

HOOKING SURVIVAL OF FISHES CAPTURED BY THE UNITED STATES ATLANTIC PELAGIC LONGLINE FISHERY: IMPACT OF THE 2004 CIRCLE HOOK RULE

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ABSTRACT

We examine the impact on pelagic fish hooking survival rates (defined as the proportion of fish alive upon gear retrieval) of the rapid switch from J-hooks to circle hooks that was required of the US pelagic longline fishery operating in the Atlantic Ocean and Gulf of Mexico after August 2004. Our focus was on 12 fish taxa that are commonly caught as bycatch or retained for the market, and for which individual disposition (live or dead) information was available from 1992 to 2010. To test the hypothesis of no change in survival before vs after the circle hook rule went into effect, we utilized a repeated measures logistic regression approach which accounted for variation in several operational, environmental, and biological covariates, including bait, fishery target, fishing zone, soak duration, water temperature, maximum fishing depth, and fish size (length). For white marlin and albacore, results were mixed, with both increases and decreases in hooking survival varying by fishing zone. For blue shark and lancetfish, no significant differences in hooking survival were detected between the pre- and post-circle hook rule time periods. However, for the remaining eight taxa (swordfish, yellowfin tuna, dolphinfish, bigeye tuna, escolar, silky shark, blue marlin, and sailfish), significant increases in survival were evident. Our results are generally consistent with previous experimental and fishery observer longline studies which suggested circle hook use has the potential to increase hooking survival. Results imply that the 2004 circle hook rule has provided increased opportunities for: (1) live release for several bycatch species; and (2) improved quality (and perhaps prices) of targeted and incidentally-caught taxa that are retained for the market.

Commercial pelagic longline fishing is conducted throughout the world's oceans. Highly effective for capturing swordfish, *Xiphias gladius* Linnaeus, 1758, and tunas (*Thunnus* spp.), a single longline set typically involves deploying hundreds to thousands of baited hooks on mainlines that can exceed 100 km in length (von Brandt 1984). In the process of catching marketable species, numerous other taxa, many of little economic value and/or of imperiled status, are also hooked, entangled, or otherwise captured. These bycatch species are typically discarded dead or returned to the sea alive with varying degrees of damage (Keene et al. 2010). Whether a captured animal is alive upon gear retrieval depends on a wide range of operational, environmental, and biological factors, including depth of capture, time on the line, prevailing water temperatures, and its size- and species-specific physiological tolerance to mechanical trauma of various types and levels. For most species examined, anatomical hooking location, i.e., where the hook ultimately engages, is one of the best predictors of both immediate and longer-term survival (Cooke et al. 2012). Among

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fishes, hooking in the mouth or jaw is associated with higher survival than “deep hooking” in the lower digestive tract, gills, or other vital, soft-tissue organs (Cooke and Suski 2004). Relative to traditionally-used J-hooks, fishing with circle hooks has been demonstrated to shift the distribution of hooking locations away from deeper, more vulnerable areas to more external, less vascularized areas, such as the jaw hinge (Cooke and Suski 2004). Such shifts have been shown to occur in a wide diversity of species, in the commercial and recreational fishery sectors, and in freshwater, estuarine, and marine systems, including the pelagic realm (Cook and Suski 2004).

Over the last decade, the use of circle hooks in pelagic longline fisheries has received increasing attention (NMFS 2008), especially given that the spatial expansion and increasing intensity of these fisheries has been accompanied by serious declines in those organisms that constitute their bycatch, including sea turtles, sharks, and billfishes (Watson and Kerstetter 2006). Experimental fishing trials, whereby hook types are alternated, are a highly effective means for revealing the potential impacts of substituting one hook for another because they allow for control of factors other than the hooks. There are several examples of such studies comparing circle hooks and J-hooks in the Atlantic (Watson et al. 2005, Kerstetter and Graves 2006a) and Pacific Oceans (Kim et al. 2006, Yokota et al. 2006, Curran and Bigelow 2011), and the Caribbean (Falterman and Graves 2002) and Mediterranean Seas (Mejuto et al. 2007). Results of these alternating-hook studies have been the basis for the promotion of circle hooks in pelagic longline fisheries around the globe, and, in the case of US Atlantic waters, these results have led to regulations making circle hook use mandatory.

In June 2001, the US National Marine Fisheries Service (NMFS) issued a Biological Opinion that found that the continued operation of the US Atlantic Pelagic Longline fleet jeopardized populations of loggerhead (*Caretta caretta* Linnaeus, 1758) and leatherback (*Dermochelys coriacea* Vandelli, 1761) sea turtles (NMFS 2001). In response to one of the Biological Opinion’s “reasonable and prudent” alternatives, in July 2001, NMFS closed the US Northeast Distant (NED) fishing zone (Northwest Atlantic, see Fig. 1) to pelagic longline fishing. This management measure prompted one of the largest alternating-hook experimental fishing trials conducted to date (Watson et al. 2005), with the objective of exploring ways to reduce sea turtle interactions without negatively impacting catch rates of target species (swordfish and tunas). Working with contracted commercial longliners in the NED, they compared catch rates for several pelagic species, including sea turtles, using 25° offset J-hooks (e.g., Mustad 7698, Eagle Claw 9015) vs catch rates obtained using each of two types of circle hook (a 10° offset or a 0° offset circle hook). Watson et al. (2005) found significant, bait-dependent catch rate differences between hook types, including circle hook-bait combinations which increased swordfish catches while decreasing sea turtle catch and deep-hooking rates. Largely based on the Watson et al. (2005) results, circle hook use became mandatory in August 2004 for all US pelagic longline fishers operating in Atlantic and Gulf of Mexico waters (Federal Register 2004). The result was an immediate switch from mostly J-hooks to a suite of different circle hooks of varying size, material, offset, etc., which also differed by fishing zone.

