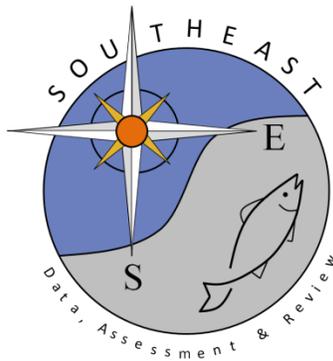


Meta-analysis of post-release fishing mortality in apex
predatory pelagic sharks and white marlin

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Meta-analysis of post-release fishing mortality in apex predatory pelagic sharks and white marlin

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Abstract

Robust assessments of the effects of fishing require accounting for components of fishing mortality, including post-release fishing mortality (F_r). Random-effects meta-analysis synthesized F_r in seven pelagic shark species captured, tagged and released with 401 pop-up satellite archival tags compiled from 33 studies and three gears (longline, purse-seine, rod & reel). The majority of F_r outcomes occurred within days of release, and the summary effect size for F_r was 0.27 [95% CI: 0.19–0.36], ranging from a low pooled effect size of 0.17 for blue shark (*Prionace glauca*, Carcharhinidae) to 0.38 (silky shark, *Carcharhinus falciformis*, Carcharhinidae). F_r rates in blue shark were consistent over dissimilar spatial and temporal scales, and results from earlier meta-analysis were replicated, which is the most powerful way to authenticate results. Condition at tagging was a strong predictor, and dichotomized survival outcomes in silky shark and no sex-, size-, location- or gear-specific F_r rates were demonstrated. Meta-analyses and sensitivity analyses indicated exposure to risk factors and conditions whilst caught on the gear probably had the largest explanatory effect on F_r , rather than stressors incurred during handling and release. Records from 549 tagged istiophorid billfishes (six species, three gears, 43 studies) demonstrated they are more robust to stressors sustained during capture, handling and release than pelagic sharks. Findings from previous meta-analysis on F_r rates in white marlin (*Kajikia albida*, Istiophoridae) were replicated. Synthesized F_r rates enable prioritizing approaches to mitigate by-catch fishing mortality, to improve the quality of stock and ecological risk assessments and to expand our knowledge of factors influencing trophic structure.

KEYWORDS

at-vessel mortality, condition, hazard, heterogeneity, longline, purse-seine, random effects, resilience, risk

1 | INTRODUCTION

Chondrichthyan fishes (sharks, batoids and chimaeras) have been around since the late Silurian–Devonian periods and comprise ~1,188 extant species (Bone & Moore, 2008; Weigmann, 2016). This successful group evolved to occupy dominant trophic positions and

play important “top-down” functional roles in shaping pelagic and coastal marine ecosystems (Heithaus, Frid, Wirsing & Worm, 2008; Schindler, Essington, Kitchell, Boggs & Hilborn, 2002; Stevens, 2000). In a recent evaluation against the IUCN Red List criteria, about one-quarter of elasmobranch species were listed as threatened due to overfishing (Dulvy, Fowler, Musick, Cavanagh & Kyne,

2014) and reducing fishing mortality is a global priority to rebuild stocks (Camhi, 2008; Dulvy, Baum, Clarke, Compagno & Cortés, 2008). Due to declining populations, more species are being protected through retention bans (IATTC, 2011; ICCAT, 2008, 2009, 2010, 2011; IOTC, 2012, 2017; Poisson, Crespo, Ellis, Chavance & Pascal, 2016; WCPFC, 2011, 2013) with implicit or explicit aims of reducing fishing mortality, which will result in higher discard (i.e. released after capture) rates. But to assess the performance and efficacy of these measures and others (e.g. fin-to-carcass ratios, bans on wire leaders, shark lines and hook shape), the fate of discards must be ascertained (Awruch, Simpfendorfer & Pankhurst, 2011; Dapp, Huveneers, Walker, Mandelman & Kerstetter, 2017; Gilman, Chaloupka, Swimmer & Piovano, 2016; Graves, Luckhurst & Prince, 2002; Gray & Kennelly, 2018; Moyes, Fragoso, Brill & Musyl, 2006; Uhlmann, Ulrich & Kennelly, 2019). Davis (2002) suggested mortality of discards was a major component in fisheries management. Crucially, by removing top predators and reducing spawning biomass, indiscriminant fishing practices can alter entire marine ecosystems with undetermined ecological as well as socioeconomic consequences (Baum & Worm, 2009; Burgess, Polasky & Tilman, 2013; Jackson, Kirby, Berger, Bjorndal & Botsford, 2001; Myers, Baum, Shepherd, Powers & Peterson, 2007).

Elasmobranchs evolved “slow” life history traits (e.g. late maturity, long gestation, slow growth, *K*-selected strategy) and behaviours (e.g. sex or age-specific migration and schooling, pronounced diel vertical diving patterns) that make populations vulnerable to exploitation and ultimately stock depletion, collapse and possible extinction (Baum, Myers, Kehler, Worm & Harley, 2003; Dulvy et al., 2008; Holden, 1973; Stevens, 2000). From a population-genetic standpoint, commercial and recreational fisheries commonly remove the largest, oldest and fittest individuals (Berkeley, Chapman & Sogard, 2004; Sibert, Hampton, Kleiber & Maunder, 2006; Sutter, Suski, Philipp, Klefoth & Wahl, 2012) and several decades of removals could produce heritable changes in maximum body size, growth rate and age-at-maturity through fisheries-induced evolution (DiBattista, Feldham, Garant, Gruber & Hendry, 2009; Enberg, Jørgensen, Dunlop, Heino & Dieckmann, 2009; Genner, Sims, Southward, Budd & Masterson, 2010; Kuparinen, Kuikka, & Merilä, 2009; Kuparinen & Merilä, 2007; Law, 2000). Fragmented and genetically isolated populations present further complications in terms of managing and protecting genetic diversity and maintaining effective population sizes (N_e) from exploitation (Clarke, Karl, Horn, Bernard & Lea, 2015). In addition, it is possible that selection pressure from global climate change might act to reduce phenotypic variability (Clark, Messmer, Tobin, Hoey & Pratchett, 2017) or skew sex ratios (Hattori, Fernandino, Kishii, Kimura & Kinno, 2009; Ospina-Álvarez & Piferrer, 2008). Due to economic and social drivers, Burgess et al. (2013) suggested multispecies fisheries were more prone to stock depletions and collapse because the incentive to target more valuable tuna and tuna-like species would outweigh the demise of less fecund, low or no-value by-catch species.

Though a few species are specifically targeted for their meat and fins (Clarke, McAllister, Milner-Gulland, Kirkwood & Michielsens,

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2006), the vast majority of apex predatory pelagic sharks are incidentally captured as by-catch in global fisheries where there is great uncertainty as to numbers that are landed and discarded (Filmlalter, Capello, Deneubourg, Cowley & Dagorn, 2013; James, Lewison, Dillingham, Curtis & Moore, 2016; Kelleher, 2005; Pauly & Zeller, 2016; Worm, Davis, Kettener, Ward-Paige & Chapman, 2013). Because of problems and uncertainty with fisheries data and in data collection systems (e.g. under-reporting, low coverage), quantifying reliable levels of discards is challenging and some authors suggest levels may actually exceed the reported number of landings by several orders of magnitude (Filmlalter et al., 2013; Gray & Kennelly, 2018; James et al., 2016; Pauly & Zeller, 2016; Simpfendorfer & Dulvy, 2017; Worm et al., 2013). Furthermore, compounding the complexity and uncertainty is that there is little or no information on at-vessel and discard mortality rates for most pelagic species captured and released in different fisheries and gears (references, Table 1).

For fisheries management and conservation, having precise survival rates of discards and at-vessel mortality rates are necessary to

TABLE 1 Metadata and results on pelagic shark and white marlin (*Kajikia albidus*) post-release mortality rates (F_r) from studies that used pop-up satellite archival tags (PSATs). For studies, “year” is deployment year (broken down by health condition code at-capture or brailled vs. non-brailled for purse-seine capture, when available) with number of mortalities over number of reporting tags provided. Non-reporting tags were not considered synonymous with mortality (Campana, Joyce & Manning, 2009; Graves et al., 2002; Musyl, Brill et al., 2011; Musyl, Domeier et al., 2011; Musyl et al., 2015). “J” = J hooks and “circle” = circle hooks. PSATs are assumed to have been rigged with fail-safe depth release mechanisms and that shed tags were positively buoyant (see Musyl, Brill et al., 2011; Musyl, Domeier et al., 2015). Microwave Telemetry with PSAT models HR (high rate) X-tag, standard archival PTT-100 and PTT-100 HR. Wildlife Computers with PAT model tags PAT1-4, MK-10, miniPAT and sPAT. The last columns indicate whether fish were tagged in the water (W) or on deck (D) with further indication whether the tagged animal was presumably healthy and resuscitated. “Y” = yes; “N” = no. “Raw” F_r rates calculated using raw, unweighted data (95% bootstrap CIs; 10,000 replications; Manly, 2007). For comparison, at-vessel mortality rates (F_v) (Dapp et al., 2017) and estimates for natural mortality (M) are provided on the summary line for species

[Study no.] and study/location	Year	Fishing method	Fishing style/hook type	F_r rate	95% CI	No. tags mort./no. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
Blue Shark, <i>Prionace glauca</i>											
[1] Weng, Castilho, Morrisette, Landeira-Fernandez and Holts (2005) So. California Bight	2002-2004	Research Longline	Circle hooks	0.12	0.03-0.37	2/17	10	D			PAT tags. Mean total length (TL) (cm) = 196.5 ± 4.1 (SE), range, 142-260; both mortalities (females [sizes 142, 185 cm]) occurred “immediately after tagging”
[2] Campana, Joyce, and Manning (2009) and Campana et al. (2015) NW Atlantic	2005-2008	Longline Swordfish-set	Circle & J hooks	0.05	0.00-0.45	0/10 ^a		W/D	Y	Y ^{b?}	PAT4 tags, tagged a random selection of sharks on deck (~3 min in air) or in the water, of which 10 were deemed healthy at-capture; companion paper (Campana et al., 2015) reanalyses the same data. Minimum soak time of 6 hr. Sharks brought on-board for tagging had their gills irrigated ^b . Hooks were left in or cut out of jaws and trailing gangion cut off close to mouth. Mean fork length (FL) = 159.3 cm, range 125-209 (Campana, Joyce & Manning, 2009; Campana et al., 2015)
[3] Campana, Joyce, and Manning (2009) and Campana et al. (2015) NW Atlantic	2005-2008	Longline	Circle & J hooks	0.33	0.18-0.53	9/27	3	W/D	N	Y ^{b?}	PAT4 tags, tagged a random selection of sharks on deck or in water of which 30 were deemed unhealthy/injured, most mortality occurred within 1 day after release (range time-to-event: 1-12 days). See Moyes et al. (2006), Campana, Joyce, Francis et al. (2009), Musyl, Brill et al. (2011) and Musyl et al. (2009) for more discussion of selection of samples. See notes for study [2] for tagging protocol
[4] Stevens, Bradford and West (2010) Eastern Australia	2004-2007	Longline		0.20	0.03-0.69	1/5		W/D			PAT4 tags, hooks and tralling line left in, mean FL = $233 \text{ cm} \pm 8.7$, range 200-271. Male (271 cm FL) “died soon after tagging”
[5] Musyl, Brill et al. (2011) Central Pacific	2001-2002	Research Longline Shallow, night-time-set	Circle hooks	0.06	0.01-0.34	1/16	16	D		N	PTT-100 tags, tagged a random selection, absence of movement in nictitating membrane used to select non-dead sharks to tag, mean TL = $168 \text{ cm} \pm 4.5$, range 120-215, wire leaders, variable soak times from ~8 to 24 hr, lifted in stretcher and tagged on-board (no hose to ventilate, ~5-7 min in air); blood samples were taken for the Moyes et al. (2006) study; see also Musyl et al. (2009), lone mortality (male, 173 TL) after 7 days
[6] Hutchinson (2016) Central Pacific/Hawaii	2016	Longline		0.08	0.01-0.41	1/12		W	Y		sPAT tags: tagged sharks “Alive and in Good Condition” (AG) from different fisheries, samples apparently tagged with gear removed or with gear and tralling line left but cut at varying lengths
[7] Musyl and Gilman (2018) Palau	2016	Longline Deep-set	Circle hooks	0.11	0.04-0.27	4/35		D	Y	N	sPAT tags, mean TL = 209 ± 3.4 , range 150-245, gaffed larger fish in mouth to bring through fish door, absence of movement in nictitating membrane used to select non-dead sharks to tag (Musyl, Brill et al., 2011), left in hook and varying length of tralling gear, random selection of sharks tagged of which 35 were deemed healthy, in air ~1 min. Most mortality occurred after one day

(Continues)

TABLE 1 (Continued)

[Study no.] and study/location	Year	Fishing method	Fishing style/hook type	F_r rate	95% CI	No. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
[8] Musyl and Gilman (2018) Palau	2016	Longline Deep-set	Circle hooks	0.31	0.12–0.59	4/13		D	N	N	sPAT tags; mean TL = 209 ± 8.5, range 150–250, gaffed larger fish in mouth to bring through fish door, absence of movement in nictitating membrane used to select non-dead sharks to tag (Musyl, Brill et al., 2011), left in hook and varying length of trailing gear , random selection of sharks tagged of which 13 were deemed unhealthy , in air ~1 min. Most mortality occurred after one day
[33] Howey, Wetherbee, Tolentino and Shivji (2017) Martha's Vineyard Atlantic		Rod & reel Longline	Circle hooks	0.13	0.04–0.34	3/23	10	W			PTT-100 and HR X-tags, fight times averaged 22.5 min (±2.61 SE), one mortality may have been result of predation by endothermic predator
Weighted Blue Shark summary effect Random-effects model				0.17	0.11–0.26	25/158					
			Raw F_r	0.16	0.10–0.22						
			F_c	0.17	0.174–0.176						$M = 0.20/\text{year}$ (Aires-da-Silva et al., 2005) $M = 0.17\text{--}0.23/\text{year}$ (Rice & Semba, 2014) $M = 0.18/\text{year}$ (Schindler et al., 2002)
Silky shark, <i>Carcharhinus falciformis</i>											
[9] Poisson, Filmalter et al. (2014) Indian Ocean	2011–2012	Purse-seine		0.67	0.27–0.92	4/6	1	D	N	N	MiniPATs, mean TL = 108 cm ± 5.8, range 86–127, sharks were tagged after being brailed (lower brail), presumably injured fish; most mortalities occurred immediately after tagging (range time-to-event: ~0–35 days, median = 7.5)
[10] Poisson, Filmalter et al. (2014) Indian Ocean	2011–2012	Purse-seine		0.10	0.01–0.67	0/4	1	D	N	N	MiniPATs, mean TL = 140 cm ± 7.7, range 122–155, sharks were tagged after being entangled , presumably healthy fish
[11] Poisson, Filmalter et al. (2014) Indian Ocean	2011–2012	Purse-seine		0.47	0.26–0.70	8/17	2	D	N	N	MiniPATs, mean TL = 133 cm ± 9.9, range 87–235, sharks were tagged after being brailed (upper brail), presumably injured fish, most mortalities occurred after tagging (range time-to-event: ~0–14 days, median = 0)
[12] Hutchinson et al. (2015) Tuvalu/Tokelau	2012	Purse-seine		0.14	0.02–0.58	1/7		D	Y^b		X-tags, miniPAT, sPAT, mean TL = 108 cm ± 4.3, range 93–127, blood sampled to analyse stress parameters, tagged " pre-set " or when encircled , mostly healthy fish. One mortality after 7 days. Note: Hutchinson et al. (2015) considered F_r to only occur within 10 days or less of the fishing insult, presumably based on biochemical disruptions
[13] Hutchinson et al. (2015) Tuvalu/Tokelau	2012	Purse-seine		0.75	0.24–0.97	3/4		D	Y^b		X-tags, miniPAT, sPAT, mean TL = 118 cm ± 4.7, range 105–137, tagged after brailed , 3 samples removed from analysis that were tagged dead at retrieval, fish mostly in poor condition, sampled blood to analyse stress parameters. Mortality after 0 days
[14] Hutchinson et al. (2015) Tuvalu/Tokelau	2012	Purse-seine		0.42	0.19–0.69	5/12	2	D	Y^b		X-tags, miniPAT, sPAT, mean TL = 123 cm ± 3.8, range 93–145, tagged when tangled , fish in good condition , sampled blood to analyse stress parameters. Mortality after 0–129 days, median = 15
[15] Eddy et al. (2016) Eastern Pacific	2011–2012	Purse-seine		0.17	0.01–0.81	0/2		D			MiniPAT, mean TL = 127 cm ± 4.0, range 123–131, tagged when snagged , coded health condition scores after Manire et al. (2001) Brailing time correlated with tonnage (catch)

(Continues)

TABLE 1 (Continued)

