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THE EFFECT OF CIRCLE HOOKS ON SHARK CATCHABILITY AND AT-VESSEL MORTALITY RATES IN LONGLINES FISHERIES

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ABSTRACT

Circle hooks have gained recent attention as a cost-effective bycatch mitigation tool in pelagic longline fisheries, particularly for marine turtles. Over the last few years, a growing number of studies have investigated the use of circle hooks and their effects on other species, including elasmobranchs. To elucidate the potential value of circle hook use as a tool for shark conservation and management in pelagic longline fisheries, we conducted a quantitative review of all available studies to date. We compiled 15 published and eight gray literature studies and where possible used random effects meta-analysis and analysis of covariance to test the effects of circle hooks on catchability and at-vessel mortality rates. Overall, results suggest that using circle hooks on pelagic longlines do not have a major effect on shark catch rates, but do reduce at-vessel mortality compared to J-hooks. Thus circle hooks should be seen as one potential tool to help reduce bycatch mortality of sharks in longline fisheries. However, the high level of heterogeneity found between studies highlights the need for shark-specific controlled experiments to provide more definitive results.

Worldwide, unintended capture (bycatch) of threatened species is one of the most prominent issues facing the commercial fishing industry. There are particular concerns regarding bycatch of marine turtles, cetaceans, seabirds, and sharks, as these are especially vulnerable to fishing mortality because of their life histories, characterized by slow growth, late maturity, long life span, and low fecundity rates (Musick 1999, Lewison et al. 2004). Substantial research efforts to reduce bycatch mortality have been devoted to marine turtles and seabirds (FAO 2009, FAO Fisheries Department 2009), but large knowledge gaps exist with regard to sharks. In recent years, the conservation and management of elasmobranchs has drawn increased attention as numerous species around the world have suffered large declines in abundance (e.g., Dulvy et al. 2008, Cahmi et al. 2009).

One of the most challenging problems to the management of sharks globally is the high bycatch rate associated with longline fisheries (Lewison et al. 2004). Longlines are passive, non-selective gears that typically catch a wide range of species. Pelagic longline fisheries generally occur on the high seas and are multispecies fisheries primarily targeting tunas (*Thunnus* spp.), swordfish, *Xiphias gladius* (Linnaeus, 1758), and mahi mahi, *Coryphaena hippurus* (Linnaeus, 1758), (Watson and Kerstetter 2006, Ward and Hindmarsh 2007). Benthic or bottom longline fisheries are generally conducted in coastal waters and target a variety of bony fishes (e.g., Serranidae and Lutjanidae), as well as elasmobranchs (e.g., Coelho and Erzini 2008).

Although practices vary and a combination of different hooks are used on commercial vessels, longliners targeting tuna typically use Japanese tuna hooks, while vessels targeting swordfish and sharks more often use J-hooks (Watson and Kerstetter 2006). For their apparent conservation benefits for marine turtles, circle hooks have been the subject of much attention over the last decade and there has

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been a growing movement to replace traditional J-hooks (i.e., J-hooks and Japanese tuna hooks) with circle hooks. Consequently, several countries have adopted or are considering the use of circle hooks as a means to reduce bycatch and increase post-release survivorship. For example, five regional fisheries management organizations (RFMOs)—Commission for the Conservation of Southern Bluefin Tuna (CCSBT), Inter-American Tropical Tuna Commission (IATTC), International Commission for the Conservation of Atlantic Tunas (ICCAT), Indian Ocean Tuna Commission (IOTC), Western and Central Pacific Fisheries Commission (WCPFC)—are encouraging their contracting parties and cooperating members (CCMs) to undertake research trials of appropriate-size circle hooks in their commercial pelagic longline fisheries. Since January 2010, WCPFC was the first RFMO to include the use of large circle hooks with an offset that does not exceed 10° as one available bycatch mitigation method required for implementation by all CCMs fishing for swordfish using shallow longline sets (WCPFC 2008). Although less attention has been directed to circle hook usage on demersal longlines, fishers using bottom longlines in the US Gulf of Mexico reef fish fishery are now required to use circle hooks to reduce marine turtle bycatch (US Fed Reg 2011).

Over the last few years, a growing number of studies have investigated the use of circle hooks and their effects on a range of species, including elasmobranchs. In the case of sharks, however, managers and scientists are confronted with multiple studies of small sample sizes with either conflicting results or no statistical significance and no clear conclusions. The goal of this review is to synthesize existing results and provide clearer overall conclusions on the value of circle hooks as a potential tool for shark conservation and management in longline fisheries.

Materials and Methods

Data Selection and Manipulation.—To examine trends in circle hook effects on sharks, we conducted a systematic review of all empirical studies that compared catch rate (i.e., catchability) and at-vessel mortality rates (i.e., if a shark was alive or dead at the vessel during haulback of the gear) between circle hooks and J-hooks in both pelagic and demersal longline fisheries. Where applicable, we also gathered information on hooking locations. Relevant published and gray literature was located via electronic database searches and additional unpublished data collected by individuals currently active in this area of research. Following the methodology used by Cooke and Suski (2004) and Serafy et al. (2009), each set of species-specific results from individual studies was considered an independent study.