Experimental fishing trials tend to have low sample sizes and, in the process of standardizing all but treatment conditions, fishing methods and animal handling often diverge from those used normally in the fishery. It is important, therefore, to follow-up experimental work with direct fishery observations to gauge the actual

conditions and outcomes of management measures, including hook regulations. Here, we investigate the consequences of the circle hook rule on the hooking survival (i.e., proportion of fish alive upon gear retrieval, the complement of hooking mortality) of 12 fish taxa that, during US pelagic longline operations, are either caught as bycatch, directly targeted, or, incidentally captured and retained for the market. The taxa examined were: swordfish, *Xiphias gladius*; yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788); dolphinfish, *Coryphaena hippurus* Linnaeus, 1758; blue shark, *Prionace glauca* (Linnaeus, 1758); bigeye tuna, *Thunnus obesus* (Lowe, 1839); escolar, *Lepidocybium flavobrunneum* (Smith, 1843), lancetfish (*Alepisaurus* sp.); albacore, *Thunnus alalunga* (Bonnaterre, 1788); silky shark, *Carcharhinus falciformis* (Müller and Henle, 1839); white marlin, *Kajikia albida* (Poey, 1860); blue marlin, *Makaira nigricans* Lacépède, 1802; and sailfish, *Istiophorus platypterus* (Shaw and Nodder, 1792).

Our objective was to test the hypothesis of no change in the probability of each taxon being alive at haul-back before vs after implementation of the 2004 circle hook requirement. We were particularly interested in addressing two questions: (1) Has the circle hook regulation led to increased opportunities for the live release of bycatch species?, and (2) Is there evidence for the circle hook rule leading to higher survival rates for the taxa destined for the market? Our rationale for pursuing the second question stemmed from the suggestion from Watson et al. (2005) and Kerstetter and Graves (2006a) that circle hooks lead to higher survival rates for fish destined for sale, and thus ultimately lead to higher quality products and prices in the market. We also compare our results with those reported in other studies, with special emphasis on the comparisons with those of Epperly et al. (2012)—an experimental trial with exceptionally high sample sizes and importance given its connection to the Watson et al. (2005) study, which formed the basis for mandating circle hook use for US Atlantic pelagic longline fishers. Finally, we discuss the strengths and weaknesses of our approach and suggest areas for future research.

METHODS

The data set examined spanned 18 yrs (1992–2010) and was a subset of that collected as part of the US NMFS Pelagic Observer Program (POP). The POP gathers detailed information on each longline set including: time and location of deployment, hook model, number of hooks, number of light sticks, bait, soak duration, sea surface temperature, and estimated hook depth. Also collected are details of catch, including the identity (genus, species) of captured taxa, their numbers, and the size (lengths) and the disposition (live/dead) of all individuals observed. Fish were classified as “dead” if they showed no visible movement. If a fish was either dead or alive, but exhibited extensive injuries the fish was classified as “damaged.” If the observer was unsure, the specimen’s disposition is classified as “unknown.” Further details of observer protocols are available at <http://www.sefsc.noaa.gov/fisheries/observers/forms.htm>. Fish classified as either damaged or unknown were excluded from the present analysis. Using coordinates corresponding to the beginning of each set, longline deployments were mapped using geographical information system software and each was assigned to one of six fishing zones (Fig. 1): Caribbean (CAR), Gulf of Mexico (GOM), Southeast coastal (SEC), Northeast coastal (NEC), Northeast distant (NED), and Southeast distant (SED).

To test the hypothesis of no hooking survival change, we compared mean survival rates before and after implementation of the 2004 circle hook requirement. However, we took several measures to reduce the impact of operational, environmental, and biological factors as well as several other management actions that could confound results. First, we eliminated from

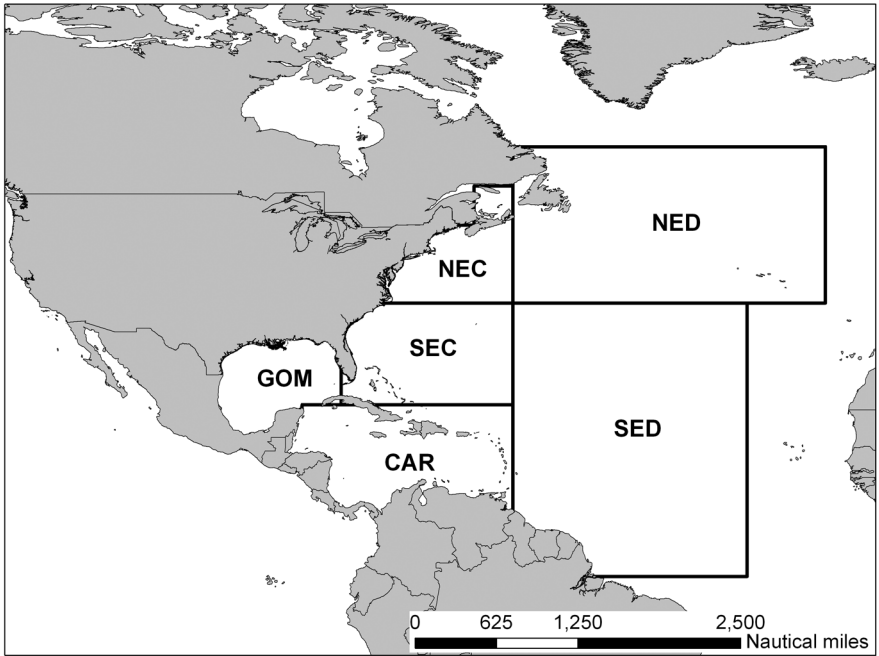


Figure 1. Map depicting the six statistical areas considered in the present study. Fishing zone codes are CAR (Caribbean), GOM (Gulf of Mexico), Southeast Coastal (SEC), NEC (Northeast Coastal), Northeast Distant (NED), and Southeast Distant (SED).