[Study no.] and study/location	Year	Fishing method	Fishing style/hook type	F _r rate	95% CI	No. tags mort./no. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
[16] Eddy et al. (2016) Eastern Pacific	2011–2012	Purse-seine		0.73	0.41–0.91	8/11		D	N		MiniPAT, mean TL = 121 cm ± 6.2, range 87–165, tagged when brailed . Coded health condition scores after Manire et al. (2001)
[17] Musyl, Brill et al. (2011) Central Pacific	2003–2005	Research longline	Circle hooks	0.05	0.00–0.45	0/10		D		N	PTT-100 tags, mean TL = 156 cm ± 11.7, range 116–200, wire leaders , tagged on-board, no hose to ventilate, blood samples were taken for the Moyes et al. (2006) study; see also Musyl et al. (2009). Study [5] describes the tagging protocol and selection of individuals
[18] Musyl and Gilman (2018) Palau	2016	Longline Deep-set	Circle hooks	0.04	0.01–0.22	1/27		D	Y	N	sPAT tags, mean TL = 131 ± 6.6, range 80–190, gaffed larger fish in mouth to bring through fish door, left in hook and varying length of trailing gear , random selection of sharks tagged of which 27 were deemed healthy . Mortality within 1 day. Studies [7–8] describe the tagging protocol
[19] Musyl and Gilman (2018) Palau	2016	Longline Deep-set	Circle hooks	0.75	0.38–0.94	6/8		D	N	N	sPAT tags, mean TL = 110 ± 3.7, range 85–110, gaffed larger fish in mouth to bring through fish door, left in hook and varying length of trailing gear , random selection of sharks tagged, of which 8 were deemed unhealthy . Mortality within 1 day. Studies [7–8] describe the tagging protocol
Weighted Silky Shark summary effect Random-effects model											
				0.38	0.21–0.59	36/108					
				Raw F _r	0.33	0.25–0.43					
				F _c	0.23	0.229–0.237					M = 0.17–0.21/year (Cortés, 2002)
Common Thresher, <i>Alopias vulpinus</i>											
[20] Heberer et al. (2010) So. California	2007–2009	Rod & reel	Trolling lures	0.26	0.11–0.50	5/19	1	W	N	N	MK-10 PATs, mean FL = 185 cm ± 4.1, range 160–221, tagged tail-hooked animals, >85 min fight time and >180 cm FL separated survivors from moribund fish, sampled blood to analyse stress parameters. All mortalities after 4 hr
[21] Sepulveda et al. (2015) So. California	2010–2012	Rod & reel	Trolling lures	0.78	0.42–0.94	7/9	1	W	N	N	MK-10 PATs, mean FL = 143 cm ± 5.4, range 111–175, tagged tail-hooked animals, left in trailing gear , sampled blood to analyse stress parameters. Most mortalities after 5 days but extended to 81 days (median = 2, range 1–81)
[22] Sepulveda et al. (2015) So. California	2011–2012	Rod & reel	Trolling lures	0.06	0.00–0.54	0/7	3	W	Y	N	MK-10 PATs, mean FL = 150 cm ± 9.0, range 125–187, tagged mouth-hooked animals, hooks removed, sampled blood to analyse stress parameters
Weighted Common Thresher summary effect Random-effects model											
				0.35	0.07–0.79	12/35					
				Raw F _r	0.34	0.20–0.51					M = 0.179/year (Cortés, Camhi, Plikitch & Babcock, 2008)
Shortfin mako, <i>Isurus oxyrinchus</i>											
[23] Abascal et al. (2011) Chile	2007	Longline		0.44	0.18–0.75	4/9		W			MK10 PAT, mean TL = 178 cm ± 9.8, range 140–220, mortality reported after 3, 32, 38 and 133 days
[24] Musyl, Brill et al. (2011) Hawaii	2002–2006	Research longline Shallow-set	Circle hooks	0.17	0.01–0.81	0/2	3	D			PTT-100 tags, mean TL = 176 cm ± 19.9, range 118–210, wire leaders , tagged on deck, Study [5] describes the tagging protocol and selection of individuals

(Continues)

TABLE 1 (Continued)

[Study no.] and study/location	Year	Fishing method	Fishing style/hook type	F_r rate	95% CI	No. tags mort./no. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
[25] French et al. (2015) Tasmania	2013	Rod & reel	J & circle hooks	0.10	0.03–0.27	3/30	3	D/W	Y ^b /N	Y ^b /N	sPAT, mean TL = 176 cm ± 6.4 range, 110–265, all mortalities occurred within ~1 day and after <30 min fight times on J hooks, sampled blood to analyse stress parameters
[26] Campana et al. (2015) NW Atlantic	2010–2014	Longline	Circle hooks	0.30	0.15–0.52	12/29		W/D	Y		MK-10 PAT, miniPAT & X-tags, mean FL = 131.5 cm, range, 80–229; tagged ostensibly healthy individuals. Campana et al. (2015) excluded six tagged samples <110 cm FL, five of which died, almost immediately after capture. For completeness, these samples are included in the meta-analysis
[27] Campana et al. (2015) NW Atlantic	2010–2014	Longline	Circle hooks	0.33	0.04–0.85	1/3		W/D	N		MK-10 PAT, miniPAT & X-tags, mean FL = 131.5 cm, range, 80–229; tagged ostensibly unhealthy/injured individuals
Weighted Shortfin mako summary effect Random-effects model				0.25	0.14–0.42	15/67					
				Raw F_r	0.22	0.13–0.33					M = 0.077–0.244/year (Chang & Liu, 2009)
				F_c	0.07	0.063–0.067					
Oceanic Whitetip, <i>Corcharchinus longimanus</i>											
[28] Musyl, Brill et al. (2011) Central Pacific	2001–2005	Research longline	Circle hooks	0.04	0.00–0.38	0/13	3	D	N	N	PTT-100 tags, mean TL = 147 cm ± 14.6, range 100–225, wire leaders, tagged on deck, Study [5] describes the tagging protocol and selection of individuals
[29] Hutchinson (2016) Central Pacific/ Hawaii		Longline		0.50	0.06–0.94	1/2		W	Y		sPAT tags: tagged sharks "Alive and in Good Condition" (AG) from different fisheries, samples apparently tagged with gear removed or trailing line cut
Weighted Oceanic Whitetip summary effect Random-effects model				0.16	0.01–0.83	1/15					
				Raw F_r	0.07	0.00–0.20					M = 0.203/year (Smith, Au, Show, Camhi & Pikitch, 2008)
				F_c	0.11	0.102–0.114					
Bigeye Thresher, <i>Alopias superciliosus</i>											
[30] Musyl, Brill et al. (2011) Central Pacific	2002–2004	Research longline	Circle hooks	0.12	0.01–0.73	0/3	8	W			PTT-100 tags, ~200 cm FL, wire leaders , left in hooks and trailing line, tagged in water with pole
[31] Hutchinson (2016) Central Pacific/ Hawaii		Longline		0.25	0.08–0.55	3/12		W	Y		sPAT tags: tagged sharks "Alive and in Good Condition" (AG) from different fisheries, samples apparently tagged with gear removed or trailing line cut
Weighted Bigeye Thresher summary effect Random-effects model				0.23	0.08–0.49	3/15					
				Raw F_r	0.20	0.00–0.40					

(Continues)

TABLE 1 (Continued)

[Study no.] and study/location	Year	Fishing method	Fishing style/hook type	F _r rate	95% CI	No. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
Scalloped Hammerhead, <i>Sphyrna lewini</i>											
[32] Eddy et al. (2016)		Purse-seine		0.88	0.27–0.99	3/3		D			MiniPAT, mean TL = 153 cm ± 4.2, range 145–159, tagged when brailed
Eastern Pacific											
Weighted Scal. Ham. summary effect Random-effects model											
			F _c	0.88	0.27–0.99	3/3					
			F _c	0.26	0.247–0.262						M = 0.279/year (Liu & Chen, 1999)
White Marlin, <i>Kajikia albida</i>											
[47] Hoolihan, Luo, Snodgrass, Orbesen and Barse (2015) ^c Maryland, No. Carolina, Aruba	2007–2012	Rod & reel		0.06	0.01–0.20	2/35	5	W		Y ^b	MK10, size (weight) ranged from 13.6 to 38.6 kg, 2 mortalities (13.6, 20.4 kg) occurred within 24 hr after release, tagging protocols followed Prince & Goodyear (2006)
[48] Graves et al. (2016) Virginia	2015	Rod & reel	Circle hooks Drop back	0.17	0.02–0.63	1/6		W		Y ^b	X-tags, mean LJFL = 149 cm ± 1.8, range 145–157, tested samples with <1 min air exposure, variable resuscitation times and hooking locations; see Graves & Horodysky (2008) for tagging protocols and bait rigging
[49] Graves et al. (2016) Virginia	2015	Rod & reel	Circle hooks Drop back	0.40	0.10–0.80	2/5		W		Y ^b	X-tags, mean LJTL = 150 cm ± 3.9, range 142–165, tested samples with <3 min air exposure, variable resuscitation times and hooking locations; see Graves & Horodysky (2008) for tagging protocols and bait rigging
[50] Graves et al. (2016) Virginia	2015	Rod & reel	Circle hooks Drop back	0.57	0.23–0.86	4/7		W		Y ^b	X-tags, mean LJTL = 154 cm ± 2.8, range 145–163, tested samples with <5 min air exposure, variable resuscitation times and hooking locations; see Graves & Horodysky (2008) for tagging protocols and bait rigging.
[51] Schlenker et al. (2016) Mid-Atlantic Coast	2012–2013		Circle hooks	0.21	0.07–0.49	3/14		D			HR X-tags, mean LJTL = 160 cm ± 1.9, range 147–173, tested samples with <2 min air exposure, variable angling times; see Graves et al. (2002) and Graves & Horodysky (2008) for tagging protocols and bait rigging, sampled blood to analyse stress parameters
[52] Schlenker et al. (2016) Mid-Atlantic Coast	2012–2013		Circle hooks	0.14	0.02–0.58	1/7		D			HR X-tags, mean LJTL = 157 cm ± 4.6, range 137–175, tested samples with <3 min air exposure, variable angling time; see Graves et al. (2002) and Graves & Horodysky (2008) for tagging protocols and bait rigging, sampled blood to analyse stress parameters

(Continues)

TABLE 1 (Continued)

[Study no.] and study location	Year	Fishing method	Fishing style/hook type	F_r rate	95% CI	No. tags mort./no. tags report	No. non-report. tags	Water/deck	Healthy	Ventilated	Notes, tag types, models, time-to-event (mortality) Key descriptors are given in bold face
[53] Vaudo, Byrne, Wetherbee, Harvey and Mendillo (2017) Isla Mujeres Mexico Gulf of Mexico	2014–2016	Rod & reel	Circle hooks	0.06	0.01–0.31	1/18	3	D		Y^b	MiniPAT tags, 145–170 cm LJFL, <2 min on deck to tag fish, lone mortality after 29 days was presumably due to predation by mako shark
Weighted White Marlin summary effect Random-effects model				0.19	0.09–0.37	14/92					
				Raw F_r	0.15	0.08–0.23					$M = 0.10-0.20/\text{year}$ (Goodyear, 1998; Porch, 2003)

^{||}The assumption was made that stainless steel crimps were incorporated in tethers as copper crimps could interfere with the functioning of the PSAT's nose cone (Musyl, Domeier et al., 2011).

^aIn studies with 2 or more deployments where no mortalities were reported, a 0.5 continuity correction factor was added to the event and non-event values to derive study F_r weights, SEs, variances and 95% CIs (see text). ^bNote that hoses with brass fittings used for irrigation/ventilation purposes could contribute additional stress and injury through copper toxicity (De Boeck, Hatink, Franklin, Bucking & Wood, 2007; Grosell, Blanchard, Brix & Gerdes, 2007). It is not known if this potential confounding risk factor was addressed in the referenced studies. ^cBracketed study numbers for white marlin continue from the numbering scheme for istiophorid billfish found in Musyl et al. (2015).

advance and justify non-retention, catch-and-release policies (Ellis, Phillips & Poisson, 2016; Graves, Marcek & Goldsmith, 2016; Moyes et al., 2006; Pine, Martell, Jensen, Walters & Kitchell, 2008) and other by-catch mitigation strategies to rebuild stocks (Carruthers, Schneider & Neilson, 2009; Dapp, Huvneers, Walker, Drew & Reina, 2016; Favaro & Côté, 2015; Gilman et al., 2016; Poisson et al., 2016; Uhlmann et al., 2019). In fisheries population biology, it is necessary to account for the two main sources of fishing mortality: at-vessel or catch (i.e. removals) (F_c) and post-release or discard (i.e. delayed) (F_r) mortality rates (Campana, Joyce & Manning, 2009; Carruthers et al., 2009; Gilman, Suuronen, Hall & Kennelly, 2013; Musyl, Brill et al., 2011; Musyl et al., 2015). The terms comprising fishing mortality (F_c and F_r) are additive but distinct mortality sources (i.e. $F = F_c + F_r + \varepsilon$; ε is an error term to account for other [i.e. unmeasured] potential sources of mortality such as pre-catch and ghost fishing; see Gilman et al., 2013). Fishing mortality (F) combines with natural mortality (M) to estimate Z , the instantaneous mortality rate or the total force of fishing mortality. Precise estimates of F_c and F_r are necessary because small changes in mortality can sometimes result in large changes in spawning biomass and therefore population growth, which ultimately impacts sustainability.

Accurate estimates of the two sources comprising fishing mortality are also essential in producing accurate stock and other forms of ecological risk assessments (Gallagher, Kyne & Hammerschlag, 2012; Hobday, Smith, Stobutzki, Bulman & Daley, 2011; Kelleher, 2005; Kitchell, Kaplan, Cox, Martell & Essington, 2004; Pine et al., 2008; Punt, Smith, Tuck & Methot, 2006; Viana, Graham, Wilson & Jackson, 2011; Viana, McNally, Graham, Reid & Jackson, 2013). The vast majority of discards are unaccounted for in most stock assessments (Dapp et al., 2017) and the uncertainty as to the true values of F_c and F_r are major impediments to effective management and resource conservation in many fisheries (Campana, Joyce & Manning, 2009; Carruthers et al., 2009; Dapp et al., 2016, 2017; Dapp, Walker, Huvneers & Reina, 2015; Molina & Cooke, 2012; Musyl et al., 2015). Fishing also has the capacity to exert sublethal effects at the population level (e.g. spawning, migration, reproduction) which, due to logistical challenges, is rarely measured in large pelagic species (Guida, 2016; Wosnick, Awruch, Adams, Gutierrez & Bornatowski, 2019).

Whilst measuring accurate F_c rates is largely dependent on the quality of fisheries observer programmes and fleet coverage (Dapp et al., 2017; Walsh, Bigelow & Sender, 2009; Walsh, Ito, Kawamoto & McCracken, 2005), F_r can be challenging to estimate due to cost-benefit and logistics (Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Musyl & Gilman, 2018; Musyl, Brill et al., 2011; Musyl, Domeier et al., 2011). It has been hypothesized that F_c and F_r rates might be expected to show congruence because prognostic factors responsible for F_c in fisheries are likely to be many of the same ones acting on F_r (Benoît, Hurlbut, Chasse & Jonsen, 2012; Braccini, Rijn & Frick, 2012; Campana, Joyce & Manning, 2009; Dapp et al., 2015, 2017; Musyl & Gilman, 2018; Musyl, Brill et al., 2011; Musyl et al., 2015). Though there are several indirect and direct methods to estimate F_r rates in pelagic sharks, each method has different strengths and weaknesses which impact cost-benefit

and ultimately experimental design and statistical power (Campana, Joyce, Fowler & Showell, 2015; Goodyear, 2002; Graves et al., 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Musyl & Gilman, 2018; Musyl, Brill et al., 2011; Musyl et al., 2015). Survival studies to determine F_r generally require several hundred samples to achieve statistical power at ~80% (Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Machin, Campbell, Tan & Tan, 2009; Murray, 2006; Musyl & Gilman, 2018; Musyl, Brill et al., 2011; Musyl et al., 2015; Ryan, 2013). As an example, pop-up satellite archival tags (PSATs) are commonly used in F_r studies but costs of PSATs has translated into small sample sizes (Table 1; Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Moyes et al., 2006; Musyl & Gilman, 2018; Musyl et al., 2015; Musyl, Moyes, Brill & Fragoso, 2009).

Though reviewed in greater detail in Davis (2002), Campana, Joyce, and Manning (2009), Musyl, Brill et al. (2011), Neilson, Busawon, Andrushchenko, Campana and Carruthers (2011), Benoît et al. (2012), Molina and Cooke (2012), Gilman et al. (2013) and Ellis et al. (2016) (see also references, Table 1), methods (both indirect and direct) to estimate F_r briefly encompass (a) conventional (plastic) tagging (Graves et al., 2002; Hueter, Manire, Tyminski, Hoenig & Hepworth, 2006; Manire, Hueter, Hull & Spieler, 2001), (b) vitality or health status condition scores at haulback (Benoît et al., 2012; Braccini et al., 2012; Hueter et al., 2006; Manire et al., 2001), (c) biochemical correlates (Mandelman & Skomal, 2009; Marshall, Field, Afiadata, Sepulveda & Skomal, 2012; Moyes et al., 2006), (d) reflex action mortality predictors (RAMP; Davis & Olla, 2001; Davis, 2007; Merremans, Yochum, Kochzius, Tuyttens & Uhlmann, 2017), (e) tank studies (Benoît et al., 2012; Braccini et al., 2012), (f) electronic tagging (e.g. PSATs and acoustic tags; Graves et al., 2002; Musyl et al., 2015) and (g) combination of techniques (Davis, 2002; Eddy, Brill & Bernal, 2016; Hutchinson, Itano, Muir & Holland, 2015; Moyes et al., 2006; Pollock & Pine, 2007; Pollock, Jiang & Hightower, 2004; Schlenker, Latour, Brill & Graves, 2016). The last (combination) method incorporating vitality or condition scores is gaining traction due to its potential to reduce costs and increase sample sizes (Benoît et al., 2012; Braccini et al., 2012; Dapp et al., 2017; Ellis et al., 2016; Meeremans et al., 2017), but the overall model needs validation from known outcome samples (Benoît et al., 2012; Braccini et al., 2012; Eddy et al., 2016; French, Lyle, Tracey, Currie & Semmens, 2015; Hutchinson et al., 2015; Musyl & Gilman, 2018; Poisson, Filmlalter, Vernet & Dagorn, 2014).

