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Original Article

Discards, hooking, and post-release mortality of porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), and blue shark (*Prionace glauca*) in the Canadian pelagic longline fishery

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Global discards of sharks greatly exceed reported landings, yet there are few estimates of mortality after release. Based on more than 21 000 fisheries observer records and the results of 109 popup satellite archival tags, all sources of fishing-induced mortality (harvest, capture, and post-release) were estimated for blue sharks (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the Canadian pelagic longline fishery between 2010 and 2014. Hooking mortality ranged from 15 to 44%, with porbeagles and makos experiencing much greater mortality than blue sharks. The post-release mortality rate varied between 10 and 31%, with porbeagle and mako again having the highest mortality rate. Overall, about one-half of the hooked porbeagles and makos died during or after fishing, with most of the post-release mortality occurring within 2 d of release. Landed catch accounted for less mortality in porbeagle and blue sharks than did the combination of hooking and post-release mortality. These results indicate that the conservation benefits of mandatory release regulations for pelagic longline gear are not nearly as great as is now assumed.

Keywords: discarding, mortality, pop-up tag, sharks.

Introduction

Fishing gear can often be non-selective with respect to the species captured, resulting in the capture of both the target species and other non-target species. Where the non-target species is considered commercially valuable, bycatch is usually retained and used, and thus is not necessarily harmful. However, bycatch of non-commercial, unretained species can lead to their injury or death, and may be driving population declines of many species on a global scale (Lewison *et al.*, 2004). Marine mega-fauna such as sea turtles, seabirds, sharks, and marine mammals appear to be particularly susceptible to bycatch mortality in fishing gear, but bycatch and discarding of less charismatic fish species is also viewed as a global problem (Harrington *et al.*, 2005). The magnitude of the issue was examined by Harrington *et al.* (2005), who reported that more than 1 million t of fish (equal to 28% of landings) were discarded annually in US waters alone. Global discards have never been accurately quantified, but a recent study estimated that unused or unmanaged bycatch accounted for a minimum of 38.5 million metric t annually, equivalent to 40% of global catches (Davies *et al.*, 2009).

Bycatch mortality can be categorized into capture mortality (e.g. immediate or hooking mortality) and post-release (or discard) mortality. Capture mortality is readily quantified, since it can be assessed onboard the fishing vessel at the time the fishing gear is pulled aboard. However, the assessment of post-release mortality is more problematic. Unpredictable and potentially large post-release mortality rates can result from injuries due to fishing and handling, as well as the stress of capture plus the complicating effects of environmental conditions at the time of release (Davis, 2002). Indeed, some studies have concluded that post-release mortality could be a larger source of mortality than harvest mortality (Cramer, 2004; Douglas *et al.*, 2010; Molina and Cooke, 2012). The difficulty in quantifying post-release mortality is due to the scarcity and/or expense of methods for tracking released fish in the wild over periods of time of up to several months. Most studies have attempted to avoid this issue by holding fish in cages or pens for several days after capture (e.g. Neilson *et al.*, 1989). However, holding pens provide a clearly artificial and spatially constrained environment, and thus have the potential to introduce (or avoid) sources of mortality that would not be present under natural, free-swimming conditions. Predation on released fish and sublethal effects on reproduction are clear examples of processes that cannot be assessed at the time of capture (Raby *et al.*, 2014; Wilson *et al.*, 2014). As a result, some sort of tag–recapture or telemetry programme is required to properly estimate the post-release mortality rate of discarded fish (Davis, 2002; Pollock and Pine, 2007; Skomal, 2007). Such a programme would be well suited for monitoring released fish in the wild for extended periods of time, and has been successfully applied in estimating discard mortality rates in several fish species (Domeier *et al.*, 2003; Butcher *et al.*, 2010). An additional advantage of such studies is that evidence of physical trauma or stress indicators from blood chemistry can ultimately be linked to the subsequent survival rate measured by telemetry, thus providing predictors for discard mortality rate (Benoit *et al.*, 2012; Renshaw *et al.*, 2012).

Global discards of elasmobranchs greatly exceed reported landings (James *et al.*, 2015), and pelagic longline fisheries for highly migratory pelagic species such as tuna and swordfish account for more shark bycatch than any other fishery (Oliver *et al.*, 2015). Blue sharks (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) are among the most common pelagic sharks caught in the North Atlantic, but the bycatch rates of blue sharks far outstrips those of other species, both in the Atlantic and worldwide (Bonfil, 1994; Oliver *et al.*, 2015). Owing to low commercial value in many countries, most of these blue sharks are discarded at sea. Discard rates of porbeagle are believed to be marginally lower (Campana *et al.*, 2011), while shortfin mako are considered to be a higher value species and thus less likely to be discarded. However, the fate of discarded porbeagle and mako sharks has never been quantified, and a previous estimate of discard mortality of blue sharks was completed at a time before the widespread introduction of the less-fatal circle hook (Campana *et al.*, 2009). As first mentioned by Bonfil (1994), the absence of discard mortality estimates seriously compromises attempts at providing credible stock assessments for North Atlantic sharks.

