significantly lower with circle hooks in 12 species, including three tuna species, three Istiophorid billfishes, swordfish (*Xiphias gladius*) and three shark species. No species had significantly greater at-vessel mortality when captured with a circle hook rather than a J-hook. While our general approach increased model variability compared to more detailed studies, results were consistent with trends identified in previous studies that compared the catch rates and at-vessel mortality (between hook types) for a number of species. Our results suggest that circle hooks can be a promising tool to reduce mortality of some bycatch species in pelagic longline fisheries, although the effects depend on the species and the metric (catch rate or at-vessel mortality), emphasizing the need for fishery-specific data in conservation and management decisions.

KEYWORDS
at-vessel mortality, bycatch, catch rate, circle hooks, meta-analysis, pelagic longline

1 | INTRODUCTION

Bycatch mortality in pelagic longline fisheries is a major factor contributing to the decline of several marine species. Such population declines have prompted fishery managers to implement regulations aimed at mitigating bycatch mortality, including both target species that are released (regulatory discards) and non-target species that are captured. Pelagic longline gear is frequently used to target swordfish (*Xiphias gladius*, Xiphiidae), tunas, dolphinfish (*Coryphaena hippurus*, Coryphaenidae) and wahoo (*Acanthocybium solandri*, Scombridae), and some fisheries may also target sharks (Graves, Horodysky, & Kerstetter, 2012; National Marine Fisheries Service (NMFS) (2014); however, many non-target species are also captured and subsequently discarded for regulatory or economic reasons. Species that are considered bycatch vary by fishery; however, several species of conservation concern are among those commonly discarded by longline fisheries, including istiophorid billfishes, sharks, sea turtles, Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae), and occasionally, marine mammals and seabirds (NMFS, 2014).

The use of circle hooks may affect the mortality rate of target and bycatch species in pelagic longline fisheries due to the influence of hook type on catch rates, at-vessel mortality (mortality during capture) and post-release mortality (mortality occurring after release from gear). Unlike traditional J-hooks, the point of a circle hook is oriented perpendicular to the shank, forming a circular shape (Serafy, Cooke, et al., 2012). The rounded shape allows a circle hook to slide over soft tissue in the mouth and oesophagus and rotate as the hook exits the mouth of a fish so that the hook sets in the jaw (Kerstetter & Graves, 2006a). Compared to J-hooks, circle hooks have been associated with lower rates of deep-hooking and foul-hooking, leading to improved condition at haulback and increased survival of released animals (Cooke & Suski, 2004; Godin, Carlson, & Burgener, 2012; Graves et al., 2012; Horodysky & Graves, 2005; Serafy, Kerstetter, & Rice, 2009). Circle hooks (vs. J-hooks) have been shown to decrease catch rates in billfish (Serafy et al., 2009) and increase catch rates of target species such as tunas (Diaz, 2008; Falterman & Graves, 2002; Graves et al., 2012; Kerstetter & Graves, 2006a; Pacheco et al., 2011), leading to both economic and conservation benefits in certain fisheries.

The benefits of circle hooks have led to the recommended use of circle hooks instead of J-hooks to reduce mortality of bycatch species in pelagic longline fisheries (Carruthers, Schneider, & Neilson, 2009; Horodysky & Graves, 2005; Serafy, Cooke, et al., 2012; Walter, Orbesen, Liese, & Serafy, 2012; Yokota, Takahisa, Minami, & Kiyota, 2012). While the conservation benefits of circle hooks have been recognized by Regional Fisheries Management Organizations (RFMOs), variable results across studies and variation in both target species and fishing practices among international fisheries have prevented enactment of more widespread regulations (Graves et al., 2012). Currently, the Western Central Pacific Fisheries Commission (WCPFC) requires the use of circle hooks on longline vessels using shallow sets to catch swordfish, unless the nation has an alternate mitigation strategy (WCPFC CMM 2008-03). Western Central Pacific Fisheries Commission is the only RFMO requiring the use of circle hooks in any part of the pelagic longline fishery. In the Atlantic, the International Commission for the Conservation of Atlantic Tunas (ICCAT) Standing Committee on Research and Statistics (SCRS) has acknowledged the conservation benefits of circle hooks to sea turtles, blue marlin (*Makaira nigricans*, Istiophoridae) and white marlin (*Kajikia albida*, Istiophoridae; ICCAT SCRS, 2016). However, ICCAT has not yet required the use of circle hooks by participating nations. Additionally, the Western Central Atlantic Fishery Commission (a United Nations Food and Agriculture Organization Regional Fisheries Advisory Commission) and partners have developed a draft Caribbean Billfish Management and Conservation Plan that recommends the use of circle hooks in longline and hook-and-line commercial fisheries (D. R. Blankinship, personal communication).

Individual countries may also enact circle hook regulations independently of a RFMO. In the Atlantic, the U.S. and Canadian pelagic longline fleets now require circle hooks, measures that were initially adopted in the USA primarily to reduce impacts to sea turtles (Wilson & Diaz, 2012) and in Canada as a bycatch reduction initiative (Andrushchenko, Hank, Whelan, Neilson, & Atkinson, 2014). Mexico is also known to use circle hooks in their pelagic longline fisheries. However, even in countries without circle hook requirements, cases have been observed in which fishers switch to circle hooks after seeing improved catch and condition of target species in their own fleet (Graves et al., 2012). Potential benefits of expanding the use of circle hooks to a greater number of large-scale commercial fisheries and artisanal fleets include increased catch of some target species and reduced post-release mortality rates of both discarded bycatch species and regulatory discards of target species.

Previous meta-analyses have examined either a single species or pooled data for species groups, for example in sharks (Godin et al., 2012) and billfishes (Serafy et al., 2009), and consequently have not assessed effects across taxa (Gilman, Chaloupka, Swimmer, & Piovano, 2016). Meta-analyses are used to synthesize results of multiple studies, providing greater power than any other study (Cohn & Becker, 2003), and to generate inference from a set of experiments that may otherwise have disparate conclusions (Gurevitch & Hedges, 1999). Our study uses a meta-analysis to quantify the relative effects of using circle hooks compared to J-hooks for target and bycatch species in pelagic longline fisheries from both the Atlantic and Pacific Oceans. Previous meta-analyses have found lower at-vessel mortality and hooking injury using circle hooks (vs. J-hooks) in sharks and billfishes (Cooke & Suski, 2004; Serafy et al., 2009). Conclusions about catch rates vary by taxa. Most studies on sharks have shown increases in catch rates (Cohn & Becker, 2003; Favaro & Côté, 2013; Gilman et al., 2016) on circle hooks, while Serafy et al. (2009) found no change in catch rate for billfishes.

Our study differs from previous meta-analyses in that we evaluate a greater number of animals using species-specific models. Ultimately, this information could be combined with fishery-specific fishing characteristics and catch and effort data to estimate conservation or management benefits of programmes encouraging the use of circle hooks instead of J-hooks. We were able to quantify the magnitude and direction of changes in catch rate and at-vessel mortality in species using relative risk (RR) as the measure of effect size.

2 | METHODS

We compiled information from studies and experiments that examined circle and J-hook catch in pelagic longline fisheries, including both Atlantic and Pacific fisheries. Published literature, technical reports and unpublished data relevant to our search were identified via Google Scholar searches, using the following keywords: circle hook, pelagic longline and pelagic longline bycatch. Initial references were collected from the *International Symposium on Circle Hooks* held in Coral Gables, Florida from 4 May to 6 May 2011 (Serafy, Cooke, et al., 2012). Collected literature was reviewed for additional references fitting the search criteria. Inclusion in our analysis required that studies used pelagic longlines, reported species-specific data for both circle and J-hooks using the same experimental design, and, at a minimum, presented data on catch numbers or catch rates. For redundant data sets, we used the more recent data source. We use the term “reference” to refer to a document; “experiment” to refer to a unique data set considered in our analysis; and “record” to refer to one comparison between circle and J-hooks for a species within an experiment. References used were collected before October 2014.

2.1 | Data collection and screening

Data collected from each reference included species name, hook type, number of hooks fished, total catch, catch rate and at-vessel mortality (e.g. number of fish dead at haulback). All records were classified as “circle” or “J” hooks. Following Kim, Moon, Boggs, Koh, and Hae An (2006) and Serafy et al. (2009) circle hooks were categorized as a type of J-hook because the point is not “blocked” by the hook shaft when the line becomes taught.

Although hook specifications were recorded when available, even standard hook parameters differ between hook type and manufacturers. Species names were standardized to reflect the current taxonomic names based on the Integrated Taxonomic Information System (ITIS, 2015).

Some values that were required, but not directly reported, were derived where possible. For example, the number of fish caught was often derived from catch rates and effort reported in the reference. Each unique experiment was assigned an identification number (ID). Experiments were considered unique if they differed with respect to attributes such as time (year of study or season), location, gear (e.g. hook size), vessel size or fleet. Results from more than one experiment could be presented in a single reference. Most references included only one or two experiment IDs, although one reference had seven experiment IDs (Andraka et al., 2013) because results were reported for three countries, two target species sets and different hook comparisons. Each experiment in our data set was treated as independent.