Because of the paucity of data on sharks, if multiple circle and J-hook sizes and offsets were compared in a given study, we pooled the data into a single hook category (i.e., circle or J-hook). In most cases, however, only one hook type was compared or results were already pooled into a single hook category. Hooks with a point parallel to the shank and no apparent curvature of the shaft were categorized as J-hooks (Serafy et al. 2009). For a detailed guide on hook types used in pelagic longline fisheries, please refer to Beverly and Park (2009).

Meta-Analyses.—To better elucidate the overall differences between circle and J-hooks, we completed a meta-analysis on pooled data of all shark species. Most rays (Dasyatidae and Mobulidae) were excluded from these analyses owing to their different biology and ecology. However, for the most common elasmobranchs, including pelagic stingray (*Pteroplatytrygon violacea* Bonaparte, 1832), we performed a meta-analysis on the pooled data at the species and family level. Contingency tables were developed using "study" as a categorical variable. Since these studies are likely to have numerous differences, between-study variability (heterogeneity) is believed to be present and for this reason, random effects meta-analyses were employed using the DerSimonian and Laird method (DerSimonian and Laird 1986). An effect size was calculated and reported as pooled Odds Ratio (OR) with 95% confidence interval (CI). Studies were weighted according to the inverse of variance of the outcomes of interest in individual studies. I^2 percentage values were calculated to assess statistical heterogeneity (Higgins et al. 2003). All analyses were conducted using *metabin* functions of the version 1.6-1 *meta* package of the R statistical programming language (R Development Core Team 2008). Influential analysis using *metainf* functions of the same package was also performed to further evaluate the effect of omitting one study at a time on the pooled estimates.

The number of sharks caught on circle and J-hooks and the total number of hooks used in each category were used to calculate odds ratios for each study in the meta-analysis on catchability. Similarly, the number of dead sharks caught on circle and J-hooks and the total numbers of sharks caught were used to calculate the odds ratios in the at-vessel mortality meta-analysis. Pooled results were tested against the null hypothesis that shark catch or at-vessel mortality is not different between hook types. Using analysis of covariance (ANCOVA), the effects of variables influencing catchability and at-vessel mortality were further quantitatively examined. Models were coded using SAS PROC GLM with bait type, taxonomic family, and study area as covariates, and hook type as a treatment. The use of different leader material (monofilament vs wire) could not be considered in the analysis because information was incomplete.

Results

We compiled 15 published and eight gray literature studies as well as unpublished data from the National Oceanic and Atmospheric Administration (NOAA). Kerstetter and Graves (2006) was treated as two separate studies in the meta-analysis because the original paper comprised two distinct data sets (spring and fall). Similarly in Bolten et al. (2005), phase 1, phase 2, and phase 4A of their experiment accounted for three individual studies in the meta-analysis. The vast majority of the studies were conducted in the northwest Atlantic and western central Pacific Oceans (Fig. 1, Table 1). No clear standards exist among hook classifications; studies employed a variety of hooks that differed in width, degree of offset, orientation of the point, and length; and hook specifications were sometimes missing. In general, in the pooled data set, >60% of the J-hooks were size 8/0 and 9/0 with some degree of offset (10°–20°) and 75% of the circle hooks were size 16/0 and 18/0 usually with zero to a minimal degree of offset (5°–10°). Two studies (Ingram et al. 2005, Hale et al. 2011) were available to generate information on the effects of circle hooks on shark catches in bottom longline fisheries. All bottom longline studies were conducted in the US Gulf of Mexico and northwest Atlantic Ocean.

Catchability.—A review of the literature from studies using pelagic longlines suggested hook type does not have a significant effect on shark catchability (Kerstetter and Graves 2006, Yokota et al. 2006, Galeana-Villasenor et al. 2008, Promjinda et al. 2008, Galeana-Villasenor et al. 2009, Ward et al. 2009, Pacheco et al. 2011). However, a higher shark catch rate (Bolten et al. 2005, Watson et al. 2005, Kim et al. 2007, Ward et al. 2009, Sales et al. 2010, Afonso et al. 2011, Pacheco et al. 2011); and less frequently, a lower shark catch rate on circle hooks have also been reported for specific species (Kim et al. 2006, Gilman et al. 2007, Curran and Bigelow 2011). For sharks, the meta-analysis conducted on 18 studies is consistent with the null hypothesis that no significant difference in catchability exists between hook types when all shark species are combined (P = 0.21, Table 2). However, the influential