analysis those longline sets which had mixed hook types (i.e., some combination of J- and circle hooks). Second, we removed those sets deployed in times and areas that were subject to fishing closures at some point during the study period (Fig. 2). Third, through their inclusion in regression models, we minimized the potential influence of several operational, environmental, and biological “nuisance” variables unrelated to hook type that, if not accounted for, could confound pre- and post-regulation results. And fourth, we accounted for within-vessel correlation by using a repeated measures approach whereby the subjects were individual fishing vessels that fished both before and after the circle hook rule. We implemented this approach because fishing practices associated with a particular vessel or crew are known to be a major source of variation in hooking survival (Campana et al. 2009). Specifically, using SAS (1990) PROC GENMOD, we applied repeated measures generalized linear models to test for a “time” (i.e., pre- vs post-regulation) effect on fish survival. The models took the form:

$$S = \text{Time} + \text{Bait} + \text{Target} + \text{Zone} + \text{Length} + \text{Temp} + \text{Soak} + \text{Depth} + \text{Time} \times \text{Zone}$$

where: S = Survival (1,0); Time (pre-, post-regulation); Bait = bait type (fish, squid, mix); Target = species targeted (tuna, swordfish, mix, as determined by the ratio of lightsticks to hooks); Zone = fishing zone (up to six categories); Length = curved lower jaw fork length measurement for billfishes and tunas and straight upper jaw/snout fork length for the remaining species (cm); Temp = sea surface temperature ($^{\circ}\text{C}$); Soak = soak duration (hrs); Depth = estimated maximum hook depth (m). The number of fishing zones considered in each analysis was tailored to the number of observations per time and zone combination. That is, if the number of observations (live or dead individuals) in a given fishing zone was <50 fish during either time period, data from that zone were eliminated from analysis. Based on regression results, appropriate least square means were generated and plotted to reveal average survival levels

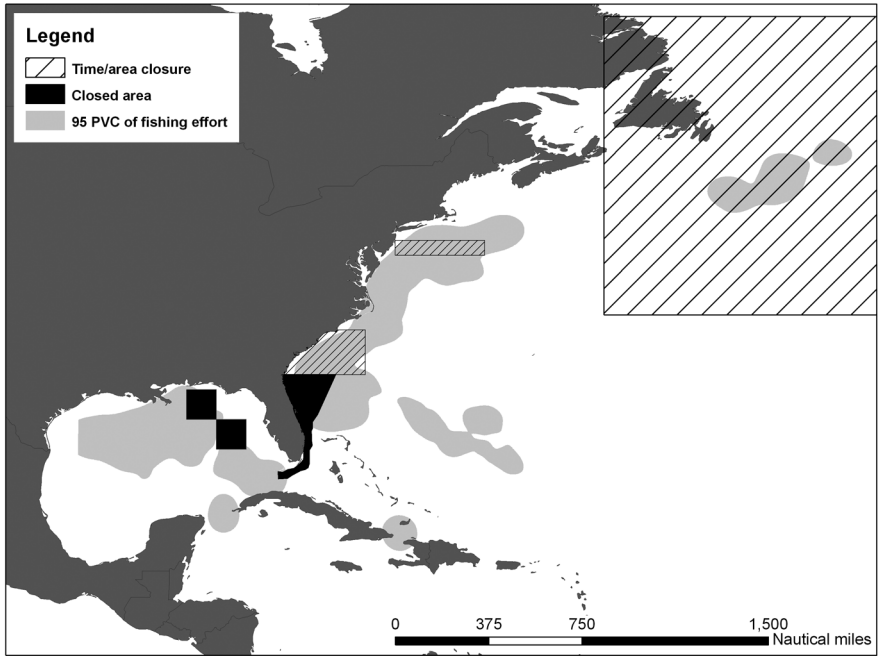


Figure 2. Map showing spatial pelagic longline fishery closures (black), time-area closures (hatched), and a spatial depiction of the fishing effort examined in the present study (gray polygons). Plotting of individual longline set coordinates is prohibited for data confidentiality reasons; therefore, presented are 95% volume contours (PVCs) of fishing effort, which were generated using Hawth's Analysis Tool for ArcGIS (Beyer 2004).

(with 95% confidence intervals) before and after the circle hook regulation, thus allowing for taxon-specific, statistical assessment of the magnitude and direction of survival change that can be attributed to this management measure.