The National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center Pelagic Observer Program (POP) data set from 1992 to 2011 was included as a single experiment in our analysis of at-vessel mortality rates. POP data were parsed into two time periods reflecting the U.S. Atlantic pelagic longline fishery before and after implementation of the 2004 circle hook regulations (i.e. 1992–2003 and 2005–2011) and 2004 data were excluded to remove the effect of changes that occurred during the calendar year. Species data from the POP were included in the analysis if the species was already included in our data set from other references. The POP data set variable “boarding status” was used to designate individual fish as dead or alive on haulback (NMFS, 2015). Serafy, Orbesen, Snodgrass, Beerkircher, and Walter (2012) also used POP data to examine the effectiveness of circle hooks; however, their data were selected based on criteria specific to their analysis and were not appropriate for our use. Similarly, we were unable to use data directly from the Epperly, Watson, Foster, and Shah (2012) and Foster, Epperly, Shah, and Watson (2012) studies and were provided raw data by the authors. Our compiled data set is available in Appendix S1 and includes records of counts (catch, at-vessel mortality and hooks fished) for all studies, including those from sources not readily available, such as the POP data set, Epperly et al. (2012) and Foster et al. (2012). Data from the POP data set are also provided in Appendix S2 and allow for replication of our analysis.

2.2 | Meta-analysis

Using the data collected, we constructed a suite of meta-analysis models to evaluate differences in catch rate and at-vessel mortality for fish and sea turtles caught on circle and J-hooks and to examine within- and among-experiment variation. Our analysis follows methods used by Godin et al. (2012), but is specific to the pelagic longline fishery, and uses relative risk (RR) rather than an odds ratio. We selected RR as an effect size measure because of its straightforward interpretation. The difference between the calculated RR and a value of 1.0 represents the mean per cent change associated with the experimental treatment, such that an RR < 1.0 indicates lower values for circle hooks compared to J-hooks. The RR is equal to:

$$RR = \frac{a_i / n_i^1}{c_i / n_i^2}$$

where for the ith experiment, a_i is the number of animals caught on experimental hook (circle hook), n_i^1 is the number of experimental hooks fished, c_i is the number of animals caught on control hooks (J-hooks), and n_i^2 is the number of control hooks fished for the analysis of catch rate. For the at-vessel mortality analysis, a_i is the number of animals dead at haulback on circle hooks, n_i^1 is the number of animals caught on circle hooks, c_i is the number of animals dead at haulback on J-hooks, and n_i^2 is the number of animals caught on J-hooks. The RR value is log-transformed to normalize the distribution of effect sizes around zero and to meet the assumption of normality for the analysis.

Catch rates and at-vessel mortality for circle and J-hooks were estimated using the *metafor* package (Viechtbauer, 2010) in R 3.11 (R Core Team, 2014) for each species. We computed a summary effect size for all taxa that had at least two experiment IDs, including scenarios in which all experiments came from a single citation. A two-sided Wald-type Z test was used to test for differences between effects mean and zero. Effect sizes were estimated using a random effects model, allowing us to account for heterogeneity among experiments. Heterogeneity was expected due to the many explicit and implicit differences in study designs included in our analysis (e.g. hook size, offset and manufacturer, capture location, fishery studied, time of fishing and target species). Although we collected data on other variables, such as hook size, offset, bait type, target species and geographic location, we did not include these as fixed effects in our model because they were not reported consistently across studies and would have resulted in a reduction in the data available to test our primary hypotheses.

Compared to fixed effects models, the random effects approach is generally considered conservative (Borenstein, Hedges, Higgins, & Rothstein, 2009) and applicable to conditions and locations outside

TABLE 1 Results of the meta-analysis on catch rates showing the summary effect size (relative risk, RR) and 95% confidence interval (CI)

	#exp.	RR	CI	I^2	*p*	References	Status
Aulopiformes							
Longnose lancetfish	8	0.96	0.74–1.25	71%	.790	Coelho et al. (2012), Curran & Bigelow (2011), Kim, An, Moon, & Hwang (2007), Kim et al. (2006), Promjinda, Siriraksophon, Darumas , & Chaidee (2008), Ward et al. (2009)	LC
Carcharhiniformes							
Silky shark	9	1.4	1.18–1.67	49%	**<.001**	Afonso et al. (2011), Andraka et al. (2013), Pacheco et al. (2011), Promjinda et al. (2008), Ward et al. (2009), Yokota et al. (2006)	NT
Oceanic whitetip shark	6	1.4	0.85–2.32	0%	.190	(Afonso et al. (2011), Kim et al. (2006, 2007), Pacheco et al. (2011), Ward et al. (2009), Yokota et al. (2006)	VU
Night shark	2	1.87	0.75–4.66	72%	.180	Afonso et al. (2011), Domingo et al. (2012)	VU
Tiger shark	4	0.87	0.12–6.4	63%	.890	Afonso et al. (2011), Coelho et al. (2012), Promjinda et al. (2008), Ward et al. (2009)	NT
Blue shark	24	1.46	1.18–1.8	99%	**<.001**	Afonso et al. (2011), Andraka et al. (2013), Bolten & Bjorndal (2005), Cambiè, Muiño, Freire, & Mingozzi (2012), Curran & Bigelow (2011), Domingo et al. (2012), Foster et al. (2012), Huang, Swimmer, Bigelow, Gutierrez, & Foster (2016), Kerstetter & Graves (2006a); Kim et al. (2006, 2007), Largacha et al. (2005), Mejuto, Garcia- Cortés, & Ramos-Cartelle (2008), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009), Yokota et al. (2006)	NT
Scalloped hammerhead	7	0.85	0.57–1.28	0%	.440	Afonso et al. (2011), Domingo et al. (2012), Kim et al. (2006, 2007), Pacheco et al. (2011), Sales et al. (2010)	EN
Smooth hammerhead	2	0.25	0.03–2.31	0%	.220	Kim et al. (2006, 2007)	VU
Lamniformes							
Pelagic thresher	6	0.6	0.25–1.42	26%	.250	Andraka et al. (2013), Domingo et al. (2012), Promjinda et al. (2008), Yokota et al. (2006)	VU
Bigeye thresher	10	1.5	0.97–2.31	84%	.070	Coelho et al. (2012), Curran & Bigelow (2011), Kim et al. (2006, 2007), Promjinda et al. (2008), Ward et al. (2009), Yokota et al. (2006)	VU
Shortfin mako	12	1.71	1.57–1.86	0%	**<0.001**	Afonso et al. (2011), Andraka et al. (2013), Domingo et al. (2012), Foster et al. (2012), Kim et al. (2006), Mejuto et al. (2008), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009), Yokota et al. (2006)	VU
Salmon shark	3	2.04	1.05–3.96	16%	**.036**	Kim et al. (2006, 2007), Yokota et al. (2006)	LC
Porbeagle shark	3	2.08	1.84–2.34	0%	**<.001**	Domingo et al. (2012), Foster et al. (2012)	VU
Crocodile shark	7	3.46	1.81–6.63	88%	**2e-04**	(Coelho et al. (2012), Kim et al. (2006, 2007), Pacheco et al. (2011), Ward et al. (2009)	NT
Lampridiformes							
Opah	4	1.18	0.68–2.02	87%	.560	Curran & Bigelow (2011), Kim et al. (2007), Ward et al. (2009)	LC
Myliobatiformes							
Pelagic stingray	15	0.64	0.36–1.13	87%	.120	Andraka et al. (2013), Cambiè et al. (2012), Coelho et al. (2012), Curran & Bigelow (2011), Domingo et al. (2012), Kerstetter & Graves (2006a), Kim et al. (2006, 2007), Pacheco et al. (2011), Promjinda et al. (2008), Ward et al. (2009)	LC
Percoidei							
Atlantic pomfret	2	3.11	0.86–11.22	90%	.084	Kim et al. (2006, 2007)	LC
Sickle pomfret	2	0.83	0.71–0.97	68%	**.022**	Curran & Bigelow (2011)	NE
Dolphinfish	21	0.84	0.74–0.97	95%	**.013**	Andraka et al. (2013), Cambiè et al. (2012), Curran & Bigelow (2011), Domingo et al. (2012), Kerstetter & Graves (2006a), Kim et al. (2006, 2007), Largacha et al. (2005), Pacheco et al. (2011), Promjinda et al. (2008), Sales et al. (2010), Ward et al. (2009)	LC
Great barracuda	3	1.35	0.25–7.18	0%	.730	Kim et al. (2007), Promjinda et al. (2008), Ward et al. (2009)	LC

(Continues)

TABLE 1 (Continued)