Porbeagle, mako, and blue sharks are highly migratory species whose distribution extends throughout most of the North Atlantic, and consequently are fished by multiple nations in international waters. Despite best attempts, stock assessments for mako and blue shark by the regional fisheries management organization (RFMO) ICCAT (International Commission for the Conservation of Atlantic Tunas) have produced ambiguous results (ICCAT, 2012); the assessment for porbeagle was less problematic because of the concentration of its fishery in national waters (Campana *et al.*, 2010). In the light of preliminary capture/post-release mortality estimates for blue shark of around 35% (Campana *et al.*, 2009), it is likely that at least some of the difficulties of determining the conservation status of the three shark species can be attributed to the exclusion of fishing-induced mortalities associated with capture and post-release mortality from the stock assessments. In this study, we used extensive observer data combined with results from 109 popup satellite archival tags (PSATs) to estimate all sources of fishing-induced shark mortality in the Canadian pelagic longline fishery. The objectives of the current study were: (i) to use recent observer data to estimate the discard rates and hooking mortality of mako, porbeagle, and blue sharks; (ii) to use PSATs to estimate post-release mortality rate in commercially discarded sharks of all three shark species; and (iii) to compare the magnitude of (documented) harvest mortality with other sources of fishing-induced mortality (normally undocumented) to better understand the conservation threats of sharks in the North Atlantic and worldwide.

Material and methods

The hooking (capture) mortality and release condition of blue sharks (*P. glauca*), shortfin mako (*I. oxyrinchus*), and porbeagle (*L. nasus*) captured as part of commercial pelagic longline fishing were analysed using data collected by the Scotia-Fundy Observer Programme (SFOP), which provides accurate, independent observations of all catch and discards. Observed fishing sets were those by Canadian pelagic longliners targeting swordfish (*Xiphias gladius*) or tuna (primarily bigeye tuna *Thunnus obesus* with smaller amounts of Atlantic bluefin (*Thunnus thynnus*) and yellowfin (*Thunnus albacares*) in the Northwest Atlantic. A total of 496 sets made between the years 2010 and 2014 were included in the analysis, a period during which increased observer attention was given to sharks. As each shark was pulled up to the rail, its status was categorized as healthy, injured, or dead, and an estimate of its length was recorded. Most sharks were removed from the hook (or had the gangion cut without first removing the hook) without being brought aboard, and could not be closely examined, thus making the status classification somewhat difficult. The status of 21% of all sharks could not be determined, largely because it was unclear if the shark was actually dead or simply immobile. These individuals were removed from the analysis, leaving a sample size of 16 795 sharks. The observers characterized an injured shark as the one that had swallowed the hook, was hooked in the gills, or was otherwise showing signs of severe trauma. Healthy sharks were characterized as those that were hooked in the mouth or jaw, with no other obvious signs of injury.

To assess the post-release mortality of sharks caught on pelagic longliners, a random sample of sharks (both injured and healthy) were tagged with pop-up satellite archival tags (PSATs) just before release. Most of the sharks were tagged on commercial fishing trips for swordfish and tuna, but some were tagged on dedicated charters on the same vessels, using identical fishing and handling techniques. The minimum soak time of the gear was 6 h always. Sharks are typically discarded at sea without being boarded, unless they are to be landed. If discarded, the hooks are either removed or cut out of the jaw as the shark is brought out of the water, or the gangion is cut off close to the mouth. For this reason, tags were either applied with a pole, while the shark was on the line and in the water, or after being brought aboard to allow easier handling. If brought aboard, sharks were on deck an average of ~3 min for tagging and measurement while the gills were being irrigated, and showed no obvious stress above and beyond that of capture. A variety of PSATs were used: Wildlife Computers (WC) Model 4 PATs in 2005–2006, Mk-10 PATs in 2006–2013, and miniPATs and Microwave Telemetry (MT) X-tags in 2013. PSATs were attached to the shark by darting a nylon umbrella tip ~8 cm into the dorsal musculature of the shark just lateral to the posterior end of the first dorsal fin. The angle of dart insertion was such that the tip engaged the pterygiophores immediately underneath the dorsal fin, thus reducing the possibility of premature release. The umbrella tip was attached to the PSAT with a monofilament leader of 400-pound test sheathed to reduce trauma to the shark near the point of insertion. Each PSAT was also fitted with an emergency cut-off device provided by the manufacturer which physically released the tag if it went below 1800 m (which is the maximum nominal safe depth for tag operation).

PSAT tags were programmed to record depth ($\pm$0.5 m), temperature ($\pm$0.1°C), and light intensity at 10 s–1 min intervals for a period of 2–12 months after release. The length of the recording period was assumed to be long enough to include any mortality due to capture and handling trauma, as well as delayed mortality due to factors such as internal damage or cessation of feeding associated with swallowed hooks. The tag data were transmitted to an Argos satellite after release of the PSAT from the shark, internally binned by 6 h intervals for the WC tags, and unbinned for the MT tags. All inferences about shark mortality during the PSAT recording period were based on analysis of the satellite-transmitted data, except four tags that were physically recovered. A total of 83% of the 131 tags transmitted successfully after release from the shark. Non-transmitting tags were excluded from subsequent analysis and were not assumed to have died. All PSATs were programmed to release from the shark if a constant depth was maintained for a period of 4 d, since a constant depth equal to that of the water depth at that location would be indicative of death in an actively swimming pelagic shark species.