Given the obvious need and importance of deriving credible F_r and F_c rates in fisheries, particularly in pelagic sharks (James et al., 2016; Molina & Cooke, 2012; Oliver, Braccini, Newman & Harvey, 2015; Poisson et al., 2016), methods to synthesize precise and credible point estimates are required (e.g. Musyl et al., 2015). Whilst single F_r studies are often context-specific, they generally are of low power, and thus, their utility is difficult to judge in the framework of mortality outcomes from other studies (Table 1; Murray, 2006; Musyl et al., 2015). In other words, low power and precision introduces uncertainty in the point estimates and large F_r studies are cost-prohibitive to design at 80% power using electronic tags

(Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Musyl & Gilman, 2018; Musyl, Brill et al., 2011; Musyl et al., 2015). Meta-analysis is an approach that can help bridge the gap between low power issues, cost-benefit and has the ability to resolve trends and test multiple hypotheses across multiple independent studies. The benefits are myriad, but if F_r rates are consistent across species, fisheries, gear types and temporal and spatial scales, then the meta-analysis provides a combined estimate that is more precise than any of the individual studies. By contrast, if the F_r rates vary across studies, the meta-analysis may allow for the identification of explanatory factors and to distinguish "Best Practices" in terms of guidelines in handling and operational procedures that enhance survival of released animals. Molina and Cooke (2012) identified handling practice as an area that required further study in fisheries as a possible way to reduce mortality but "Best Handling Practices" would be more appropriately determined from meta-analysis (i.e. large numbers of similar studies), rather than using single, low powered studies.

To provide precision in true mortality rates, researchers are turning to evidence-based methods such as meta-analysis not only to increase overall power and cut costs, but also to test various hypotheses unavailable in single studies (Benoît et al., 2012; Dapp et al., 2015; Favaro & Côté, 2015; Gilman et al., 2016; Godin, Carlson & Burgener, 2012; Musyl, Brill et al., 2011; Musyl et al., 2015; Reinhardt, Weaver, Latham, Dell'Apa & Serafy, 2017; Serafy, Orbesen, Snodgrass, Beerkircher & Walter, 2012). Synthesizing precise F_r rates in pelagic fisheries by meta-analysis has been limited to Musyl, Brill et al. (2011) on blue shark, Musyl et al. (2015) on istiophorid billfish and Dapp et al. (2015) on several species of pelagic and coastal sharks. Hammerschlag, Gallagher and Lazarre (2011) and Musyl, Domeier et al. (2011) also conducted meta-analysis on the performance and reliability of PSATs which are an important tool to measure F_r rates. Dapp et al. (2015) used meta-analyses on F_r rates in sharks to test hypotheses concerning respiratory mode (i.e. pelagic sharks are obligate ram-ventilators compared to coastal species which have spiracles which allow buccal pumping for ventilation) and gear type (i.e. trawl, gillnet, longline). In his review, Davis (2002) cautioned that confidence in generalizing results from F_r studies was limited and would need to be validated under a wide range of fishing conditions and factor interactions (e.g. light conditions, temperature, air exposure, anoxia, sea conditions, pressure changes, fish size and species, behaviour, physiology and potential mortality). Meta-analysis can help address these concerns as well as providing confidence in the estimates and generalizing results.

By compiling and synthesizing effect sizes across multiple independent studies and fisheries, the pooled F_r estimates presented herein are the best and most precise available for several species of pelagic sharks and white marlin. White marlin were included in the study for several reasons, including (a) concerns about their stock status (Graves et al., 2016; Schlenker et al., 2016), (b) demonstrating the utility meta-analyses and (c) comparing the robustness of apex predatory pelagic species to the effects of fishing. Moreover, to

validate the efficacy and usefulness of the technique and to increase precision in point estimates, the current meta-analysis demonstrates the ability to act like a “living document” in that addition of new studies increased precision in earlier meta-analyses on F_r rates for blue shark and white marlin. The synthesized F_r rates indicate istiophorid billfish are more robust to the effects of fishing than pelagic sharks which have implications for management, ecosystem dynamics and trophic structure in pelagic environments (Hunsicker, Olson, Essington, Maunder & Duffy, 2012; Kitchell, Essington, Boggs, Schindler & Walters, 2002; Schindler et al., 2002). Should they be warranted, this meta-analysis will be used to design better survival studies and ultimately serve as a guide to help researchers interpret their results and to prioritize by-catch mitigation strategies for animals with high mortality rates.

2 | METHODS

Methods for random-effects meta-analysis followed Musyl, Brill et al. (2011) and Musyl et al. (2015) and the general PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) format (Moher, Liberati, Tetzlaff & Altman, 2009). A brief summary of these methods is provided below.

2.1 | Identification of post-release mortality outcomes

PSATs are a common device used to discriminate mortality outcomes in pelagic sharks and istiophorid billfishes (Table 1; Hammerschlag et al., 2011; Musyl, Domeier et al., 2011; Musyl et al., 2015). The tags are fishery independent and are equipped with fail-safe mechanisms (either mechanical or within the device's software) that allow downloaded pressure (depth), temperature and ambient light data to discriminate a dead sinking animal (sharks do not possess a swim bladder and are negatively buoyant) from a shed tag or live animal (Eddy et al., 2016; French et al., 2015; Hutchinson et al., 2015; Kerstetter & Graves, 2006; Moyes et al., 2006; Musyl, Brill et al., 2011; Musyl, Domeier et al., 2011; Musyl et al., 2015; Poisson, Filmlalter et al., 2014; Schlenker et al., 2016) or even from tags presumably ingested by sharks (Kerstetter, Polovina & Graves, 2004). Most F_r studies failed to indicate whether PSATs would float if shed, and therefore, it was assumed tags were rigged to allow discrimination of survival outcomes after tag detachment (Domeier, Dewar & Nasby-Lucas, 2003; Musyl & Gilman, 2018; Musyl et al., 2015).

2.2 | Selection of studies and eligibility criteria

Using the keywords and various combinations of post-release mortality, discards, survival, PSAT, pop-up satellite archival tag, sharks, pelagic sharks, fisheries, purse-seine, longline, rod & reel, fail-safe release mechanism (or software) and positively buoyant, we performed an unstructured search on the published and grey

literature using Google Scholar and Web of Science, tuna Regional Fisheries Management Organizations (t-RFMO) websites, fisheries agency websites, personal databases and contacted colleagues for references. We excluded studies with biased sampling designs that selectively tagged and/or reported results from only healthy individuals (e.g. movement studies), as inclusion of these studies would have biased the pooled estimates. Studies were included whose stated goals were to investigate F_r and/or that provided full disclosure about the fate of deployments. Most studies were designed to match fish handling procedures presumed to be most common in the fishery and indicated a random mixture of samples were tagged (Table 1). Selection of white marlin studies followed Musyl et al. (2015).

2.3 | Data extraction and quality control

Research that purposely categorized multiple independent deployments of sharks with different health condition scores, anatomical hooking location (e.g. mouth, in the oesophagus or more deeply, or foul hooked in the body such as tail-hooked) or from different access positions in purse-seine fishing (e.g. snagged, encircled, brailed) were treated as separate studies. Occasionally two or more articles were found describing different aspects of the same PSAT deployments (e.g. Campana, Joyce & Manning, 2009; Campana et al., 2015) and we reported results from these studies once. Studies that provided full disclosure about the status of tags were selected, but non-reporting tags were not considered synonymous with mortality and were not included in the meta-analysis because many factors can cause failure in electronic tags (Chaloupka, Parker & Balazs, 2004; Goodyear, 2002; Graves et al., 2002; Hays, Bradshaw, James, Lovell & Sims, 2007; Musyl, Brill et al., 2011; Musyl, Domeier et al., 2011; Musyl et al., 2015). Samples were also excluded from the analysis where presumably dead animals were tagged at-retrieval (Table 1; Hutchinson et al., 2015) as including these samples would bias the mortality estimates (Campana, Joyce & Manning, 2009; Campana, Joyce, Francis & Manning, 2009; Musyl, Brill et al., 2011; Musyl et al., 2009).

2.4 | Meta-analysis model

Random-effects meta-analysis was selected because studies were assumed to represent random samples (i.e. mixtures of samples, environmental conditions, health condition scores, fishing gear, handling practices and location) in which the underlying (infinite-sample) effect sizes have a distribution rather than a single value. Inverse-variance weighting and estimated variability between studies (τ^2) as I^2 was calculated by the method of moments (DerSimonian & Laird, 1986; Kontopantelis & Reeves, 2010) on the logit of the proportion of pelagic sharks that ultimately died using Comprehensive Meta-Analysis (Borenstein, Hedges, Higgins & Rothstein, 2009) and Open Meta-Analyst (Wallace, Dahabreh, Trikalinos, Lau & Trow, 2012). Cochran's Q statistic was used to test for heterogeneity and was also used in a mixed-effects ANOVA design to test F_r within and across subgroups (i.e. species, gear type,

condition code; Gurevitch & Hedges, 1999). I^2 , derived from the Q statistic, described the proportion of observed dispersion between studies that was real (Borenstein et al., 2009). The Q statistic was also used in meta-regression (unrestricted maximum likelihood, mixed-effects model) to test effect sizes against study latitude. Forest plots were used to depict effect sizes where the area of the boxes for each study are proportional to the inverse of the variance, and any side of the box is proportional to the inverse of the standard error. The 95% confidence intervals (horizontal bars) for each study are proportional to the standard error and related to sample size. Diamonds represent the summary effect size and the width is proportional to the 95% CI. Cumulative meta-analysis and sensitivity analysis were used to look for bias and patterns (Borenstein et al., 2009; Sutton, Abrams, Jones, Sheldon & Song, 2000). Begg and Mazumdar's (1994) rank correlation test (Kendall's tau with continuity correction), Egger's regression intercept method (Egger, Davey Smith, Schneider & Minder, 1997), Orwin's fail-safe N (Orwin, 1983), Duval and Tweedie's (2000a, 2000b) "trim and fill" and funnel plots were used to test for publication bias using Comprehensive Meta-Analysis.

In studies reporting zero mortality events (24% of studies and ~13% of tags, Table 1), the 0.5 continuity correction factor was applied because calculations in meta-analysis do not work with zero events (Cox, 1970; Haldane, 1955; Higgins & Green, 2011; Yates, 1934). To examine potential confounding effects in one-arm studies (i.e. non-comparative binary outcomes) using the 0.5 continuity correction factor, exact non-parametric inference tests (Pearson's chi-square tests) were implemented in StatXact v.11 (Cytel Inc., Cambridge, MA, USA; 2015) to verify the results because exact tests do not require the continuity correction (Friedrich, Adhikari & Beyene, 2007; Sweeting, Sutton & Lambert, 2004). Point probabilities (i.e. measure of discreteness) were provided for each test, which is the probability of getting exactly the observed test statistic given the marginals (i.e. row and column totals). Kaplan–Meier survival and hazard curves were used to examine F_r in nine studies where requisite survival time (i.e. time-to-event) and censor information (0, 1) were provided (Hosmer & Lemeshow, 1999; Kleinbaum & Klein, 2005).

2.5 | IPD survival analysis of silky shark

In the silky shark meta-analysis, it was possible to extract individual participant data (IPD) common to several studies (Table 1; Eddy et al., 2016; Hutchinson et al., 2015; Musyl & Gilman, 2018; Poisson, Filmlalter et al., 2014) to test the binary response (survival) variable δ (0 = censored, 1 = mortality event) against several prognostic variables and covariates including health condition scores, body size, sex, fishing gear and a dummy variable for fishing location/study using logistic regression (Hilbe, 2016; Hosmer & Lemeshow, 2000; Kleinbaum & Klein, 2010; Sutton et al., 2000) implemented in LogXact v.11 (Cytel Inc.; 2015). In order to make meaningful comparison, we synonymized condition code into three categories across studies where 1 = best condition, 2 = medium condition and 3 = worst condition (i.e. two extreme condition codes with one in

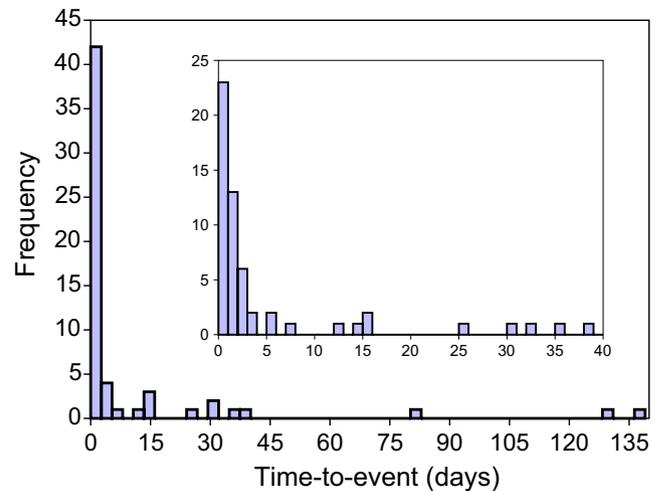


FIGURE 1 Time-to-event (days) frequency histogram indicating post-release mortality outcomes after release from fishing gear for pelagic sharks equipped with pop-up satellite archival tags. Inset figure provides detail on the first 40 days post-release

the middle; Musyl & Gilman, 2018). Two of the studies (Eddy et al., 2016; Hutchinson et al., 2015) used 4- and 5-category condition codes and in these instances, we pooled the worst condition categories into category 3 arguing that healthy sharks were easier to distinguish whereas subtleties across poorer condition codes were harder to distinguish. Next, we compared condition codes to access points in purse-seine operations and likely severity of injury (free swimming around FADs, handline = 1, snagged, encircled = 2 and brailed = 3) with Cronbach's alpha and the value (~0.80) indicated our synonymized condition code was adequate for research purposes (Bland & Altman, 1997).

Overfitting data is a problem in survival and logistic models using too many prognostic variables in small samples and interpretations can be erroneous due to bias and random errors (Harrell, 2001; Ogundimu, Altman & Collins, 2016; Peduzzi, Concato, Feinstein & Holford, 1995). Several authors recommended a ratio of ~10 mortality "events per variable" (EPV) in survival models (but see Ogundimu et al., 2016 recommended >20 EPV). With 36 mortalities in the silky shark IPD, ~2–3 variables were considered appropriate for possible candidate models without overfitting the data. For logistic regression survival models, Peduzzi et al. (1995) recommended minimum sample sizes of $n = 10 k/p$, where k is the number of variables (determined from EPV) and p is the effect size for F_r . As an example, for 2–3 variables and $p = 0.20$, $n = 100$ –150. Based on these guidelines, with a total sample size of $n = 98$, our IPD analysis was considered adequate for testing combinations of ~2 variables. The suite of prognostic variables were entered manually or by forward, backward and stepwise selection procedures and competing models were compared against the null model (contained intercept) with Akaike's information criteria (Akaike, 1974; Burnham & Anderson, 2002; Hilbe, 2016; Hosmer & Lemeshow, 2000; Kleinbaum & Klein, 2010; Lee & Wang, 2003). Receiver operator characteristic (ROC) curves (MedCalc Statistical Software

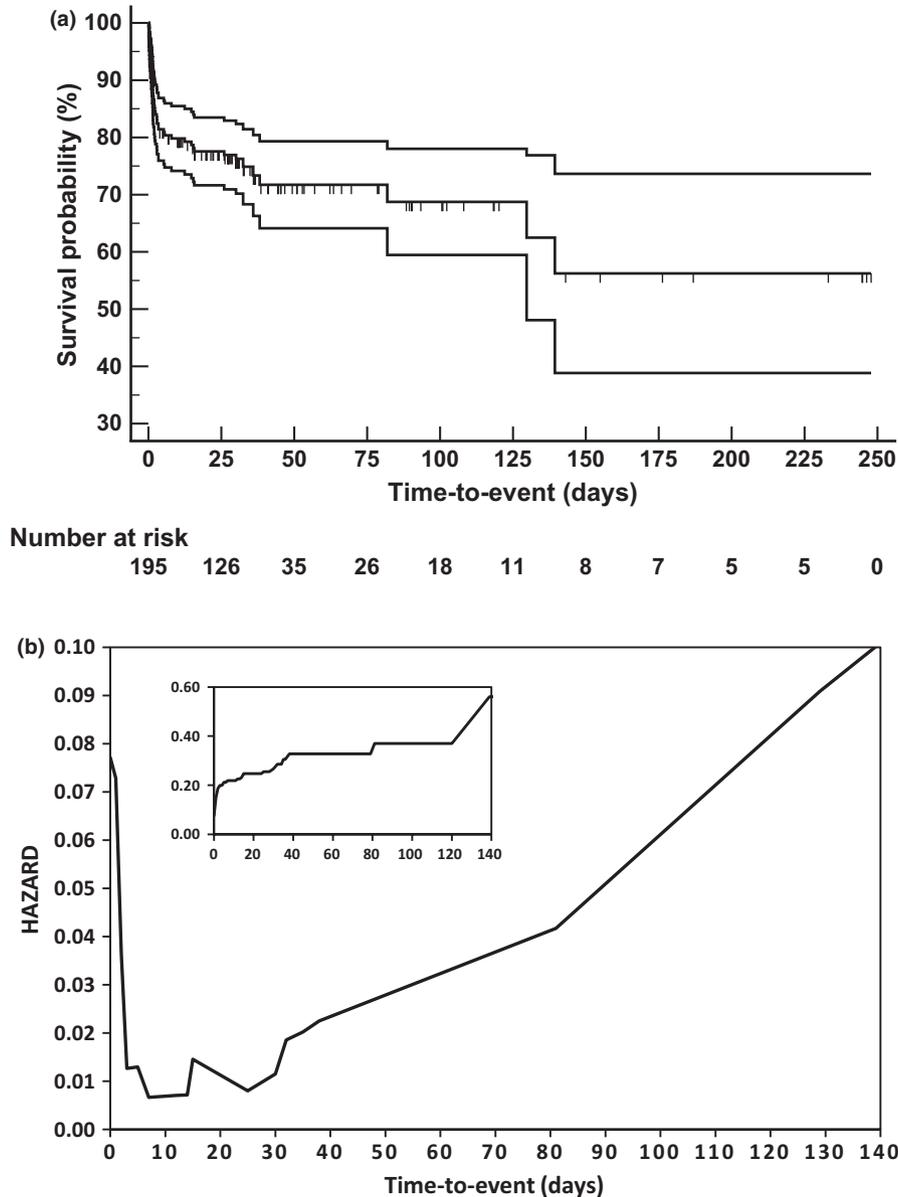


FIGURE 2 (a) Kaplan–Meier survival curves from nine studies on pelagic sharks with requisite information (i.e. time-to-event data on survivors and mortality outcomes). The survival curve (censored individuals indicated by tick marks) \pm 95% confidence intervals. Each downward step indicates an F_r outcome. (b) Hazard rate function for the same time-to-event and censor information used in the Kaplan–Meier curve with the inset showing the cumulative hazard

version 17.6, Ostend, Belgium) and classification matrix were used to examine signal strength, model diagnostics and model fit (Hilbe, 2016; Hosmer & Lemeshow, 2000; Kleinbaum & Klein, 2010). Statistical tests were performed at the $p = 0.05$ level of significance.

