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14	pelagic longline fisheries: management and conservation benefits
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- 38 **Running title**: Meta-analysis of circle hooks vs J-hooks
- 39
- 40 Abstract
- 41 We conducted a meta-analysis of literature reporting on the use of circle hooks and J-hooks
- 42 in pelagic longline fisheries. Our study included more data than previous meta-analyses of
- 43 the effects of hook type, due to both a larger number of relevant studies available in recent
- 44 years and a more general modeling approach. Data from 42 empirical studies were
- 45 analyzed using a random effects model to compare the effects of circle hooks and J-hooks
- 46 on catch rate (43 species) and at-vessel mortality (31 species) of target and bycatch
- 47 species. Catch rates with circle hooks were greater for 11 species, including four tuna

48 species, six shark species, and one Istiophorid billfish. Catch rates on circle hooks were

- 49 lower for seven species, including two Istiophorid billfishes and two species of sea turtle.
- 50 At-vessel mortality was significantly lower with circle hooks in 12 species, including three
- 51 tuna species, three Istiophorid billfishes, swordfish (*Xiphias gladius*), and three shark
- 52 species. No species had significantly greater at-vessel mortality when captured with a circle
- 53 hook rather than a J-hook. While our general approach increased model variability
- 54 compared to more detailed studies, results were consistent with trends identified in
- 55 previous studies that compared the catch rates and at-vessel mortality (between hook
- 56 types) for a number of species. Our results suggest that circle hooks can be a promising tool
- 57 to reduce mortality of some bycatch species in pelagic longline fisheries, although the
- 58 effects depend on the species and the metric (catch rate or at-vessel mortality),
- 59 emphasizing the need for fishery-specific data in conservation and management decisions.
- 60 **Keywords:** At-vessel mortality, bycatch, catch rate, circle hooks, meta-analysis, pelagic

61 longline

Author Ma

62 Introduction

- 63 Methods
- 64 Data collection and screening
- 65 Meta-analysis
- 66 Results
- 67 Catch-rate
- 68 At-vessel mortality
- 69 IUCN status
- 70 Discussion
- 71 Tunas
- 72 Sharks
- 73 Billfish, swordfish, and dolphinfish
- 74 Sea turtles
- 75 IUCN
- 76 Analysis considerations and implications
- 77 Conclusions
- 78 Acknowledgements
- 79 References
- 80 Introduction
- 81 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
- 83 implement regulations aimed at mitigating bycatch mortality, including both target species

84 that are released (regulatory discards) and non-target species that are captured. Pelagic 85 longline gear is frequently used to target swordfish (*Xiphias gladius*, Xiphiidae), tunas, 86 common dolphinfish (Corvphaena hippurus, Corvphaenidae), and wahoo (Acanthocybium 87 solandri, Scombridae), and some fisheries may also target sharks (National Marine 88 Fisheries Service (NMFS), 2014; Graves, Horodysky, & Kerstetter, 2012); however, many 89 non-target species are also captured and subsequently discarded for regulatory or 90 economic reasons. Species that are considered by catch vary by fishery; however, several 91 species of conservation concern are among those commonly discarded by longline 92 fisheries, including istiophorid billfishes, sharks, sea turtles, Atlantic bluefin tuna (*Thunnus* 93 thynnus, Scombridae), and occasionally, marine mammals and seabirds (NMFS, 2014). 94 The use of circle hooks may affect the mortality rate of target and bycatch species in 95 pelagic longline fisheries due to the influence of hook type on catch rates, at-vessel 96 mortality (mortality during capture), and post-release mortality (mortality occurring after 97 release from gear). Unlike traditional I- hooks, the point of a circle hook is oriented perpendicular to the shank, forming a circular shape (Serafy, Cooke, Diaz, Graves, Hall, 98 99 Shivji, & Swimmer, 2012a). The rounded shape allows a circle hook to slide over soft tissue 100 in the mouth and esophagus and rotate as the hook exits the mouth of a fish so that the 101 hook sets in the jaw (Kerstetter and Graves, 2006a). Compared to J-hooks, circle hooks 102 have been associated with lower rates of deep-hooking and foul-hooking, leading to 103 improved condition at haulback and increased survival of released animals (Cooke and 104 Suski, 2004: Serafy, Kerstetter, & Rice, 2009: Godin, Carlson, & Burgener, 2012: Graves et 105 al., 2012; Horodysky and Graves, 2005). Circle hooks (vs. J-hooks) have been shown to 106 decrease catch rates in billfish (Serafy et al., 2009) and increase catch rates of target species such as tunas (Pacheco et al., 2011; Graves et al., 2012; Diaz, 2008, Falterman and 107 108 Graves, 2002; Kerstetter and Graves, 2006a), leading to both economic and conservation 109 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 (Horodysky and
Graves, 2005; Walter, Orbesen, Liese, & Serafy, 2012; Carruthers, Schneider, & Neilson,
2009; Serafy et al., 2012a; Yokota, Takahisa, Minami, & Kiyota, 2012). While the
conservation benefits of circle hooks have been recognized by Regional Fisheries

115 Management Organizations (RFMOs), variable results across studies and variation in both 116 target species and fishing practices among international fisheries have prevented 117 enactment of more widespread regulations (Graves et al., 2012). Currently, the Western 118 Central Pacific Fisheries Commission (WCPFC) requires the use of circle hooks on longline 119 vessels using shallow sets to catch swordfish, unless the nation has an alternate mitigation 120 strategy (WCPFC CMM 2008-03). Western Central Pacific Fisheries Commission is the only 121 RFMO requiring the use of circle hooks in any part of the pelagic longline fishery. In the 122 Atlantic, the International Commission for the Conservation of Atlantic Tunas (ICCAT) 123 Standing Committee on Research and Statistics (SCRS) has acknowledged the conservation 124 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 125 126 vet required the use of circle hooks by participating nations. Additionally, the Western 127 Central Atlantic Fishery Commission (a United Nations Food and Agriculture Organization 128 Regional Fisheries Advisory Commission) and partners have developed a draft Caribbean 129 Billfish Management and Conservation Plan that recommends the use of circle hooks in 130 longline and hook-and-line commercial fisheries (David R. Blankinship, pers. comm.). 131 Individual countries may also enact circle hook regulations independently of a RFMO. In 132 the Atlantic, the U.S. and Canadian pelagic longline fleets now require circle hooks, 133 measures that were initially adopted in the USA primarily to reduce impacts to sea turtles (Wilson and Diaz, 2012) and in Canada as a bycatch reduction initiative (Andrushchenko, 134 135 Hank, Whelan, Neilson, & Atkinson, 2014), Mexico is also known to use circle hooks in their 136 pelagic longline fisheries. However, even in countries without circle hook requirements, 137 cases have been observed in which fishers switch to circle hooks after seeing improved 138 catch and condition of target species in their own fleet (Graves et al., 2012). Potential 139 benefits of expanding the use of circle hooks to a greater number of large-scale commercial 140 fisheries and artisanal fleets include increased catch of some target species and reduced 141 post-release mortality rates of both discarded by catch species and regulatory discards of 142 target species. 143 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,

146 Swimmer, & Piovano, 2016). Meta-analyses are used to synthesize results of multiple studies, providing greater power than any one study (Cohn and Becker, 2003), and to 147 148 generate inference from a set of experiments that may otherwise have disparate 149 conclusions (Gurevitch and Hedges, 1999). Our study uses a meta-analysis to quantify the 150 relative effects of using circle hooks compared to J-hooks for target and bycatch species in 151 pelagic longline fisheries from both the Atlantic and Pacific Oceans. Previous meta-analyses 152 have found lower at-vessel mortality and hooking injury using circle hooks (vs. J-hooks) in 153 sharks and billfishes (Serafy et al., 2009; Cooke and Suski, 2004). Conclusions about catch 154 rates vary by taxa. Most studies on sharks have shown increases in catch rates (Favaro and 155 Côté, 2013; Gilman et al., 2016; Cohn and Becker, 2003) on circle hooks, while Serafy et al. 156 (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 programs 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-

162 vessel mortality in species using relative risk (RR) as the measure of effect size.