Two potentially important variables that we were unable to incorporate directly in our models were hook size and degree offset. Table 1 indicates the distribution of hook types, sizes, and degree offset by fishing zone as reflected in the POP data set. Hook size designations between J- and circle hooks are not comparable and can vary widely among manufactures, even within hook types. Similarly problematic is that degree offset measurements were only consistently recorded in the POP data set during the post-regulation time period. Many sets were made with an unspecified mix of hook sizes and offset values which further complicated matters. For these reasons, observations were either absent or insufficient in number for application of the repeated measures approach, which would require a balance of vessel- and zone-specific data for each hook type, size, and offset level both before and after the circle hook regulation—data that do not exist in the POP database. As indicated in Table 1, changes in circle hook use pre- vs post-regulation were accompanied by changes in hook size and offset and these differed by fishing zone. Therefore, the present analysis does not test for a hook effect per se; rather it tests for a hook regulation effect on the survival probabilities of target and bycatch species. This is an important distinction from most experimental fishing studies, which focus on specific hook effects as opposed to the response of the fishery to a mandatory hook type rule that may or may not be accompanied by hook size or offset requirements.

Table 1. Distribution of hook types, sizes, and degree offset by fishing zone before (pre) and after (post) the 2004 mandatory circle hook rule. U° indicates degree offset unknown. MIX and MIX° indicate that more than one hook size or degree offset was used in a given set. Numbers given are number of hooks per fishing zone.

Time	Hook type	Hook		Fishing zone					
		Size	Offset	CAR	GOM	NEC	NED	SEC	SED
Pre	J-hook	7/0	U°	–	800,857	5,202	–	–	–
	J-hook	8/0	U°	–	341,877	193,861	55,993	78,674	–
	J-hook	9/0	U°	128,380	86,091	229,117	100,916	497,288	220,676
	J-hook	9/0	25°	–	–	2,400	–	–	–
	J-hook	10/0	U°	2,376	3,406	5,380	10,095	12,728	18,602
	J-hook	11/0	U°	–	–	–	–	6,316	–
	J-hook	13/0	U°	–	–	–	–	550	–
	J-hook	14/0	U°	–	–	–	–	282	–
	J-hook	MIX	U°	10,420	60,603	130,653	6,693	103,439	37,955
	J-hook	U	U°	–	6,272	–	–	–	–
	Circle hook	14/0	U°	–	1,405	–	–	–	–
	Circle hook	15/0	U°	–	84,194	–	–	–	–
	Circle hook	16/0	U°	–	176,283	10,334	–	–	–
	Circle hook	17/0	U°	–	–	–	–	–	–
	Circle hook	18/0	U°	–	–	–	12,506	–	–
	Circle hook	MIX	U°	–	3,945	–	–	–	–
Post	Circle hook	16/0	U°	–	88,400	4,360	–	2,045	–
	Circle hook	16/0	0°	–	2,452,242	143,088	–	142,005	69,945
	Circle hook	16/0	10°	–	–	–	–	1,430	–
	Circle hook	16/0	MIX°	–	–	–	–	2,836	–
	Circle hook	18/0	0°	–	40,136	1,260	–	46,945	15,960
	Circle hook	18/0	5°	–	2,268	–	–	–	–
	Circle hook	18/0	10°	32,845	1,460	586,254	177,617	496,484	–
	Circle hook	18/0	U°	–	–	14,064	72,119	–	–
	Circle hook	18/0	MIX°	–	–	4,500	–	5,317	–
	Circle hook	MIX	U°	3,164	14,996	5,760	–	532	–
	Circle hook	MIX	0°	–	7,796	6,222	–	1,300	–
	Circle hook	MIX	10°	–	1,460	6,300	–	6,746	–
	Circle hook	MIX	MIX°	–	29,957	130,650	–	137,410	–

RESULTS

Total numbers of live and dead individuals (observations) per taxon ranged from 777 (sailfish) to over 39,000 (swordfish); fish sizes (lower or upper jaw-fork length, depending on species) ranged from 25 (dolphinfish) to 400 cm (blue marlin, Table 2). Numbers of unique vessels with records of fishing and capturing the focal taxa both before and after the circle hook rule ranged from 32 (albacore tuna) to 65 (swordfish) and the number of fishing zones considered in each analysis ranged from two to six (Table 3).

The prime objective of our study was to test for a “Time” or “Time × Zone” effect on fish survival at boatside after accounting for the influence of a set of operational, environmental, and biological variables. Statistically significant effects were detected for the majority (10 of 12) taxa examined (Table 3); only blue shark and lancetfish survival was found to be equivalent before vs after the circle hook rule. The repeated

Table 2. Fish taxa examined in the present hooking survival study. Shown are species codes, total numbers (n), and length information (i.e., minimum, mean, and maximum curved lower jaw fork length measurement for billfishes and tunas, and straight upper jaw/snout fork length for the remaining species).

Species	Common name	n	Length (cm)		
			Min	Mean	Max
<i>Xiphias gladius</i>	Swordfish	39,225	29	132	298
<i>Thunnus albacares</i>	Yellowfin tuna	19,301	30	124	190
<i>Coryphaena hippurus</i>	Dolphinfish	12,071	25	99	150
<i>Prionce glauca</i>	Blue shark	10,977	30	162	366
<i>Thunnus obesus</i>	Bigeye tuna	5,881	35	115	195
<i>Lepidocybium flavobrunneum</i>	Escolar	4,166	28	93	178
<i>Alepisaurus</i> sp.	Lancetfish	3,815	30	106	180
<i>Thunnus alalunga</i>	Albacore tuna	3,225	25	100	123
<i>Carcharhinus falciformis</i>	Silky shark	2,071	45	124	305
<i>Kajikia albida</i>	White marlin	1,220	60	149	211
<i>Makaira nigricans</i>	Blue marlin	1,016	71	197	400
<i>Istiophorus platypterus</i>	Sailfish	777	90	149	210

measures regression results (Table 3) revealed that a different set of model terms (covariates) emerged as significant for each taxon. This was an expected outcome given that hooking survival probabilities are likely species-specific and that no two analyses in the present study were based on an identical set of vessels operating in the same set of fishing zones. Although taxon-specific regression results were unique, the overall pattern of model term significance for the 12-taxa suite lends insight into the relative importance of “nuisance” variable adjustment in non-experimental studies of this kind. For example, of all variables included in the models, “Depth” was significant in only one analysis, whereas “Length” was significant in eight. Similarly, the terms “Temperature” and “Soak” were significant in most (seven of the 12) analyses performed; while the terms “Bait,” “Target,” and “Zone” (main effect) emerged as significant variables in fewer than or equal to five of the 12 analyses.