3 | RESULTS

Individual studies (indicated in text and figures by numbers in brackets that match Table 1) compiled for the meta-analysis on F_r rates in pelagic sharks included 33 studies, comprising 401 working PSAT tags, seven species (bigeye thresher *Alopias superciliosus*, Alopiidae; blue shark

Prionace glauca, Carcharhinidae; common thresher *Alopias vulpinus*, Alopiidae; oceanic whitetip *Carcharhinus longimanus*, Carcharhinidae; scalloped hammerhead *Sphyrna lewini*, Sphyrnidae; shortfin mako *Isurus oxyrinchus*, Lamnidae; silky shark, *Carcharhinus falciformis*, Carcharhinidae) and three gear types (Table 1; Supporting Information Figure S1). The meta-analysis for pelagic sharks comprised published (30 studies, \sim 91% of total) and unpublished reports (three studies, \sim 9%). Eight studies (25% of studies) had results from a combined total of 51 tag deployments indicating survival after release. Two studies (\sim 6%) reported successful deployments of ≥ 30 reporting tags and six studies (\sim 18%) reported results of >20 successful tag deployments. Median number of reporting tags deployed in studies was 10 (range: 2–35; mean = 12.2 [95% CI: 9.1–15.2]). The primary fishing gear was longline

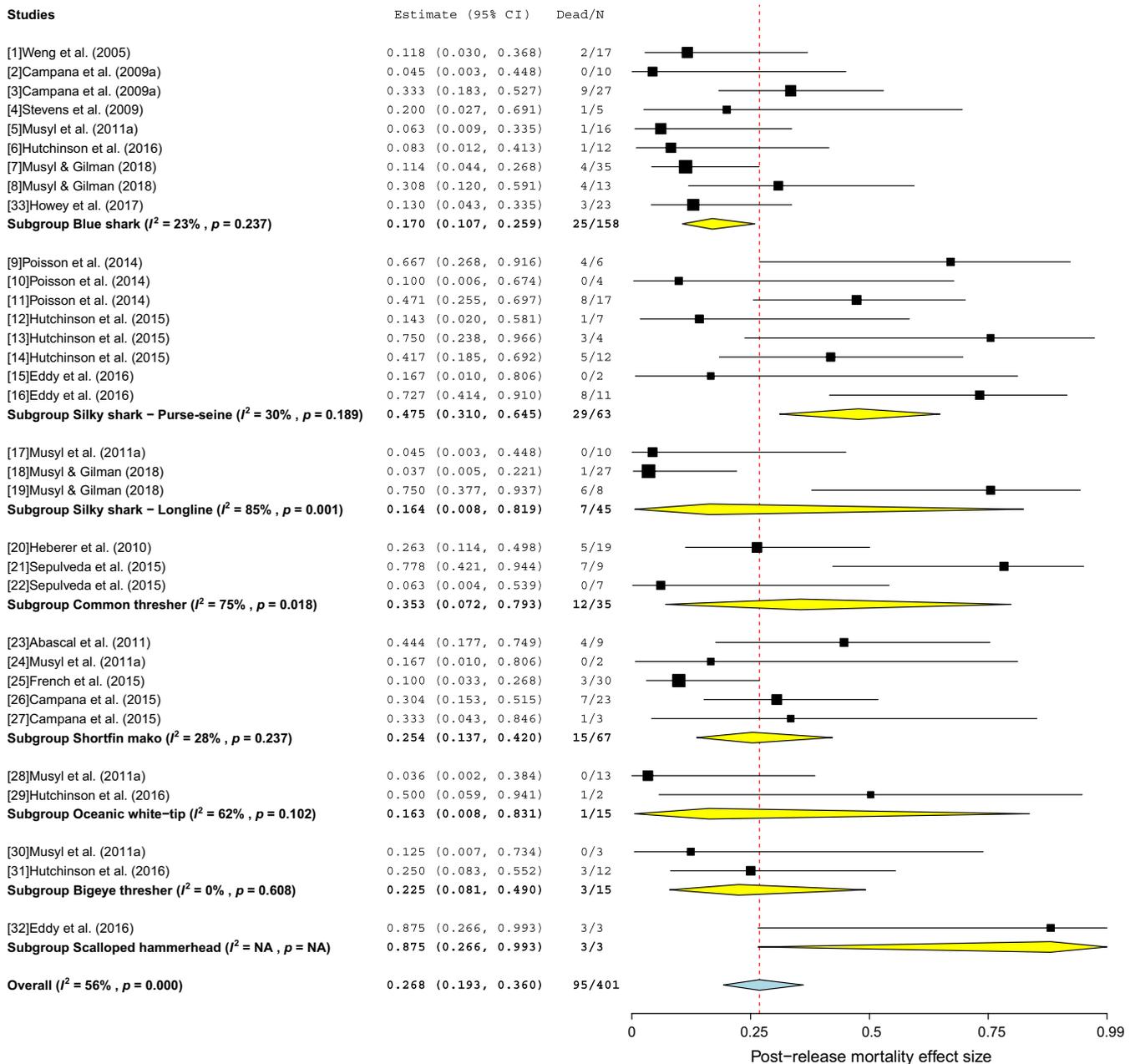


FIGURE 3 Forest plot for the effect size of post-release mortality (F_r) in pelagic sharks released from fishing gear. Study number is provided (in brackets) along with the reference for each study grouped by species. Effect sizes, 95% CIs and number of tags indicating mortality and total sample size (i.e. Dead/N) are provided for each study. I^2 , the amount of variability among studies within species, along with a p value testing for heterogeneity (Cochran's Q), are provided. For studies with zero mortality, a 0.5 continuity factor was added to the events and non-events (see text). Forest plots were constructed where the area of the boxes for each study is proportional to the inverse of the variance, and any side of the box is proportional to the inverse of the standard error. The 95% confidence intervals (horizontal bars) for each study are proportional to the standard error and are related to sample size. The diamonds represent the summary effect size and the width is proportional to the 95% CI. Note especially the much narrower widths of the diamonds indicating more precision in the estimates

(19 studies, ~65% of tags), followed by purse-seine (nine studies, ~17% of tags) and rod & reel (five studies, ~18% of tags). Seven new F_r studies (92 tags, rod & reel) on white marlin (*Kajikia albida*, Istiophoridae) were compared to a previous meta-analysis comprising six studies (94 tags, longline, rod & reel) and to an existing F_r meta-database on six species of istiophorid billfish comprising 36 studies, 457 tags and three gear types (Musyl et al., 2015). In total, F_r results from 76 studies, 950 tags,

13 species and four gear types (harpoon, longline, purse-seine, rod & reel) are analysed and presented in the report.

3.1 | Temporal distribution of mortality outcomes

Post-release mortality events were documented in 95 cases in pelagic sharks of which time-to-event was reported in only 59 cases.

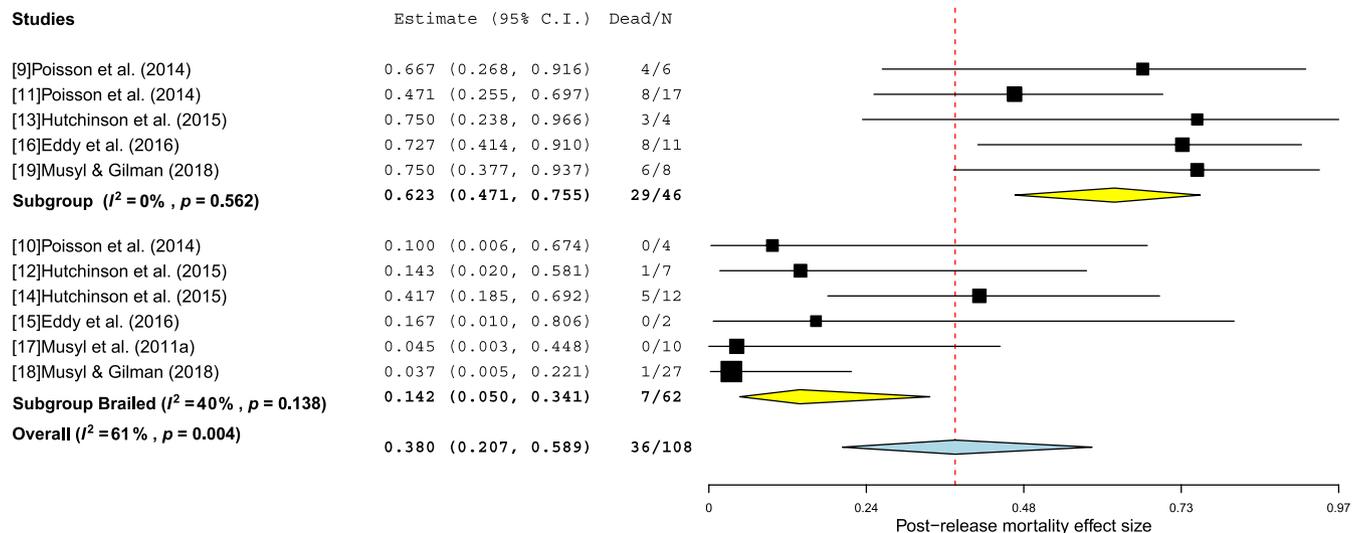


FIGURE 4 Forest plot for the effect size of post-release mortality (F_r) comparing silky sharks released from longline and purse-seine fishing gear broken down by health assessment into two groups. The “brailed” group comprised silky sharks judged the most severely injured/unhealthy by study authors from longline and purse-seine studies and the “non-brailed” group comprised those deemed healthy from longline and purse-seine studies. Silky sharks that were brailed (i.e. crushed, suffocated) from purse-seine interaction [9, 11, 13, 16] and unhealthy sharks released from longline gear [19] had the highest F_r rates. Descriptions follow Figure 3

Most authors used “zero” to indicate immediate mortality occurring within 1 day after release and whole numbers thereafter. Mean time-to-event was 10.4 days ([95% CI: 3.4–17.4], median = 1, mode = 0, range: 0–139) and the distribution for mortality outcomes was positively skewed (coefficient of skewness = 3.8, $p < 0.0001$) with a heavy tail (coefficient of kurtosis = 14.8, $p < 0.0001$; Figure 1). Sixty-one per cent of F_r occurred within 1 day after release, 80% within 7 days, 83% within 14 days, 90% within 30 days and 95% within 40 days. The positively skewed shape of the distribution indicates high initial F_r immediately after release (i.e. riskiest period) with the rate rapidly diminishing after 2 weeks and mostly gone >40 days. We decided to investigate this distribution further but there were two problems. Firstly, mortality is a continuous random variable (i.e. time-to-event must be >0) and to investigate F_r outcomes further, we needed to randomly select decimal numbers between whole numbers. From 56 candidate distributions, the Anderson–Darling test (Laio, 2004; Razali & Wah, 2011) indicated the transformed data best fit a three-parameter Fréchet (extreme value or reciprocal Weibull) distribution ($\alpha = 0.65115$, $\beta = 0.63838$, $\gamma = -0.03853$). The second problem was that the tags were programmed with different pop-up schedules (i.e. 30–250 days). Therefore, it is possible F_r was underestimated given that ~10% of mortality outcomes were reported >30 days which could not be measured with 30-day tags. For the sizes and ages of sharks in the study, it is possible the long tail of the F_r distribution may contain the juncture between F_r and M . Kaplan–Meier survival curves for applicable studies (Supporting Information Figure S2) indicated most mortality outcomes in the early part of the curves—where risk was largest—and then, it gradually tapered off at ~40 days (Figure 2a). The hazard curve (Figure 2b) showed the typical initial burn-in period (high mortality) and bathtub shape that suggest an increasing hazard rate after 40 days which is

based on limited mortality outcomes ($n = 3$) reported >40 days (81, 129 and 133 days; ~5% of reported time-to-event outcomes).

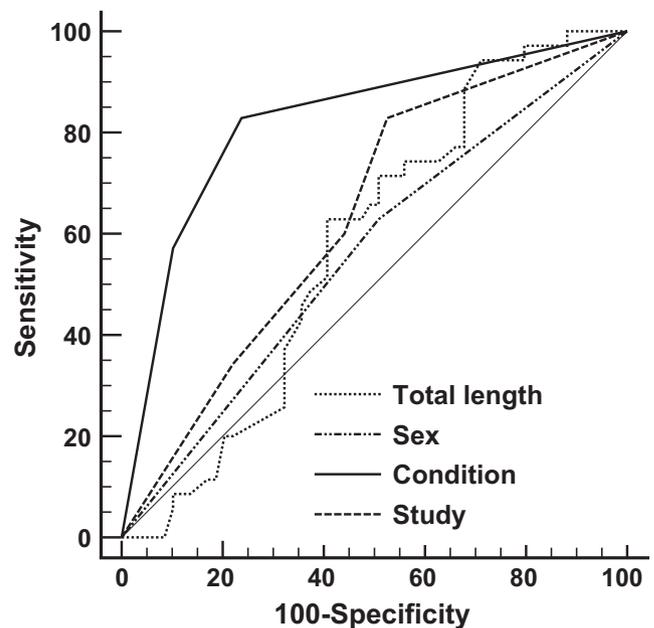


FIGURE 5 Receiver operator characteristic (ROC) curve for the prognostic variables used in the individual participant data meta-analysis of silky sharks. Sensitivity is the true positive rate and 100-specificity is the false positive rate. The further away from the diagonal line represents better discriminatory power of the particular variable in classifying survival outcomes. Condition code confers the best discriminatory power (area under the ROC curve (AUC) = 0.84 [0.75–0.91])

3.2 | Blue shark

The meta-analysis comprised nine studies (eight longline, one rod & reel), 158 reporting tags (Table 1; Figure 3). There were no significant differences in F_r rates between blue shark studies ($Q_{(8)} = 10.416$, $p = 0.237$, $T^2 = 0.15$, $I^2 = 23.20$) and the summary effect size was 0.17 [95% CI: 0.11–0.26]. This result was confirmed by exact chi-square tests ($\chi^2 = 12.8$, $p = 0.1144$, *point probability* = 2.534×10^{-6}). The high-low cumulative analysis (to identify possible bias) indicated no significant trends or shifts in the data (Supporting Information Figure S3).

Next, a sensitivity analysis (Supporting Information Figure S4) indicated that no single blue shark study had a significant impact on the summary effect (i.e. 95% CIs overlapped and there were no significant outliers). No significant differences in F_r by set type for longline gear (deep vs. shallow) or targeting strategies (tuna and swordfish) was evident in the studies (Table 1; Figure 3). The

sensitivity analysis did, however, show a 0.032 drop in mortality rates when study [3] was removed and 0.017 drop when study [8] is removed. When excluding these two studies [3, 8] indicating unhealthy/injured sharks (Table 1), the summary effect size dropped to 0.11 [95% CI: 0.06–0.18] and both T^2 and I^2 dropped to zero, indicating heterogeneity between studies was accounted for by these two studies. In this situation, F_r can be attributed to random events within studies since by definition the between-studies variance was $T^2 = 0.00$ (Borenstein et al., 2009).