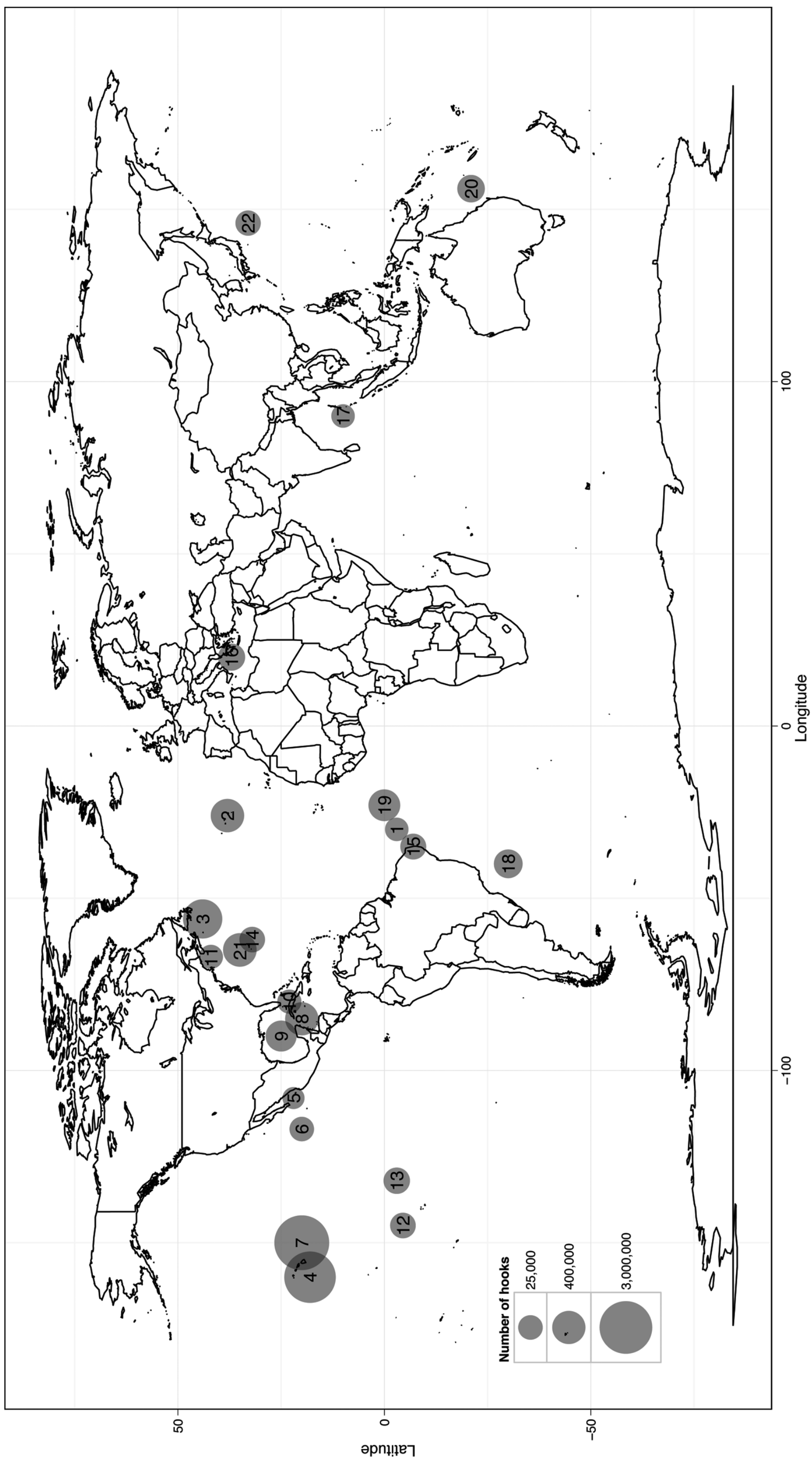

Figure 1. Summary of fishing area of each study that compared the performance of circle hook and J-hooks. The sizes of the points reflect the total number of hooks tested or analyzed in each study. The numbers correspond to the study identification number of Table 1.

Table 1. List of studies and sample size (total number of hooks) comprised in this review. Asterisk (*) indicates studies that have not been included in meta-analysis because data required for the analysis were not accessible; however, summary of the results was included in the discussion.

#	Study	Total number of hooks
1	Afonso et al. (2011)	7,800
2	Bolten et al. (2005; phase 1, 2, 4A)	416,199
3	Carruthers et al. (2009)	949,999
4	Curran and Bigelow (2011)	2,773,427
5	Galeana-Villasenor et al. (2008)*	2,400
6	Galeana-Villasenor et al. (2009)*	22,560
7	Gilman et al. (2007)	3,433,422
8	Hale et al. (2011)	400,000
9	Ingram et al. (2006)	254,500
10	Kerstetter and Graves (2006, spring)	16,560
11	Kerstetter and Graves (2006, fall)	14,040
12	Kim et al. (2006)	44,100
13	Kim et al. (2007)	62,464
14	NOAA (unpubl data)	>400,000
15	Pacheco et al. (2011)	50,170
16	Piovano et al. (2010)	86,116
17	Promjinda et al. (2008)	6,227
18	Sales et al. (2010)	145,828
19	Coelho et al. (2012)	305,352
20	Ward et al. (2009)	95,150
21	Watson et al. (2005)	427,312
22	Yokota et al. (2006)	35,027

analysis revealed that the results of Gilman et al. (2007) had a significant effect on the pooled results and when removed from the analysis, the effect size led to in a slight increase in shark catch on circle hooks (OR = 1.2, CI = 1.07–1.33, P = 0.0016).