	#exp.	RR	CI	I^2	*p*	References	Status
Scombroidei							
Snake mackerel	4	0.34	0.31–0.37	0%	**<.001**	Curran & Bigelow (2011), Promjinda et al. (2008), Ward et al. (2009)	LC
Escolar	11	1.31	0.94–1.82	82%	.110	Andraka et al. (2013), Curran & Bigelow (2011), Domingo et al. (2012), Kerstetter & Graves (2006a), Kim et al. (2006, 2007), Pacheco et al. (2011), Promjinda et al. (2008), Ward et al. (2009)	LC
Oilfish	6	0.76	0.49–1.18	0%	.220	Cambiè et al. (2012), Domingo et al. (2012), Kim et al. (2006, 2007), Largacha et al. (2005)	LC
Wahoo	9	1.08	0.69–1.69	73%	.730	Andraka et al. (2013), Curran & Bigelow (2011), Domingo et al. (2012), Kim et al. (2006, 2007), Pacheco et al. (2011), Ward et al. (2009)	LC
Skipjack tuna	7	1.08	0.69–1.69	57%	.730	(Andraka et al. (2013), Curran & Bigelow (2011), Kim et al. (2006, 2007), Ward et al. (2009)	LC
Albacore	11	1.46	1.01–2.1	93%	**.044**	(Curran & Bigelow (2011), Domingo et al. (2012), Foster et al. (2012), Huang et al. (2016), Kim et al. (2006, 2007), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009)	NT
Yellowfin tuna	16	1.32	1.07–1.62	87%	**.010**	Andraka et al. (2013), Curran & Bigelow (2011), Domingo et al. (2012), Huang et al. (2016), Kim et al. (2006, 2007), Largacha et al. (2005), Pacheco et al. (2011), Promjinda et al. (2008), Sales et al. (2010), Ward et al. (2009)	NT
Bigeye tuna	14	1.38	1.13–1.68	92%	**.002**	Andraka et al. (2013), Curran & Bigelow (2011), Domingo et al. (2012), Foster et al. (2012), Huang et al. (2016), Kim et al. (2006, 2007), Largacha et al. (2005), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009))	VU
Bluefin tuna	2	1.87	1.3–2.7	27%	**<.001**	(Cambiè et al. (2012), Foster et al. (2012)	EN
Squaliformes							
Velvet dogfish	2	3.48	0.41–29.32	75%	.250	Kim et al. (2006, 2007)	NE
Testudines							
Loggerhead sea turtle	16	0.58	0.36–0.92	91%	**.021**	Andraka et al. (2013), Boggs & Swimmer (2007), Bolten & Bjorndal (2005), Cambiè et al. (2012), Domingo et al. (2012), Foster et al. (2012), Gilman et al. (2007), Huang et al. (2016), Mejuto et al. (2008), Piovano et al. (2012), Sales et al. (2010)	VU
Green sea turtle	10	0.72	0.49–1.06	37%	.100	Andraka et al. (2013), Largacha et al. (2005), Pacheco et al. (2011), Sales et al. (2010)	EN
Hawksbill sea turtle	6	0.8	0.31–2.02	7%	.630	Andraka et al. (2013)	CR
Olive ridley sea turtle	14	0.69	0.53–0.89	60%	**.005**	Andraka et al. (2013), Huang et al. (2016), Kim et al. (2006, 2007), Largacha et al. (2005), Mejuto et al. (2008), Pacheco et al. (2011), Santos, Coelho, Fernandez-Carvalho, & Amorim (2012)	VU
Leatherback sea turtle	10	0.64	0.38–1.08	89%	.093	Andraka et al. (2013), Domingo et al. (2012), Foster et al. (2012), Gilman et al. (2007), Huang et al. (2016), Mejuto et al. (2008), Pacheco et al. (2011), Sales et al. (2010), Santos et al. (2012)	VU
Tetraodontiformes							
Ocean sunfish	6	0.99	0.73–1.35	7%	.970	Cambiè et al. (2012), Coelho et al. (2012), Domingo et al. (2012), Ward et al. (2009)	VU
Xiphioidei							
Black marlin	2	1.11	0.78–1.58	0%	.560	Andraka et al. (2013), Promjinda et al. (2008)	DD
Sailfish	8	1.2	1.00–1.44	38%	**.048**	Andraka et al. (2013), Kim et al. (2006, 2007), Pacheco et al. (2011), Promjinda et al. (2008)	LC
White marlin	2	0.98	0.77–1.25	0%	.880	Andraka et al. (2013), Pacheco et al. (2011)	VU

(Continues)

TABLE 1 (Continued)

	#exp.	RR	CI	I^2	*p*	References	Status
Striped marlin	5	0.86	0.76–0.97	56%	**.015**	Curran & Bigelow (2011), Kim et al. (2006, 2007), Ward et al. (2009)	NT
Blue marlin	7	0.96	0.63–1.46	69%	.840	Andraka et al. (2013), Curran & Bigelow (2011), Kim et al. (2006, 2007), Pacheco et al. (2011), Ward et al. (2009)	VU
Shortbill spearfish	6	0.66	0.51–0.84	56%	**.001**	Curran & Bigelow (2011), Huang et al. (2016), Kim et al. (2006, 2007), Ward et al. (2009)	DD
Swordfish	26	1	0.81–1.23	97%	.980	Andraka et al. (2013), Boggs & Swimmer (2007), Bolten & Bjorndal (2005), Cambiè et al. (2012), Curran & Bigelow (2011), Domingo et al. (2012), Foster et al. (2012), Gilman et al. (2007), Huang et al. (2016), Kerstetter & Graves (2006a), Kim et al. (2006, 2007), Mejuto et al. (2008), Pacheco et al. (2011), Piovano et al. (2012), Promjinda et al. (2008), Sales et al. (2010), Ward et al. (2009)	LC

RR > 1 indicates a higher catch was calculated on circle hooks compared to J-hooks. I^2 describes the percentage of total variation caused by between-study heterogeneity rather than within-study variance. *p*-Values that are ≤.05 are in bold to indicate significance. Status refers to IUCN Red List conservation status category where LC—least concern, NT—near threatened, VU—vulnerable, EN—endangered and CR—critically endangered are categories with increasing extinction risk. The categories, DD—data deficient and NE—not evaluated, are not categorized as an extinction risk.

of the scope of the studies analysed. The random effects model computes a global mean effect size based on a weighted mean of the studies' effect sizes, where the global mean estimate represents the average of the true underlying distribution of effect sizes from which the studies were drawn (Hedges & Vevea, 1998). Weights were computed as the inverse of the sample variance and the between-study variance (τ^2), thereby placing more weight on experiments with estimates having greater precision and de-emphasizing those weights with high between-study variance. Sample variance, v_i, for ln(RR) of the *i*th experiment was calculated as:

$$v_i = \frac{1}{a_i} - \frac{1}{n_i^1} + \frac{1}{c_i} - \frac{1}{n_i^2}$$

We computed the heterogeneity factor I^2 as a measure of total variation across experiments due to variability among experiments (Higgins, Thompson, Deeks, & Altman, 2003). Values of I^2 vary from 0% to 100%, with higher values indicating greater heterogeneity between experiments due to variation among experiments that was unaccounted for in our model (e.g. hook size, hook offset).

3 | RESULTS

We identified 33 unique references as part of our data compilation and screening process, of which 25 were used in our meta-analyses. In total, we analysed 43 of 54 experiments identified during our literature search and extracted information for 62 species. Species not included in more than one experiment were excluded from the analysis. Catch rate analyses were performed for 43 species (Table 1 and Appendix S3) and at-vessel mortality estimates were obtained for 31 species (Table 2 and Appendix S4).

Meta-analysis results for 43 species are reported here to evaluate differences in catch rate and at-vessel mortality among target and bycatch species caught with circle and J-hooks in the pelagic longline fishery. Forest plots of catch rate and at-vessel mortality for species included in our meta-analysis are provided in Appendices S3 and S4 and present the results and variation among the individual studies used in our meta-analysis. Results for swordfish and yellowfin tuna (*Thunnus albacares*, Scombridae) are presented in Figures 1–4 as examples. The meta-analysis found that swordfish catch rates were not significantly different between circle and J-hooks (Table 1). Forest plots of the individual experiments show 13 experiments with higher swordfish catch rates and the remaining 13 with lower, or no difference in, catch rates with circle hooks (Figure 2). At-vessel mortality in swordfish was lower (or showed no difference) when caught with circle hooks (Table 2) and only one experiment found greater at-vessel mortality in swordfish with circle hooks (vs. J-hooks; Figure 3). For yellowfin tuna, the forest plots show lower catch rates on circle hooks in four experiments, higher in 12 experiments (Figure 4), and the summary effect size (RR = 1.32) was significant (Table 1). Forest plots of at-vessel mortality of yellowfin tuna (Figure 5) indicate lower (four experiments) or no difference (one experiment) in mortality on circle hooks (vs. J-hooks), combined with an overall significant reduction in at-vessel mortality (RR = 0.84, p = .003; Table 2).

3.1 | Catch rate

The difference in catch rate with circle hooks (vs. J-hooks) was significantly greater ($p \le .05$) for 11 of the 43 species evaluated (Table 1, Figure 6) and significantly lower for seven species ($p \le .05$). For presentation and discussion purposes, fish were classified as tunas, elasmobranchs, billfishes or "other fish" (e.g. dolphinfish). Overall, catch rates with circle hooks (vs. J-hooks) were higher for the shark and tuna species, lower for sea turtle species and other fish species and mixed for the billfish species.