The meta-analysis replicated the results of an earlier meta-analysis by Musyl, Brill et al. (2011) but increased precision in the estimate. Tests for publication bias were non-significant (Begg & Mazumdar, 1994) and Orwin's fail-safe N indicated 25 additional biased studies (~450 tags) with an F_r rate of 0.50 would be required to nullify the summary results and significantly double F_r to above 0.40. That is, the higher number of additional biased studies

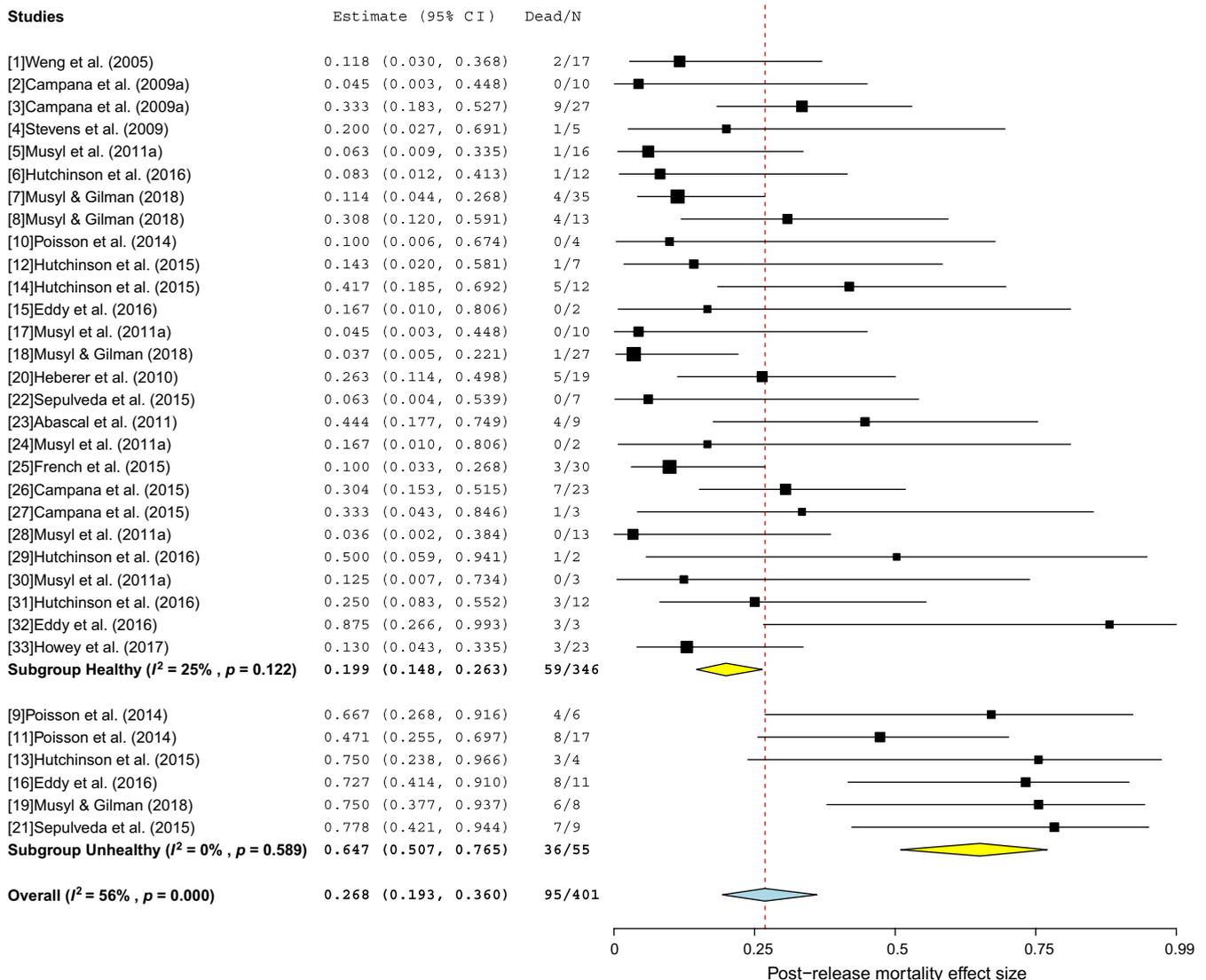


FIGURE 6 Forest plot for the effect size of post-release mortality (F_r) comparing “healthy” and “unhealthy” pelagic sharks. As reported by study authors, the unhealthy group comprised silky sharks that were brailed from purse-seine interaction [9, 11, 13, 16], silky sharks in unhealthy condition from longline capture [19] and tail-hooked caught common thresher sharks [21] had the highest F_r rates. Descriptions for the plot follow Figure 3

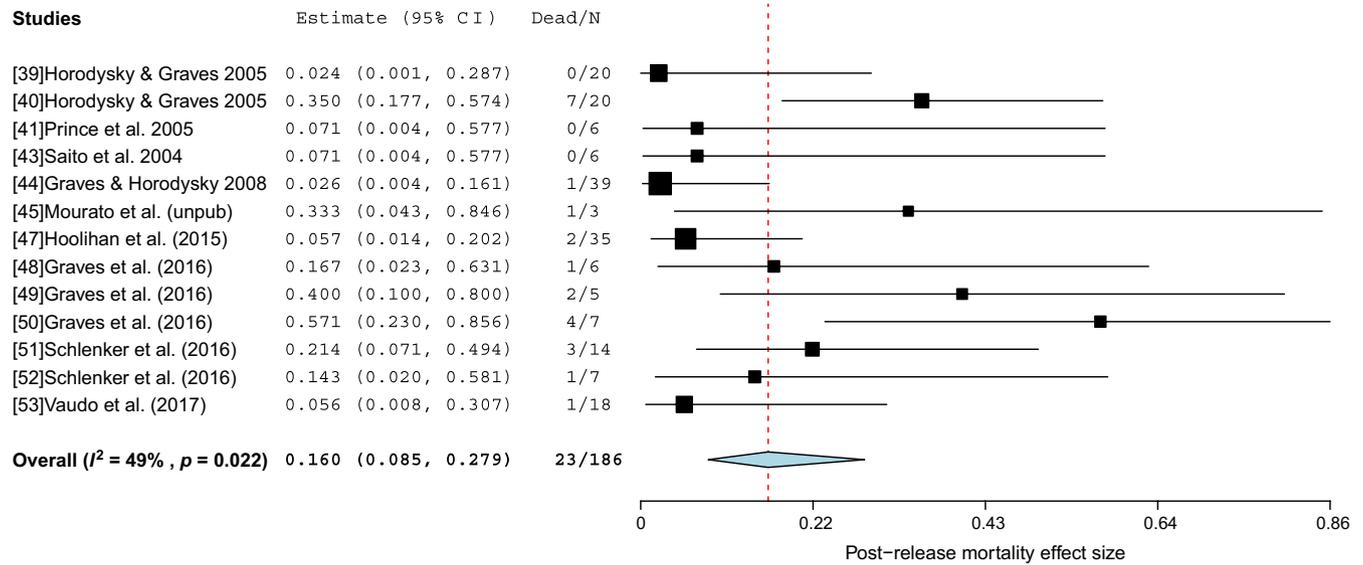


FIGURE 7 Forest plot for the effect size of post-release mortality (F_r) in white marlin studies. Descriptions for the plot follow Figure 3

indicates increased likelihood that studies with higher F_r rates were not missed in the analysis. For example, as a comparison, Duval & Tweedie's analysis suggested only two small missing studies (i.e. imputed studies) were required to balance the funnel plot but the result was non-significant (i.e. imputed and observed summary effect sizes overlapped; Supporting Information Figure S5).

3.3 | Silky shark

The meta-analysis for silky shark comprised 11 studies, 108 reporting tags and two gear types (longline, purse-seine; 1; Figure 3). For all silky shark studies, Cochran's Q indicated highly significant heterogeneity in F_r rates between longline and purse-seine studies ($Q_{(10)} = 25.629$, $p = 0.004$, $T^2 = 1.14$, $I^2 = 60.98$) and the result was confirmed by exact tests ($\chi^2 = 41.68$, $p = 8.322 \times 10^{-7}$, *point probability* = 1.349×10^{-11}). The summary effect size for all silky shark studies was 0.38 [95% CI: 0.21–0.59]. In the sensitivity analysis, silky sharks that were brailed (i.e. crushed and suffocated) from purse-seine interaction [9, 11, 13, 16] and sharks in presumably unhealthy condition released by longline gear [19] had the largest impact on F_r rates (Supporting Information Figure S6).

As indicated above, though there was significant heterogeneity among F_r rates in silky shark studies presumably from combining a mixture of condition codes and gear types, within groups based on health assessment codes or injury, there were no significant differences in pooled mortality rates (Figure 4): (a) the "brailed group" comprising the most severely injured/unhealthy silky shark from longline and purse-seine studies [9, 11, 13, 16, 19] exhibited the highest (0.62 [95% CI: 0.47–0.76]) but most homogeneous F_r rates ($Q_{(4)} = 2.977$, $p = 0.562$, $T^2 = 0.00$, $I^2 = 0.00$), whereas (b) the "non-brailed group" consisting of presumably healthy silky sharks released from purse-seine (snagged or encircled) and longlines exhibited the lowest F_r rates (0.14 [95% CI: 0.05–0.34]) but with ~40% heterogeneity explained between the mixture of studies ($Q_{(5)} = 8.340$, $p = 0.138$, $T^2 = 0.775$, $I^2 = 40.05$). Tests for

publication bias in silky shark studies were non-significant (Begg & Mazumdar, 1994) and Orwin's fail-safe N indicated 21 additional studies (~210 tags) with an F_r rate of 0.50 would be required to nullify the overall summary results and significantly increase F_r by 10%. Duval & Tweedie's analysis indicated three missing studies (Supporting Information Figure S7).

3.4 | Silky shark IPD

To further explore patterns in heterogeneity of F_r rates in greater detail, IPD from silky shark studies [9–16, 18–19] was analysed by logistic regression and indicated condition code was the only significant factor to explain survival outcomes in models (Figure 5). The odds of dying were ~6 times higher (odds ratio, OR = 5.64 [95% CI: 1.51–21.04]) going from the healthiest condition code (1) to the middle health code (2) and the odds more than doubled (OR = 13.68 [95% CI: 3.56–52.51]) going from code (2) to the poorest condition code (3). The logistic model was ~78% accurate in correctly classifying survival outcomes using condition code (area under the ROC [AUC] = 0.84 [95% CI: 0.75–0.91]; Hosmer & Lemeshow test was $\chi^2 = 6.73$, $p = 0.566$; Nagelkerke R^2 was 0.423) and diagnostics indicated strong overall predictive power (Hilbe, 2016). Classification results were duplicated using stepwise discriminant function analysis. In addition to the IPD and censor data, some of the studies [9–14, 18–19] provided time-to-event data in which case Cox proportional hazards models (Hosmer & Lemeshow, 1999; Kleinbaum & Klein, 2005) could be run, but they confirmed results from the logistic regression model with condition code as the only significant variable.

3.5 | Shortfin mako

The meta-analysis for shortfin mako comprised five studies, 67 reporting tags and two gear types (longline, rod & reel; Table 1;

Figure 3). There were no significant differences in F_r rates between shortfin mako studies ($Q_{(4)} = 5.528$, $p = 0.237$, $T^2 = 0.20$, $I^2 = 27.65$) and the summary effect size was 0.25 [95% CI: 0.14–0.42]. This result was also confirmed by exact chi-square tests ($\chi^2 = 6.81$, $p = 0.14$, *point probability* = 0.001088). Sensitivity analysis indicated a 0.043 drop in mortality when longline study [23] was removed and the recalculated summary effect size was 0.21 [95% CI: 0.11–0.37].

3.6 | Meta-analysis of pelagic sharks

By combining a mixture of species, body sizes, sexes, gear types, handling characteristics, operational factors in the fishery, healthy and unhealthy samples, spatial and temporal scales, environmental variables and many other variables and nuances unknown in the individual studies, it was expected that significant heterogeneity in F_r rates would be observed between studies ($Q_{(32)} = 71.938$, $p \ll 0.001$, $T^2 = 0.74$, $I^2 = 55.52$; Monte Carlo $\chi^2 = 110.5$, 99% CI for p value [0.0–0.0004604]), and the overall summary effect size was 0.27 [95% CI: 0.19–0.36] (Figure 3).

High–low cumulative analysis suggested minor bias in smaller studies (i.e. shift to the right) but these were not significant and the F_r rates converged at ~345 tags (study [19], Supporting Information Figure S8). The highest reduction in mortality rates were observed when brailed/severely injured silky sharks [9, 11, 13, 16, 19] and tail-hooked common thresher sharks [21] were removed in the sensitivity analysis (Supporting Information Figure S9). These six studies, indicating severe injury and the lowest health condition codes reported by study authors, were not significantly different ($Q_{(5)} = 3.732$, $p = 0.589$, $T^2 = 0.00$, $I^2 = 0.00$, effect size 0.65 [95% CI: 0.51–0.77], $\chi^2 = 3.893$, $p = 0.597$, *point probability* = 0.001729). When excluding these six extreme injury outlier studies in the analysis, the remaining 27 studies, comprising 7 species, 3 gear types and $n = 346$ tags (86% of tags), were homogeneous ($Q_{(26)} = 34.539$, $p = 0.122$, $T^2 = 0.20$, $I^2 = 24.72$; $\chi^2 = 8.975$, $p = 0.1694$, *point probability* = 1.217×10^{-5}) and the overall summary effect size for F_r was 0.20 [95% CI: 0.15–0.27] (Figure 6).

Meta-regression indicated no significant trends in F_r effect sizes with study latitude for pelagic shark studies (Supporting Information Figure S10; $b_1 = -0.022$ [–0.052, 0.007], $p = 0.142$). However, higher mortality (but not significantly so) was observed at lower latitudes.

The funnel plot indicated symmetry at the top for the larger studies but an absence of smaller studies (near the base) with high mortality rates (Supporting Information Figure S11). These small studies, however, had minor impact in the analysis. Duval & Tweedie's analysis indicated only four small imputed missing studies were needed to balance the plot. Tests for publication bias were non-significant (Begg & Mazumdar, 1994; Egger et al., 1997) and Orwin's fail-safe N indicated 61 additional studies (~732 tags) with an F_r rate of 0.50 would be required to nullify the results and significantly increase F_r to above 0.42.

3.7 | White marlin

Seven additional studies [47–53] were added to the meta-analysis performed by Musyl et al. (2015) on white marlin (Table 1; Figure 7).

For the 13 combined white marlin studies (186 reporting tags, two gear types), F_r was significantly different between studies ($Q_{(12)} = 23.757$, $p = 0.022$, $T^2 = 0.77$, $I^2 = 49.49$), and the summary effect size was 0.16 [95% CI: 0.09–0.28]. About half of the variance (~50%) was explained between studies and exact chi-square tests confirmed the result ($\chi^2 = 38.51$, $p = 0.0005314$, *point probability* = 2.961×10^{-7}). The high–low cumulative meta-analysis indicated F_r rates converging near the bottom with no evidence of bias (Supporting Information Figure S12).

As identified previously in Musyl et al. (2015), the primary source contributing to the variability in F_r was the use of J hooks in study [40] (Horodysky & Graves, 2005). Sensitivity analysis on the 13 studies (Supporting Information Figure S13) indicated a 0.021 drop in mortality rates when study [40] was removed, a drop of 0.023 when study [50] was removed and a drop of 0.016 when study [49] was removed. Notice the linear pattern in studies [48–50] and studies [51–52] correlating F_r rates with varying time of air exposure (i.e. higher survival rates correlated with lower air exposure times) (Figure 7). If studies [40–J hook] and [49, 50–increased air exposure time] were removed from the analysis, the remaining studies were not significantly different ($Q_{(9)} = 8.174$, $p = 0.517$; $\chi^2 = 13.7$, $p = 0.1257$, *point probability* = 0.0007222) and the heterogeneity statistics drop to zero ($T^2 = 0.00$, $I^2 = 0.00$) indicating all variability is randomly distributed within studies. The summary effect size was 0.10 [95% CI: 0.06–0.17]. Tests for publication bias were non-significant (Begg & Mazumdar, 1994) and Orwin's fail-safe N indicated 33 additional studies (~472 tags) with an F_r rate of 0.50 would be required to nullify the results and significantly increase F_r to above 0.40. Duval & Tweedie's analysis indicated five missing studies (Supporting Information Figure S14).