Minor differences were found when data were examined at the species-specific level. For pelagic stingrays, all reviewed studies report lower catchability on circle hooks (Kerstetter and Graves 2006, Promjinda et al. 2008, Piovano et al. 2010, Curran and Bigelow 2011, Pacheco et al. 2011). Our meta-analysis was consistent with this trend although results were not significant (Table 3). Sufficient data were available to further evaluate circle hook effects on catchability for blue shark, *Prionace glauca* (Linnaeus, 1758), shortfin mako, *Isurus oxyrinchus* (Rafinesque, 1810), and crocodile shark, *Pseudocarcharias kamoharai* (Matsubara, 1936), and at the family level for mackerel shark, Lamnidae, thresher shark, Alopiidae, and all remaining requiem sharks, Carcharhinidae (excluding blue shark). No significant differences in catchability between hook types were found in any of these analyses. For most meta-analyses, I^2 percentages were extremely high indicating severe heterogeneity among studies (Table 3). ANCOVA indicated that bait type, study area, and taxonomic family were significant covariates ($P < 0.05$) in the catchability of circle vs J-hooks (Table 4).

In bottom longline fisheries, Ingram et al. (2005) found a significantly higher catch rate on circle hooks for all shark species combined and for five species individually in pairwise comparisons (11 species, total catch of 4469 individuals). However,

Table 2. Meta-analysis on catchability showing the summary effect and each study effect size (odd ratio, OR) and 95% confidence interval (CI). OR > 1 means a higher shark catch was calculated on circle hooks vs J-hooks. "Events" represent the total number of sharks caught on each hook category and "Total" represent the total number of hooks used in each category. The area of each square is proportional to the study's weight in the meta-analysis (W). The dotted vertical line shows the pooled random effects estimate. Species included in each study: Afonso et al. (2011)—silky shark *Carcharhinus falciformis*, bull shark *Carcharhinus leucas*, oceanic whitetip shark *Carcharhinus longimanus*, dusky shark *Carcharhinus obscurus*, night shark *Carcharhinus signatus*, tiger shark *Galeocerdo cuvier*, nurse shark *Ginglymostoma cirratum*, shortfin mako *Isurus oxyrinchus*, blue shark *Prionace glauca*, scalloped hammerhead *Sphyrna lewini*. Bolten and al. 2005 (1,2,4A)—*P. glauca*. Carruthers et al. (2009)—*P. glauca*, *I. oxyrinchus*, porbeagle shark *Lamna nasus*. Curran and Bigelow 2011—*P. glauca*, bigeye thresher *Alopias superciliosus*. Gilman et al. (2007)—*P. glauca*. Kerstetter and Graves (2006, spring)—*Carcharinus* spp. Kerstetter and Graves (2006, fall)—*P. glauca*. Kim et al. (2006)—*A. superciliosus*, *C. longimanus*, *P. glauca*, salmon shark *Lamna ditropis*, crocodile shark *Pseudocarcharias kamoharai*, Smallmouth knifetooth dogfish *Scymnodon obscurus*. Kim et al. (2007)—*A. superciliosus*, *C. longimanus*, *P. glauca*, *L. ditropis*, *P. kamoharai*. Pacheco et al. (2011)—*P. glauca*, *P. kamoharai*, *C. longimanus*, *I. oxyrinchus*, *S. lewini*, *C. falciformis*. Promjinda et al. (2008)—pelagic thresher shark *Alopias pelagicus*, *A. superciliosus*, *C. falciformis*, *G. cuvier*. Sales et al. (2010)—*Carcharinus* spp., *P. glauca*, *I. oxyrinchus*, *S. lewini*, smooth hammerhead shark *Sphyrna zigaena*. Coelho et al. (2012). Ward et al. (2009)—*C. falciformis*, *C. longimanus*, *G. cuvier*, *P. glauca*, *I. oxyrinchus*, *P. kamoharai*. Watson et al. (2005)—*P. glauca*. Yokota et al. (2006)—*P. glauca*, *I. oxyrinchus*, *L. ditropis*, *Alopias* spp.