TABLE 2 Results of the meta-analysis on at-vessel mortality showing the summary effect size (relative risk, RR) and 95% confidence interval (CI)

	#exp.	RR	CI	I^2	*p*	References	Status
Aulopiformes							
Longnose lancetfish	2	1.07	0.9–1.28	98%	.420	Curran & Bigelow (2011)	LC
Carcharhiniformes							
Silky shark	2	0.57	0.24–1.32	54%	.190	Afonso et al. (2011), NMFS (2011)	NT
Oceanic whitetip shark	2	0.38	0.16–0.9	0%	**.028**	Afonso et al. (2011), Pacheco et al. (2011)	VU
Dusky Shark	2	0.63	0.35–1.16	42%	.140	Afonso et al. (2011), NMFS (2011)	VU
Tiger shark	2	1.08	0.31–3.71	40%	.910	Afonso et al. (2011), NMFS (2011)	NT
Blue shark	9	0.99	0.88–1.12	88%	.930	Afonso et al. (2011), Curran & Bigelow (2011), Epperly et al. (2012), Huang et al. (2016), NMFS (2011), Pacheco et al. (2011), Yokota et al. (2006)	NT
Scalloped hammerhead	2	0.79	0.72–0.86	0%	**<.001**	Afonso et al. (2011), NMFS (2011)	EN
Lamniformes							
Bigeye thresher	4	1.08	0.9–1.3	61%	.400	Coelho et al. (2012), Curran & Bigelow (2011), NMFS (2011)	VU
Shortfin mako	6	0.89	0.82–0.96	1%	**.005**	Afonso et al. (2011), Epperly et al. (2012), NMFS (2011), Pacheco et al. (2011), Yokota et al. (2006)	VU
Porbeagle shark	2	0.89	0.79–1.01	9%	.074	Epperly et al. (2012), NMFS (2011)	VU
Crocodile shark	2	0.97	0.51–1.85	0%	.930	Coelho et al. (2012), Pacheco et al. (2011)	NT
Lampridiformes							
Opah	2	0.78	0.66–0.93	0%	**.006**	Curran & Bigelow (2011)	LC
Myliobatiformes							
Pelagic stingray	4	1.07	0.48–2.41	0%	.860	Coelho et al. (2012), Curran & Bigelow (2011), Pacheco et al. (2011)	LC
Percoidei							
Sickle pomfret	2	0.95	0.7–1.29	0%	.740	Curran & Bigelow (2011)	NE
Dolphinfish	4	0.83	0.76–0.91	50%	**<.001**	Curran & Bigelow (2011), NMFS (2011), Pacheco et al. (2011)	LC
Scombroidei							
Snake mackerel	2	0.97	0.85–1.09	0%	.590	Curran & Bigelow (2011)	LC
Escolar	3	0.7	0.61–0.8	0%	**<.001**	Curran & Bigelow (2011), NMFS (2011)	LC
Wahoo	3	1.01	0.96–1.07	0%	.700	Curran & Bigelow (2011), Pacheco et al. (2011)	LC
Skipjack tuna	2	0.97	0.95–1	0%	**.077**	Curran & Bigelow (2011)	LC
Albacore	6	0.99	0.92–1.07	60%	.840	Curran & Bigelow (2011), Epperly et al. (2012), Huang et al. (2016), NMFS (2011), Pacheco et al. (2011)	NT
Yellowfin tuna	5	0.84	0.75–0.94	74%	**.003**	(Curran & Bigelow, 2011, Huang et al., 2016, NMFS, 2011, Pacheco et al., 2011)	NT
Bigeye tuna	6	0.91	0.76–1.09	95%	.310	Curran & Bigelow (2011), Epperly et al. (2012), Huang et al. (2016), NMFS (2011), Pacheco et al. (2011)	VU
Bluefin tuna	2	0.86	0.81–0.91	0%	<.001	Epperly et al. (2012), NMFS (2011)	EN
Testudines							
Loggerhead sea turtle	5	1.41	0.61–3.26	8%	.420	Cambiè et al. (2012), Gilman et al. (2007), Mejuto et al. (2008), NMFS (2011), Sales et al. (2010)	VU
Leatherback sea turtle	4	1.49	0.49–4.56	25%	.480	Huang et al. (2016), Mejuto et al. (2008), NMFS (2011), Pacheco et al. (2011)	VU

(Continues)

TABLE 2 (Continued)

	#exp.	RR	CI	I^2	*p*	References	Status
Xiphioidei							
Sailfish	2	0.71	0.5–1	3%	**.048**	NMFS (2011), Pacheco et al. (2011)	LC
White marlin	2	0.84	0.77–0.9	0%	**<.001**	NMFS (2011), Pacheco et al. (2011)	VU
Striped marlin	2	1.06	0.8–1.41	62%	.670	Curran & Bigelow (2011)	NT
Blue marlin	4	0.82	0.75–0.9	0%	**<.001**	Curran & Bigelow (2011), NMFS (2011), Pacheco et al. (2011)	VU
Shortbill spearfish	3	1.01	0.94–1.08	33%	.870	Curran & Bigelow (2011), Huang et al. (2016)	DD
Swordfish	6	0.92	0.87–0.97	80%	**.004**	Curran & Bigelow (2011), Epperly et al. (2012), Huang et al. (2016), NMFS (2011), Pacheco et al. (2011)	LC

RR > 1 indicates a higher at-vessel mortality was calculated on circle hooks compared to J-hooks. I^2 describes the percentage of total variation caused by between-study heterogeneity rather than within-study variance. *p*-values that are ≤.05 are in bold to indicate significance. Status refers to IUCN Red List conservation status category where LC—least concern, NT—near threatened, VU—vulnerable, EN—endangered and CR—critically endangered are categories with increasing extinction risk. The categories, DD—data deficient and NE—not evaluated, are not categorized as an extinction risk.

The 11 species with higher catch rates included four species of tuna: yellowfin tuna, albacore (*Thunnus alalunga*, Scombridae), bigeye tuna (*Thunnus obesus*, Scombridae) and Atlantic bluefin tuna; Atlantic sailfish (hereafter simply "sailfish" *Istiophorus platypterus*, Istiophoridae); and six species of sharks: silky shark (*Carcharhinus falciformis*, Carcharhinidae), shortfin mako shark (*Isurus oxyrinchus*, Lamnidae), salmon shark (*Lamna ditropis*, Lamnidae), porbeagle shark (*Lamna nasus*, Lamnidae), blue shark (*Prionace glauca*, Carcharhinidae) and crocodile shark (*Pseudocarcharias kamoharai*, Pseudocarchariidae). The seven species that showed lower catch rates with circle hooks (vs. J-hooks) were two species of sea turtles: loggerhead sea turtle (*Caretta caretta*, Cheloniidae) and olive ridley sea turtle (*Lepidochelys olivacea*, Cheloniidae), two billfishes: striped marlin (*Kajikia audax*, Istiophoridae) and shortbill spearfish (*Tetrapturus angustirostris*, Istiophoridae), sickle pomfret (*Taractichthys steindachneri*, Bramidae), snake mackerel (*Gempylus serpens*, Gempylidae) and dolphinfish.

Effect sizes for species with significant differences in catch rate between circle hooks and J-hooks (Figure 6) illustrate general trends among taxonomic groupings, with higher catch rates for tunas and elasmobranchs and lower catch rates for sea turtles and "other fish" (i.e. snake mackerel, sickle pomfret and dolphinfish). The billfishes were the only taxonomic group with both lower and higher catch rates.

Increases in catch rate with circle hooks (vs. J-hooks) ranged from 20% greater in the sailfish (RR = 1.20; p = .05) to 246% greater in the crocodile shark (RR = 3.46; p < .001). Catch rate more was more than doubled for species in the genus *Lamna* (porbeagle shark RR = 2.08; p < .001 and salmon shark RR = 2.44; p = .04) caught using circle hooks compared to J-hooks. Among thunnid tunas, catch rates ranged from 32% greater in yellowfin tuna (RR = 1.32; p = .0098) to 87% greater in bluefin tuna (RR = 1.87; p < 0.001) when circle hooks were used. For the Carcharhiniformes, increases in catch rates were 40% (RR = 1.40; p < .001) and 46% (RR = 1.46; p < .001) higher with circles hooks for the silky and blue sharks, respectively.

Effect sizes for catch rates that were lower with circle hooks (vs. J-hooks) ranged from 16% lower catch rate (RR = 0.84; p = 0.01) in dolphinfish to 66% lower catch rate (RR = 0.34; p < .001) in snake mackerel. Catch rates for loggerhead and olive ridley sea turtles were 42% (RR = 0.58; p = .02) and 31% (RR = 0.69; p = .0049) lower, respectively, when circle hooks were used rather than J-hooks.

3.2 | At-vessel mortality

Twelve species evaluated had significantly (p ≤ .05) lower at-vessel mortality rate when caught on circle hooks (vs. J-hooks), including three species of shark (oceanic whitetip shark, shortfin mako shark and scalloped hammerhead—*Sphyrna lewini*), two species of tuna (yellowfin and bluefin), four billfishes (blue marlin, sailfish, white marlin and swordfish), dolphinfish and opah (*Lampris guttatus*, Lampridae; Table 2, Figure 7). Reductions in at-vessel mortality ranged from 62% in the oceanic whitetip shark (RR = 0.38, p = .03) to eight per cent in the swordfish (RR = 0.92, p = .0036). However, 10 of the 12 species had reductions ranging from 14% to 30%.

No significant differences in at-vessel mortality due to capture by circle hook (vs. J-hook) were found for the remaining 12 species, which include species of shark, tuna, billfish, other fish and sea turtles. Five species had significant differences in both at-vessel mortality and catch rates in comparisons between circle and J-hooks. Only one species, the dolphinfish, had both lower catch rate and lower at-vessel mortality. The remaining four species had higher catch rates and lower at-vessel mortality when caught with circle hooks (vs. J-hooks): shortfin mako shark, yellowfin tuna, bluefin tuna and sailfish.