3.8 | Istiophorid billfish

Metadata on F_r rates in istiophorid billfish from Musyl et al. (2015) were combined with the present report comprising 43 studies, 549 tags, six species and three gear types (harpoon, longline, rod & reel). F_r was not significantly different between istiophorid studies ($Q_{(42)} = 44.242$, $p = 0.377$, $T^2 = 0.05$, $I^2 = 5.07$; $\chi^2 = 10.17$, $p = 0.0705$, *point probability* = 4.635×10^{-6}) and the summary effect size was 0.14 [95% CI: 0.11–0.18] (Supporting Information Figure S15). The cumulative meta-analysis by study year suggests F_r levels have been steady since ~1999 with a minor, non-significant shift at study [40] (Figure 8) but there was no evidence of bias (Supporting Information Figure S16). There was no significant trend between F_r and study latitude in istiophorid billfish studies (Supporting Information Figure S17, $b_1 = 0.037$ [–0.001, 0.075], $p = 0.053$) although higher mortality (but not significantly so) was observed at higher latitudes. Tests for publication bias were non-significant (Begg & Mazumdar, 1994; Egger et al., 1997) and Orwin's fail-safe N indicated 145 additional studies (~1,851 tags) with an F_r rate of 0.50 would be required to nullify the results and significantly increase F_r to above 0.40. Duval & Tweedie's analysis suggested 12 missing studies but the imputed summary effect size (black diamond) was not significantly different

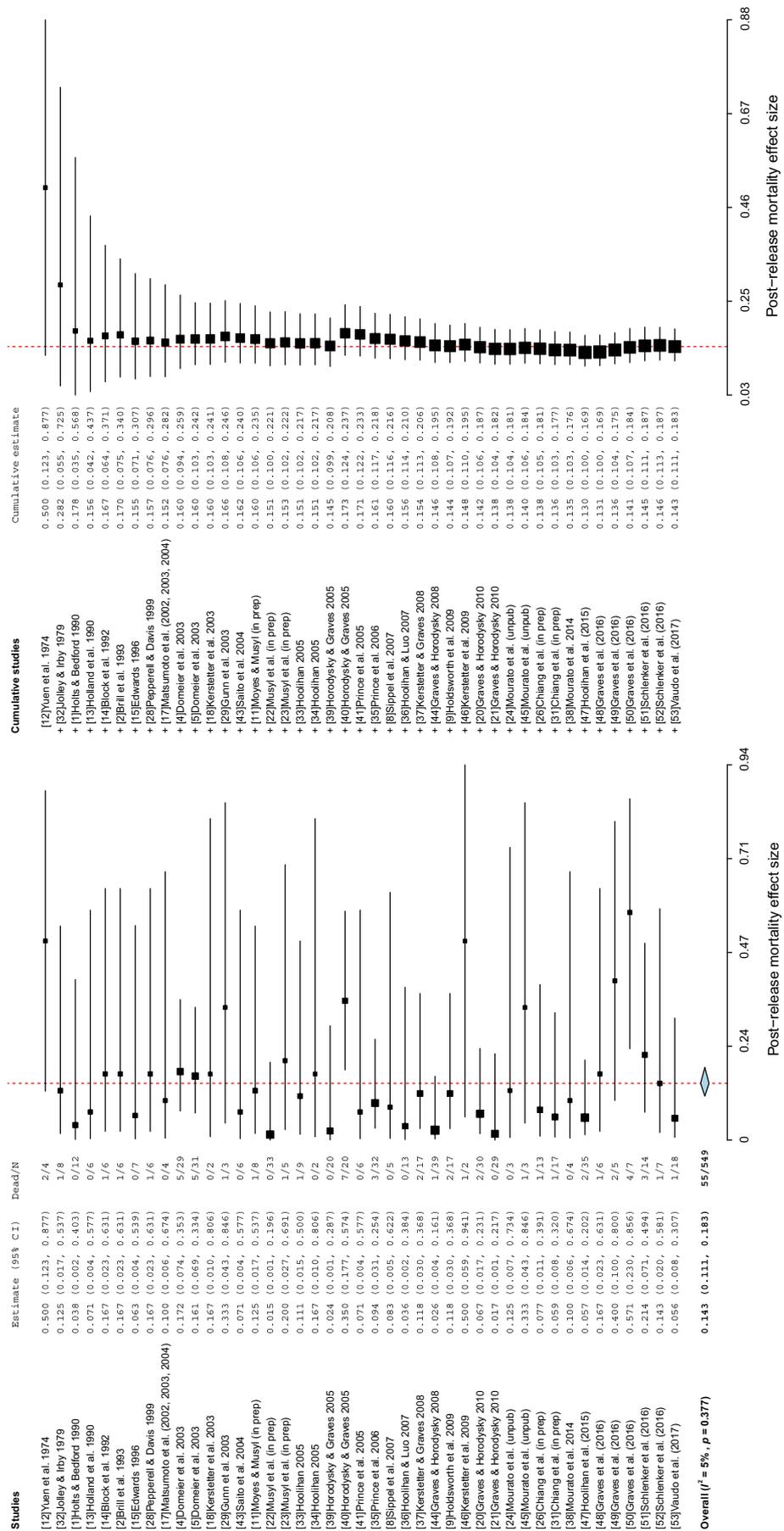


FIGURE 8 Cumulative Forest plot (right panel) arranged by study year is provided for the effect size of post-release mortality (F_p) in istiophorid billfish released from fishing gear. Descriptions for the plot follow Figure 3

the observed summary effect size (open diamond; Supporting Information Figure S18). Over 90% of F_r outcomes in istiophorid billfish occurred within 10 days after release.

4 | DISCUSSION

By consolidating and synthesizing current research on global F_r rates in pelagic shark and istiophorid billfish studies across dissimilar spatial and temporal scales, from different species, environmental conditions, fisheries, handling practices and gear types (Table 1), the meta-analysis findings have implications for fisheries management and prioritizing future F_r studies to fill identified gaps in our understanding of what influences F_r rates in fisheries. Due to the mixture of studies, a random-effects meta-analysis approach produced wide-ranging results that can be extrapolated over diverse settings and contexts (Sutton et al., 2000). This is certainly applicable in the context of latitudinal trends in F_r rates where no significant correlation was found across a diverse array of pelagic shark and istiophorid billfish studies, species, fisheries and gear types. Given the overall meta-analysis on F_r rates and the generalizability of results, where information is lacking on a particular species, by examining similar species with concordant distributions, it would be justifiable to use the summary effect size (e.g. Oliver et al., 2015).

Results from single studies are sometimes inconsistent or contradictory, often making it difficult to draw conclusions or find non-zero baselines against which future results can be compared (Ellis, 2010). Thus, this study provides a credible baseline to which future F_r studies can be compared and designed. Single F_r studies are rarely definitive because they are often context-specific but the larger deficiency is that they are too small which increases the chance of type II errors (failing to find a meaningful result because study size was small; Table 1). For example, most F_r studies in Musyl et al. (2015) had statistical power <9%.

By pooling relevant studies, random errors can be reduced to produce a more reliable and precise estimate of the true effect size. Moreover, the ability to replicate F_r rates across independent studies was demonstrated which is fundamental in increasing the proportion of true research findings (Carver, 1978, 1993; Ellis, 2010; Errington, Iorns, Gunn, Tan & Lomax, 2014; Ioannidis, 2014, 2016; Kandela, Jin, Owen & Reproducibility Project: Cancer Biology, 2015). A dedicated effort, The Reproducibility Project: Cancer Biology, was specifically established amid growing concerns about reproducibility in clinical research where researchers seldom replicate experiments of existing results (Errington et al., 2014; Kandela et al., 2015). Fisheries biology needs to emulate this best practice of demonstrating and testing reproducibility in F_r and F_c studies (and for that matter, results from any studies that repeatedly test or measure similar things).

4.1 | Blue shark mortality

A previous meta-analysis on F_r rates in blue shark using four studies produced a summary effect size of 0.17 [95% CI: 0.07–0.34] (Musyl,

Brill et al., 2011). Confidence intervals are based on the concept of repetition of the study under consideration (Campbell & Machin, 1993). If the study is repeated many times, the expectation is that the calculated 95% CIs would include the population effect size 95% of the time. Despite conducting studies over disparate temporal and spatial scales and across different fisheries (Table 1; Figure 3), the ability to replicate results of blue shark F_r studies was clearly demonstrated. For example, to give an idea of the consistency of results and robustness of the estimates, the effect size (0.15) of the new (i.e. independent) studies [6–8, 33] added to the updated meta-analysis was well within the limits (more near the mean) of the previous 95% CIs estimated by Musyl, Brill et al. (2011). Overall, there was no significant heterogeneity in F_r across studies but the addition of new studies produced more precise point estimates. In brief, the best and most precise estimate would be the combined summary effect size synthesized for blue shark that has remained consistent over spatial and temporal scales. In other words, there is no compelling reason to ignore commonalities in mortality rates across different fisheries and locations. This finding is critical because blue shark make up the majority of by-catch in global longline fisheries (Gilman, Chaloupka, Merrifield, Malsol & Cook, 2015; Oliver et al., 2015) and precise estimates for F_r are required for robust stock assessments and ecological risk assessments and to manage by-catch at sustainable levels (Simpfendorfer & Dulvy, 2017).

Findings from the sensitivity analysis on blue shark F_r rates indicated a ~3% drop in mortality when study [3] was removed and a ~2% drop when study [8] was removed. In study [3], sharks occasionally had their jaws detached from crew cutting out hooks and/or were severely injured from crew body-gaffing them before they were discarded. There was also some indication that J hooks were used in study [3] (Carruthers et al., 2009; Diaz, 2008; Gilman et al., 2012, 2016; Godin et al., 2012; Reinhardt et al., 2017; Serafy et al., 2012), but the number of tagged individuals by hook type was not reported. It remains unknown what factors affected condition scores for mortality outcomes in study [8] but at the time of tagging, all blue sharks were handled in a similar fashion (Table 1).

Poisson, Gaertner, Taquet, Durbec and Bigelow (2010) demonstrated that blue and oceanic whitetip sharks could survive after spending ~14 hr hooked on longline gear. Soak time and time-in-air, however, were not significant factors to explain F_r rates in blue sharks released from longline gear in the Canadian Atlantic (Campana, Joyce & Manning, 2009) or in Palau (Musyl & Gilman, 2018). Time on deck for tagging and handling ranged from ~50 s (Musyl & Gilman, 2018) to ~3 min (Campana, Joyce & Manning, 2009). Out of water, sharks' body weight is not supported and internal organs can get damaged (McLoughlin & Eliason, 2008; Patterson, Hansen & Larcombe, 2014; Poisson, Séret, Vernet, Goujon & Dagorn, 2014; Poisson, Séret, Vernet, Goujon & Dagorn, 2012), but despite prolonged time on deck (~5–7 min) for blood sampling and affixing PSATs with no hose for ventilation, higher F_r rates were not observed in the central Pacific (Moyes et al., 2006; Musyl, Brill et al., 2011). Despite the obvious bias in mortality rates from severe handling practices in Campana, Joyce and Manning (2009; see also Campana, Joyce, Francis et al.,

2009; Musyl et al., 2009; Musyl, Brill et al., 2011), there were no significant differences in mortality rates between blue shark F_r studies. Moreover, Campana, Joyce and Manning (2009) and Musyl and Gilman (2018) used similar survival models and prognostic variables and independently reached the same conclusion: the only significant variable to explain survival outcomes was health condition code at retrieval and tagging. However, in terms of practical and clinical significance and “Best Handling Practices” to promote survival, it is clear that eliminating severely injurious handling practices could lower mortality rates (Favaro & Côté, 2015; Molina & Cooke, 2012; Poisson, Filmlalter et al., 2014; Poisson et al., 2012, 2016; Poisson, Séret et al., 2014).

4.2 | Silky shark mortality

Results of the meta-analysis on silky shark F_r rates were paradoxical and included an unexpected dichotomy based on condition code, rather than fishing gear. Firstly, due to the mixture of different studies, locations, fishing gear (purse-seine, longline), fisheries and presumably random selection of individuals with varying condition codes, significant variability in F_r rates was expected across studies.

Mode of death and physical injury suffered by silky sharks captured by purse-seine, however, is unlike injuries suffered by sharks interacting with longline gear or rod & reel. Sharks that are brailed suffer the most severe physical injuries which are the result of being crowded, confined, abraded (i.e. obligate ram-ventilators must swim actively or extend their gape to oxygenate the gills, Carlson & Parsons, 2001), suffocated and/or crushed (Poisson, Filmlalter et al., 2014). Duration of purse-seine fishing typically lasts ~1 hr but occasionally extends to ~2 hr [9–16]. Yet, silky sharks deemed unhealthy at the time of retrieval at longline capture (study [19], mean soak time was ~13 hr and ranged ~9–24 hr) had similar F_r rates compared to brailed sharks released from purse-seine gear. Soak time for longline gear should not be interpreted as the time sharks are hooked and struggling. A logical extension, however, is that longline captured sharks have the opportunity for protracted and varied capture periods which increases stress but variability in soak time did not translate into higher F_r rates for pelagic sharks (Campana, Joyce & Manning, 2009; Musyl & Gilman, 2018; Poisson et al., 2010). Conversely, silky sharks liberated from purse-seine before they were brailed (i.e. snagged or encircled) exhibited similar F_r rates compared to presumably healthy sharks released from longline gear.

To further investigate patterns of survival outcomes, IPD from longline and purse-seine studies were analysed by logistic regression to explain F_r rates and the only significant prognostic factor was condition code. As a prognostic variable, condition code makes practical sense to predict survival outcomes because health and injury might be expected to show congruence (Benoît et al., 2012; Braccini et al., 2012; Davis, 2002; Eddy et al., 2016; Hutchinson et al., 2015; Meeremans et al., 2017; Musyl & Gilman, 2018; Poisson, Filmlalter et al., 2014). In other words, the commonality in explaining mortality in silky shark longline and purse-seine studies was condition code and not gear type, sex, location or body size. In the combined sample

regardless of gear, the odds of silky shark dying were ~6 times higher going from the healthiest category to the medium condition category and ~14 times higher going to the poorest condition category. Condition code as a prognostic factor to explain F_r was found to be 78% accurate. Similarly, Musyl and Gilman (2018), reported condition code was ~83% accurate in classifying silky and blue shark F_r rates released from longline gear and was the only significant factor found in survival models, similar to what Campana, Joyce, and Manning (2009) reported. The obvious parallels in condition code and mortality suggest mitigation measures that improve health condition would increase survival (Butcher, Peddemors, Mandelman, McGrath & Cullis, 2015). Discerning factors responsible for condition code, however, appear to be complex and probably need to be examined in conjunction with F_c rates to increase resolving power (Musyl & Gilman, 2018).

4.3 | Mortality comparisons of pelagic sharks

It was evident severely injured and/or unhealthy silky sharks comprising six studies released from purse-seine and longline gear and tail-hooked common thresher sharks exhibited the highest and most homogenous F_r rates in the study. This association appeared to be based on severity of injury and/or health condition as reported by study authors. No other high F_r clusters were evident in the metadata. Tail-hooked common thresher sharks are obligate ram-ventilating species and the synergy of restricted forward motion (preventing the acquisition of oxygen) and high stress translated into short survival times (Heberer, Aalbers, Bernal, Kohin & DiFiore, 2010; Sepulveda, Heberer, Aalbers, Spear & Kinney, 2015). Brailed silky sharks have high F_r rates but it is not clear what prognostic factors influence silky sharks released from longline gear in poor condition to suffer similar F_r rates (Musyl & Gilman, 2018). Regardless of this clustering, when these six high F_r studies ($n = 55$ tags) were excluded from the overall analysis, F_r rates were homogeneous across seven pelagic shark species, 27 studies, $n = 346$ tags (86% of tags) and three gear types (longline, purse-seine, rod & reel). This finding, in particular, suggests that whilst species-specific differences to stress may be apparent (Hight, Holts, Graham, Kennedy & Taylor, 2007; Mandelman & Skomal, 2009; Mandelman, Cooper, Werner & Lagueux, 2008; Moyes et al., 2006), it is also incumbent to point out that stress does not necessarily translate into species-specific F_r rates in pelagic shark species. For coastal elasmobranch species, species-specific differences in F_r rates were reported (Braccini et al., 2012; Butcher et al., 2015; Dapp et al., 2015; Frick, Renia & Walker, 2009; Frick, Renia & Walker, 2010; Gallagher, Orbesen et al., 2014; Gallagher, Serafy et al., 2014; Marshall, Skomal, Ross & Bernal, 2015; Morgan & Carlson, 2010). Moyes et al. (2006) and Hight et al. (2007) indicated blue sharks exhibited significantly lower plasma lactate and catecholamine levels, respectively, than shortfin mako during retrieval of longline gear but there were no differences in F_r rates between these species. It appears that regardless of species, fisheries or gear type, health condition at tag and release largely dictated survival outcomes. It is not known whether sublethal effects

were manifested at the population level (i.e. spawning, migration, reproduction) for pelagic sharks released from fishing gear but carrying PSATs was probably not detrimental to their health (Jepsen, Thorstad, Havn & Lucas, 2015; Lynch, Marcek, Marshall, Bushnell & Bernal, 2017; Musyl, Domeier et al., 2011). Should PSATs or other tags remain attached for prolonged periods, the possibility exists that extra drag and energetic costs could affect long-term fitness and health outcomes (Bouyoucos, Montgomery, Brownscombe, Cooke & Suski, 2017; Bouyoucos, Suski, Mandelman & Brooks, 2017; Lear, Gleiss & Whitney, 2018), but there was no evidence of increased mortality with time-to-event and the bulk of F_r occurred within 40 days of release. Finally, Guida (2016) and Wosnick et al. (2019) demonstrated population-level effects in small rays and sharks exposed to fishing, but it remains unresolved whether these findings can be extrapolated to other pelagic elasmobranchs.

4.4 | White marlin and istiophorid billfish meta-analysis

Due to their overfished status in the Atlantic, it is critical to assess the survival of white marlin released from fishing gear [references for studies 47–52, Table 1]. Though Graves et al. (2016) analysed F_r data from several studies, they did not synthesize precise F_r rates nor did they account for between-study variability. Musyl et al. (2015) conducted a meta-analysis on F_r rates in white marlin using six studies and $n = 94$ tags, and the summary effect size was 0.11 [95% CI: 0.03–0.32]. The addition of seven new studies and $n = 92$ tags (0.24 [95% CI: 0.12–0.43]) increased both the estimate and precision in the updated meta-analysis (0.16 [95% CI: 0.09–0.28], 13 studies, $n = 186$ tags). Again, it is worthwhile to note that the new effect size calculated from the seven additional studies in the updated meta-analysis (0.24) was contained in the original 95% CIs using six studies indicating precision in the earlier estimate. The upgraded estimate is, of course, preferred as it more reliably captures an array of diverse handling conditions, including varying air exposure times, experienced by captured and released marlin. This example, along with blue shark, serves to indicate why the meta-analysis should be continually updated to derive the most precise and credible estimates that are available for management and conservation purposes.