163 Methods

164 We compiled information from studies and experiments that examined circle and J-hook 165 catch in pelagic longline fisheries, including both Atlantic and Pacific fisheries. Published 166 literature, technical reports, and unpublished data relevant to our search were identified 167 via Google Scholar searches, using the following keywords: circle hook, pelagic longline, 168 and pelagic longline bycatch. Initial references were collected from the *International* 169 Symposium on Circle Hooks held in Coral Gables, Florida from May 4-6, 2011 (Serafy et al., 170 2012a). Collected literature was reviewed for additional references fitting the search 171 criteria. Inclusion in our analysis required that studies used pelagic longlines, reported 172 species-specific data for both circle and J-hooks using the same experimental design, and, at 173 a minimum, presented data on catch numbers or catch rates. For redundant datasets, we 174 used the more recent data source. We use the term 'reference' to refer to a document; 175 'experiment' to refer to a unique dataset considered in our analysis; and 'record' to refer to

- 176 one comparison between circle and J-hooks for a species within an experiment. References
- 177 used were collected before October 2014.
- 178 *`Data collection and screening*

179 Data collected from each reference included species name, hook type, number of hooks

180 fished, total catch, catch rate, and at-vessel mortality (e.g., number of fish dead at

181 haulback). All records were classified as 'circle' or 'J' hooks. Following Kim, Moon, Boggs,

182 Koh, & Hae An (2006) and Serafy et al. (2009) circle hooks were categorized as a type of J-

183 hook because the point is not 'blocked' by the hook shaft when the line becomes taught.

184 . Although hook specifications were recorded when available, even standard hook

185 parameters differ between hook type and manufacturers. Species names were

186 standardized to reflect the current taxonomic names based on the Integrated Taxonomic

187 Information System (ITIS, 2015).

188 Some values that were required, but not directly reported, were derived where 189 possible. For example, the number of fish caught was often derived from catch rates and 190 effort reported in the reference. Each unique experiment was assigned an identification 191 number (ID). Experiments were considered unique if they differed with respect to 192 attributes such as time (year of study or season), location, gear (e.g., hook size), vessel size, 193 or fleet. Results from more than one experiment could be presented in a single reference. 194 Most references included only one or two experiment IDs, although one reference had 195 seven experiment IDs (Andraka et al., 2013) because results were reported for three 196 countries, two target species sets, and different hook comparisons. Each experiment in our 197 dataset was treated as independent.

198 The National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center 199 Pelagic Observer Program (POP) dataset from 1992-2011 was included as a single 200 experiment in our analysis of at-vessel mortality rates. POP data were parsed into two time 201 periods reflecting the U.S. Atlantic pelagic longline fishery before and after implementation 202 of the 2004 circle hook regulations (i.e., 1992-2003 and 2005-2011) and 2004 data were 203 excluded to remove the effect of changes that occurred during the calendar year. Species 204 data from the POP were included in the analysis if the species was already included in our 205 dataset from other references. The POP dataset variable "boarding status" was used to 206 designate individual fish as dead or alive on haulback (NMFS, 2015). Serafy, Orbesen,

207 Snodgrass, Beerkircher, & Walter (2012b) also used POP data to examine the effectiveness 208 of circle hooks; however, their data were selected based on criteria specific to their analysis 209 and were not appropriate for our use. Similarly, we were unable to use data directly from 210 the Foster, Epperly, Shah, & Watson (2012) and Epperly, Watson, Foster, and Shah (2012) 211 studies and were provided raw data by the authors. Our compiled dataset is available in 212 Supplemental Material A and includes records of counts (catch, at-vessel mortality, and 213 hooks fished) for all studies, including those from sources not readily available, such as the 214 POP dataset, Foster et al. (2012) and Epperly et al. (2012). Data from the POP dataset is 215 also provided in Supplemental Material B and allows for replication of our analysis. 216 Meta-analysis 217 Using the data collected, we constructed a suite of meta-analysis models to evaluate

218 differences in catch rate and at-vessel mortality for fish and sea turtles caught on circle and 219 I-hooks and to examine within- and among- experiment variation. Our analysis follows 220 methods used by Godin et al. (2012), but is specific to the pelagic longline fishery, and uses 221 relative risk (RR) rather than an odds ratio. We selected RR as an effect size measure 222 because of its straightforward interpretation. The difference between the calculated RR and 223 a value of 1.0 represents the mean percent change associated with the experimental treatment, such that an RR less than 1.0 indicates lower values for circle hooks compared 224 225 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 226 (circle hook), n_i^1 is the number of experimental hooks fished, c_i is the number of animals 227 caught on control hooks (J-hooks), and n_i^2 is the number of control hooks fished for the 228 229 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 230 number of animals dead at haulback on J-hooks, and n_i^2 is the number of animals caught on 231 232 I-hooks. The RR value is log-transformed to normalize the distribution of effect sizes 233 around zero and to meet the assumption of normality for the analysis.

234 Catch rates and at-vessel mortality for circle and I-hooks were estimated using the 235 *metafor* package (Viechtbauer, 2010) in R 3.11 (R Core Team, 2014) for each species. We 236 computed a summary effect size for all taxa that had at least two experiment IDs, including 237 scenarios in which all experiments came from a single citation. A two-sided Wald-type Z-238 test was used to test for differences between effects mean and zero. Effect sizes were 239 estimated using a random effects model, allowing us to account for heterogeneity among 240 experiments. Heterogeneity was expected due to the many explicit and implicit differences 241 in study designs included in our analysis (e.g., hook size, offset, and manufacturer, capture 242 location, fishery studied, time of fishing, and target species). Although we collected data on 243 other variables, such as hook size, offset, bait-type, target species, and geographic location, 244 we did not include these as fixed effects in our model because they were not reported 245 consistently across studies and would have resulted in a reduction in the data available to 246 test our primary hypotheses.

247 Compared to fixed effects models, the random effects approach is generally considered 248 conservative (Borenstein, Hedges, Higgins, & Rothstein, 2009) and applicable to conditions 249 and locations outside of the scope of the studies analyzed. The random effects model 250 computes a global mean effect size based on a weighted mean of the studies' effect sizes, 251 where the global mean estimate represents the average of the true underlying distribution 252 of effect sizes from which the studies were drawn (Hedges and Vevea, 1998). Weights were 253 computed as the inverse of the sample variance and the between-study variance (τ^2), 254 thereby placing more weight on experiments with estimates having greater precision and 255 de-emphasizing those weights with high between-study variance. Sample variance, v_i , for 256 ln(RR) of the *ith* 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 *P* as a measure of total variation across experiments due to variability among experiments (Higgins, Thompson, Deeks, & Altman, 2003). Values of *P* 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). 262 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 analyzed 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 Supplemental Material C) and atvessel mortality estimates were obtained for 31 species (Table 2 and Supplemental Material D).

270 Meta-analysis results for 43 species are reported here to evaluate differences in catch 271 rate and at-vessel mortality among target and bycatch species caught with circle and J-272 hooks in the pelagic longline fishery. Forest plots of catch rate and at-vessel mortality for 273 species included in our meta-analysis are provided in Supplemental Material C and D and 274 present the results and variation among the individual studies used in our meta-analysis. 275 Results for swordfish and yellowfin tuna (Thunnus albacares, Scombridae) are presented 276 in Figures 1-4 as examples. The meta-analysis found that swordfish catch rates were not 277 significantly different between circle and J-hooks (Table 1). Forest plots of the individual 278 experiments show 13 experiments with higher swordfish catch rates and the remaining 13 279 with lower, or no difference in, catch rates with circle hooks (Fig. 2). At-vessel mortality in 280 swordfish was lower (or showed no difference) when caught with circle hooks (Table 2) 281 and only one experiment found greater at-vessel mortality in swordfish with circle hooks 282 (vs. I-hooks) (Fig. 3). For vellow fin tuna, the forest plots show lower catch rates on circle 283 hooks in four experiments, higher in 12 experiments (Fig. 4), and the summary effect size 284 (RR=1.32) was significant (Table 1). Forest plots of at-vessel mortality of yellowfin tuna 285 (Fig. 5) indicate lower (four experiments) or no difference (one experiment) in mortality 286 on circle hooks (vs. I-hooks), combined with an overall significant reduction in at-vessel 287 mortality (RR=0.84, p= 0.003) (Table 2).