	Circle hook		J-hook				
Study	Events	Total	Events	Total	OR	95%-CI	W (random)%
Promjinda et al. (2008)	7	3,113	16	3,113	0.44	[0.18; 1.06]	2.6
Gilman et al. (2007)	30,109	2,150,674	28,092	1,282,748	0.63	[0.62; 0.64]	6.4
Kim et al. (2006)	82	29,400	61	14,700	0.67	[0.48; 0.94]	5.3
Kerstetter and Graves (2006, fall)	27	7,020	37	7,020	0.73	[0.44; 1.20]	4.4
Kerstetter and Graves (2006, spring)	12	8,280	15	8,280	0.80	[0.37; 1.71]	3.1
Curran and Bigelow (2011)	4,229	1,386,713	5,051	1,386,713	0.84	[0.80; 0.87]	6.4
Yokota et al. (2006)	2,318	32,400	1,060	16,200	1.10	[1.02; 1.19]	6.4
Coelho et al. (2012)	6,027	203,568	2,691	101,784	1.11	[1.07; 1.15]	6.4
Watson et al. (2005)	6,555	213,621	5,915	213,691	1.12	[1.07; 1.18]	6.4
Bolten et al. (2005) (1)	796	46,040	1,333	92,081	1.20	[1.10; 1.31]	6.3
Sales et al. (2010)	2,116	72,914	1,773	72,914	1.20	[1.12; 1.28]	6.4
Carruthers et al. (2010)	8,573	458,964	2,587	165,890	1.20	[1.15; 1.26]	6.4
Pacheco et al. (2011)	68	25,085	56	25,085	1.21	[0.85; 1.73]	5.2
Bolten et al. (2005) (4A)	976	27,225	350	13,613	1.41	[1.24; 1.59]	6.3
Ward et al. (2009)	73	47,575	44	47,575	1.66	[1.14; 2.41]	5.1
Bolten et al. (2005) (2)	3,095	58,767	896	29,383	1.77	[1.64; 1.91]	6.4
Kim et al. (2007)	232	46,848	42	15,616	1.85	[1.33; 2.56]	5.3
Afonso et al. (2011)	92	3,900	42	3,900	2.22	[1.54; 3.21]	5.1
Pooled effects estimate	65,387	4,822,107	50,061	3,500,306	1.13	[0.94; 1.35]	100.0

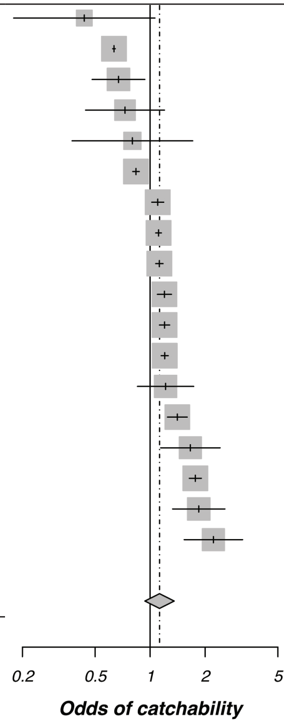

Table 3. Summary of the results of the meta-analysis on catchability showing the summary effect size (odd ratio, OR) and 95% confidence interval (CI). OR > 1 indicates a higher shark catch was calculated on circle hooks vs J-hooks. I^2 describes the percentage of total variation across studies that are due to heterogeneity rather than chance. Values >25%, 50%, and 75% are categorized has low, moderate, and high, respectively.

Category	# studies	OR	CI (%)	I^2 (%)
All sharks combined	18	1.13	0.94–1.35	99.3
Prionace glauca	15	1.15	0.92–1.44	99.4
Pteroplatytrygon violacea	9	0.44	0.19–1.03	97.5
Isurus oxyrinchus	6	1.08	0.69–1.71	70.3
Pseudocarcharias kamoharai	4	2.07	0.93–4.64	61.1
Other requiem, Carcharhinidae	8	1.13	0.72–1.77	68.8
Mackerel, Lamnidae	8	0.97	0.33–2.83	96.9
Thresher, Alopiidae	5	0.75	0.46–1.22	58.8

Studies included in "all sharks combined" analysis: refer to Figure 2.
Prionace glauca—Afonso et al. (2011), Bolten et al. (2005; 1, 2, 4A), Carruthers et al. (2009), Curran and Bigelow (2011), Gilman et al. (2007), Kerstetter and Graves (2006, fall), Kim et al. (2006, 2007), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009), Watson et al. (2005), Yokota et al. (2006).
Pteroplatytrygon violacea—Carruthers et al. (2009), Curran and Bigelow (2011), Kerstetter and Graves (2006, fall), Kim et al. (2006, 2007), Pacheco et al. (2011), Piovano et al. (2010), Promjinda et al. (2008), Ward et al. (2009).
Isurus oxyrinchus—Afonso et al. (2011), Carruthers et al. (2009), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009), Yokota et al. (2006).
Pseudocarcharias kamoharai—Kim et al. (2006, 2007), Pacheco et al. (2011), Ward et al. (2009).
Other Requiem, Carcharhinidae—Afonso et al. (2011), Kerstetter and Graves (2006, spring), Kim et al. (2006, 2007), Pacheco et al. (2011), Promjinda et al. (2008), Sales et al. (2010), Ward et al. (2009).
Mackerel, Lamnidae: Afonso et al. (2011), Carruthers et al. (2009), Kim et al. (2006, 2007), Pacheco et al. (2011), Sales et al. (2010), Ward et al. (2009), Yokota et al. (2006).
Thresher, Alopiidae—Curran and Bigelow (2011), Kim et al. (2006, 2007), Promjinda et al. (2008), Yokota et al. (2006).

an analysis from data in Hale et al. (2011) found significantly higher catch rates on J-hooks for all sharks combined as well as by all individual species (eight species).