In random-effects meta-analysis, Jackson and Turner (2017) reported ~5 or more studies were required to achieve power greater than the individual studies that contributed to them. The standard error for the summary effect in the random-effects model (SE_{M*}) contains two terms:

$$SE_{M*} = \sqrt{\frac{\sigma^2}{k \times n} + \frac{\tau^2}{k}}$$

The first term is the standard error (SE_M) for the fixed-effect model where σ^2 is the within-study variance, k is the number of one-group studies and n is the sample size of each study. In this term,

large sample sizes can reduce the standard error but the fixed-effect model does not take into account between-studies dispersion. The random-effects model, however, contains a second term to account for the between-studies variance (τ^2), and the standard error will approach zero as the number of studies approaches infinity (Borenstein et al., 2009). In other words, in the random-effects model, the number of studies is important and not necessarily sample sizes within studies.

The sensitivity analysis suggests adoption of circle hooks over J hooks (on baited hooks) and limiting air exposure times to <1 min could potentially reduce mortality rates by ~6% in white marlin. Globally, as previously reported (Musyl et al., 2015), there was no significant relationship between study latitude and F_r rates in istiophorid billfish and F_r was homogeneous across contrasting spatial and temporal scales, six species, 43 studies, $n = 549$ tags and three gear types. Finally, to give an example of the power and types of hypotheses that can be tested, if the question was deriving credible and precise F_r rates in istiophorid billfish, the meta-analysis analysis could have been stopped at ~50 tags (eight studies) in ~1999 (Figure 8), thus saving costs associated with the deployment of another ~500 tags (~1,700,000 USD; not including added deployment costs such as vessel charters, lodging and salaries for personnel). Precision in the trend (measured $\pm 95\%$ CI) is ± 0.11 points in ~1999 [28] and increases to ± 0.04 in the most recent study [53] (Figure 8). Although the time series contains a quasi-break at ~2005, it was minor and due to the inclusion of the J hook study [40] with higher F_r . The year ~1999 is also relevant because it demarcates the use of heavier and larger acoustic tags (primarily attached to larger istiophorid billfish ~200–300 kg; Musyl et al., 2015) and the prevalence of PSATs after year 2000 attached to a more diverse size range. The trend underscores the lack of significant differences in F_r rates between tag types, species, locations, gears and body sizes over a substantial time period. Moreover, most of the variability was expressed randomly within studies with very little dispersion expressed between studies. Orwin's fail-safe N analysis supported the temporal stability of the trend by indicating ~145 additional biased studies would be required to invalidate the current results if F_r rates in the "new studies" were above 0.50, which seems unlikely. Given these findings, the gain in new information from additional F_r studies is probably not cost-effective and therefore not warranted. However, compiling information on F_c rates and prognostic factors in istiophorid billfish is warranted (Musyl et al., 2015).

Though subjected to different fisheries, one of the most compelling findings was the large contrast in F_r rates between r -selected istiophorid billfish (~14%) and K -selected pelagic sharks (~27%). Pelagic sharks appear to be ~50% less resilient to the effects of F_r than istiophorid billfishes. Added to their "slow" life history strategy, this lower resiliency to the effects of fishing has implications for management, population biology and ecosystem dynamics. Given their already low P/B (Production/Biomass) values, low turnover rates and slow recovery (Bornatowski, Angelini, Coll, Barreto & Amorim, 2017; Kitchell et al., 2002; Schindler et al., 2002; Stevens, 2000), it

is evident pelagic sharks require efforts to mitigate their by-catch mortality and to preserve their functional roles (Bird, Veríssimo, Magozzi, Abrantes & Auilar, 2018; Stein, Mull, Kuhn, Aschliman & Davidson, 2018). Based on energetics and diet, Kitchell et al. (2002, 2006) and colleagues suggested that pelagic sharks were not the primary drivers of ecosystem dynamics in the central North Pacific. Those simulations, however, used much different F_r rates for pelagic species than reported in present report because only a few single F_r studies were available at the time (Kaplan, Cox & Kitchell, 2007; Kitchell et al., 2002, 2006). But if pelagic sharks are being removed at nearly double the rate of istiophorid billfishes from ecosystems (assumes fishing pressure from different gears is steady), coupled with their slow life history strategy, it is possible this hitherto unknown magnitude in apex predator F_r rates could have ramifications for intraguild predation and top-down compensatory effects (Hunsicker et al., 2012). Furthermore, it is not clear whether fishing pressure affects population-level processes differently in pelagic sharks and istiophorid billfishes and how stochastic variability may impact these processes. In any event, it appears reparametrizing these ecosystem models with more precise F_r and F_c rates, synthesized by meta-analysis, will provide more credible simulations.

4.5 | Precision in F_r studies

Though researchers are cognizant of required sample sizes in pelagic sharks and istiophorid billfishes needed to achieve sufficient power to reduce type II errors in survival studies, most studies rarely attain ~30% power (Table 1; Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Musyl & Gilman, 2018; Musyl et al., 2015). Goodyear (2002) recommended a minimum of 100 tags in F_r studies, but none of the individual studies in Table 1 come close to this sample size. About 200 samples would provide power at 80% ($\alpha = 0.05$) testing a medium effect size ($\Delta p = 0.15$) between two survival curves with a log-rank test (Machin et al., 2009; Ryan, 2013). For the most part, the individual studies in Table 1 (and in Musyl et al., 2015) were relatively small and imprecise (i.e. wide 95% CIs). Based on Monte Carlo simulations of reconstructed catch data, Pauly and Zeller (2016) indicated confidence bands of ± 0.10 points coincided with the “High agreement and robust evidence” category based on Intergovernmental Panel on Climate Change (IPCC) criteria. Doubling the number of tags and studies from the previous meta-analysis in blue shark to 158 tags in the present meta-analysis increased power and precision in point estimates from ± 0.14 points to ± 0.08 points (i.e. reduction of 0.06 points). Adding 92 tags to the updated meta-analysis in white marlin increased power and precision in point estimates from ± 0.15 points to ± 0.10 points illustrating an important issue: precision is expensive! The electronic tags used in Musyl et al. (2015) and Table 1 cost anywhere from ~2,000 to 4,200 USD each. Specifically because of the costs and exposure, it was not unreasonable to collect the majority of available survival studies using PSATs on pelagic sharks and istiophorid billfishes for the meta-analysis. The funnel plots indicating symmetry in larger studies and tests for possible publication

bias suggests the majority of possible influential studies were collected in the report. Horodysky and Graves (2005) and Musyl and Gilman (2018) calculated several 100s of tags would be needed to achieve ~80% power in F_r studies with a medium effect size. Unless meta-analysis is used to synthesize estimates, this design is cost-prohibitive using PSATs. Researchers and managers need to be aware of the uncertainty of point estimates inherent in small studies and perform meta-analyses to synthesize precise rates. Should future F_r be warranted, these precise rates are needed to design appropriate survival studies.

As an example, the lack of location-specific differences in F_r rates across studies suggest that better and more powerful studies could be undertaken in a few locations instead of the “Salami Science” approach where several small, low powered PSAT studies are conducted at several different locations (Table 1). In studying reproducibility rates in preclinical animal research studies, Voelkl, Vogt, Sena and Würbel (2018) suggested excessive standardization within studies obscured important biological variability. Furthermore, Voelkl et al. (2018) demonstrated that conducting ~2–4 suitably powered independent experiments in tandem was preferred over standardized single experiments for reproducing consistent effect sizes. In essence, the random-effects meta-analysis model captures this variability by treating each study unique in terms of distribution of effect sizes and sampling errors (i.e. the analysis does not obscure relevant biological information and phenotypic variability within studies) and appears to be adequately powered (Jackson & Turner, 2017). As far as planning and experimental design purposes, it appears that as little as two sufficiently powered studies are probably better than single studies using standardized protocols to produce credible effect sizes (Voelkl et al., 2018). In terms of cost-benefit and logistics, conducting a few large studies would also make the overall study cheaper.

Finally, the question researchers need to ask is “What level of precision is required in F_r studies?” as this will directly translate into cost-benefit considerations (Murray, 2006). There is little guidance on this for F_r studies on pelagic species and it appears precision (= sample size) is mostly driven by availability of funding for PSATs and electronic tagging studies (Goodyear, 2002; Horodysky & Graves, 2005; Kerstetter & Graves, 2006; Musyl & Gilman, 2018; Musyl, Domeier et al., 2011; Musyl et al., 2015). Precision, however, in F_r studies needs to be appraised in the context in which it is used or required. If matched to the precision of F_c rates, however, then from a cost-benefit perspective, this is not feasible using PSATs as precision in F_c point estimates for blue shark is reported $\pm \sim 0.001$ points (Dapp et al., 2017) whereas precision in F_r is $\pm \sim 0.08$ points (nearly a 100 fold difference). Clearly, in this situation, alternative methods like condition code offers a cost-effective remedy to predict F_r with some level of accuracy (Benoît et al., 2012; Braccini et al., 2012; Merremans et al., 2017; Musyl & Gilman, 2018). On the other hand, estimates for M in pelagic shark species are usually imprecise (Aires-da-Silva, Taylor, Punt, Gallucci & Kohler, 2005; Brodziak, Gedamke, Porch, Walter & Courtney, 2012; Chang & Liu, 2009). To aid in interpretation and context, Musyl and Gilman (2018)

suggested comparing F_r and F_c rates to M to look for correlation [see estimates for M and F_c on the species summary line in Table 1].

Musyl and Gilman (2018) and others, suggested that since F_r and F_c were subjected to many of the same prognostic factors and risks in fisheries, they might show congruence. In addition, these authors reported correspondence between these components of F and M in blue and silky shark but their F_r rates were synthesized from single studies. In the meta-analysis for blue shark, the summary effect size for F_r was 0.17, and Dapp et al. (2017), also from meta-analysis, synthesized a summary effect size of $F_c = 0.17$. Next, estimates for M in the species ranged from 0.17 to 0.23/year (Table 1). Clearly, F_c , F_r and M were similar, but the synthesized F (i.e. $F_c + F_r = 0.34$ [95% CI: 0.27–0.43]) was almost ~4 orders of magnitude larger than the reference F (0.09) used in Rice, Harley and Kai (2014). The authors also used a range of F values in their simulations from 0.07 to 0.22, but even these values did not correlate with the range in synthesized F values. Similarly, silky shark ($F_c = 0.23$, $F_r = 0.16$ longline, $F_r = 0.48$ purse-seine, $M = 0.17$ –21/year) F values estimated by meta-analyses (purse-seine $F = 0.48$, longline $F = 0.39$) were similar to the reference F (0.37) used by Rice and Harley (2013) for longline gear and within the range of values for purse-seine (0.17–0.54) and other gears (0.0–0.52). For white marlin, F_r and M were equivalent but to our knowledge, no synthesized F_c rates are available for comparison. The effect sizes for F_c and F_r rates synthesized by meta-analysis suggest that where data are lacking on a particular species, it may be beneficial to use the synthesized F estimated by meta-analysis. Moreover, the synthesized F by meta-analysis is an independent method that can be used to compare and verify F estimated by other (conventional) methods. The F rates synthesized by random-effects meta-analysis are reported with high precision and take into account both within- and between-studies dispersion in a consistent fashion. Regardless of the application, it is clear precise F_r and F_c rates need to be synthesized for many target and by-catch species in fisheries to estimate true effect sizes.

4.6 | One-arm vs. two-arm studies

The majority of F_r studies did not provide an obvious comparator in their design (e.g. circle vs. J hook) to use a comparative binary outcome (e.g. risk ratio) for a two-arm study. To utilize as many of the studies as possible, a one-arm or non-comparative binary outcome approach was used (Borenstein et al., 2009; Musyl, Brill et al., 2011; Musyl et al., 2015; Sutton et al., 2000). For discovery, we converted applicable studies into a two-arm design using the risk ratio (as the effect size for F_r) on condition code. To do this most, multiple health condition codes needed to be collapsed from 3 condition codes into 2 (healthy vs. unhealthy), but this concealed some of the true variability in studies (Supporting Information Figure S19). The one-arm approach uncovered significant variability whereas the converted two-arm approach did not. Another option would be to use network meta-analysis and multiple study arms (e.g. Sydes, Parmar, James, Clarke & Dearnaley, 2009), but clearly the F_r studies were not designed with these dimensions, sample sizes or purposes in mind.

Though conservative, the one-arm approach is transparent and preserves the original intent (and design) of the studies and highlights gaps where information is needed. The random-effects model place weight on the information contained in studies, including small ones. Though information on F_r rates is limited for some species, in some cases it is the only information available.

4.7 | PSATs to measure F_r outcomes

Measurement error did not appear to be an issue in the meta-analysis (i.e. only working PSAT tags were used) but attributing F_r outcomes to fishing can be challenging the longer tags remain attached before the subject presumably succumbs to injuries related to the fishing bout (Graves et al., 2002; Hutchinson et al., 2015; Musyl et al., 2015; Poisson, Filmlalter et al., 2014). In other words, mortality events closer to capture-tag-release would be attributable to F rather than to natural mortality occurring later on (Goodyear, 2002; Graves et al., 2002). As a conservative strategy, several researchers suggested using electronic tags with short pop-off periods (Graves et al., 2002; Hutchinson et al., 2015) that would better demarcate or disentangle F_r from M (Goodyear, 2002; Graves et al., 2002; Hutchinson et al., 2015; Musyl & Gilman, 2018; Musyl et al., 2015). For example, Graves et al. (2002) recaptured tagged blue marlin after 5 days and considered this period sufficient for recovery and to measure F_r rates whereas Hutchinson et al. (2015) considered 10 days post-release for silky shark released from purse-seine but provided no justification (i.e. mortality events outside this bound were not considered attributable to F_r). The bulk of time-to-event data in the meta-analysis suggests these periods, though conservative, coincide with ~80% of reported mortality outcomes in F_r studies in pelagic sharks and istiophorid billfish (Musyl et al., 2015).

PSAT-tagged pelagic sharks and istiophorid billfish exhibit type III survivorship curves (high initial mortality where risk is largest) and by continually adding precise time-to-event F_r data and analysing outcomes by size and age intervals, it might be feasible to locate the point to delineate F_r from M in the survival distribution. If electronic tags remained attached to the subject for several years (Musyl, Domeier et al., 2011) it could be feasible to locate this juncture on a short-lived species like mahi mahi (*Coryphaena hippurus*, Coryphaenidae) in the hazard curve. But firstly, in order to maximize data integration, researchers need to report precise time-to-event data in F_r studies (i.e. mortality is a continuous random variable). Only 62% of time-to-event information was extracted from the reports, but these data were mostly reported as whole numbers. Time stamps in the data downloaded by some early model PSATs, however, did not provide data at the necessary resolution or format. In any event, time-to-event >2 months in the study ($n = 3$ tags or ~5% of reported mortality outcomes—see below) must be viewed with caution and considered rare events but 5–10 day pop-up periods may underestimate mortality by ~20%. The rare event outcomes could represent a mixture of F_r and M events. The present data are inadequate to determine this. Additional time-to-event data are needed to evaluate and parametrize this trend. Our working hypothesis

suggests F_r outcomes conform to a positively skewed distribution which are common in survival studies and failures of manufactured components (Lee & Wang, 2003; Meeker & Escobar, 1999). Given the distribution of mortality outcomes, we strongly recommend researchers use a minimum 3-month pop-up period which matches the average retention period (79 days [95% CI: 73–85]), determined from a meta-analysis of 577 PSATs attached to elasmobranchs and teleosts (Musyl, Domeier et al., 2011), to determine the juncture between F_r and M .

Abascal, Quintans, Ramos-Cartelle and Mejuto (2011) reported mortality in shortfin mako 133 days after release from longline gear. Musyl, Domeier et al. (2011) and Musyl et al. (2015) offered an alternative explanation for the possible simulation of events that could be misinterpreted as F_r after extended PSAT retention times: biofouling and/or infection. In this scenario, a shed (~80% of PSATs prematurely release before their scheduled pop-up times), heavily fouled (i.e. negatively buoyant) tag could sink, thus mimicking a dead sinking animal (Musyl, Domeier et al., 2011; Musyl et al., 2015). This scenario makes the assumption that fail-safe features in the PSAT's nose cone engages at the threshold pressure, thereby jettisoning the tether and tag head and allowing the tag to float to the surface and download data to Argos. Next, from 577 PSATs affixed to various pelagic animals, it was determined that epipelagic species have significantly shorter PSAT retention times than deeper-dwelling mesopelagic I or II species which was attributable to biofouling and/or infection (Hays et al., 2007; Musyl, Domeier et al., 2011). For example, as epipelagic creatures, istiophorid billfish spend most of their time in the photic zone (surface to ~200 m) where there is increased exposure to fouling and necrotizing organisms (Hays et al., 2007; Musyl, Domeier et al., 2011). The accumulation of fouling organisms on PSATs results in extra drag and vibration that are maximized at the tag head, and over time, these forces delay tag-insertion wounds from healing, providing a route for infection, inflammation and tissue necrosis (Musyl, Domeier et al., 2011). In other words, the tag head rots out over time and may sink if it is heavily fouled. As mesopelagic I sharks, however, shortfin mako regularly undertake excursions beneath the mixed-layer depth where the combination of temperature and pressure oscillations tend to retard the growth and accumulation of fouling and necrotizing organisms (Musyl, Domeier et al., 2011; Musyl et al., 2015). Consequently, biofouling on the tag is probably not a convincing argument for mimicking F_r after 133 days in shortfin mako. On the other hand, though Hutchinson et al. (2015) did not consider mortality outcomes after 10 days post-release to be attributable to F_r , epipelagic silky shark presumably succumbing to injuries after 129 days fit the biofouling hypothesis but tail-hooked common thresher sharks (mesopelagic II) expiring after 81 days (Sepulveda et al., 2015) do not. In the meta-analysis, we specifically made the explicit assumption that study authors deployed rigged PSATs (i.e. tag head and tether attached) that would float (i.e. positively buoyant) when shed as this condition is necessary to allow discrimination of a shed tag from a dead sinking animal. For all that, Campana, Joyce, and Manning (2009) suggested that swallowed hooks or hooks lodged in the oesophagus could interfere with feeding and

cause eventual death. Moreover, it appears F_r outcomes could eventuate after several months. Hooks lodged in the oesophagus or stomach can penetrate the body cavity causing chronic proliferative responses resulting in opportunity for bacterial or algal infection, inflammation, systemic infection and possible death over the course of several months (Adams, Borucinska, Maillott, Whitburn & Sander, 2015; Borucinska, Kohler, Natanson & Skomal, 2002; Borucinska, Martin & Skomal, 2001).