Least squares mean hooking survival rates (Figs. 3, 4) suggested the focal taxa can be categorized into those with high, intermediate, and low probability of survival upon gear retrieval. Mean survival values for lancetfish (Fig. 3A), albacore tuna (Fig. 4A), and swordfish (Fig. 4B) were consistently below 30% during the pre-regulation time period. The survival change for these three species before vs after the regulation indicated no significant difference in lancetfish survival, a mixed, fishing zone-dependent response in albacore tuna (ranging from +6% to -11%), and a consistent increase (averaging approximately 8%) in swordfish survival (Fig. 4B). The highest apparent survival gain for swordfish was 21% in the SED fishing zone and the lowest gain (<2%) was in the GOM. Intermediate mean hooking survival probabilities (i.e., 30%–60% survival pre-regulation) were estimated for seven fishes: yellowfin tuna (Fig. 3B), bigeye tuna (Fig. 3C), escolar (Fig. 3D), silky shark (Fig. 3E), white marlin (Fig. 4C), blue marlin (Fig. 3F), and sailfish (Fig. 3G). With one exception, consistent post-regulation survival gains (i.e., ranging from 12% to 19%) were observed for these taxa. The exception was white marlin with an apparent increase of 15% in the SEC fishing zone, but minor decreases in the GOM and NEC fishing zones (i.e., <0.1% and 3%, respectively). Blue shark (Fig. 3H) and dolphinfish (Fig. 4D) emerged as the species with the highest probability of survival upon gear retrieval, averaging 88% for blue shark during the pre-regulation time period and values ranging from 72% to 81% for dolphinfish, depending on fishing zone. While blue shark survival appeared

Table 3. Summary of hooking survival results for species-specific repeated measures generalized linear models indicating the fishing zones examined and the number of vessels and fish considered in each analysis. Statistically significant (i.e., $P < 0.05$) and non-significant model terms are indicated by asterisks and ns, respectively. See Figure 1 for fishing zone codes. See text for model term descriptions.

Taxon	Fishing zones	Number of vessels	Number of fish	Time	Bait	Target	Zone	Length	Temp	Soak	Depth	Time x Zone
Swordfish	CAR, GOM, SEC, NEC, NED, SED	65	39,225	*	ns	*	*	ns	*	*	ns	*
Yellowfin tuna	GOM, SEC, NEC, SED	63	19,301	*	*	*	*	*	*	*	ns	ns
Dolphinfish	GOM, SEC, NEC, SED	63	12,071	ns	*	ns	*	*	ns	*	ns	*
Blue shark	SEC, NEC, NED	40	10,977	ns	ns	*	*	*	ns	ns	ns	ns
Bigeye tuna	GOM, SEC, NEC, SED	61	5,881	*	ns	ns	*	ns	*	*	ns	ns
Escolar	GOM, SEC	52	4,166	*	*	*	ns	*	*	*	*	ns
Lancetfish	GOM, SEC, NEC, SED	59	3,815	ns	*	ns	ns	ns	*	*	ns	ns
Albacore tuna	SEC, NEC	32	3,225	*	ns	*	ns	*	*	ns	ns	*
Silky shark	GOM, SEC, NEC	57	2,071	*	ns	ns	ns	*	*	*	ns	ns
White marlin	GOM, SEC, NEC	57	1,220	ns	ns	ns	ns	*	ns	ns	ns	*
Blue marlin	GOM, SEC	52	1,016	*	ns	ns	ns	ns	ns	ns	ns	ns
Sailfish	GOM, SEC	47	777	*	ns	ns	ns	*	ns	ns	ns	ns