Post-release mortality was usually readily detected in the PSAT data, and characterized by a rapid descent to the ocean bottom followed by a 4-d cessation of vertical movement (Campana *et al.*, 2009). Only two mortality events were considered unattributable to fishing (both in mako), but given their extended time at liberty (>80 d) and their apparently normal behaviour before death, their movement to the ocean bottom was considered unconnected with capture. Premature tag release did not prevent the interpretation of transmitted data, and non-reporting tags were excluded from any mortality calculations.

Preliminary examination of the post-release PSAT data identified a single trip where five out of six of the healthy makos that were tagged died almost immediately after tagging. All were tagged by a single fisheries observer, all were small (FL < 110 cm) sharks, and all were tagged on board the vessel. Such a high mortality rate on otherwise healthy sharks lies well outside the bounds of any other observations in this study, suggesting that inappropriate handling/tagging methods or an excessive period on deck might have been responsible. For this reason, these six sharks were excluded from further analysis. If subsequent study indicates that these were valid observations, the post-release mortality rates reported for makos in this study are underestimated.

To summarize the PSAT sample size, 109 of the 131 PSATs deployed on longlines successfully transmitted. Of these, six of the mako tags were disqualified (see above) and seven other tags were excluded from the mortality calculations (only) because they were applied on short-duration longline sets, leaving a sample size of 96 in the analysis. An additional four PSATs applied on an otter trawler will be referred to later in the paper, but were not included in any mortality calculations.

Overall shark mortality rate due to capture and discard mortality was calculated as the species-specific sum of post-release mortality rates for injured and healthy sharks, weighted by the relative frequency of these two injury status categories as recorded by fisheries observers between 2010 and 2014, plus the observed frequency of dead sharks. The 95% confidence interval around this proportion was calculated based on Monte Carlo (mc) draws from the binomial distributions corresponding to both the observed injury status categories and the observed PSAT mortalities within each category, as in:

$$(N_D + N_I \times M_I + N_H \times M_H) \cdot n^{-1},$$

where N is the number of sharks, M the mortality rate, N_{mc} is drawn randomly from a binomial distribution with an observed injury status (D, dead; I, injured; H, healthy) proportion and sample size n, and M_{mc} is drawn randomly from a binomial distribution with an observed PSAT-derived mortality rate and a sample size equal to the number of tags applied to that injury status category.

Shark bycatch in the large pelagic fishery was estimated by country, fishery, quarter, and year from Scotia-Fundy Observer Programme (SFOP) observations made between 2010 and 2014, with bycatch defined as the summed weight of the kept and discarded sharks relative to the summed large pelagic catch (tuna, swordfish, and porbeagle). The summed large pelagic catch accounted for most of the catch, and its use in the estimation avoided problems associated with the species sought being unknown. The analysis was restricted to Canadian, Japanese, and Faroese vessels, since they accounted for more than 99% of the shark catch. Bycatch in the foreign fisheries was fully observed, so estimation was used more to calculate bycatch proportion than bycatch weight for foreign vessels. Total pelagic catch for each cell was determined from Fisheries and Oceans catch statistics for Canadian vessels, and from SFOP for foreign vessels. Full details on the estimation protocol are presented in Campana *et al.* (2015).

This research was conducted in accordance with the animal care guidelines of Fisheries and Oceans Canada and the Canadian Council on Animal Care.

Results

Fishing sets ($n = 496$) in the Northwest Atlantic observed by SFOP between 2010 and 2014 most often occurred on the edge of the Canadian continental shelf, offshore of the shelf in the waters bordering the Gulf Stream, and in deep basins of the shelf itself (Figure 1). On the 76 trips, all vessels used circle hooks (#16 or #18), except in 2010 and 2011 when some vessels also used J or modified J hooks. Overall, 88% of all hooks fished were circle hooks. The soak time of the gear was generally 8–12 h, and the mean surface

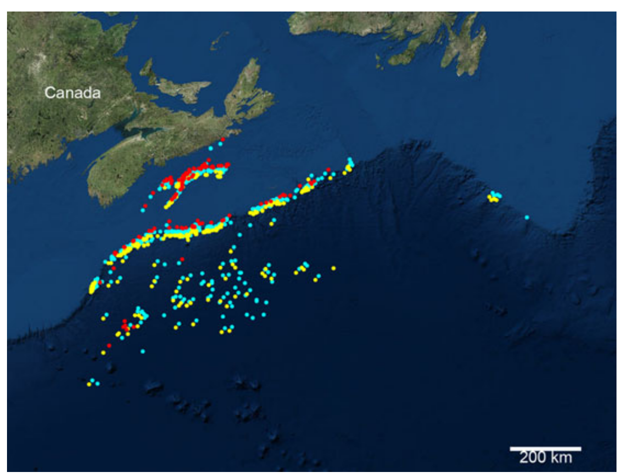

Figure 1. Map of the Northwest Atlantic off of eastern Canada showing observer-recorded catch locations of blue sharks (blue), shortfin mako (yellow), and porbeagle (red) in commercial large pelagic longline catches between 2010 and 2014.