3.3 | IUCN status

The IUCN programme *Red List of Threatened Species* lists risk status of species on a global scale in an effort to highlight taxa threatened with extinction and promote their conservation (Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006). The IUCN designations, in order of decreasing risk, are "endangered," "vulnerable," "near

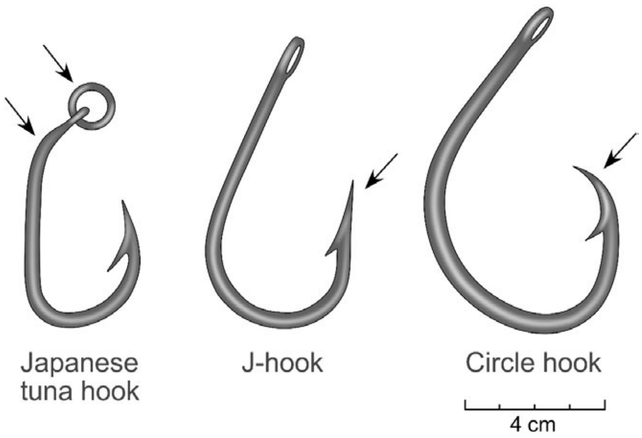

FIGURE 1 Diagram of circle, tuna and J-hook. Arrows represent the distinctive characteristics of each style of hook. Tuna hook—the curved shaft, J-hook—the point is parallel to the shaft, Circle hook—the point is turned inward relative to the shaft

threatened" and "least concern" ("data deficient" and "not evaluated" are also included, but are not related to risk). IUCN designations for species with significant differences in catch rate (18 species) or at-vessel mortality (12 species) between circle and J-hooks are indicated in Figures 6 and 7, respectively.

Of the 11 species that had greater catch rates with circle hooks, one (bluefin tuna) is IUCN-designated as endangered, three as vulnerable (bigeye tuna, porbeagle shark and shortfin mako shark), five as near threatened (albacore and yellowfin tunas, and crocodile, blue, and silky sharks), and two (salmon shark and sailfish) are listed as species of least concern (Figure 6). Among these, five of the six shark species that had higher catch rates on circle hooks, are considered near threatened or vulnerable by the IUCN (none had higher at-vessel mortality with circle hooks). The five species with lower catch rates with circle hooks (vs. J-hooks) are listed as vulnerable (both sea turtles), near threatened (striped marlin) and of least concern (snake mackerel and dolphinfish). The shortbill spearfish and sickle pomfret are designated as "data deficient" and "not evaluated," respectively.

The bluefin tuna and scalloped hammerhead are the only species listed as endangered on the IUCN *Red List of Threatened Species* that had lower at-vessel mortality with circle hooks (vs. J-hooks) (Figure 7). The remaining species with lower at-vessel mortality are IUCN-listed as vulnerable (oceanic whitetip shark, shortfin mako shark, blue marlin, striped marlin), near threatened (yellowfin tuna) and of least concern (swordfish, sailfish, opah, dolphinfish and escolar—*Lepidocybium flavobrunneum*, Gempylidae).

Of the five species demonstrating significant differences in both catch rate and at-vessel mortality when captured with circle hooks (vs.

Authors	Circle hook Events	Circle hook Total	J-hook Events	J-hook Total	% *W*	RR [95% CI]
Piovano et al. 2012 [23]	8	4,275	36	4,275	2.84%	0.22 [0.10, 0.48]
Bolten & Bjorndal 2005[36]	264	46,040	723	46,040	4.40%	0.37 [0.32, 0.42]
Andraka et al. 2013[53]	83	65,603	181	69,040	4.20%	0.48 [0.37, 0.63]
Curran & Bigelow 2011[6]	120	1,176,471	231	1,172,589	4.28%	0.52 [0.42, 0.65]
Kerstetter & Graves 2006a[18]	49	7,650	72	7,650	3.97%	0.67 [0.47, 0.97]
Curran & Bigelow 2011[41]	19	215,909	27	214,286	3.34%	0.70 [0.39, 1.26]
Domingo et al. 2012[7]	148	19,911	195	19,911	4.29%	0.76 [0.61, 0.94]
Kerstetter & Graves 2006a[63]	233	7,650	282	7,650	4.36%	0.83 [0.70, 0.98]
Sales et al. 2010[27]	715	72,914	833	72,914	4.44%	0.86 [0.78, 0.95]
Piovano et al. 2012 [22]	100	9,011	113	9,012	4.19%	0.89 [0.68, 1.16]
Pacheco et al. 2011[21]	301	25,085	307	25,085	4.38%	0.98 [0.84, 1.15]
Cambie et al. 2012[48]	1	2,320	1	2,322	0.52%	1.00 [0.06, 15.99]
Foster et al. 2012[9]	11,035	156,164	8,110	116,359	4.48%	1.01 [0.99, 1.04]
Domingo et al. 2012[8]	148	22,571	139	22,571	4.26%	1.06 [0.85, 1.34]
Andraka et al. 2013[49]	223	177,942	210	178,732	4.33%	1.07 [0.88, 1.29]
Boggs & Swimmer 2007[57]	65	8,250	60	8,250	4.00%	1.08 [0.76, 1.54]
Kim et al. 2006[30]	12	14,700	11	14,700	2.70%	1.09 [0.48, 2.47]
Ward et al. 2009[43]	127	47,575	111	47,575	4.21%	1.14 [0.89, 1.48]
Gilman et al. 2007[42]	33,142	2,150,674	17,086	1,282,748	4.48%	1.16 [1.14, 1.18]
Bolten & Bjorndal 2005[39]	212	13,613	138	13,613	4.29%	1.54 [1.24, 1.90]
Huang et al. 2016[45]	341	203,838	220	203,838	4.36%	1.55 [1.31, 1.84]
Bolten & Bjorndal 2005[37]	357	29,383	203	29,383	4.36%	1.76 [1.48, 2.09]
Mejuto et al. 2008[59]	4,232	143,413	2,172	143,473	4.47%	1.95 [1.85, 2.05]
Andraka et al. 2013[54]	38	36,834	20	38,207	3.48%	1.97 [1.15, 3.39]
Promjinda et al. 2008[26]	12	6,277	4	6,277	1.98%	3.00 [0.97, 9.30]
Kim et al. 2007[20]	52	15,616	15	15,616	3.38%	3.47 [1.95, 6.15]
RE model					100.00%	1.00 [0.81, 1.23]

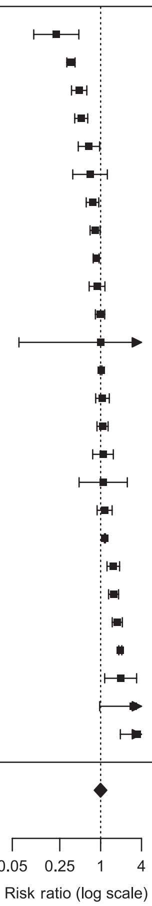

FIGURE 2 Effect size of hook type on catch rate for swordfish for experiments considered in this analysis and estimated by the resulting model (RE model). "Events" refer to observed catch, and "total" indicates the number of hooks fished. Effect size (relative risk—RR), 95% confidence intervals (CI) and weights (%W) are shown indicated for each study and the meta-analysis model. Numeric superscript refers to the experiment identification number provided to distinguish between experiments within a reference

J-hooks), the bluefin tuna (endangered), shortfin mako shark (vulnerable), yellowfin tuna (near threatened) and sailfish (least concern) had higher catch rate and lower at-vessel mortality, while the dolphinfish (least concern) had a lower catch rate and lower at-vessel mortality (Table 3).

4 | DISCUSSION

Reducing bycatch is an important component in the conservation of threatened species and recovery of declining fisheries and, therefore, a focus of fisheries conservation and management (Alverson, 1994; Andraka et al., 2013; Crowder & Murawski, 1998; Kerstetter & Graves, 2006a; Lewison, Crowder, Read, & Freeman, 2004). The results of our meta-analysis suggest that substituting circle hooks for J-hooks in pelagic longline fisheries may increase the catch rates of some target and bycatch species and decrease catch rates of others; in contrast, we found only decreases or no change in at-vessel mortality.

4.1 | Tunas

Our results found increases in catch rate on circle hooks for all four *Thunnus* species analysed. Except for the bluefin tuna, tunas were well represented in the analysis because they are the target of many pelagic longline fisheries and, therefore, data are available from numerous studies. Although the results of our meta-analysis suggest that transition to circle hooks may increase catch rates of tunas, at-vessel mortality was lower for yellowfin and bluefin tuna. Similarly, Pacheco et al. (2011) found that bigeye and yellowfin tuna had lower at-vessel mortality and were hooked externally more than internally, indicating a greater potential for post-release survival. This may also translate into conservation benefits in fisheries that release undersized tunas, assuming that circle hook effects on fish survival are size-independent.

Yellowfin tuna is one of the primary targets of pelagic longline fisheries on a global scale (Allen, 2010) and higher catch rates with circle hooks may help overcome the scepticism of fishers and clear the way for adoption of circle hooks. Furthermore, landing live tuna leads to a higher quality (i.e. more valuable) ex-vessel product; therefore, increasing the number of fish alive at haulback may be an additional incentive for circle hook adoption by tuna fishers (Clucas, 1997; Foster, Parsons, Snodgrass, & Shah, 2015; Serafy, Orbesen, et al., 2012). For example, Venezuelan pelagic longline fishers targeting yellowfin tuna were reluctant to experiment with circle hooks because of perceived catch reductions (Falterman & Graves, 2002). However, after higher catches and lower immediate mortality rates were demonstrated in their fishery, they adopted the use of circle hooks (Graves et al., 2012). These financial gains may be significant enough to offset the cost of gear conversion to circle hooks, as was demonstrated in the Australian fisheries targeting bigeye and yellowfin tuna and swordfish (Ward et al., 2009).

4.2 | Elasmobranch

Significant results for shark species showed only increases in catch rates and decreases in mortality with respect to hook type. Among shark species, catch rates increased (six species) or showed no difference (seven species), while at-vessel mortality rates decreased (three species) or showed no difference (seven species).