288 Catch rate

289 The difference in catch rate with circle hooks (vs. J-hooks) was significantly greater

290 ($p \le 0.05$) for 11 of the 43 species evaluated (Table 1, Fig. 6) and significantly lower for

seven species ($p \le 0.05$). 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 turtlespecies and other fish species, and mixed for the billfish species.
- The 11 species with higher catch rates included four species of tuna: yellowfin tuna,
 albacore *(Thunnus alalunga,* Scombridae), bigeye tuna (*Thunnus obesus,* Scombridae), and
- 297 Atlantic bluefin tuna; Atlantic sailfish (hereafter simply "sailfish" *Istiophorus platypterus*,
- 298 Istiophoridae); and six species of sharks: silky shark (*Carcharhinus falciformis,*
- 299 Carcharhinidae), shortfin mako shark (*Isurus oxyrinchus*, Lamnidae), salmon shark (*Lamna*
- 300 *ditropis*, Lamnidae), porbeagle shark (*Lamna nasus*, Lamnidae), blue shark (*Prionace*
- 301 glauca, Carcharhinidae), and crocodile shark (Pseudocarcharias kamoharai,
- 302 Pseudocarchariidae). The seven species that showed lower catch rates with circle hooks
- 303 (vs. J-hooks) were two species of sea turtles: loggerhead sea turtle (*Caretta caretta,*
- 304 Cheloniidae) and olive ridley sea turtle (*Lepidochelys olivacea*, Cheloniidae), two billfishes:
- 305 striped marlin (*Kajikia audax*, Istiophoridae) and shortbill spearfish (*Tetrapturus*
- 306 angustirostris, Istiophoridae), sickle pomfret (Taractichthys steindachneri, Bramidae),
- 307 snake mackerel (*Gempylus serpens*, Gempylidae), and dolphinfish.
- Effect sizes for species with significant differences in catch rate between circle hooks and J-hooks (Fig. 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.
- 313 Increases in catch rate with circle hooks (vs. I-hooks) ranged from 20% greater in the 314 sailfish (RR=1.20; p=0.05) to 246% greater in the crocodile shark (RR=3.46; p<0.001). 315 Catch rate more was more than doubled for species in the genus *Lamna* (porbeagle shark 316 RR = 2.08; p<0.001 and salmon shark RR = 2.44; p=0.04) caught using circle hooks 317 compared to I-hooks. Among thunnid tunas, catch rates ranged from 32% greater in 318 vellow fin tuna (RR=1.32; p=0.0098) to 87% greater in blue fin tuna (RR=1.87; p<0.001) 319 when circle hooks were used. For the Carcharhiniformes, increases in catch rates were 320 40% (RR=1.40; p<0.001) and 46% (RR=1.46; p<0.001) higher with circles hooks for the 321 silky and blue sharks, respectively. 322 Effect sizes for catch rates that were lower with circle hooks (vs. J-hooks) ranged from
- 323 16% lower catch rate (RR=0.84; p=0.01) in dolphinfish to 66% lower catch rate (RR=0.34;

p<0.001) in snake mackerel. Catch rates for loggerhead and olive ridley sea turtles were

325 42% (RR=0.58; p=0.02) and 31% (RR=0.69; p=0.0049) lower, respectively, when circle

326 hooks were used rather than J-hooks.

327 At-vessel mortality

328 Twelve species evaluated had significantly ($p \le 0.05$) lower at-vessel mortality rate when

- 329 caught on circle hooks (vs. J-hooks), including three species of shark (oceanic whitetip
- 330 shark, shortfin mako shark, and scalloped hammerhead– *Sphyrna lewini*), two species of
- tuna (yellowfin and bluefin), four billfishes (blue marlin, sailfish, white marlin, and
- 332 swordfish, dolphinfish, and opah (*Lampris guttatus*, Lamprididae) (Table 2, Fig. 7).
- Reductions in at-vessel mortality ranged from 62% in the oceanic whitetip shark (RR=0.38,
- p=0.03) to eight percent in the swordfish (RR=0.92, p=0.0036). However, 10 of the 12
- 335 species had reductions ranging from 14% to 30%.

No significant differences in at-vessel mortality due to capture by circle hook (vs. Jhook) 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.

343 IUCN status

344 The IUCN program *Red List of Threatened Species* lists risk status of species on a global 345 scale in an effort to highlight taxa threatened with extinction and promote their 346 conservation (Rodrigues, Pilgrim, Lamoreux, Hoffman, & Brooks, 2006). The IUCN designations, in order of decreasing risk, are "endangered", "vulnerable", "near threatened", 347 348 and "least concern" ("data deficient" and "not evaluated" are also included, but are not 349 related to risk). IUCN designations for species with significant differences in catch rate (18) 350 species) or at-vessel mortality (12 species) between circle and I-hooks are indicated in 351 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,

355 blue, and silky sharks), and two (salmon shark and sailfish) are listed as species of least 356 concern (Fig. 6). Among these, five of the six shark species that had higher catch rates on 357 circle hooks, are considered near threatened or vulnerable by the IUCN (none had higher 358 at-vessel mortality with circle hooks). The five species with lower catch rates with circle 359 hooks (vs. I-hooks) are listed as vulnerable (both sea turtles), near threatened (striped 360 marlin), and of least concern (snake mackerel and dolphinfish). The shortbill spearfish and 361 sickle pomfret are designated as "data deficient" and "not evaluated", respectively. 362 The bluefin tuna and scalloped hammerhead are the only species listed as endangered 363 on the IUCN *Red List of Threatened Species* that had lower at-vessel mortality with circle 364 hooks (vs. I-hooks) (Fig. 7). The remaining species with lower at-vessel mortality are IUCN-365 listed as vulnerable (oceanic whitetip shark, shortfin mako shark, blue marlin, striped 366 marlin), near threatened (yellowfin tuna), and of least concern (swordfish, sailfish, opah, 367 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. 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).

373 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; Crowder and Murawski, 1998; Lewison, Crowder, Read, &
Freeman, 2004; Kerstetter and Graves, 2006a; Andraka et al., 2013). 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.

381 Tunas <

382 Our results found increases in catch rate on circle hooks for all four *Thunnus* species

analyzed. 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.

392 Yellowfin tuna is one of the primary targets of pelagic longline fisheries on a global 393 scale (Allen, 2010) and higher catch rates with circle hooks may help overcome the 394 skepticism of fishers and clear the way for adoption of circle hooks. Furthermore, landing 395 live tuna leads to a higher quality (i.e., more valuable) ex-vessel product; therefore, 396 increasing the number of fish alive at haulback may be an additional incentive for circle 397 hook adoption by tuna fishers (Foster, Parsons, Snodgrass, & Shah, 2015; Serafy et al., 398 2012b; Clucas, 1997). For example, Venezuelan pelagic longline fishers targeting yellowfin 399 tuna were reluctant to experiment with circle hooks because of perceived catch reductions 400 (Falterman and Graves, 2002). However, after higher catches and lower immediate 401 mortality rates were demonstrated in their fishery, they adopted the use of circle hooks 402 (Graves et al., 2012). These financial gains may be significant enough to offset the cost of 403 gear conversion to circle hooks, as was demonstrated in the Australian fisheries targeting 404 bigeye and yellowfin tuna and swordfish (Ward et al., 2009).