Table 1. Breakdown of shark condition by species and year at the time of unhooking, as recorded by fisheries observers.

Species	Year	Unknown	Healthy	Injured	Dead	Total	% dead	% injured
Porbeagle	2010	20	143	42	56	261	0.23	0.17
	2011	0	129	38	202	369	0.55	0.10
	2012	52	11	19	37	119	0.55	0.28
	2013	172	0	0	0	172		
	2014	4	1	1	4	10	0.67	0.17
	Total	248	284	100	299	931	0.44	0.15
Blue	2010	392	3513	1779	843	6527	0.14	0.29
	2011	774	3712	475	542	5503	0.11	0.10
	2012	652	1759	1563	761	4735	0.19	0.38
	2013	609	301	71	67	1048	0.15	0.16
	2014	1751	98	32	76	1957	0.37	0.16
	Total	4178	9383	3920	2289	19 770	0.15	0.25
Mako	2010	5	63	13	18	99	0.19	0.14
	2011	1	51	7	17	76	0.23	0.09
	2012	2	102	86	90	280	0.32	0.31
	2013	0	28	8	5	41	0.12	0.20
	2014	0	23	3	6	32	0.19	0.09
	Total	8	267	117	136	528	0.26	0.23

Table 2. Breakdown of post-release survival by species and condition at the time of PSAT tagging.

Species	Condition at tagging	Lived	Died	Total
Blue	Healthy	10	0	10
	Injured	18	9	27
Mako	Healthy	16	7	23
	Injured	2	1	3
Porbeagle	Healthy	26	3	29
	Injured	1	3	4

water temperature was 19.4°C (range between 11 and 28°C). The number of hooks fished per daily set ranged up to 1770, with an overall mean of 1060.

The catch rates of the three shark species differed markedly, and were often associated with particular target species. Overall, blue shark catch rates averaged 1.37 (s.e. = 0.08) kg hook^{-1}, while catch rates for makos (0.05 ± 0.004) and porbeagles (0.06 ± 0.01) were significantly lower (ANOVA, $p < 0.01$). Up to 534 blue sharks were caught in one set, representing 35% of the available hooks on the line.

Hooking (capture) mortality

More than 21 000 sharks were observed on large pelagic longline fishing vessels between 2010 and 2014 (Table 1). Of those where condition could be assessed at release, the mean annual percentage of dead blue sharks was 14.7% (range 12–37%). The mean hooking mortality rate for porbeagles was 43.8% (range 0–67%), while that for mako was 26.2% (range 12–32%). The interspecific differences in hooking mortality rates were highly significant (χ^2, $p < 0.001$). In addition, there was also significant variation in hooking mortality within the pelagic longline category if disaggregated by species sought or fishing vessel: for example, porbeagle hooking mortality was twice as high when bluefin tuna was the species sought rather than swordfish. Although it was difficult to distinguish between the effects of species sought and fishing vessel, the effect was real and independent of observer. The hooking mortality rates by species did not differ significantly between the periods when a small proportion of J hooks were used (2010 and 2011) compared with the period when only circle hooks were used (2012–2014).

For unknown reasons, reporting rates differed substantially across years, with 78% of sharks being recorded as "status unknown" in 2013 and 2014 compared with 11% in previous years (Table 1). Most of the status-unknown sharks were blue sharks. In part, this was due to significantly different reporting rates across individual observers (ANOVA; $p < 0.01$), with one observer apparently unable to distinguish between dead and "status unknown" sharks out of more than 2000 examined.

The proportion of injured sharks also differed significantly across species, with 25% of blue sharks, 15% of porbeagles, and 23% of makos being reported as injured at the time of capture (Table 1; χ^2, $p < 0.001$).

Post-release (discard) mortality

A total of 109 of the sharks caught by commercial pelagic longliners were tagged with PSATs, and subsequently transmitted successfully to document post-release survival or mortality. Tagged individuals ranged in fork length from 80 to 249 cm FL, with shortfin mako tending to be smaller (mean FL = 131.5 cm, range 80–229 cm) than either blue sharks (mean FL = 159.3 cm, range 125–209 cm) or porbeagle (mean FL = 173.5 cm, range 101–249 cm). Both healthy and injured sharks were tagged and released, with a mean time at liberty of 92 d (range 0–356 d).

The post-release mortality rate of all three shark species differed with condition at release (Table 2). Healthy blue sharks showed 0% mortality ($n = 10$), while injured blue sharks ($n = 27$) experienced a 33% mortality. Similarly, healthy porbeagles ($n = 29$) experienced a 10% mortality rate, while 75% of injured porbeagles ($n = 4$) subsequently died. Healthy makos ($n = 23$) experienced the highest mortality rate at 30%, which was similar to the 33% mortality rate of injured makos ($n = 3$). Single-digit sample sizes for two of the categories render those estimates imprecise, an uncertainty that was later incorporated into the Monte Carlo estimation of confidence intervals.

The post-release mortality rate of healthy shortfin makos was significantly higher than that of healthy individuals of the other two species (χ^2, $p < 0.05$). In addition, this was the only species where some individuals were tagged while in the water, while other individuals were brought on board for tagging (as was the case with all porbeagle and blue sharks). The possibility that mako post-release mortality rate was influenced by the boarding practice was tested with a GLM using a binomial-dependent variable (mortality), boarding as a main effect, fork length as a covariate, plus the interaction term. None of the GLM terms were significant (25 d.f.; $p > 0.4$), indicating that the fate of the healthy makos was independent of boarding practice or size.