These results are consistent with a previous meta-analysis on the effect of pelagic longline fishing gear factors on sharks (species combined), in which the use of circle hooks increased catch rates and reduced at-vessel mortality (Gilman et al., 2016). Gilman et al. speculated that reduced deep-hooking of sharks caught on circle hooks likely accounted for the reduced mortality, which may also lead to an increase in post-release survival for sharks. Literature reviewed for this analysis included findings of no differences in catch rate between hook type (Pacheco et al., 2011; Ward et al., 2009; Yokota, Kiyota, & Minami, 2006), higher catch rates (Afonso et al., 2011; Pacheco et al., 2011; Ward et al., 2009; Watson, Epperly, Shah, & Foster, 2005) and (infrequently) lower catch rates (Curran & Bigelow, 2011; Gilman et al., 2007; Kerstetter & Graves, 2006a) for pelagic shark species.

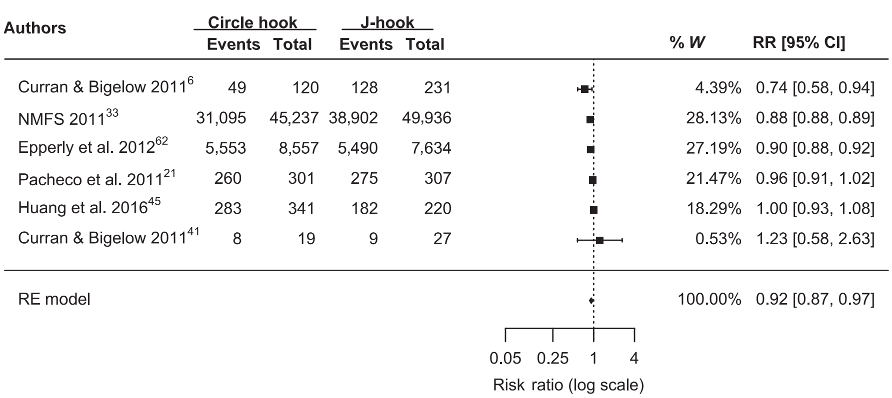

FIGURE 3 Effect size of hook type on at-vessel mortality for swordfish for experiments considered in this analysis and estimated by the resulting model (RE model). "Events" refer to observed mortalities, and "total" indicates the number fish caught. Effect size (relative risk—RR), 95% confidence intervals (CI) and weights (%W) are indicated for each study and the meta-analysis model. Numeric superscript refers to the experiment identification number provided to distinguish between experiments within a reference

Godin et al. (2012) evaluated effects of circle vs. J-hooks reported in 30 studies and found higher catch rates with circle hooks, except for blue, shortfin mako, crocodile and common thresher (*Alopias vulpinus*, Alopiidae) sharks, which showed no significant effects. An analysis of circle vs. J-hooks by Gilman et al. (2016) demonstrated higher catch rates in crocodile, whitetip and silky sharks, consistent with results of the present study, but lower catch rates in blue sharks. Both Godin et al. (2012) and Gilman et al. (2016) demonstrated lower at-vessel mortality (or greater survival), consistent with our results for pelagic species.

One potentially confounding factor was the use of different leader types with different hook types. Experiments conducted by Watson et al. (2005) found that circle hooks had a significantly higher catch rate and lower gut hooking rate of blue shark when compared to J-hooks; however, the authors hypothesized that use of monofilament leaders may have confounded catch rate comparisons because gut-hooked sharks are more likely to bite off these leaders and escape detection. Afonso, Santiago, Hazin, and Hazin (2012) found that wire leaders had higher shark catch rates and that significantly more sharks were captured alive on wire vs. monofilament leaders [but see Yokota et al. (2006) for a counterexample]. They cautioned that, in longline fisheries, shark catch and mortality rates may be underestimated when monofilament leaders were used. Unfortunately, the data available did not allow us to control for this factor in our analysis, but, due to the paired nature of most studies included in our analysis, leader type was controlled for on longline sets within experiments by simply alternating hook type with otherwise identical terminal gear. Piovano, Basciano, Swimmer, and Giacoma (2012) provide an exception, where one fishing crew bunched experimental hooks on portions of the line. This control was not possible for the pelagic observer data, and the potential bias previously noted (Beerkircher, Cortés, & Shivji, 2003). The effect of leader type on and mortality metrics is an area for future research, especially with respect to sharks. Respiratory mode is a key factor controlling post-release mortality in elasmobranchs. Dapp, Walker, Huveneers, and Reina (2016) and Ellis, McCully Phillips, and Poisson (2017) found that obligate ram-venting sharks, such as carcharhinids and lamnids, have higher discard mortality (combined at-vessel mortality and post-release mortality) than stationary-respiring species because their respiration is impaired during capture. Ram-ventilating pelagic fish species, such as tunas, mackerels and billfishes, may also have impaired respiration during capture (Wegner, Sepulveda, Aalbers, & Graham, 2013), although to our knowledge there are no comparable analyses available for bony fish. Water temperature and soak time are other factors influencing shark discard mortality. Shark survival in pelagic longline fisheries significantly decreases with increasing water temperature (and corresponding lower dissolved oxygen concentration) and soak time, which favours asphyxiation and increases capture stress in sharks (Gallagher, Orbesen, Hammerschlag, & Serafy, 2014; Skomal & Bernal, 2010).

Our results suggest that circle hooks would reduce at-vessel mortality in three ram-ventilating sharks—oceanic whitetip, scalloped hammerhead and shortfin mako. This result is particularly promising for their management because these species are commonly caught in pelagic longline fisheries (Coelho, Santos, & Amorim, 2012), and their conservation status is a matter of international concern. A decrease in at-vessel mortality for bycatch of these shark species does not necessarily translate to a decrease in post-release mortality of released individuals, however, some proportion of post-release mortality is related to physiological stress and injuries experienced during capture (Skomal, 2007). To our knowledge, no studies specifically address post-release mortality of scalloped hammerhead from pelagic longlines (Gallagher et al., 2014). Few studies have estimated such rates in other large pelagic shark species, but see examples for oceanic whitetip and shortfin mako (Musyl et al., 2011), the blue shark (Campana, Joyce, & Manning, 2009; Moyes, Fragoso, Musyl, & Brill,

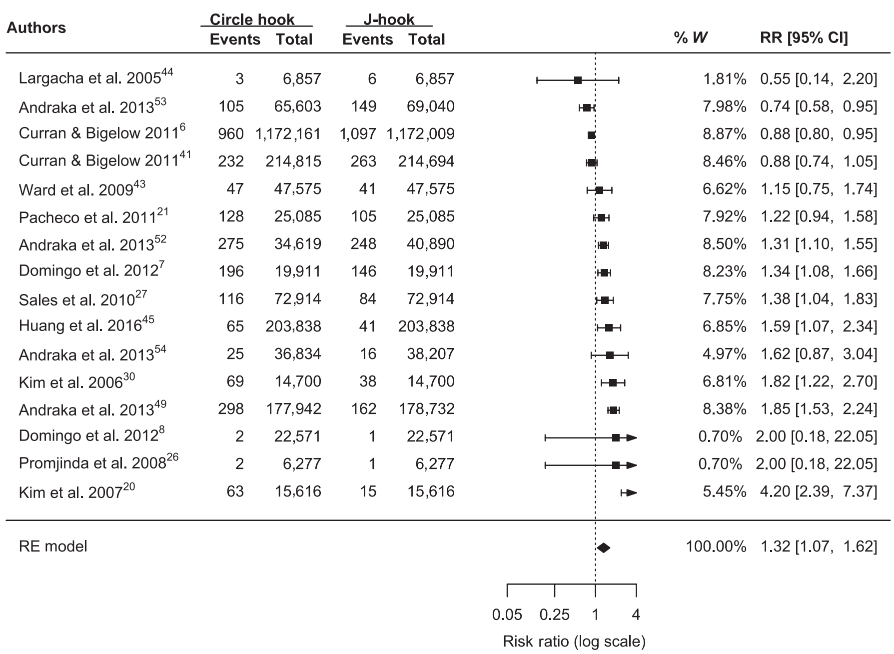

FIGURE 4 Effect size of hook type on catch rate for yellowfin tuna for experiments considered in this analysis and estimated by the resulting model (RE model). "Events" refer to observed catch, and "total" indicates the number of hooks. Effect size (relative risk—RR), 95% confidence intervals (CI) and weights (%W) are indicated for each study and the meta-analysis model. Numeric superscript refers to the experiment identification number provided to distinguish between experiments within a reference

2006) and common thresher shark (Heberer et al., 2010; Sepulveda et al., 2015).

4.3 | Billfishes, swordfish and dolphinfish

Replacing J-hooks with circle hooks may increase catch rates of several targeted tuna species without a corresponding increase in catch rates of other target (swordfish) and secondary target (billfishes and dolphinfish) species. Our results indicate that the use of circle hooks will lead to a decrease in at-vessel mortality for these species. Previous work documented relatively high post-release survival in several billfish species (white marlin, blue marlin and swordfish) captured in the pelagic longline fishery (Kerstetter & Graves, 2006b, 2008; Kerstetter, Luckhurst, Prince, & Graves, 2003); therefore, the differences in at-vessel mortality that we observed are likely to result in a conservation benefit to the species. These species are particularly important to recreational fisheries in tropical and subtropical oceanic waters, and similar reductions in immediate mortality and injury due to hook trauma have been observed in recreational billfish fisheries, although survival is generally higher in the recreational fishery than in pelagic longline fisheries (Horodysky & Graves, 2005; Kerstetter & Graves, 2006b; Prince et al., 2007).