405 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 (Yokota, Kiyota, & Minami, 2006; Ward et al., 2009; Pacheco et al.,

417 2011), higher catch rates (Watson, Epperly, Shah, & Foster, 2005; Ward et al., 2009; Afonso 418 et al., 2011; Pacheco et al., 2011), and (infrequently) lower catch rates (Gilman et al., 2007; 419 Curran and Bigelow, 2011; Kerstetter and Graves, 2006a) for pelagic shark species. Godin 420 et al. (2012) evaluated effects of circle vs. J-hooks reported in 30 studies and found higher 421 catch rates with circle hooks, except for blue, shortfin mako, crocodile, and common 422 thresher (*Alopias vulpinus*, Alopiidae) sharks, which showed no significant effects. An 423 analysis of circle vs. J-hooks by Gilman et al. (2016) demonstrated higher catch rates in 424 crocodile, whitetip, and silky sharks, consistent with results of the present study, but lower 425 catch rates in blue sharks. Both Godin et al. (2012) and Gilman et al. (2016) demonstrated 426 lower at-vessel mortality (or greater survival), consistent with our results for pelagic 427 species.

428 One potentially confounding factor was the use of different leader types with different 429 hook types. Experiments conducted by Watson et al. (2005) found that circle hooks had a 430 significantly higher catch rate and lower gut hooking rate of blue shark when compared to 431 I-hooks; however, the authors hypothesized that use of monofilament leaders may have 432 confounded catch rate comparisons because gut-hooked sharks are more likely to bite off 433 these leaders and escape detection. Afonso, Santiago, Hazin, & Hazin (2012) found that 434 wire leaders had higher shark catch rates and that significantly more sharks were captured 435 alive on wire vs. monofilament leaders (but see Yokota (2006) for a counterexample). They 436 cautioned that, in longline fisheries, shark catch and mortality rates may be 437 underestimated when monofilament leaders were used. Unfortunately, the data available 438 did not allow us to control for this factor in our analysis, but, due to the paired nature of 439 most studies included in our analysis, leader type was controlled for on longline sets within 440 experiments by simply alternating hook type with otherwise identical terminal gear. 441 Piovano, Basciano, Swimmer, & Giacoma (2012) provide an exception, where one fishing 442 crew bunched experimental hooks on portions of the line. This control was not possible for 443 the pelagic observer data, and the potential bias previously noted (Beerkircher, Cortes, & 444 Shivji, 2003). The effect of leader type on and mortality metrics is an area for future 445 research, especially with respect to sharks. Respiratory mode is a key factor controlling 446 post-release mortality in elasmobranchs. Dapp, Walker, Huveneers, & Reina (2016) and 447 Ellis, McCully Phillips, & Poisson (2017) found that obligate ram-venting sharks, such as

448 Carcharhinids and Lamnids, have higher discard mortality (combined at vessel mortality 449 and post-release mortality) than stationary-respiring species because their respiration is 450 impaired during capture. Ram-ventilating pelagic fish species, such as tunas, mackerels, 451 and billfishes, may also have impaired respiration during capture (Wegner, Sepulveda, 452 Aalbers, & Graham, 2013), although to our knowledge there are no comparable analyses 453 available for bony fish. Water temperature and soak time are other factors influencing 454 shark discard mortality. Shark survival in pelagic longline fisheries significantly decreases 455 with increasing water temperature (and corresponding lower dissolved oxygen 456 concentration) and soak time, which favors asphyxiation and increases capture stress in 457 sharks (Skomal and Bernal, 2010; Gallagher, Orbesen, Hammerschlag, & Serafy, 2014). 458 Our results suggest that circle hooks would reduce at-vessel mortality in three ram 459 ventilating sharks – oceanic whitetip, scalloped hammerhead, and shortfin mako. This 460 result is particularly promising for their management because these species are commonly 461 caught in pelagic longline fisheries (Coelho, Santos, & Amorim, 2012), and their 462 conservation status is a matter of international concern. A decrease in at-vessel mortality 463 for bycatch of these shark species does not necessarily translate to a decrease in post-464 release mortality of released individuals, however, some proportion of post-release 465 mortality is related to physiological stress and injuries experienced during capture (Skomal 466 2007). To our knowledge, no studies specifically address post-release mortality of 467 scalloped hammerhead from pelagic longlines (Gallagher et al., 2014). Few studies have 468 estimated such rates in other large pelagic shark species, but see examples for oceanic 469 whitetip and shortfin mako (Musyl et al. 2011), the blue shark (Moyes, Fragoso, Musyl, & 470 Brill, 2006; Campana, Joyce, & Manning, 2009) and common thresher shark (Heberer et al., 471 2010; Sepulveda et al., 2015).

472 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, Luckhurst,

479 Prince, & Graves, 2003; Kerstetter and Graves, 2006b; Kerstetter and Graves, 2008); 480 therefore, the differences in at-vessel mortality that we observed are likely to result in a 481 conservation benefit to the species. These species are particularly important to 482 recreational fisheries in tropical and subtropical oceanic waters, and similar reductions in 483 immediate mortality and injury due to hook trauma have been observed in recreational 484 billfish fisheries, although survival is generally higher in the recreational fishery than in 485 pelagic longline fisheries (Horodysky and Graves, 2005, Kerstetter and Graves, 2006b, Prince et al., 2007). 486

487 Billfishes are among the most common highly migratory species targeted by for-hire 488 charter boats. Recreational catch of white marlin along the Atlantic and Gulf coasts ranges 489 between 4,000 and 12,000 individuals annually (Goodyear and Prince, 2003; NMFS, 2006) 490 and recreational fishing for dolphinfish and other pelagic fish species along the U.S. Mid-491 Atlantic has increased in recent years due to improved access of anglers to offshore pelagic 492 waters (Dell'Apa et al., 2015). Management and other conservation measures are needed 493 for these fish, particularly in consideration of the rapid expansion of the recreational 494 fishery in developing countries (Pitcher and Hollingworth, 2002; Alió, 2012) and on a 495 global scale (Ihde, Wilberg, Loewensteiner, Secor, & Miller, 2011). The potential reduction 496 in mortality due to pelagic longline interactions provided by conversion to circle hooks is 497 promising for the conservation and management of these species, particularly in the 498 Atlantic, Regulations requiring the use of circle hooks could be part of a broader 499 management strategy to curtail the impacts of recreational and commercial fishing to 500 billfish populations. Further research into post-release survival rates in secondary target 501 species, an issue which has only been marginally explored in longline fisheries (Graves and 502 Horodysky, 2008), would be helpful to management and conservation efforts. 503 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 nonsignificant increase in at-vessel mortality, which mirrors the results found in other studies. Additionally, differences in mortality rates were typically attributed 510 to combinations of covarying factors, for example, Cambiè, Muiño, Freire, & Mingozzi.

511 (2012) found that mortality of sea turtles increased with soak time and decreased in

512 relation to the size of the animal.

513 *IUCN*

The results of our analysis indicated increased catch rates with circle hooks in four pelagic 514 515 species (shortfin mako and porbeagle sharks, bigeye, and bluefin tuna) identified as 516 vulnerable or endangered by the IUCN. Reduced at-vessel mortality with circle hooks 517 (compared with I-hooks) was found in three shark species, bluefin tuna, and two billfish 518 species listed as endangered or vulnerable by the IUCN (Table 3). These results are 519 consistent with those previously reported for sharks (Gilman et al., 2016, Serafy et al., 520 2012a), billfishes (Prince, Prince, Ortiz, & Venizelos, 2002; Domeier, Dewar, & Nasby-Lucas, 521 2003; Horodysky and Graves, 2005; Prince et al., 2007; Skomal, 2007), and bluefin tuna 522 (Skomal, Chase, Prince, Lucy, & Studholme, 2002; Prince et al., 2002), which presume that 523 external (vs. internal) hooking results in reduced mortality. In addition, we found reduced 524 catch rates for two sea turtle species when circle hooks were used, consistent with findings 525 of previous studies (e.g., Watson et al., 2005, Foster et al., 2012). We believe the use of 526 circle hooks may be helpful in reducing at-vessel mortality for several at-risk species in the 527 list, and therefore provide a valuable tool for management and conservation of bycatch 528 species.