Although the statistical analysis of the healthy mako survival data showed no effect of boarding, similar analyses could not be carried out with the porbeagles and blue sharks in our study because they were all tagged on board. Nevertheless, two independent sets of observations suggest that the boarding effect in our study was negligible. First, four porbeagles caught by commercial otter trawlers fishing on Georges Bank in summer were brought aboard for PSAT tagging; all survived post-release. Second, six healthy porbeagles PSAT-tagged on board after short duration (1–2 h) sets as part of a pelagic longline charter using standard swordfish gear and commercial handling techniques showed no post-release mortality; the one injured porbeagle tagged on the same trip subsequently died. Neither the porbeagles tagged on the otter trawl nor those tagged on the charter were included in any analyses used in this study, since the short duration of the sets and the otter trawl are not representative of commercial pelagic longline fishing. Nevertheless, the results support the premise that the post-release survival of sharks in this study was not compromised by having been tagged on board.

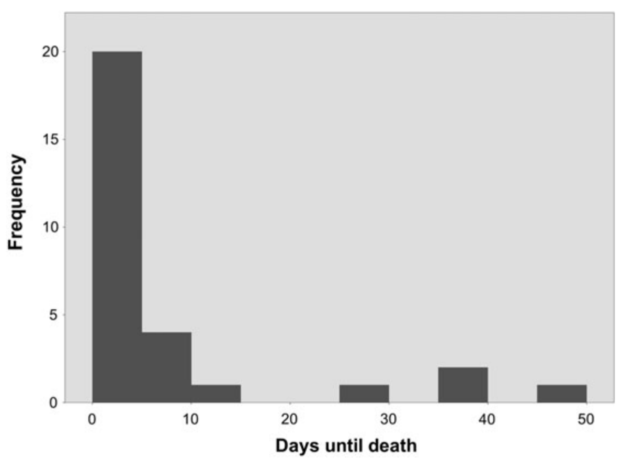

Figure 2. Frequency histogram of the number of days between tagging and death for porbeagles, makos, and blue sharks combined.

The survival time of sharks that subsequently died was highly skewed, with most sharks dying within a few days of release (Figure 2). Survival times ranged from 0.04 to 48 d, with a median survival time of 0.25 d. There was no significant difference in survival times across species (Kruskal–Wallis test, $p = 0.5$), nor was there a significant difference between injured and healthy sharks (Mann–Whitney U-test, $p = 0.25$).

Table 1 indicates that an annual percentage of 10–38% of the assessed blue sharks were reported by observers as being injured at the time of release, with an overall mean of 25.1%. Applying the 33.3% mortality rate to the 25.1% injury rate for sharks not already dead at capture implies that the overall post-release mortality of live (healthy and injured) blue sharks was 9.8% (s.e. = 4.7%; Figure 3a). According to the observers who made the observations, this estimate of fishing mortality is probably a minimum estimate, since observers often got only a quick glimpse of each blue shark as it was brought up to the rail and cut-off, leaving only those that were badly injured or clearly dead being recorded as such.

A mean annual percentage of 14.6% of the porbeagle were reported by observers as being injured at the time of release from pelagic longlines (Table 1). Healthy sharks accounted for 41.6%. Applying the 10% PSAT-based mortality rate to the 41.6% healthy rate, and the 75% PSAT-based mortality rate to the 14.6% injury rates, implies that the overall post-release mortality rate of live porbeagle was 27.2% (s.e. = 12%) (Figure 3a).

The mean annual percentage of makos that were observed as being injured was 22.5%, while 51.3% were healthy (Table 1). Given a 30% PSAT-based mortality rate for the healthy sharks, and a 33% PSAT-based mortality rate for the injured sharks (Table 2), the overall post-release mortality rate of live makos was 31.3% (s.e. = 18%; Figure 3a).