Billfishes are among the most common highly migratory species targeted by for-hire charter boats. Recreational catch of white marlin along the Atlantic and Gulf coasts ranges between 4,000 and 12,000 individuals annually (Goodyear & Prince, 2003; NMFS, 2006) and recreational fishing for dolphinfish and other pelagic fish species along the U.S. Mid-Atlantic has increased in recent years due to improved access of anglers to offshore pelagic waters (Dell'Apa et al., 2015). Management and other conservation measures are needed for these fish, particularly in consideration of the rapid expansion of the recreational fishery in developing countries (Alió, 2012; Pitcher & Hollingworth, 2002) and on a global scale (Ihde, Wilberg, Loewensteiner, Secor, & Miller, 2011). The potential reduction in mortality due to pelagic longline interactions provided by conversion to circle hooks is promising for the conservation and management of these species, particularly in the Atlantic. Regulations requiring the use of circle hooks could be part of a broader management strategy to curtail the impacts of recreational and commercial fishing to billfish populations. Further research into post-release survival rates in secondary target species, an issue which has only been marginally explored in longline fisheries (Graves & Horodysky, 2008), would be helpful to management and conservation efforts.

4.4 | Sea turtles

Catch rates on circle hooks were reduced in two sea turtle species, the loggerhead and olive ridley. These results are consistent with the large-scale experiment described in Watson et al. (2005), which was the basis of mandatory circle hook use in the U.S. pelagic longline fishers operating in Atlantic and Gulf of Mexico waters since 2004 (69 F.R. 6621). Both species showed a non-significant increase in at-vessel mortality, which mirrors the results found in other studies. Additionally, differences in mortality rates were typically attributed to combinations of covarying factors, for example Cambiè, Muiño, Freire, & Mingozzi. (2012) found that mortality of sea turtles increased with soak time and decreased in relation to the size of the animal.

4.5 | IUCN

The results of our analysis indicated increased catch rates with circle hooks in four pelagic species (shortfin mako and porbeagle sharks, bigeye and bluefin tuna) identified as vulnerable or endangered by the IUCN. Reduced at-vessel mortality with circle hooks (compared with J-hooks) was found in three shark species, bluefin tuna and two billfish species listed as endangered or vulnerable by the IUCN (Table 3). These results are consistent with those previously reported for sharks (Gilman et al., 2016; Serafy, Cooke, et al., 2012), billfishes (Domeier, Dewar, & Nasby-Lucas, 2003; Horodysky & Graves, 2005; Prince, Prince, Ortiz, & Venizelos, 2002; Prince et al., 2007; Skomal, 2007) and bluefin tuna (Prince et al., 2002; Skomal, Chase, Prince, Lucy, & Studholme, 2002), which presume that external (vs. internal) hooking results in reduced mortality. In addition, we found reduced catch rates for two sea turtle species when circle hooks were used, consistent with findings of previous studies (e.g. Foster et al., 2012; Watson et al., 2005). We believe the use of circle hooks may be helpful in reducing at-vessel mortality for several at-risk species in the list, and therefore provide a valuable tool for management and conservation of bycatch species.

Cortés et al. (2010), in an assessment of the vulnerability of sharks in the Atlantic pelagic longline fishery, found that as a group, pelagic sharks are particularly vulnerable to pelagic longline fisheries, primarily due to their low productivity and high susceptibility to capture and subsequent mortality. The study ranked silky and shortfin mako sharks as the first and second most vulnerable, respectively, followed by the oceanic whitetip shark (ranked 5), blue shark (ranked 7), scalloped hammerhead (ranked 9) and porbeagle (ranked 10). Of these ranked species, the shortfin mako, porbeagle and oceanic whitetip shark are IUCN-designated as vulnerable and scalloped hammerhead as endangered. The remaining species are listed as of least concern or not threatened. Although higher catch rates may not translate into higher mortality, concern remains regarding the ability of circle hooks to contribute to the conservation of some species of sharks. Reduced at-vessel mortality with circle hooks is expected to benefit sharks caught in regulated fisheries by increasing the number of sharks released alive, while higher catch rates remain a concern in unregulated fisheries because both dead and live sharks may be retained (Serafy, Cooke, et al., 2012). We used the IUCN *Red List of Threatened Species* to evaluate, at a high level, the potential conservation implications of hook type changes in pelagic longline fisheries. While we recognize that formal stock assessments are the best source of information for evaluating stock status, not all species evaluated here have been formally assessed. We consider the IUCN *Red List of Threatened Species* to be a useful

Authors	Circle hook Events	Circle hook Total	J-hook Events	J-hook Total	% W	RR [95% CI]
Pacheco et al. 2011[21]	56	128	67	105	13.02%	0.69 [0.54, 0.88]
NMFS 2011[33]	11,138	31,696	12,185	26,915	33.20%	0.78 [0.76, 0.79]
Curran & Bigelow 2011[6]	396	960	509	1,097	26.65%	0.89 [0.81, 0.98]
Curran & Bigelow 2011[41]	96	232	112	263	15.60%	0.97 [0.79, 1.19]
Huang et al. 2016[45]	44	65	28	41	11.54%	0.99 [0.76, 1.30]
RE model					100.00%	0.84 [0.75, 0.94]

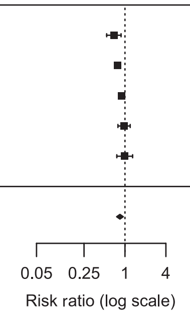

FIGURE 5 Effect size of hook type on at-vessel mortality for yellowfin tuna for experiments considered in this analysis and estimated by the resulting model (RE model). "Events" refer to observed mortalities, and "total" indicates the number of fish caught. Effect size (relative risk—RR), 95% confidence intervals (CI) and weights (%W) are indicated for each experiment and the meta-analysis model. Numeric superscript refers to the experiment identification number provided for the purpose of distinguishing between experiments within a reference

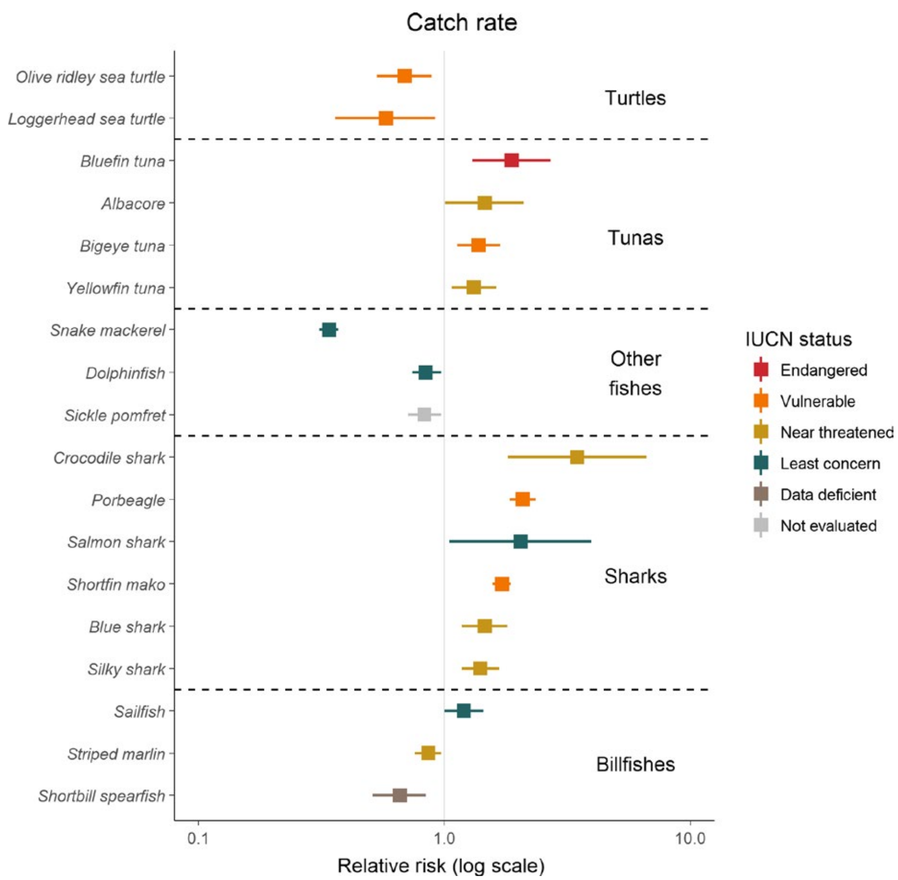

FIGURE 6 Effect size (relative risk—RR) of hook type on catch rate for species for which a significant difference was observed. Squares represent mean values, and lines show the Wald-type 95% confidence intervals estimated by the model. Values <1 represent significantly lower at-vessel mortality on circle hooks relative to J-hooks. IUCN status refers to IUCN Red List conservation status category

proxy, as the IUCN process provides a formal and consistent evaluation of population risk (Rodrigues et al., 2006) across species, and stock assessments are considered during the designation process (e.g. Collette et al., 2011).