529 Cortés et al. (2010), in an assessment of the vulnerability of sharks in the Atlantic 530 pelagic longline fishery, found that as a group, pelagic sharks are particularly vulnerable to 531 pelagic longline fisheries, primarily due to their low productivity and high susceptibility to 532 capture and subsequent mortality. The study ranked silky and shortfin mako sharks as the 533 first and second most vulnerable, respectively, followed by the oceanic whitetip shark 534 (ranked 5), blue shark (ranked 7), scalloped hammerhead (ranked 9), and porbeagle 535 (ranked 10). Of these ranked species, the shortfin make, porbeagle, and oceanic whitetip 536 shark are IUCN-designated as vulnerable, and scalloped hammerhead as endangered. The 537 remaining species are listed as of least concern or not threatened. Although higher catch 538 rates may not translate into higher mortality, concern remains regarding the ability of 539 circle-hooks to contribute to the conservation of some species of sharks. Reduced at-vessel 540 mortality with circle hooks is expected to benefit sharks caught in regulated fisheries by

541 increasing the number of sharks released alive, while higher catch rates remain a concern 542 in unregulated fisheries because both dead and live sharks may be retained (Serafy et al., 543 2012a). We used the IUCN *Red List of Threatened Species* to evaluate, at a high level, the 544 potential conservation implications of hook type changes in pelagic longline fisheries. 545 While we recognize that formal stock assessments are the best source of information for 546 evaluating stock status, not all species evaluated here have been formally assessed. We 547 consider the IUCN *Red List of Threatened Species* to be a useful proxy, as the IUCN process 548 provides a formal and consistent evaluation of population risk (Rodrigues et al., 2006) 549 across species, and stock assessments are considered during the designation process (e.g.,

550 Collette et al., 2011).

551 *Analysis considerations and implications*

552 Our results are consistent with previous studies of the effects of circle hooks on pelagic 553 fishes, in which reduced at-vessel mortality in sharks (Godin et al., 2012; Favaro and Côté, 554 2013; Gilman et al., 2016), billfishes (Graves et al., 2012; Horodysky and Graves; 2005, Graves and Horodysky, 2008; Serafy et al., 2009; Prince et al., 2002), and tunas (Cooke and 555 556 Suski, 2004; Pacheco et al.; 2011, Skomal et al.; 2002) were found. However, ours is the first 557 meta-analysis to examine these differences at the species level for a large number of 558 species and provides new information regarding differences in catch rates and at-vessel 559 mortality between species. For example, Serafy et al. (2009) found no species-specific 560 patterns in catch rate or mortality for billfishes between circle hooks and I-hooks but found 561 higher mortality and injury rates on J-hooks across studies analyzed. Since the publication 562 of that review, several other studies have been published that we were able to include in 563 our analysis. Our findings were consistent with Serafy et al. (2009), in that all billfishes had 564 significant decreases or no change in at-vessel mortality with circle hooks. However, we 565 found significant, mixed results for catch rates – sailfish catch rates increased on circle 566 hooks, while striped marlin and shortbill spearfish catch rates were reduced on circle 567 hooks relative to I-hooks.

Variability among datasets (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 and Suski, 2004; Serafy et al., 2009; Serafy et al., 2012b; Graves et al., 2012).

572 We did observe heterogeneity across studies (as measured by I^2) and recognize that it is 573 due to variability among datasets that was accounted for as a random effect rather than 574 fixed-factors. By grouping at the highest level of hook type (circle or]) rather than 575 including additional fixed-factors such as hook manufacturer model, hook size, and hook 576 offset, we risk losing information. However, our estimates of effect are useful as estimates 577 of benefits over a wider range of conditions, particularly because there is a limit to the level 578 of control that regulations or conservation projects may place on the fishing characteristics 579 of participating vessels or fisheries. Including additional factors, such as hook size and 580 offset, would have reduced the available data by restricting the study dataset to those 581 studies that included the additional variables of interest. We considered binning species 582 into higher taxonomic categories (e.g., order-level analysis), which would allow for the 583 inclusion of more data; however, this greatly increased between-study heterogeneity. 584 Additionally, we recognize that for analyses that included few experiments, RR estimates 585 should be used with caution and should only be considered a first-order approximation of the population mean (Hedges and Vevea, 1998), as they are based on datasets that cover 586 587 fewer variations in gear configuration and less geographic range, which may not overlap 588 with a species' primary range.

589 Compared to Serafy et al. (2012b), which included a smaller data set but accounted for a 590 larger number of variables, our species-specific estimates for at-vessel mortality were 591 generally more conservative in representing the magnitude of change, but in all cases 592 reflected the same trends in the direction of change. The agreement between our results 593 and similar studies suggest that our estimates could be applicable to fisheries for which we 594 lack fishery-specific estimates to generate a reasonable estimate of the benefits of using 595 circle hooks. However, we recognize the need for fishery-specific estimates of the impacts 596 of circle hooks in conjunction with the implementation of potential projects that attempt to 597 increase circle hook use in fisheries.

598 Greater coordination across scientific and management bodies with respect to common 599 study parameters and variables might allow smaller scale studies to be combined more 600 easily and, therefore, increase the power of meta-analyses. If the information provided by 601 the studies were standardized, it would expand the availability of appropriate data and 602 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 ofhooks 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.
Conclusions

610 Results of our analysis indicate that circle hooks can benefit the management and 611 conservation of target species and some common bycatch species caught in commercial 612 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 613 614 hooks to be effective in fostering species conservation, international adoption of this 615 fishing gear (and proper handling/release procedures) is needed, given the migratory 616 behavior 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 617 618 some recreational fisheries.

619 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 620 621 measure for reducing by catch mortality for a specific fishery should be evaluated prior to 622 implementation either experimentally or more specific analysis, consistent with other findings (Graves et al., 2012; Cooke and Suski, 2004). Particular attention should be given 623 624 to species that had high *P*, where the heterogeneity may indicate differences in 625 experimental design or fishery characteristics (e.g., bait type, hook depth, and hook types) 626 can lead to divergent results. Transition to circle hooks may be expedited by direct 627 outreach that provides fishers with opportunities to evaluate the potential for circle hooks 628 to increase catch rate of target species while decreasing catch and mortality of bycatch 629 species. Impacts to a specific fishery with respect to target species, catch rates, bycatch, 630 and management goals should be evaluated to assess the potential conservation benefits of 631 circle hooks.

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- 640 **References** – * indicates articles used in the meta-analysis
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- 925 **1.1 Catch rate and at-vessel mortality of circle hooks versus J-hooks**
- 926 in pelagic longline fisheries: a global meta-analysis: Tables
- 927

Table 1: Results of the meta-analysis on catch rates showing the summary effect size (relative risk, RR) and
95% confidence interval (CI). RR > 1 indicates a higher catch was calculated on circle hooks compared to Jhooks. *P* describes the percentage of total variation caused by between-study heterogeneity rather than
within-study variance. P-values that are less than or equal to 0.05 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 with an extinction risk.