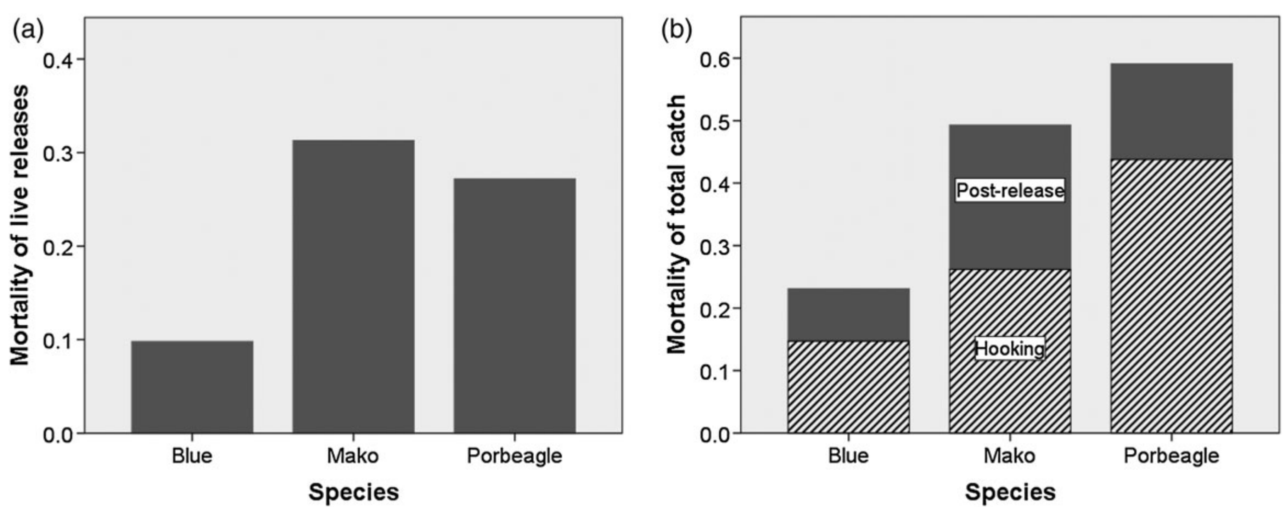

Figure 3. Shark mortality due to capture or hooking mortality in commercial pelagic longline fishing, broken down by species: (a) proportion that die after live release as recorded by PSATs; (b) proportion of the total catch that die during hooking (striped pattern) and after live release (solid grey). Confidence intervals for all of the estimates are reported in the text.

Total mortality

Calculations of total mortality must take account of both hooking mortality and overall post-release mortality. The hooking mortality of blue sharks was 14.7%. When combined with an overall post-release mortality of live (healthy and injured) blue sharks of 9.8%, the overall non-landed fishing mortality of blue sharks captured in the pelagic longline fishery was estimated at 23.1% (95% CI: 16–30%). Similar calculations for porbeagles and makos (assuming that no live sharks were retained) yield overall fishing-related mortality rate estimates of 59.1% (95% CI: 46–72%) for porbeagles and 49.3% (95% CI: 23–73%) for makos (Figure 3b).

A comparison of the mortality rates across species indicates that porbeagle and makos were considerably more likely to die after live release than were blue sharks (Figure 3a). This pattern was compounded by the higher hooking mortality rates of porbeagles and makos, resulting in total mortality rates for these species that were about twice that of blue sharks (Figure 3b). The species-specific hooking mortality rate tended to be comparable to the post-release mortality rate of live sharks of the same species. However, when calculated as a percentage of the entire catch, species-specific hooking mortality rates accounted for more deaths than did post-release mortality (Figure 3b).

Commercial landings of blue shark in the Canadian tuna and swordfish fisheries averaged <1 mt annually between 2010 and 2014, due to a 100% discarding rate. In contrast, annual bycatch estimates averaged ~1612 mt annually between 2010 and 2014. Given the discard mortality rate discussed earlier, an average of 372 mt of blue sharks were estimated to die annually in the Canadian pelagic longline fishery due to a combination of hooking and post-release mortality (Figure 4). Estimated discard rates and amounts were considerably lower for porbeagles (84% discard rate; 59 mt annual discards) and makos (32% discard rate; 22 mt annual discards), resulting in total estimated annual hooking/discard mortalities in the Canadian pelagic longline fisheries of 35 and 11 mt for porbeagles and makos, respectively. Except makos, the combination of hooking and post-release mortality accounted for more fishing-related mortality than did landings.

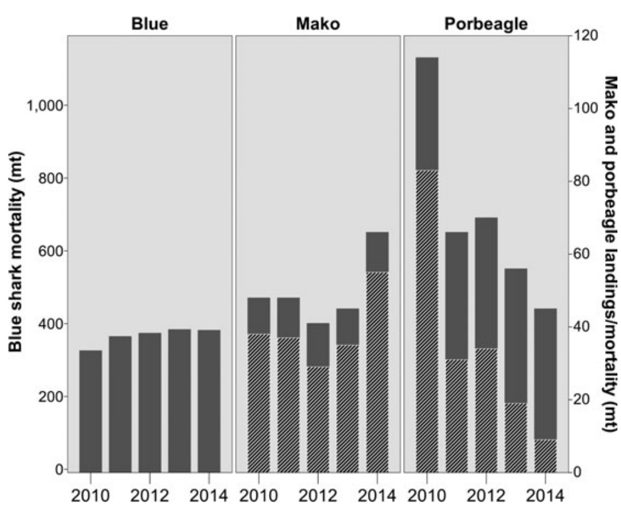

Figure 4. Estimated mortality of blue, shortfin mako, and porbeagle sharks between 2010 and 2014 due to landings (hatched pattern) and discard mortality (both hooking and post-release; solid bars). Blue shark values have been scaled differently from makos and porbeagles to improve visibility.