4.6 | Analysis considerations and implications

Our results are consistent with previous studies of the effects of circle hooks on pelagic fishes, in which reduced at-vessel mortality in sharks (Favaro & Côté, 2013; Gilman et al., 2016; Godin et al., 2012), billfishes (Graves & Horodysky, 2008; Graves et al., 2012; Horodysky and Graves; 2005; Prince et al., 2002; Serafy et al., 2009) and tunas (Cooke & Suski, 2004; Pacheco et al.; 2011, Skomal et al.; 2002) were found. However, ours is the first meta-analysis to examine these differences at the species level for a large number of species and provides new information regarding differences in catch rates and at-vessel mortality between species. For example, Serafy et al. (2009) found no species-specific patterns in catch rate or mortality for billfishes between circle hooks and J-hooks but found higher mortality and injury rates on J-hooks across studies analysed. Since the publication of that review, several other studies have been published that we were able to include in our analysis. Our findings

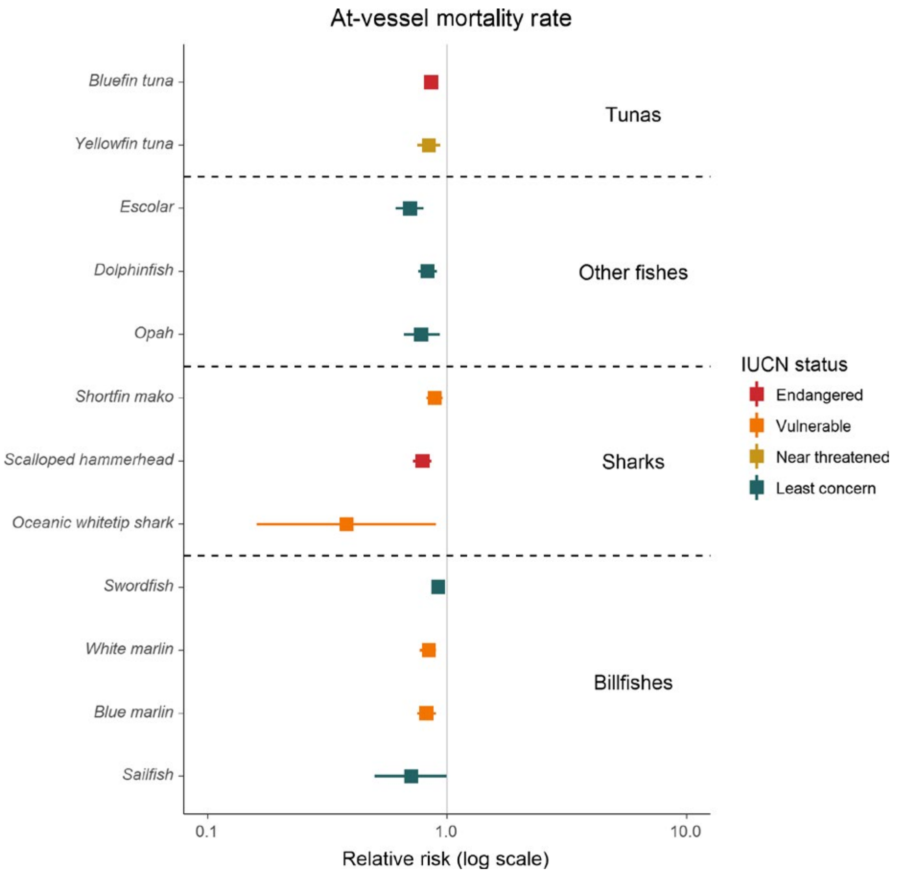

FIGURE 7 Effect size (relative risk—RR) of hook type on at-vessel mortality for species for which a significant difference was observed. Squares represent the mean values and lines show the Wald-type 95% confidence intervals estimated by the model. Values <1 represent significantly lower at-vessel mortality of fish caught on circle hooks relative to J-hooks. IUCN status refers to IUCN Red List conservation status category

TABLE 3 Species by IUCN status. See text for details on status determination

IUCN Status	Species
CR	Hawksbill sea turtle
EN	Green sea turtle, **Scalloped hammerhead(–,↓)**, **Bluefin tuna(↑,↓)**
VU	Bigeye thresher, **Oceanic whitetip shark(–,↓)**, Dusky shark, Night shark, **Loggerhead sea turtle(↓,–)**, Leatherback sea turtle, **Shortfin mako(↑,↓)**, **White marlin(–,↓)**, **Porbeagle(↑,–)**, **Olive ridley sea turtle(↓,–)**, **Blue marlin(–,↓)**, Ocean sunfish, Smooth hammerhead, **Bigeye tuna(↑,–)**
NT	**Silky shark(↑,–)** Tiger shark, **Striped marlin(↓,–)**, **Blue shark(↑,–)**, **Crocodile shark(↑,–)**, **Albacore(↑,–)**, **Yellowfin tuna(↑,↓)**
LC	Wahoo, Longnose lancetfish, Atlantic pomfret, **Dolphinfish(↓,↓)**, **Snake mackerel(↓,–)**,**Sailfish(↑,↓)**, Skipjack tuna, **Salmon shark(↑,–)**, **Opah(–,↓)**, **Escolar(–,↓)**, Pelagic stingray, Oilfish, Great barracuda, Blackfin tuna, **Swordfish(–,↓)**
DD	Black Marlin, **Shortbill spearfish(↓,–)**
NE	Velvet dogfish, **Sickle pomfret(↓,–)**

IUCN status refers to IUCN Red List conservation status category where LC—least concern, NT—near threatened, VU—vulnerable, EN—endangered and CR—critically endangered are categories with increasing extinction risk. The categories, DD—data deficient and NE—not evaluated, are not categorized as an extinction risk. Species in bold were found to have a relative risk of catch rate or at-vessel mortality significantly different from zero. Those species are followed by an indication of the direction of the relative risk (catch rate, at-vessel mortality). A dash (–) indicates not significantly different from zero for that parameter (catch rate, at-vessel mortality).

were consistent with Serafy et al. (2009), in that all billfishes had significant decreases or no change in at-vessel mortality with circle hooks. However, we found significant, mixed results for catch rates—sailfish catch rates increased on circle hooks, while striped marlin and shortbill spearfish catch rates were reduced on circle hooks relative to J-hooks.

Variability among data sets (e.g. geography, hook size, shape and manufacturers, depth, bait type) has previously limited the ability of meta-analyses and reviews to draw definitive conclusions about the conservation value of circle hooks for target and bycatch species (Cooke & Suski, 2004; Graves et al., 2012; Serafy, Orbesen, et al., 2012; Serafy et al., 2009). We did observe heterogeneity across studies (as measured by I^2) and recognize that it is due to variability among data sets that was accounted for as a random effect rather than fixed-factors. By grouping at the highest level of hook type (circle or J) rather than including additional fixed-factors such as hook manufacturer model, hook size and hook offset, we risk losing information. However, our estimates of effect are useful as estimates of benefits over a wider range of conditions, particularly because there is a limit to the level of control that regulations or conservation projects may place on the fishing characteristics of participating vessels or fisheries. Including additional factors, such as hook size and offset, would have reduced the available data by restricting the study data set to those studies that included the additional variables of interest. We considered binning species into higher taxonomic categories (e.g. order-level analysis), which would allow for the inclusion of more data; however, this greatly increased between-study heterogeneity. Additionally, we recognize that for analyses that included few experiments, RR estimates should be used with caution and should only be considered a first-order approximation of the population mean (Hedges & Vevea, 1998), as they are based on data sets that cover fewer variations in gear configuration and less geographic range, which may not overlap with a species' primary range.

Compared to Serafy, Orbesen, et al. (2012), which included a smaller data set but accounted for a larger number of variables, our species-specific estimates for at-vessel mortality were generally more conservative in representing the magnitude of change, but in all cases reflected the same trends in the direction of change. The agreement between our results and similar studies suggest that our estimates could be applicable to fisheries for which we lack fishery-specific estimates to generate a reasonable estimate of the benefits of using circle hooks. However, we recognize the need for fishery-specific estimates of the impacts of circle hooks in conjunction with the implementation of potential projects that attempt to increase circle hook use in fisheries.

Greater coordination across scientific and management bodies with respect to common study parameters and variables might allow smaller scale studies to be combined more easily and, therefore, increase the power of meta-analyses. If the information provided by the studies were standardized, it would expand the availability of appropriate data and increase the ease with which meta-analyses such as ours could be conducted. In our case, we were unable to use several studies because they did not present the total number of hooks fished or species caught per hook type.

Overall, our results suggest that a transition to circle hooks in pelagic longline fisheries could lead to lower fishing mortality for some species, including several species of conservation concern. Additionally, circle hooks have been shown to increase post-release survival in billfishes (Horodysky & Graves, 2005) which contributes to lower mortality.

5 | CONCLUSIONS

Results of our analysis indicate that circle hooks can benefit the management and conservation of target species and some common bycatch species caught in commercial pelagic longline fisheries. The conversion to circle hooks in recreational rod-and-reel fisheries also could enhance the conservation of billfishes and sharks. However, for circle hooks to be effective in fostering species conservation, international adoption of this fishing gear (and proper handling/release procedures) is needed, given the migratory behaviour of the majority of target and bycatch species of pelagic longline fisheries and the inherent overlap in fishing effort among pelagic longline fleets and between longline and some recreational fisheries.

The effects of circle hooks on catch rates and at-vessel mortality were mixed across studies and species. Therefore, expanding the use of circle hooks as a management measure for reducing bycatch mortality for a specific fishery should be evaluated prior to implementation either experimentally or more specific analysis, consistent with other findings (Cooke & Suski, 2004; Graves et al., 2012). Particular attention should be given to species that had high I^2, where the heterogeneity may indicate differences in experimental design or fishery characteristics (e.g. bait type, hook depth and hook types) can lead to divergent results. Transition to circle hooks may be expedited by direct outreach that provides fishers with opportunities to evaluate the potential for circle hooks to increase catch rate of target species while decreasing catch and mortality of bycatch species. Impacts to a specific fishery with respect to target species, catch rates, bycatch and management goals should be evaluated to assess the potential conservation benefits of circle hooks.

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SUPPORTING INFORMATION

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