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	#exn	RR	CI	<u>p</u>	n	References	Status
Aulopiformes	"схр.	Ĩ	ŭ		Ρ	References	Status
<u> </u>						(Coelho et al., 2012, Curran and Bigelow, 2011, Kim et al.,	
Longnose lancetfish	8	0.96	0.74-1.25	71%	0.790	2007, Kim et al., 2006, Promiinda et al., 2008, Ward	LC
V						et al., 2009)	
Carcharhiniformes							
Silky shark	9	1.4	1.18-1.67	49%	<0.001	(Afonso et al., 2011, Andraka	NT

et al., 2013, Pacheco et al., 2011, Promjinda et al., 2008, Ward et al., 2009, Yokota et al., 2006) (Afonso et al., 2011, Kim et al., 2007, Kim et al., 2006, Oceanic whitetip shark 0.85-2.32 0% 0.190 VU 6 1.4 Pacheco et al., 2011, Ward et al., 2009, Yokota et al., 2006) (Afonso et al., 2011, Domingo Night shark VU 2 1.87 0.75-4.66 72% 0.180 et al., 2012) (Afonso et al., 2011, Coelho et Tiger shark 0.890 al., 2012, Promjinda et al., NT 0.87 0.12-6.4 63% 2008, Ward et al., 2009) (Afonso et al., 2011, Andraka et al., 2013, Bolten and Bjorndal, 2005, Cambiè et al., 2012, Curran and Bigelow, 2011, Domingo et al., 2012, Foster et al., 2012, Huang et al., 2016, Kerstetter and Blue shark 99% <0.001 24 NT 1.46 1.18 - 1.8Graves, 2006a, Kim et al., 2007, Kim et al., 2006, Largacha et al., 2005, Mejuto et al., 2008, Pacheco et al., 2011, Sales et al., 2010, Ward et al., 2009, Yokota et al., 2006) (Afonso et al., 2011, Domingo et al., 2012, Kim et al., 2007, Scalloped hammerhead 7 0.85 0.57 - 1.280% 0.440 EN Kim et al., 2006, Pacheco et al., 2011, Sales et al., 2010)

Smooth hammerhead	2	0.25	0.03-2.31	0%	0.220	(Kim et al., 2007, Kim et al., 2006)	VU
Lamniformes							
Pelagic thresher	6	0.6	0.25-1.42	26%	0.250	(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%	0.070	(Coelho et al., 2012, Curran and Bigelow, 2011, Kim et al., 2007, Kim et al., 2006, 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%	0.036	(Kim et al., 2007, Kim et al., 2006, Yokota et al., 2006)	LC
Porbeagle shark	3	2.08	1.84-2.34	0%	<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., 2007, Kim et al., 2006, Pacheco et al., 2011, Ward et al., 2009)	NT

Lampridiformes

Opah	4	1.18	0.68-2.02	87%	0.560	(Curran and Bigelow, 2011, Kim et al., 2007, Ward et al., 2009)	LC
Myliobatiformes							
Pelagic stingray	15	0.64	0.36-1.13	87%	0.120	(Andraka et al., 2013, Cambiè et al., 2012, Coelho et al., 2012, Curran and Bigelow, 2011, Domingo et al., 2012, Kerstetter and Graves, 2006a, Kim et al., 2007, Kim et al., 2006, Pacheco et al., 2011, Promjinda et al., 2008, Ward	LC
Percoidei						et al., 2009)	
Atlantic pomfret	2	3.11	0.86-11.22	90%	0.084	(Kim et al., 2007, Kim et al., 2006)	LC
Sickle pomfret	2	0.83	0.71-0.97	68%	0.022	(Curran and Bigelow, 2011)	NE
Dolphinfish	21	0.84	0.74-0.97	95%	0.013	(Andraka et al., 2013, Cambiè et al., 2012, Curran and Bigelow, 2011, Domingo et al., 2012, Kerstetter and Graves, 2006a, Kim et al., 2007, Kim et al., 2006, 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%	0.730	(Kim et al., 2007, Promjinda et al., 2008, Ward et al., 2009)	LC

Scombroidei

Snake mackerel	4	0.34	0.31-0.37	0%	<0.001	(Curran and Bigelow, 2011, Promjinda et al., 2008, Ward et al., 2009)	LC
Escolar Book	11	1.31	0.94–1.82	82%	0.110	(Andraka et al., 2013, Curran and Bigelow, 2011, Domingo et al., 2012, Kerstetter and Graves, 2006a, Kim et al., 2007, Kim et al., 2006, Pacheco et al., 2011, Promjinda et al., 2008, Ward et al., 2009)	LC
Oilfish	6	0.76	0.49-1.18	0%	0.220	(Cambiè et al., 2012, Domingo et al., 2012, Kim et al., 2007, Kim et al., 2006, Largacha et al., 2005)	LC
Wahoo O	9	1.08	0.69-1.69	73%	0.730	(Andraka et al., 2013, Curran and Bigelow, 2011, Domingo et al., 2012, Kim et al., 2007, Kim et al., 2006, Pacheco et al., 2011, Ward et al., 2009)	LC
Skipjack tuna	7	1.08	0.69-1.69	57%	0.730	(Andraka et al., 2013, Curran and Bigelow, 2011, Kim et al., 2007, Kim et al., 2006, Ward et al., 2009)	LC
Albacore	11	1.46	1.01-2.1	93%	0.044	(Curran and Bigelow, 2011, Domingo et al., 2012, Foster et al., 2012, Huang et al., 2016, Kim et al., 2007, Kim et al., 2006, Pacheco et al., 2011,	NT

						Sales et al., 2010, Ward et al., 2009)	
Yellowfin tuna	16	1.32	1.07-1.62	87%	0.010	(Andraka et al., 2013, Curran and Bigelow, 2011, Domingo et al., 2012, Huang et al., 2016, Kim et al., 2007, Kim et al., 2006, 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%	0.002	(Andraka et al., 2013, Curran and Bigelow, 2011, Domingo et al., 2012, Foster et al., 2012, Huang et al., 2016, Kim et al., 2007, Kim et al., 2006, 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%	<0.001	(Cambiè et al., 2012, Foster et al., 2012)	EN
Squaliformes Velvet dogfish Testudines	2	3.48	0.41-29.32	75%	0.250	(Kim et al., 2007, Kim et al., 2006)	NE
Loggerhead sea turtle	16	0.58	0.36-0.92	91%	0.021	(Andraka et al., 2013, Boggs and Swimmer, 2007, Bolten and Bjorndal, 2005, Cambiè et al., 2012, Domingo et al., 2012, Foster et al., 2012, Gilman et al., 2007, Huang et	VU

						al., 2016, Mejuto et al., 2008, Piovano et al., 2012, Sales et al., 2010)	
Green sea turtle	10	0.72	0.49-1.06	37%	0.100	(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%	0.630	(Andraka et al., 2013)	CR
Olive ridley sea turtle	14	0.69	0.53-0.89	60%	0.005	(Andraka et al., 2013, Huang et al., 2016, Kim et al., 2007, Kim et al., 2006, Largacha et al., 2005, Mejuto et al., 2008, Pacheco et al., 2011, Santos et al., 2012)	VU
Leatherback sea turtle	10	0.64	0.38-1.08	89%	0.093	(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%	0.970	(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%	0.560	(Andraka et al., 2013, Promjinda et al., 2008)	DD
Sailfish	8	1.2	1-1.44	38%	0.048	(Andraka et al., 2013, Kim et	LC

al., 2007, Kim et al., 2006, Pacheco et al., 2011, Promjinda et al., 2008)

White marlin	2	0.98	0.77-1.25	0%	0.880	(Andraka et al., 2013, Pacheco et al., 2011)	VU
Striped marlin	5	0.86	0.76-0.97	56%	0.015	(Curran and Bigelow, 2011, Kim et al., 2007, Kim et al., 2006, Ward et al., 2009)	NT
Blue marlin	7	0.96	0.63-1.46	69%	0.840	(Andraka et al., 2013, Curran and Bigelow, 2011, Kim et al., 2007, Kim et al., 2006, Pacheco et al., 2011, Ward et al., 2009)	VU
Shortbill spearfish	6	0.66	0.51-0.84	56%	0.001	(Curran and Bigelow, 2011, Huang et al., 2016, Kim et al., 2007, Kim et al., 2006, Ward et al., 2009)	DD
Swordfish	26	1	0.81-1.23	97%	0.980	 (Andraka et al., 2013, Boggs and Swimmer, 2007, Bolten and Bjorndal, 2005, Cambiè et al., 2012, Curran and Bigelow, 2011, Domingo et al., 2012, Foster et al., 2012, Gilman et al., 2007, Huang et al., 2016, Kerstetter and Graves, 2006a, Kim et al., 2007, Kim et al., 2006, 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

- 936 Table 2: Results of the meta-analysis on at-vessel mortality showing the summary effect size (relative risk,
- 837 RR) and 95% confidence interval (CI). RR > 1 indicates a higher at-vessel mortality was calculated on circle
- 938 hooks compared to J-hooks. *P* describes the percentage of total variation caused by between-study
- 939 heterogeneity rather than within-study variance. P-values that are less than or equal to 0.05 are in bold to
- 940 indicate significance. Status refers to IUCN Red List conservation status category where LC Least Concern,
- 941 NT Near Threatened, VU Vulnerable, EN Endangered, and CR Critically Endangered are categories with
- 942 increasing extinction risk. The categories DD Data Deficient, and NE Not Evaluated, are not categorized
- 943 with an extinction risk.