Discussion

There is a recent, but growing, realization that mortality induced by fishing extends to far more than just harvest (Molina and Cooke, 2012). Excluding indirect effects associated with damage to habitat by fishing gear, one can define three components of fishing-induced mortality: harvest or retained catch (classically defined as "fishing mortality"), capture mortality (i.e. hooking mortality), and post-release (discard) mortality. In situations where the entire catch is retained, there is no post-release mortality, and the magnitude of capture mortality is irrelevant. Such situations appear to be rare, due to the prevalence of quota allocations, minimum legal sizes, and market demands. But where there is discarded catch, the magnitude of capture and post-release mortality are potentially important, both with respect to the conservation status of the species and the accuracy of the stock assessment which attempts to account for all losses in population numbers (Cramer, 2004; Pine *et al.*, 2008). This is particularly true of elasmobranchs, given their typically high discard rates (James *et al.*, 2015). The results of the current study highlight this issue, demonstrating that about one-fourth of the blue sharks that are caught by Canadian pelagic longliners die either during capture or after discarding. The mortality rate of porbeagles and makos due to fishing-related causes is about twice as high, with about half of them dying due to fishing-induced causes. By any measure, such mortality rates are substantial, and would serve to undercut any conservation measures based on mandatory release from fishing gear.

Hooking mortality

Perhaps more so than the post-release mortality rate, the hooking mortality rate appears to reflect both the sensitivity of the species and the mode and handling practices of commercial fishers. Increased soaking time of the fishing gear, warmer water temperatures, smaller shark sizes, and individual boat practices have all been identified as producing significant increases in shark hooking mortality (Diaz and Serafy, 2005; Campana *et al.*, 2009; Gallagher *et al.*, 2014), whereas the shift from J hooks to circle hooks has resulted in a significant decrease in hooking mortality (Godin *et al.*, 2012). The importance of handling practices is clearly evident in the large reported variability among reported hooking mortality rates for blue shark, which range from a low of <3% in the Brazilian and Hawaiian tuna fisheries (Curran and Bigelow, 2011; Pacheco *et al.*, 2011) to as high as 51% in the Réunion (Indian Ocean) swordfishery (Poisson *et al.*, 2010). Most studies report a hooking mortality of 12–27% (Francis *et al.*, 2004; Mandelman *et al.*, 2008; Campana *et al.*, 2009; Afonso *et al.*, 2011; Coelho *et al.*, 2012; Gallagher *et al.*, 2014), which encompasses the 14.7% value observed for blue sharks in this study. There are far fewer reported estimates for shortfin makos, but the reported range of 16–47% (Francis *et al.*, 2004; Megalofonou *et al.*, 2005; Mandelman *et al.*, 2008; Walsh *et al.*, 2009; Pacheco *et al.*, 2011; Coelho *et al.*, 2012; Gallagher *et al.*, 2014) is consistent with our estimate of 26.2%. Published hooking mortality rates for porbeagle were similar or higher than those of makos (range of 30–40%; Francis *et al.*, 2004; Coelho *et al.*, 2012), and again consistent with our observed rate of 43.8%. Lamnid sharks are well known for having high metabolic rates and correspondingly high oxygen requirements, which presumably explains why porbeagle and mako are more likely than blue sharks to die on the hook, due to a reduced ability to ram ventilate while hooked (Bernal *et al.*, 2012).

Post-release mortality

Unlike harvest and capture mortality, post-release mortality is not readily observed nor measured, rendering it a "hidden mortality". Our study indicated that the post-release mortality rate of the two lamnid shark species was similar at 27–31%, and considerably higher than the 10% rate recorded for blue sharks. There are few published values against which to compare. Musyl *et al.* (2011) reported only one post-release mortality in 71 PSAT-tagged blue sharks released off Hawaii. However, the PSATs were applied during research charters, and as such, may better reflect the careful handling practices of the authors rather than the handling practices characteristic of a commercial fishery. We are unaware of any other measurements of post-release mortality in sharks caught on pelagic longline. Gallagher *et al.* (2014) reported 0% post-release mortality in tiger sharks (*Galeocerda cuvier*), 26% in bull sharks (*Carcharhinus leucas*), and 43% in great hammerhead sharks (*Sphyrna mokarran*) caught on drumlines, although the mortality rates were based on SPOT tag reporting rates, and thus may be slightly overestimated. An 84% post-release mortality rate was recorded for silky sharks *Carcharhinus falciformis* caught in purse-seines (Hutchinson *et al.*, 2015), while 26% of recreationally caught thresher sharks (*Alopias vulpinus*) hooked in the tail died after release (Heberer *et al.*, 2010). Post-release mortality rates of 17–26% have also been recorded for recreationally caught large pelagic teleosts such as marlins (Domeier *et al.*, 2003; Horodysky and Graves, 2005), 45% mortality in skates caught with bottom trawlers (Enever *et al.*, 2009), and anywhere between 0 and 69% for cod (*Gadus morhua*) caught with groundfish longlines (Milliken *et al.*, 2009), indicating that the post-release mortality rates of pelagic sharks are comparable with those of teleosts and bottom-dwelling elasmobranchs. Less direct inferences of post-release mortality rate also suggest mortality rates of up to 68% in sharks and teleosts (Wilson and Burns, 1996; Benoit *et al.*, 2012; Braccini *et al.*, 2012). Therefore, it is difficult to avoid the conclusion that post-release mortality can be a substantial source of mortality for bycatch species in many fisheries.