At-vessel Mortality.—A review of the literature from studies of pelagic longline fisheries indicates at-vessel mortality varied among studies with some reporting reduced at-vessel mortality with the use of circle hooks (Carruthers et al. 2009, Afonso et al. 2011), while others found no significant differences between circle and J-hooks (Kerstetter and Graves 2006, Yokota et al. 2006, Curran and Bigelow 2011, Pacheco et al. 2011). The meta-analysis on eight pelagic longline studies is consistent with a reduction of at-vessel mortality when using circle hooks vs J-hooks for all shark species combined (P = 0.0062, Table 5) and individually for blue shark (P = 0.025, Table 6). The influential analysis did not identify any study with a significant effect on the pooled results. Severe levels of heterogeneity were calculated for both analyses (Table 6). ANCOVA indicated that bait type was a significant covariate (P < 0.05) in the effect of circle vs J-hooks on at-vessel mortality (Table 7). Data for bottom longlines were available only from Hale et al. (2011) and indicated no significant difference in at-vessel mortality rates between hook types for 15 species of sharks.

Hooking Location.—Information on hooking location was available only from studies of pelagic longline gear. Because most studies focused on species other than sharks or because sharks were caught in insufficient quantities to allow meaningful comparisons, hooking location data are not readily reported and a meta-analysis

Table 4. ANCOVA results for the effects of bait type, taxonomic family, and study area (covariate) and hook type on catchability.

	df	Type III SS	MS	*F*-Ratio	*P*
Bait type					
Model	5	1.9041	0.3808	1.87	0.104
Hook	1	0.0075	0.0075	0.04	0.847
Bait type	2	1.8354	0.9177	4.51	0.013
Hook*Bait type	2	0.0664	0.0332	0.16	0.850
Family					
Model	13	3.5684	0.2744	1.35	0.194
Hook	1	0.0365	0.0365	0.18	0.672
Family	6	3.3223	0.5537	2.72	0.016
Hook*Family	6	0.2439	0.0406	0.20	0.976
Area					
Model	7	3.4172	0.4881	2.51	0.019
Hook	1	0.2697	0.2697	1.39	0.241
Area	3	3.0263	1.0087	5.19	0.002
Hook*Area	3	0.3886	0.1295	0.67	0.574

could not be completed. Hooking locations were reported as percentages of external or internal (deep) hooking in a consistent fashion across studies. Researchers generally defined deep-hooking events as those in which the hook was lodged beyond the jaw or mouth and not visible to the data recorder when the shark was brought to the side of the vessel. In general, most studies found that a higher percentage of sharks are hooked externally (i.e., mouth or jaw) on circle hooks as opposed to J-hooks, which tend to lodge mostly internally (i.e., in the throat, esophagus, or gut; Watson et al. 2005, Carruthers et al. 2009, Afonso et al. 2011, Pacheco et al. 2011). However, two other studies found no significant differences and indicated that sharks are hooked externally regardless of hook type (Kerstetter and Graves 2006, Ward et al. 2009). All studies reporting hooking location for pelagic stingrays found that regardless of hook type, stingrays are most often hooked in the mouth or jaw (Promjinda et al. 2008, Carruthers et al. 2009, Piovano et al. 2010).

Discussion

Catchability.—Using circle hooks instead of J-hooks can be a valuable tool for conservation of a bycatch species if their usage reduces mortality or catchability. However, to be widely accepted by the industry, such gear modification must maintain fishing efficiency for the target species (Gilman et al. 2006). Results from our review and meta-analyses suggest that, overall, circle hooks on pelagic longlines do not affect shark catch rates. For all meta-analyses, moderate and severe heterogeneity was present, indicating that differences among results of the studies are not due to chance alone and that other factors affect variability in catchability and contribute to the high inconsistency of the results. It is likely the variety of hooks and other fishing practices combined with low sample sizes contributed to the heterogeneity. Additionally, morphology and predation behavior of sharks differ markedly among species. For example, the common thresher shark, *Alopias vulpinus* (Bonnaterre, 1788), is typically hooked at the caudal fin as they utilize their elongate upper caudal