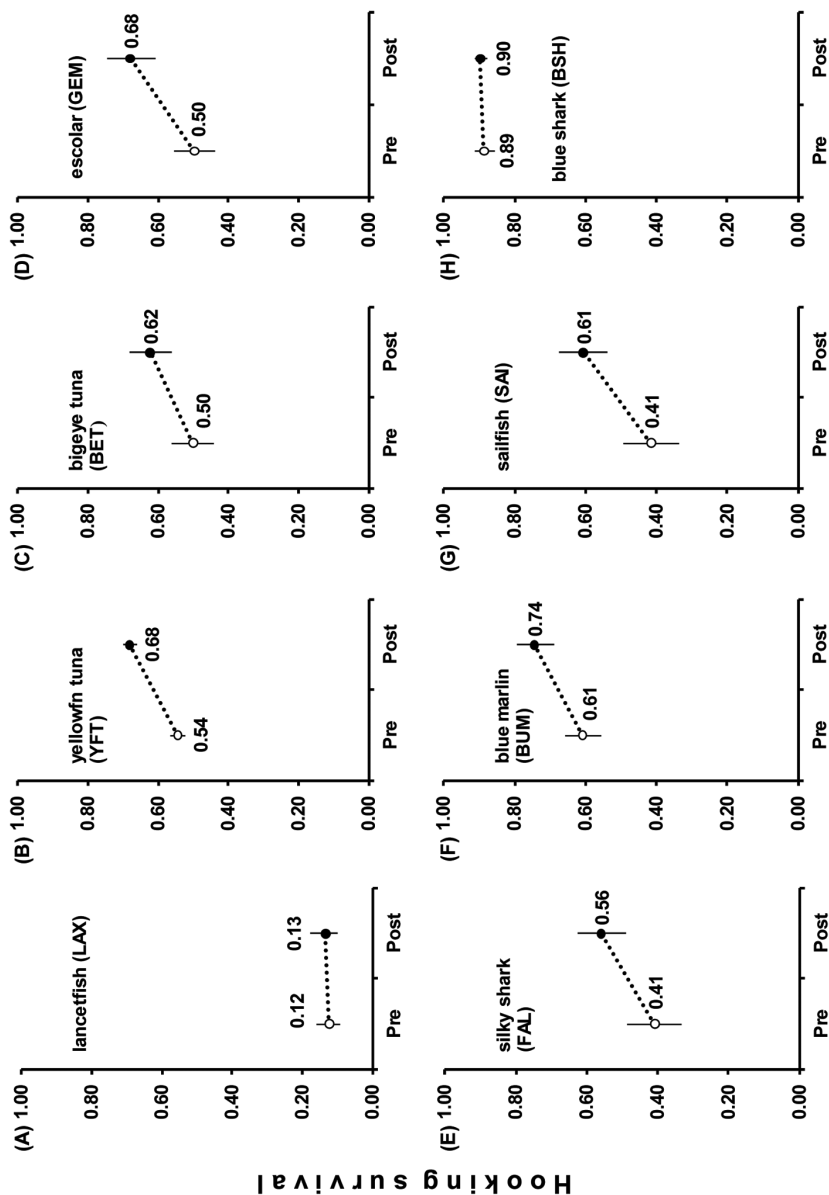


Figure 3. Hooking survival (proportion alive upon gear retrieval) plots for fishes for which no Time x Zone interaction was found. Shown are proportions of fish alive upon gear retrieval before (white circles) vs after (black circles) imposition the circle hook regulation (August 2004). Vertical lines indicate 95% confidence intervals.

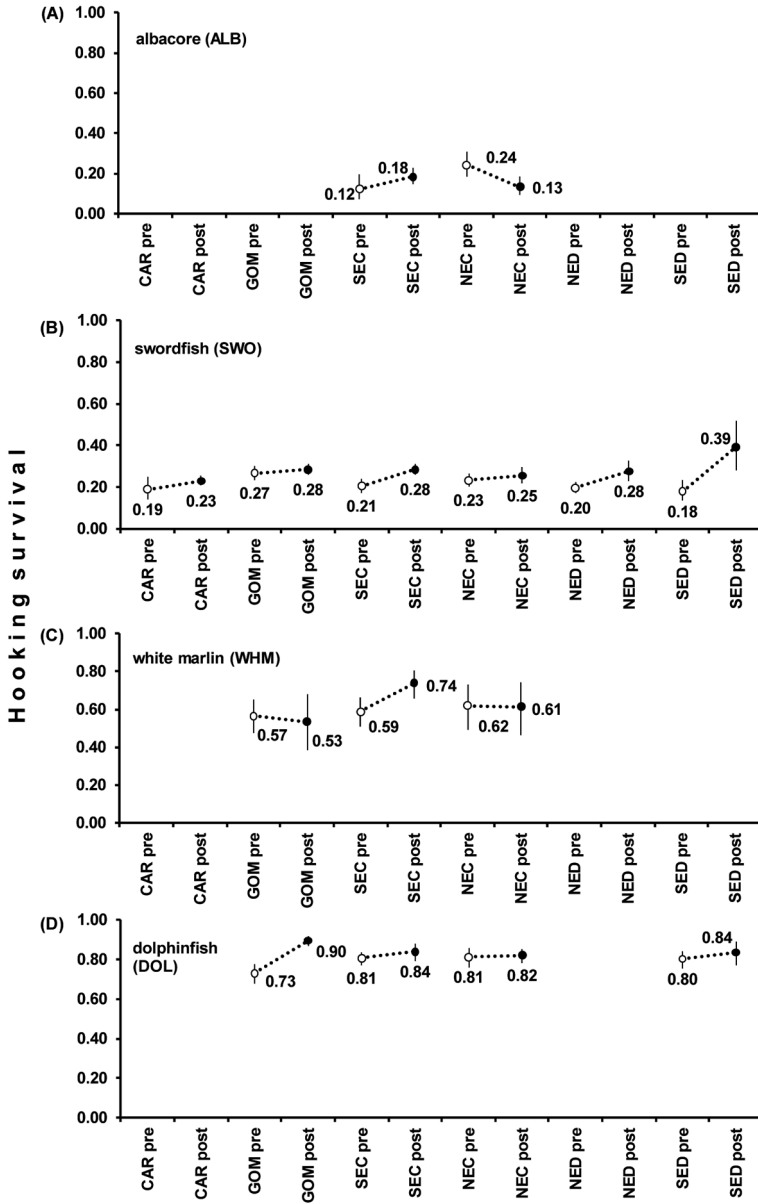


Figure 4. Hooking survival (proportion alive upon gear retrieval) plots for fishes for which a significant Time \times Zone interaction was found. Shown are proportions of fish alive upon gear retrieval before (white circles) vs after (black circles) imposition the circle hook regulation (August 2004). See Table 1 and Figure 1 for species and fishing zone codes. Vertical lines indicate 95% confidence intervals.

stable over the entire pre- and post-regulation time period, dolphinfish survival increased in all fishing zones, by as much as 17% in the GOM, but by comparatively modest increments ($\leq 4\%$) in the SEC, NEC, and SED.