	#exp.	RR	CI	P	р	References	Status
Aulopiformes Longnose lancetfish	2	1.07	0.9- 1.28	98%	0.420	(Curran and Bigelow, 2011)	LC
Carcharhiniformes							
Silky shark	2	0.57	0.24- 1.32	54%	0.190	(Afonso et al., 2011, NMFS, 2011)	NT
Oceanic whitetip shark	2	0.38	0.16- 0.9	0%	0.028	(Afonso et al., 2011, Pacheco et al., 2011)	VU
Dusky Shark	2	0.63	0.35- 1.16	42%	0.140	(Afonso et al., 2011, NMFS, 2011)	VU
Tiger shark	2	1.08	0.31- 3.71	40%	0.910	(Afonso et al., 2011, NMFS, 2011)	NT
Blue shark	9	0.99	0.88- 1.12	88%	0.930	(Afonso et al., 2011, Curran and Bigelow, 2011, Epperly et al., 2012, Huang et al., 2016, Pacheco et al., 2011, Yokota et al., 2006, NMFS, 2011)	NT
Scalloped hammerhead	2	0.79	0.72- 0.86	0%	<0.001	(Afonso et al., 2011, NMFS, 2011)	EN

Lamniformes



Escolar	3	0.7	0.61- 0.8	0%	<0.001	(Curran and Bigelow, 2011, NMFS, 2011)	LC
Wahoo	3	1.01	0.96- 1.07	0%	0.700	(Curran and Bigelow, 2011, Pacheco et al., 2011)	LC
Skipjack tuna	2	0.97	0.95–1	0%	0.077	(Curran and Bigelow, 2011)	LC
Albacore	6	0.99	0.92- 1.07	60%	0.840	(Curran and Bigelow, 2011, Epperly et al., 2012, Huang et al., 2016, Pacheco et al., 2011, NMFS, 2011)	NT
Yellowfin tuna	5	0.84	0.75- 0.94	74%	0.003	(Curran and Bigelow, 2011, Huang et al., 2016, Pacheco et al., 2011, NMFS, 2011)	NT
Bigeye tuna	6	0.91	0.76- 1.09	95%	0.310	(Curran and Bigelow, 2011, Epperly et al., 2012, Huang et al., 2016, Pacheco et al., 2011, NMFS, 2011)	VU
Bluefin tuna	2	0.86	0.81- 0.91	0%	9e-08	(Epperly et al., 2012, NMFS, 2011)	EN
Testudines							
Loggerhead sea turtle	5	1.41	0.61- 3.26	8%	0.420	(Cambiè et al., 2012, Gilman et al., 2007, Mejuto et al., 2008, Sales et al., 2010, NMFS, 2011)	VU
Leatherback sea	4	1.49	0.49- 4.56	25%	0.480	(Huang et al., 2016, Mejuto et al., 2008, Pacheco et al., 2011, NMFS, 2011)	VU
Xiphioidei							
Sailfish	2	0.71	0.5-1	3%	0.048	(Pacheco et al., 2011, NMFS, 2011)	LC
White marlin	2	0.84	0.77- 0.9	0%	<0.001	(Pacheco et al., 2011, NMFS, 2011)	VU



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(↓,-)

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957 Figure 1. Diagram of circle, tuna, and J-hook. Arrows represent the distinctive

958 characteristics of each style of hook. Tuna hook – the curved shaft, J-hook - the point is
959 parallel to the shaft, Circle hook – the point is turned inward relative to the shaft.

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.

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.

- 972 Figure 4. Effect size of hook type on catch rate for yellowfin tuna for experiments
- 973 considered in this analysis and estimated by the resulting model (RE model). 'Events' refer

974 to observed catch and 'total' indicates the number of hooks. Effect size (relative risk - RR),

- 975 95% confidence intervals (CI), and weights (%W) are indicated for each study and the
- 976 meta-analysis model. Numeric superscript refers to the experiment identification number
- 977 provided to distinguish between experiments within a reference.

978 Figure 5. Effect size of hook type on at-vessel mortality for yellowfin tuna for experiments

- 979 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
- 982 experiment and the meta-analysis model. Numeric superscript refers to the experiment
- 983 identification number provided for the purpose of distinguishing between experiments
- 984 within a reference.

Figure 6. Effect size (relative risk - RR) of hook type on catch rate for species for which a

986 significant difference was observed. Squares represent mean values and lines show the
987 Wald-type 95% confidence intervals estimated by the model. Values < 1 represent

value type vs // connuclice intervals estimated by the model. values < 1 represent

988 significantly lower at-vessel mortality on circle hooks relative to J-hooks. IUCN status

989 refers to IUCN Red List conservation status category.

990 Figure 7. Effect size (relative risk - RR) of hook type on at-vessel mortality for species for

991 which a significant difference was observed. Square represent the mean values and lines

show the Wald-type 95% confidence intervals estimated by the model. Values < 1

993 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.

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	Even	ts Total	Even	ts Total		% W	RR [95% CI]
Piovano et al. 2012 ²³	8	4275	36	4275	⊢ ∎−1	2.84%	0.22 [0.10, 0.
Bolten & Bjorndal 2005 ³⁶	264	46040	723	46040		4.40%	0.37 [0.32, 0.
Andraka et al. 2013 ⁵³	83	65603	181	69040	H=-1	4.20%	0.48 [0.37, 0.
Curran & Bigelow 2011 ⁶	120	1176471	231	1172589	H=1	4.28%	0.52 [0.42, 0.
Kerstetter & Graves 2006	a ¹⁸ 49	7650	72	7650	⊦∎⊀	3.97%	0.67 [0.47, 0.
Curran & Bigelow 201141	19	215909	27	214286	⊢■┿	3.34%	0.70 [0.39, 1
Domingo et al. 2012 ⁷	148	19911	195	19911	: I=f:	4.29%	0.76 [0.61, 0
Kerstetter & Graves 2006	a ⁶³ 233	7650	282	7650		4.36%	0.83 [0.70, 0
Sales et al. 2010 ²⁷	715	72914	833	72914	×.	4.44%	0.86 [0.78, 0
Piovano et al. 2012 ²²	100	9011	113	9012	H	4.19%	0.89 [0.68, 1
Pacheco et al. 2011 ²¹	301	25085	307	25085		4.38%	0.98 [0.84, 1
Cambie et al. 2012 ⁴⁸	1	2320	1	2322	⊢•	0.52%	1.00 [0.06, 15
Foster et al. 2012 ⁹	11035	156164	8110	116359	•	4.48%	1.01 [0.99, 1
Domingo et al. 2012 ⁸	148	22571	139	22571	i.	4.26%	1.06 [0.85, 1
Andraka et al. 2013 ⁴⁹	223	177942	210	178732	i ja i	4.33%	1.07 [0.88, 1
Boggs & Swimmer 2007 ⁵	⁷ 65	8250	60	8250	⊢≢-i	4.00%	1.08 [0.76, 1
Kim et al. 2006 ³⁰	12	14700	11	14700	⊢ ∎1	2.70%	1.09 [0.48, 2
Ward et al. 2009 ⁴³	127	47575	111	47575	Heri	4.21%	1.14 [0.89, 1
Gilman et al. 2007 ⁴²	33142	2150674	17086	1282748		4.48%	1.16 [1.14, 1
Bolten & Bjorndal 2005 ³⁹	212	13613	138	13613	H=1	4.29%	1.54 [1.24, 1
Huang et al. 2016 ⁴⁵	341	203838	220	203838	Hel	4.36%	1.55 [1.31, 1
Bolten & Bjorndal 2005 ³⁷	357	29383	203	29383	Heri	4.36%	1.76 [1.48, 2
Mejuto et al. 2008 ⁵⁹	4232	143413	2172	143473	•	4.47%	1.95 [1.85, 2
Andraka et al. 2013 ⁵⁴	38	36834	20	38207	┝╼┥	3.48%	1.97 [1.15, 3
Promjinda et al. 2008 ²⁶	12	6277	4	6277		1.98%	3.00 [0.97, 9
Kim et al. 2007 ²⁰	52	15616	15	15616	++	3.38%	3.47 [1.95, 6
RE Model					•	100.00%	1.00 [0.81, 1
					0.05 0.25 1 4		
					Risk Ratio (log scale)		
ure 2. Swordfish	catch	rate					