4.8 | Prognostic factors

Both Campana, Joyce, and Manning (2009) and Musyl and Gilman (2018) reported most F_r outcomes within 1 day after release and 80% of all reported outcomes in the meta-analysis occurred within 1 week which suggests antecedent conditions (i.e. stress, physical insults) during capture were probably responsible for the condition of sharks at tagging and release rather than fish handling practices. Using different survival models testing prognostic factors including handling practices, Musyl and Gilman (2018) argued the condition of pelagic sharks was most likely determined before they were handled, tagged and released. Moreover, condition code did not change after sharks were tagged and released. This finding was also supported in the logistic regression analysis of IPD in silky shark, from two gear types, where condition code was the only significant factor in F_r models. For longline F_r studies, after being hooked for varying amounts of time, exposed to varying exogenous (e.g. temperature, dissolved oxygen, predation) and endogenous factors (e.g. stress, injury), the most parsimonious explanation was that short handling times (Campana, Joyce & Manning, 2009; Musyl & Gilman, 2018; Musyl, Brill et al., 2011) would not be the critical juncture to explain mortality outcomes unless handling practices were severe (Campana, Joyce & Manning, 2009; Campana, Joyce, Francis et al., 2009; Musyl, Brill et al., 2011; Musyl et al., 2009). Using the random-effects models, each study was assumed to embody a "mixture" of samples and antecedent conditions (exogenous and endogenous) in terms of tagging location (i.e. ~4–45°N), body size–age–sex, fishing gear, hook type (circle and J), soak or time spent hooked, selection of individuals, handling conditions, stress, injury and probably many other co-variables such as environmental conditions (e.g. capture depth and resultant level of barotrauma, dissolved oxygen, salinity, temperature) unknown in the analysis. Sensitivity analyses suggested mortality attributed to handling practices accounted for only a fraction of F_r which lends support to this hypothesis. Moreover, the bulk of F_r occurs within the first 2 weeks after release from fishing gear in most pelagic sharks which presumably coincides with the period necessary to offset respiratory and metabolic acidosis and to recover from injury as identified by electronic tagging data (estimated recovery periods: mean = 7.1 ± 1.5 days [95% CI] for seven species of pelagic teleosts ($n = 126$) and 10.8 ± 4.1 days [95% CI] for six species of pelagic sharks ($n = 57$); Hoolihan, Luo, Abascal, Campana & Metrio, 2011; see also discussion in Musyl et al., 2015).

In the various F_r studies, many potentially important prognostic factors were simply not measured and it is possible that other factors that affected survival outcomes were unknown in the analysis. Due to logistical challenges and costs, factors such as *in situ* measured dissolved oxygen and time spent hooked are rarely measured in mortality studies but are probably influential to explain survival outcomes (Butcher et al., 2015; Lotti, Wetherbee, Grace & Driggers, 2011). Certainly these factors may synergize with other operational (e.g. hook type, leader material, handling practices, depth of fishing, time of day, gear type), environmental (e.g. temperature, dissolved oxygen, salinity, temperature–depth gradients) and biological factors (e.g. species, respiratory mode, habitat class, sex, body size, skin thickness, predation, soak time or time spent hooked/fight time, hooking location, vitality or condition code, biochemical correlates of morbidity and mortality) to influence survival outcomes (Awruch et al., 2011; Braccini et al., 2012; Butcher et al., 2015; Campana, Joyce & Manning, 2009; Carruthers et al., 2009; Dapp et al., 2015, 2016, 2017; Davis, 2002; Diaz & Serafy, 2005; Gallagher, Orbesen et al., 2014; Gallagher, Serafy et al., 2014; Marshall et al., 2015; Morgan & Carlson, 2010; Moyes et al., 2006; Musyl, Brill et al., 2011; Musyl et al., 2015). Moreover, there are also data that suggest sharks may suffer from gas emboli from rapid temperature changes (Garner, 2013) accompanied during retrieval from deep-set longline gear (Rodríguez-Cabello & Sánchez, 2017). Trailing line, however, was not a significant factor to explain F_r in blue and silky sharks released from longline gear in Palau (Musyl & Gilman, 2018). Latitude is a proxy for temperature, and temperature and dissolved oxygen are generally correlated. Temperature greatly influences physiology, metabolism, movement, stress and survival outcomes (Angilletta, 2009; Fry, Hoar & Randall, 1971; Hochachka & Somero, 2002) of captured and released coastal sharks (Braccini et al., 2012; Lotti et al., 2011; Morgan & Burgess, 2007), but no significant F_r trends by latitude were observed in pelagic sharks or istiophorid billfish (Musyl et al., 2015). Natural mortality has been shown to correlate with body size and temperature in pelagic sharks and teleosts (Gislason, Daan, Rice & Pope, 2010; Griffiths & Harrod, 2007; Pauly, 1980; Peterson & Wroblewski, 1984), but we did not have the necessary size ranges in the metadata to test this. Synthesized summary effect sizes, however, for F_r and F_c were clearly correlated with estimates for M in blue shark, silky shark and white marlin (Table 1).

Lastly, we did not see any evidence to suggest size was a factor to explain F_r rates in the meta-analysis. In general, body size appears to be equivocal to explain F_r outcomes (Bartholomew & Bohnsack, 2005; Braccini et al., 2012; Campana, Joyce & Manning, 2009; Carruthers et al., 2009; Diaz & Serafy, 2005; Ellis et al., 2016; Gallagher, Orbesen et al., 2014; Gallagher, Serafy et al., 2014; Gallagher et al., 2012; Lotti et al., 2011; Morgan & Carlson, 2010; Muonelke & Childress, 1994; Musyl & Gilman, 2018; Musyl et al., 2015). Converting continuous variables into ordinal categorical ones can ameliorate measurement errors and increase statistical power, but when body size was converted to a categorical variable in the silky shark IPD meta-analysis, however, it did not alter the interpretation of the logistic regression model. Given the mixture of gear

types, studies, locations and species, the consistent trend in istiophorid billfish F_r rates since ~1999 (Figure 8) suggests body size was not a factor to explain mortality outcomes.

4.9 | Best Practices to improve post-release survival (S_r)

As demonstrated in the meta-analysis, “Best Handling Practices” to promote survival outcomes in pelagic sharks should focus on maximizing health condition (Butcher et al., 2015). Mortality and/or injury can be reduced and/or lessened with these simple (common sense) guidelines (Fowler, 2016; Gilman, 2011; McLoughlin & Eliason, 2008; Patterson et al., 2014; Poisson, Filmlalter et al., 2014; Poisson, Séret et al., 2014; Poisson et al., 2012):

- (1). Eliminate severe handling practices such as body-gaffing sharks and cutting hooks out of jaws (Musyl et al., 2009) which could reduce mortality by as much as ~3% (determined from sensitivity analysis on blue sharks in the meta-analysis).
- (2). Eliminate wire leaders. Sharks can bite through monofilament leader material and since pelagic sharks are obligate ram-ventilators, it is likely survival chances would be enhanced using monofilament leaders (Ward, Lawrence, Darbyshire & Hindmarsh, 2008). Leaders made of wire and other durable materials such as multifilament usually translate into added time on the hook and causing abrasion and cuts (Ward et al., 2008; Ward, Myers & Blanchard, 2004).
- (3). Eliminate the dragging of sharks and using “lazy lines” on longline gear (clipping branchlines with captured sharks onto a line (usually off the stern) until the end of the gear haulback). Sharks drown, gear becomes damaged (i.e. monofilament gets “smoked”) and line weights can shoot back into crew areas during line breaks and consequently this practice represents a large crew safety and liability risk (Fowler, 2016; Gilman, 2011; Poisson, Filmlalter et al., 2014; Poisson, Séret et al., 2014; Poisson et al., 2012).
- (4). When possible, adopt circle hooks over J hooks to reduce both F_c and F_r rates (Andraka, Mug, Hall, Pons & Pacheco, 2013; Caneco, Donovan & Harley, 2014; Serafy et al., 2012; Ward, Epe, Kreutz, Lawrence & Robins, 2009) with a trade-off of increased shark catch rates (Gilman et al., 2016; Reinhardt et al., 2017). In the sensitivity analysis, elimination of J hooks (on baited hooks) in istiophorid billfish studies reduced mortality by ~3.3%. In a small study documented in the meta-analysis (French et al., 2015), 100% reduction in F_r rates was observed in recreationally caught shortfin mako switching from J to circle hooks. For retained hooks, material and construction might be altered to lessen impacts. For example, McGrath, Butcher, Broadhurst and Cairns (2011) documented wire diameter and material as important factors to accelerate hook decay (e.g. nickel-plated carbon-steel hooks decayed faster than stainless hooks).
- (5). Release captured sharks immediately in the water, leave hooks in (if embedded firmly—see above) and cut off as much trailing line next to the hook as possible. Since trailing line is presumed to be

an important factor in mortality outcomes for many marine species (Fowler, 2016; Parga, 2012; Wells, Hofmann & Moors, 1998), requiring shorter leaders (i.e. ~30–60 cm) might reduce the amount of trailing line (i.e. crew generally cuts the leader at a position to salvage most of the hardware and gangion; e.g. Musyl & Gilman, 2018). Fiskars® tree pruning saw (<http://www2.fiskars.com/>, Helsinki, Finland) is an appropriate tool to precisely cut the leader next to the hook. For concerns about possible tag retention rates, Musyl, Domeier et al. (2011) demonstrated higher PSAT retention rates for animals tagged in water as opposed to those brought on deck. Though sample sizes were small, Sepulveda et al. (2015) demonstrated that switching terminal angling tackle to catch common threshers in the mouth (as opposed to tail-hooked sharks that are released with varying lengths of trailing gear), could dramatically lower mortality rates by ~70%. In Sepulveda et al. (2015), it was not known if trailing gear was influential to explain mortality outcomes since mouth-hooked sharks had the hooks removed. Fight times >85 min in Heberer et al. (2010) delimited survival outcomes for tail-hooked threshers and it is apparent survival could be enhanced by heavier pound test lines in recreational gear to reduce fight times. Catch and rapid release of white marlin, limiting air exposure times to <1 min (Graves et al., 2016; Schlenker et al., 2016) was shown to reduce mortality by ~3% in the sensitivity analysis.

- (6). Since pelagic sharks are obligate ram-ventilators, captured sharks could benefit from longer gangions that might allow for extra movement (Gallagher, Orbesen, Hammerschlag & Serafy, 2014). Adding a section of shock cord near longline clips (i.e. hardware used to attached gangions to the mainline) in conjunction with longer gangions might facilitate and encourage movement. A reduction in number of hooks between floats or other adjustments, however, would be needed to accommodate longer gangions to prevent line tangles. Making longline clips easier to slide on the mainline would allow for extra movement but line tangles would probably outweigh any benefits.
- (7). In purse-seine fisheries, it is obvious to release sharks before they are brailled (see references for purse-seine studies on silky shark in Table 1). Given the confinement in purse-seine nets, repellents (e.g. electropositive metals, magnets), which appear to work in confined areas (Brill, Bushnell, Smith, Speaks & Sundaram, 2009), could be tried to manipulate silky sharks to escape panels (Poisson et al., 2016) or repel them from FADs (Gilman, 2011).
- (8). In longline fisheries, setting hooks deeper than ~100 m in daytime can reduce interactions with epipelagic species such as istiophorid billfishes and pelagic sharks (Beverly, Curran, Musyl & Molony, 2009). As an example, PSAT tagging data from Musyl, Brill et al. (2011) indicate this strategy would reduce 98% and 86% of oceanic whitetip and silky shark interactions, respectively, and blue shark encounters by an estimated 53% and shortfin mako by 46%. The trade-off, however, is that this strategy would increase encounters with deeper-habitat mesopelagic II species, including bigeye thresher sharks (Gilman, Chaloupka, Dagorn, Hall & Hobday, 2019).

4.10 | Future study design and methodology

Fisheries biology needs to adopt similar methodology and decision-making processes that are used in medical and epidemiological research to investigate survival outcomes and possible intervention (Borenstein et al., 2009; Ionnidis, 2014, 2016; Sutton et al., 2000; Welton, Sutton, Cooper, Abrams & Ades, 2012). In meta-analysis examining decision-making in conservation management, Pullin and Knight (2001, 2003) and Pullin, Knight, Stone and Charman (2004) concluded that the majority of decisions were experience- rather than evidence-based. In other words, though evidence was available, decisions were based mostly on prior practices and subjective assumptions and biases, thus neglecting the best available evidence. Below is an outline of suggested topics to include whilst investigating F_c and F_r rates in fisheries.

- (1). Due to the similarity in prognostic factors, it is increasingly apparent that correlation exists between F_c and F_r rates in fisheries (Table 1; Musyl & Gilman, 2018). To more fully analyse and interpret F_c and F_r rates across species, fisheries and gear types, it is imperative to develop and harmonize simple and intuitive health condition codes that are transferable across fisheries (Benoit et al., 2012; Braccini et al., 2012; Meeremans et al., 2017; Musyl & Gilman, 2018).
- (2). Campana, Joyce, and Manning (2009) and Campana et al. (2015) reported that the condition status of ~11%–78% of captured sharks could not be classified as dead or alive by observers. Part of this ambiguity could be resolved by observers performing a simple reflex test on sharks at the rail before they are discarded. As described in Musyl, Brill et al. (2011), Gallagher, Serafy, Cooke and Hammerschlag (2014), Dapp et al. (2016) and Musyl and Gilman (2018), light touching of the nictitating membrane (found only in the Carcharhiniformes, comprising ~270 species) can be used to distinguish mortality of sharks (Bell & Satchell, 1963). If observers are on boats with high freeboard, a pole with a padded probe could be used to administer the test. This is a simple yet inexpensive prognostic test that could be consistently applied across many fisheries with shark by-catch to provide more precise information on F_c rates.
- (3). Before soliciting requests for proposals to undertake survival or by-catch mitigation studies (or any study that repeats an intervention or measurement of some kind), it should be mandatory to quantitatively review existing information by meta-analysis before decisions are made (Borenstein et al., 2009; Chalmers, 2007; Ellis, 2010; Sutton et al., 2000; Welton et al., 2012). It is possible, depending on the research question(s), that available data already exist that would obviate wasting resources on new studies. Next, should they be warranted, by analysing the available information, the meta-analysis can be used to design better studies. The medical literature is rife with such examples where practitioners, researchers and research proposals have not adequately discovered what has already been done. For example, ineffective treatments were being recommended whilst highly effective treatments were not

(Sutton et al., 2000). Besides wasting limited resources, failure to adequately compile and “cumulate” prior research findings has directly translated into lives that could have been saved (Borenstein et al., 2009; Chalmers, 2007; Ellis, 2010; Sutton et al., 2000).

- (4). Given the ambiguity of results from small F_r studies, more cooperation should be made in gathering and analysing pooled meta-data or IPD across studies to increase sample sizes and power. Instead of focusing on future studies, our report indicates a more pragmatic and parsimonious approach should be made on analysing data already collected (this is especially true for F_c rates; e.g. Dapp et al., 2017). It is possible sufficient information already exists on F_r and F_c rates to test hypotheses for survival outcomes under varying conditions.
- (5). Researchers of survival studies using PSATs need to provide more details about their study so attempts to replicate the results or incorporate results into IPD studies or meta-analysis to synthesize precise point estimates can be accomplished (Musyl et al., 2015). In particular, researchers need to disclose information on time-to-event and the censor variable as these variables will dictate what type(s) of survival analyses can be conducted (Hosmer & Lemeshow, 1999; Kleinbaum & Klein, 2005; Lee & Wang, 2003).
- (6). A reasonable suite of common prognostic variables should be measured in survival studies on pelagic fishes and sharks that include species, sex, vitality or health condition code, body size, hook type/size, leader material, trailing line, hooking location, whether the hook remained after release, time hooked on the line or soak time, water temperature (e.g. acquired from electronic tags or TDRs), location, time, tagging location (deck vs. water), time-in-air and, if possible, dissolved oxygen from *in situ* portable probes.

5 | CONCLUSIONS

Survival outcomes in pelagic sharks appear to be dichotomized by health condition status. No species-, location- or gear-specific mortality rates were evident. The majority of mortality outcomes occur within days of release, and therefore, it is likely exposure to proximate factors and antecedent conditions by captured sharks was mostly responsible for mortality outcomes rather than short handling times at release. Updated meta-analyses on blue shark and white marlin F_r rates confirmed earlier findings from meta-analysis and increased precision in the point estimates. The ability to replicate findings across temporal and spatial scales was demonstrated, which is the best and most powerful way to authenticate results. Though improved handling practices can enhance survival of released sharks, improving health condition at haulback could dramatically reduce mortality rates. Istiophorid billfish appear to be more robust to the effects of fishing than pelagic sharks. Synthesized F_c and F_r represent a new method for estimating total fisheries mortality (F). Baseline data are provided to serve as a guide to design better F_r studies and to assist researchers, managers and policymakers in interpreting results from survival studies.

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