DISCUSSION

For most fish taxa examined (i.e., 10 of 12), we rejected the hypothesis of no change in survival before vs after the mandatory switch from J- to circle hooks was implemented. We found significant increases in hooking survival post-regulation for all but two of the bycatch taxa (blue shark and lancetfish) and for all of the taxa that are typically retained for the market. Results were mixed, however, for white marlin, a bycatch species, and for albacore, a marketable species. For these fishes, opposite trends (i.e., both increase and decrease) in hooking survival were found among fishing zones. Below, we compare our results with those of several previous studies (see Table 4).

BYCATCH TAXA.—Two fishes for which no change in hooking survival was detected were blue shark and lancetfish, which are fishes that often constitute the majority of bycatch in the US Atlantic and Gulf of Mexico pelagic longline fishery (Beerkircher et al. 2004, Mandelman et al. 2008). In our analyses, blue shark and lancetfish, respectively, had the highest and lowest survival rates of all the species considered—a result consistent with very high and very low potential for live release, regardless of hook type used.

Our blue shark finding of no appreciable change in hooking survival is consistent with the experimental fishing results of Kerstetter et al. (2007), Kerstetter and Graves (2006a), and Curran and Bigelow (2011). However, they differ from those of Epperly et al. (2012), which revealed significantly increased survival (by about 5%) for blue shark with circle hooks in comparison to J-hooks under experimental fishing conditions in the NED fishing zone. Although we tentatively conclude that, under normal US longline fishing operations in Atlantic and GOM waters, use of circle hooks conveys no benefits to blue shark, this conclusion contradicts analyses of Canadian fishery observer data performed by Carruthers et al. (2009) and Campana et al. (2009) which found survival increases from 6% to 13% with circle hooks vs J-hooks. Because the Epperly et al. (2012), Carruthers et al. (2009), and Campana et al. (2009) studies were all conducted in fishing zones at or beyond the northern extent of the present study's spatial domain, one might suspect water temperatures to underlie the Canada-US study discrepancies. However, this does not appear to be the case, as water temperature did not emerge as a significant contributor to blue shark survival in our analyses, which incorporated the widest temperature range of all the longline studies in question (i.e., present study: 6–30 °C; Campana et al. 2009: 11–25 °C; Epperly et al. 2012: 12–23 °C). Therefore, further research into the apparent blue shark hooking survival discrepancy may be warranted.

For lancetfish hooking survival, our results of no change are consistent with those of Kerstetter and Graves (2006a), Carruthers et al. (2009), and Epperly et al. (2012). Precisely why Curran and Bigelow (2011) found a significant decrease (12%) in survival of lancetfish with circle hooks when compared to J-hooks in experimental trials conducted in the Pacific Ocean is unknown.

Table 4. Summary of hooking survival results in the literature where circle hook performance was compared to J-hooks, including results of the present study. Arrows indicate a statistically significant increase (↑) or decrease (↓) in hooking survival was associated with circle hooks as compared to J-hooks. MIX indicates that results were not uniform among fishing areas; ns indicates the hooking survival difference observed between the focal hook types was not statistically significant.

Taxon	Kerstetter et al. (2007)	Kerstetter and Graves (2006a)	Campana et al. (2009)	Carruthers et al. (2009)	Diaz (2008)	Curran and Bigelow (2011)	Epperly et al. (2012)	Present study
Swordfish	ns	ns				ns	↑	↑
Yellowfin tuna	ns	ns				ns		↑
Dolphinfish		↑				↑		ns
Blue shark	ns	ns	↑	↑		ns	↑	ns
Bigeye tuna	↑	ns				ns	↑	↑
Escolar		↑				ns		↑
Lancetfish	ns	ns		ns		↓		ns
Albacore tuna		ns				ns	ns	MIX
Silky shark								↑
White marlin	ns	ns			↑			MIX
Blue marlin	ns				↑	ns		↑
Sailfish	↑	ns						↑

For the remaining bycatch species we considered (i.e., silky shark, sailfish, blue marlin, and white marlin), we observed mostly significant increases in hooking survival between the pre- vs post-regulation time period, although there were mixed results for white marlin. Silky shark is listed as “near threatened” by the International Union for the Conservation of Nature (IUCN 2011) and ours appears to be the first report of an association between circle hook use and increased hooking survival for silky shark. In the experimental fishing trials conducted by Ward et al. (2009), silky shark hooking survival rates were examined between circle hooks and tuna hooks and were found to be statistically equivalent; however, their sample sizes were considerably lower (25 individuals) than the present study (2071 individuals). Therefore, based on our hooking survival analysis, the circle hook rule appears to have had the unanticipated benefit of increasing opportunities for the live release of silky shark in the US pelagic longline fishery.

We also attribute the significant changes in hooking survival that we observed for sailfish and blue marlin to the circle hook rule. Pelagic longline and recreational hooking survival for the Atlantic marlins and sailfish have been examined in several studies, and a review of their collective findings was reported by Serafy et al. (2009). For sailfish, results of the present study are consistent with, but of lesser magnitude than, the experimental longline fishing trials conducted off Brazil by Kerstetter et al. (2007). We observed a 19% increase after the circle hook rule, whereas sailfish caught on circle hooks in the Kerstetter et al. (2007) trial had a 40% higher hooking survival rate than those caught on J-hooks. Both the direction and magnitude of our blue marlin results bear strong resemblance to those of Diaz (2008), which pertained to longline observer data in the Gulf of Mexico prior to 2004. Diaz (2008) found a statistically-significant +17% difference in hooking survival for blue marlin captured using circle hooks vs J-hooks; the present study indicates 13% higher hooking survival rate for this species after the circle hook regulation was implemented.