Our study results indicated that if a released shark was going to die, it would usually do so quickly, typically within a day or two of release. Similar observations have been made by others, both for discarded sharks (Heberer *et al.*, 2010) and for teleosts (Horodysky and Graves, 2005). Trauma, hypoxia, and exercise-induced stress can all contribute to rapid mortality shortly after release (Renshaw *et al.*, 2012; Skomal and Mandelman, 2012). However, reduced feeding ability (due, for example, from having had a hook torn out of a jaw) could induce delayed mortality, and may well explain some of our observations of mortality events that occurred more than a few weeks after release. Altered behaviour, reduced growth, and disrupted reproduction are all examples of sublethal effects of capture which might not induce mortality after release, but would reduce fitness and thus potentially produce population-level effects (Wilson *et al.*, 2014). Our study would not be able to detect such effects. In contrast, predation on released individuals such as PSAT-tagged eels (*Anguilla rostrata*; Béguer-Pon *et al.*, 2012) would be detectable, and was not detected in our study. Although post-release mortality from predation is undoubtedly a significant risk in many fish species (Raby *et al.*, 2014), it is probably less so in large pelagic sharks.

Direct measurements of post-release mortality in a natural environment remain scarce, largely because of the high cost of PSATs or other means of remote monitoring. As such, indirect proxies of post-release mortality continue to be actively explored. There appeared to be a weak correlation between capture and post-release mortality rates in our study and that of others, suggesting that a post-release mortality equivalent to 0.25–0.50 of the capture mortality rate could be used if no other measure of post-mortality rate were available. More promising are two other indirect proxies: physical condition at release and biochemical indices in the blood plasma. Our study indicated that condition at release was a useful but incomplete predictor of subsequent survival, with injured sharks of all three species much more likely to die post-release than healthy sharks. Similar results were reported by Hutchinson *et al.* (2015), who recorded the condition of silky sharks before release with PSATs. Although injured sharks were much more likely to die, the fate of apparently healthy sharks was much more difficult to predict. Nevertheless, release condition appears to be an easily observed variable which can be recorded in large numbers of untagged individuals, and thus used to stratify releases into categories for which direct measurements of survival are available (Benoit *et al.*, 2012).

Biochemical predictors of survival are a second promising proxy for direct measurement, with blood lactate in particular often being correlated with measures of stress such as fight time on the fishing gear (Heberer *et al.*, 2010; Gallagher *et al.*, 2014). However, it is well established that threshold lactate levels are highly species-specific, and that levels that would be fatal in one species would be inconsequential in another (Renshaw *et al.*, 2012). As is true with condition at release, lactate and other biochemical indices are most useful when calibrated against direct measurements of survival (Marshall *et al.*, 2012). Several studies have reported increased lactate levels in highly stressed sharks and teleosts, but were not able to measure any subsequent mortality in the assayed individuals under natural conditions (Moyes *et al.*, 2006; Frick *et al.*, 2010; Heberer *et al.*, 2010; Gallagher *et al.*, 2014). We are aware of only one study to date where the same individuals were assayed and then PSAT-tagged to monitor subsequent survival; significant differences in blood lactate were observed between the survivors and those that died (Hutchinson *et al.*, 2015). Once similar calibration studies have been completed for other species, biochemical predictors of post-release survival are likely to become much more useful (Marshall *et al.*, 2012).

Implications

It is usually taken as a given in fisheries stock assessments that the amount of retained catch (and dead discards, if known) is sufficient to account for all fishing mortality, although it has been demonstrated that ignoring discards in the assessment can bias the output (Punt *et al.*, 2006). The results of our study demonstrate that the combination of hooking and post-release mortality can exceed mortality due to harvest (for porbeagle and blue shark), or form a substantial portion of total mortality (for shortfin mako). Douglas *et al.* (2010) reached similar conclusions when evaluating the impact of recreational fishing discards of Murray cod (*Maccullochella peelii peelii*). In populations where discards are significant, ignoring dead discards and post-release mortality could conceivably (and unknowingly) push an otherwise well-managed fishery into an overexploited state. The post-release mortality of three marlin species was sufficiently influential in fishery yield calculations that it reduced the effectiveness of catch-and-release programmes and size limits if ignored (Pine *et al.*, 2008). For widely discarded species like sharks, dead discards and/or post-release mortality greatly exceed nominal catch worldwide (James *et al.*, 2015).

The implications of this study extend to the conservation status of sharks both in the Northwest Atlantic and worldwide. Our findings indicate that a substantial portion of fishing-induced mortality of pelagic sharks in Canadian waters is not accounted for by landed catch. For porbeagle, the immediate and delayed mortality of discards accounted for close to one-third of the total mortality allowed by current Species at Risk management (DFO, 2015). Shortfin mako is also under fisheries restrictions in Canada, whereby all live catch is to be released. However, our findings indicate that only about half of the catch will survive fishing, thus blunting the effectiveness of the regulations. Other nations fishing for swordfish and tuna in the Northwest Atlantic use similar fishing methods and gear as those used in the current study, suggesting that the benefits of mandatory release of sharks from pelagic longline gear are not nearly as large as is now assumed by RFMOs such as ICCAT (ICCAT, 2014). Given that the current global annual estimate of 34 000 mt of unharvested global shark mortality is based on conservative approximations of capture and post-release mortality (Worm *et al.*, 2013), it appears that actual mortality may be even larger.

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