	Authors	Circle I	<u>nook</u>	J-ho	ook			
		Events	Total	Events	s Total		% W	RR [95% CI]
	Curran & Bigelow 2011 ⁶	⁶ 49	120	128	231	-	4.39%	0.74 [0.58, 0.94]
	NMFS 2011 ³³	31095	45237	38902	49936	•	28.13%	0.88 [0.88, 0.89]
	Epperly et al. 2012 ⁶²	5553	8557	5490	7634	•	27.19%	0.90 [0.88, 0.92]
	Pacheco et al. 2011 ²¹	260	301	275	307	•	21.47%	0.96 [0.91, 1.02]
	Huang et al. 2016 ⁴⁵	283	341	182	220		18.29%	1.00 [0.93, 1.08]
	Curran & Bigelow 2011 ⁴	8	19	9	27		0.53%	1.23 [0.58, 2.63]
	RE Model					4	100.00%	0.92 [0.87, 0.97]
						0.05 0.25 1 4		
1003						Risk Ratio (log scale)		
1004	Figure 3. Swordfish	at-ves	sel mo	ortality	y			
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Authors	<u>Circle</u> Event	<u>hook</u> s Total	J-ł Event	<u>nook</u> ts Total		% W	RR [95% CI]
Largacha et al. 2005 ⁴⁴	3	6857	6	6857	F	1.81%	0.55 [0.14, 2
Andraka et al. 2013 ⁵³	105	65603	149	69040	H a -f	7.98%	0.74 [0.58, 0
Curran & Bigelow 2011 ⁶	960	1172161	1097	1172009	-	8.87%	0.88 [0.80, 0
Curran & Bigelow 2011 ⁴¹	232	214815	263	214694	H	8.46%	0.88 [0.74, 1
Ward et al. 2009 ⁴³	47	47575	41	47575	r ∍ -i	6.62%	1.15 [0.75, 1
Pacheco et al. 2011 ²¹	128	25085	105	25085	(= +	7.92%	1.22 [0.94, 1
Andraka et al. 2013 ⁵²	275	34619	248	40890	HE	8.50%	1.31 [1.10, 1
Domingo et al. 2012 ⁷	196	19911	146	19911	HEH	8.23%	1.34 [1.08, 1
Sales et al. 2010 ²⁷	116	72914	84	72914	}∎+	7.75%	1.38 [1.04, 1
Huang et al. 2016 ⁴⁵	65	203838	41	203838	-∎-1	6.85%	1.59 [1.07, 2
Andraka et al. 2013 ⁵⁴	25	36834	16	38207	⊨ ∎+	4.97%	1.62 [0.87, 3
Kim et al. 2006 ³⁰	69	14700	38	14700	⊢∎⊣	6.81%	1.82 [1.22, 2
Andraka et al. 2013 ⁴⁹	298	177942	162	178732	HEH	8.38%	1.85 [1.53, 2
Domingo et al. 2012 ⁸	2	22571	1	22571		0.70%	2.00 [0.18, 22
Promjinda et al. 2008 ²⁶	2	6277	1	6277		0.70%	2.00 [0.18, 22
Kim et al. 2007 ²⁰	63	15616	15	15616	⊨►	5.45%	4.20 [2.39, 7
RE Model					•	100.00%	1.32 [1.07, 1
					0.05 0.25 1 4		
					Risk Ratio (log scale)		
gure 4. Yellowfin tu	na ca	tch rate	ć				

1026							
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1029	O						
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	Authors 0	Circle hook Events Tota	J- I Ever	<u>hook</u> nts Total		% W	RR [95% CI]
	Decharge at al. 2011 ²¹	50 40	B 67	105		13.02%	0.69 [0.54, 0.88]
	Pacheco et al. 2011	50 12	5 07		- ·		
	NMFS 2011 ³³	11138 3169	5 07 6 12185	26915	-	33.20%	0.78 [0.76, 0.79]
	NMFS 2011 ³³ Curran & Bigelow 2011 ⁶	11138 3169 396 96	5 07 6 12185 0 509	26915 1097	-	33.20% 26.65%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98]
	NMFS 2011 ³³ Curran & Bigelow 2011 ⁶ Curran & Bigelow 2011 ⁶	56 12 11138 3169 396 96 ¹ 96 23	6 12185 0 509 2 112	26915 1097 263		33.20% 26.65% 15.60%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98] 0.97 [0.79, 1.19]
	NMFS 2011 ³³ Curran & Bigelow 2011 ⁶ Curran & Bigelow 2011 ⁴ Huang et al. 2016 ⁴⁵	56 12 11138 3169 396 96 ¹ 96 23 44 6	5 07 6 12185 0 509 2 112 5 28	26915 1097 263 41		33.20% 26.65% 15.60% 11.54%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98] 0.97 [0.79, 1.19] 0.99 [0.76, 1.30]
	NMFS 2011 ³³ Curran & Bigelow 2011 ⁶ Curran & Bigelow 2011 ⁴ Huang et al. 2016 ⁴⁵ RE Model	56 12 11138 3169 396 96 ¹ 96 23 44 6	6 12185 0 509 2 112 5 28	26915 1097 263 41		33.20% 26.65% 15.60% 11.54% 100.00%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98] 0.97 [0.79, 1.19] 0.99 [0.76, 1.30] 0.84 [0.75, 0.94]
	Pacheco et al. 2011 NMFS 2011 ³³ Curran & Bigelow 2011 ⁶ Curran & Bigelow 2011 ⁴ Huang et al. 2016 ⁴⁵ RE Model	56 12 11138 3169 396 96 ¹ 96 23 44 6	6 12185 0 509 2 112 5 28	26915 1097 263 41	0.05 0.25 1 4	33.20% 26.65% 15.60% 11.54% 100.00%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98] 0.97 [0.79, 1.19] 0.99 [0.76, 1.30]
1031	NMFS 2011 ³³ Curran & Bigelow 2011 ⁶ Curran & Bigelow 2011 ⁴ Huang et al. 2016 ⁴⁵ RE Model	56 12 11138 3169 396 96 ¹ 96 23 44 6	6 12185 0 509 2 112 5 28	26915 1097 263 41	0.05 0.25 1 4 Risk Ratio (log scale	33.20% 26.65% 15.60% 11.54% 100.00%	0.78 [0.76, 0.79] 0.89 [0.81, 0.98] 0.97 [0.79, 1.19] 0.99 [0.76, 1.30] 0.84 [0.75, 0.94]

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