Table 5. Meta-analysis on at-vessel mortality showing the summary effect and each study effect size (odd ratio, OR) and 95% confidence interval (CI). "Events" represent the total number of sharks identified as dead on each hook category and "Total" represent the total number of sharks caught in each category. The area of each square is proportional to the study's weight in the meta-analysis (W). The dotted vertical line shows the pooled random effects estimate. Species included in each studies: Afonso et al. (2011)—silky shark *Carcharhinus falciformis*, bull shark *Carcharhinus leucas*, oceanic whitetip shark *Carcharhinus longimanus*, dusky shark *Carcharhinus obscurus*, night shark *Carcharhinus signatus*, tiger shark *Galeocerdo cuvier*, nurse shark *Ginglymostoma cirratum*, shortfin mako *Isurus oxyrinchus*, blue shark *Prionace glauca*, scalloped hammerhead *Sphyrna lewini*. Curran and Bigelow (2011)—bigeye thresher *Alopias superciliosus*, *P. glauca*. Carruthers et al. (2009)—*P. glauca*, *I. oxyrinchus*, *Lamna nasus*. Kerstetter and Graves (2006, spring)—unidentified carcharhinid shark, (fall)—*P. glauca*. Pacheco et al. (2011)—*C. falciformis*, *C. longimanus*, *I. oxyrinchus*, *P. glauca*, crocodile shark *Pseudocarcharias kamoharai*, *S. lewini*. Yokota et al. (2006)—*P. glauca*. NOAA (unpubl data)—*P. glauca*, *I. oxyrinchus*, *L. nasus*.

	Circle hook		J-hook				
Study	Events	Total	Events	Total	OR	95%-CI	W (random)%
Afonso et al. (2011)	40	92	34	42	0.18	[0.08; 0.43]	9.2
Kerstetter and Graves (2006, fall)	2	27	8	37	0.29	[0.06; 1.49]	4.0
Pacheco et al. (2011)	8	68	15	56	0.36	[0.14; 0.94]	8.5
Carruthers et al. (2009)	559	8,397	313	2,152	0.42	[0.36; 0.49]	18.9
Kerstetter and Graves (2006, spring)	4	12	7	15	0.57	[0.12; 2.75]	4.2
NOAA (unpubl data)	2,267	11,355	1,619	7,073	0.84	[0.78; 0.90]	19.4
Yokota et al. (2006)	200	2,330	99	1,066	0.92	[0.71; 1.18]	17.9
Curran and Bigelow (2011)	127	4,229	137	5,051	1.11	[0.87; 1.42]	17.9
Pooled effects estimate	3,207	26,510	2,232	15,492	0.60	[0.42; 0.86]	100.0

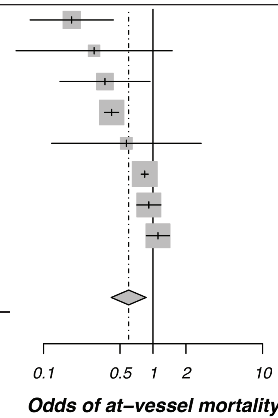

Table 6. Summary of the results of meta-analysis on at-vessel mortality showing the summary effect size (odd ratio, OR) and 95% confidence interval (CI). OR > 1 indicates that a higher at-vessel mortality rate was calculated on circle hooks vs J-hooks. I^2 describes the percentage of total variation across studies that was due to heterogeneity rather than chance. Values >25%, 50%, and 75% are categorized has low, moderate, and high, respectively. * $P < 0.05$, ** $P < 0.01$.

Category	# studies	OR	CI (%)	I^2 (%)
All sharks combined	8	0.60**	0.42–0.86	92.7
Prionace glauca	7	0.65*	0.45–0.95	92.3

Studies included in "all sharks combined" analysis: refer to Figure 3.
Studies included in "*Prionace glauca*" analysis: Afonso et al. (2011), Carruthers et al. (2009), Curran and Bigelow (2011), Kerstetter and Graves (2006, fall), Pacheco et al. (2011), Yokota et al. (2006), NOAA (unpubl data).

lobe to immobilize their prey (Nakano et al. 2003, Aalbers et al. 2010). The lower catch rate for pelagic stingray observed on larger circle hooks is likely explained by their morphology and feeding behavior. This species possesses a small subterminal mouth and employs a different feeding pattern (i.e., sucking) than other shark species. Moreover, based on interviews conducted with pelagic longline fishers from eight different countries, their qualitative experience suggests that hook type may not have a large effect on shark catch rates (Gilman et al. 2007). Consequently, pooled results should be interpreted with considerable caution and differences may exist at the species level.

Bait type, study area, and taxonomic family were found to significantly affect catchability on pelagic longlines. Of these factors, bait type appears to contribute most to shark catchability. For example, interviews conducted with Italian and Japanese longline fishers indicate that to reduce shark interactions, fishers avoid using squid as bait (Gilman et al. 2008). The largest reduction in catch regardless of hook type is found when squid is replaced with fish (usually mackerel species; Watson et al. 2005, Gilman et al. 2007, Galeana-Villasenor et al. 2009). This may be explained in part by the fact that squid baits have longer "longevity" [i.e., remain longer on the hooks, are less likely to deteriorate or lose their attractant qualities over time, and hence have an ability to catch more fish (Ward et al. 2004)]. It would be valuable to examine in greater detail how the use of different bait affects soak time, shark attractant qualities, and overall catch rates of sharks.

The study by Gilman et al. (2007) had a significant influence on the pooled result of the meta-analysis for all shark species combined. This study had the largest sample size (total number of hooks analyzed) and had one of the lowest odds ratios (i.e., much lower shark catch on circle hooks vs J-hooks). When omitted, a slight increase in shark catch on circle hooks was apparent. In fact, the significant drop in shark catches (36%) analyzed in Gilman et al. (2007) in the Hawaiian swordfish longline fishery following the regulations to mitigate bycatch of marine turtles (i.e., the fishery was required to switch from using J-hooks with squid baits to larger 18/0

Table 7. ANCOVA results for the effects of bait type (covariate) and hook type on at vessel mortality.

	df	Type III SS	MS	*F*-ratio	*P*
Model	3	2.1614	0.7204	6.47	0.003
Hook	1	1.3558	1.3558	12.18	0.002
Bait type	1	0.7762	0.7762	6.97	0.015
Hook*Bait type	1	0.1895	0.1895	1.70	0.205

circle hooks 10° offset with fish bait) was primarily attributed to the change of bait rather than the hook, although this was not statistically tested. Other studies have previously demonstrated that catch rates on circle hooks exceed those on J-hooks for a number of teleost species, such as swordfish and yellowfin, *Thunnus albacares* (Bonnaterre, 1788) (e.g., Falterman and Graves 2002, Kerstetter and Graves 2006, Ward et al. 2009). In fact, circle hooks were designed to increase fish catchability (Cooke and Suski 2004) and other studies have shown a similar pattern for some species of sharks (e.g., Ward et al. 2009, Sales et al. 2010, Alfonso et al. 2011, Pacheco et al. 2011). Our pooled data also suggest that for all shark species, blue shark, shortfin mako, crocodile shark, and other requiem sharks, circle hooks tend to be associated with slightly higher shark catches; however, this was not significant.

At Vessel Mortality and Hooking Location.—There is a clear association between hooking location and the severity of the injury. Hooking in the mouth usually induces less of an injury to the fish than deep-hooking, and is associated with lower at-vessel mortality rate and post-release mortality (i.e., species released alive but subsequently dying from injuries or stress). For example, Campana et al. (2009) observed that 96% of sharks that had swallowed the hook were either severely injured or dead, while 97% of sharks that were hooked superficially (mouth or jaw) were released healthy (lively with no apparent trauma). Moreover, postmortem pathology studies have also indicated that deeply embedded hooks (i.e., oesophagus and gastric wall) in the blue shark caused chronic systemic disease (Borucinska et al. 2001, 2002). In contrast to J-hooks, circle hooks are expected to reduce deep hooking and result in higher jaw or mouth hooking frequency because of their round shape, which is expected to rotate more readily inside a fish's mouth (Cooke and Suski 2004). Our review indicates that the majority of the studies found that sharks are more often mouth or jaw hooked (i.e., external) on circle hooks. Results from the meta-analysis are consistent with the notion that circle hooks help reduce at-vessel mortality for all shark species combined and individually for blue shark.

At-vessel mortality rates differ among species (e.g., Carruthers et al. 2009), but due to limitation of data availability, only blue shark at-vessel mortality could be statistically analyzed separately. Blue sharks are known to be a hardy species compared to others, with many studies reporting survival rates of 70%–95% when the shark is brought along the vessel (e.g., Diaz and Serafy 2005, Campana et al. 2006, Campana et al. 2009). However, for all species of shark and blue shark separately, at-vessel mortality was significantly lower with circle vs J-hooks.

In conclusion, our review and meta-analysis indicate that the use of circle hooks does not affect catches of shark species (data combined), but does contribute to reducing at-vessel mortality of shark species (data combined) and individually for the blue shark. While this suggests a tendency for circle hooks to benefit shark conservation, these advantages may not outweigh their negative effect on shark catch rates (i.e., increased catchability) for some species. Nevertheless, as a first step, we contend that, where experimental results support the conservation benefits of using circle hooks and where live-release is legislated and monitored adequately, there is sufficient evidence to promote the use of circle hooks in commercial pelagic longline fisheries. As for demersal longline fisheries, too few data are available to draw conclusions. As noted by previous studies, circle hooks are not a panacea for species conservation (e.g., Cook and Suski 2004, Serafy et al. 2009). In fisheries where there is regulatory framework for sharks and a desire to further minimize shark bycatch and subsequent mortality, managers and scientists are urged to explore additional bycatch mitigation options, such as bait type, which could work in conjunction with the promotion of circle hooks. The high level of heterogeneity found among studies highlights the need for additional controlled experiments designed specifically for sharks over a range of treatments, such that all probable factors affecting catch rates (including hook type) can be effectively modeled.

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