For white marlin, our results are less clear and are only somewhat consistent with those reported by Diaz (2008), which revealed a +12% difference in hooking survival in the GOM for white marlin captured on circle hooks relative to J-hooks. We observed a 15% hooking survival increase after the circle hook rule, however, this estimate pertained only to the SEC fishing zone. In the GOM and NEC fishing zones, we observed a small ($\leq 4\%$) hooking survival rate reduction after the circle hook rule was implemented. Why the circle hook rule appears to have conferred a potential conservation benefit for white marlin in the SEC fishing zone and not in the fishing zones directly adjacent to it may relate to sample size differences—further investigation is warranted.

MARKETED TAXA.—Six fish taxa examined in the present study (swordfish, yellowfin tuna, bigeye tuna, albacore, dolphinfish, and escolar) are either directly targeted or incidentally captured by the US Atlantic pelagic longline fishery and, depending on size, quality, and other considerations, are typically retained for the market (Keene et al. 2010). Although proper handling and storage after capture are critical, highest seafood quality is typically associated with fishing methods where fish are alive upon gear retrieval (Clucas 1997). Correlated with fight time, reduced tuna meat quality results from muscle cell degeneration, which begins prior to death and proceeds more rapidly after death (Cramer et al. 1981). For the marketable fishes examined in the present study, hooking survival rates were quite variable before vs after the circle hook rule; however, for all but albacore, a consistent pattern of increase emerged across species and fishing zones.

Our hooking survival results for swordfish, whereby a mean increase of approximately 8% after the circle hook rule was observed, was remarkably consistent with the experimental results of Epperly et al. (2012), which compared survival rates of swordfish caught on circle hooks with those caught on J-hooks. Our results for bigeye tuna (i.e., 12% increase in survival after the regulation) fall between those of Epperly et al. (2012) and the experimental fishing results of Kerstetter et al. (2007), which reported up to 7% and 24% increases, respectively.

Neither Kerstetter and Graves (2006a), Kerstetter et al. (2007), nor Curran and Bigelow (2011) found significant differences in survival for yellowfin tuna on circle hooks vs J-hooks in their experimental fishing trials. Our finding of a 14% increase in hooking survival rate for yellowfin tuna, therefore, partially corroborates the actions of the early circle hook adopters in the GOM. Our findings on escolar and dolphinfish are generally consistent with those obtained in the experimental fishing trial of Kerstetter and Graves (2006a) which reported significant differences between hook types for these species. In their fishing trial, escolar and dolphinfish survival rates were 32% and 24% higher, respectively, on circle hooks relative to J-hooks. Curran and Bigelow (2011) also observed a significant increase in survival of dolphinfish caught on circle hooks relative to J-hooks (by approximately 6%). In the present study, escolar hooking survival increased by 17% after the circle hook rule, whereas corresponding survival rates for dolphinfish were increases of 1%–17%, depending on fishing zone. Our hooking survival results for albacore were mixed with a 6% increase after the circle hook rule in one fishing zone (SEC) and an 11% decrease in another (NEC). No other study comparing albacore hooking survival has revealed significant differences associated with hook type (i.e., Kerstetter and Graves 2006a,

Curran and Bigelow 2011, Epperly et al. 2012), thus our finding appears worthy of additional investigation.

Although the above taxa are primarily marketed, the higher probabilities of being alive at haulback observed after the switch to circle hooks also has important conservation benefits, particularly for fish managed under size limit regulations. Currently, US regulations in the Atlantic and Gulf of Mexico prohibit retention of yellowfin and bigeye tuna <68.6 cm curved fork length and swordfish <119.4 cm lower jaw fork length. High release mortality or, similarly, a low likelihood of surviving the capture process, reduces the effectiveness of size limits in achieving yield-per-recruit or maintaining spawner-per-recruit management goals (Coggins et al. 2007, Pine et al. 2008). While we did not explicitly test for survival differences in undersized marketed fish, any potential increases would improve the effectiveness of the size limits as a management strategy.

CAVEATS, IMPLICATIONS, AND FUTURE RESEARCH.—Properly-designed experimental fishing studies, such as those that alternate hook types (e.g., Watson et al. 2005, Curran and Bigelow 2011), are well-suited for quantifying hook effects as they can minimize the influence of confounding factors. However, the realized effects of a sweeping regulatory change can only be determined from evaluation of fishery performance. For this reason, data collected from onboard observers is essential to estimating these effects. In the present study, we examined fishery observer data to gauge the apparent effects of the hook regulation on a single variable—hooking survival. In doing so, our focus was narrowed toward the beginning of a chain of events that ultimately determine whether the circle hook rule has led to: (1) increased live release of bycatch fishes, and (2) economic gains to the fishery via improved seafood quality. For most taxa, our hooking survival estimates are consistent with mainly positive impacts of the rule; however, there are important caveats to keep in mind when considering our hooking survival findings.

First, we cannot strictly attribute all changes in hooking survival with the change from J- to circle hooks because they are inextricably confounded with time. In the future, a phased approach to regulation implementation would allow for more rigorous evaluation of regulatory effects and would be consistent with the adaptive management approach (Walters 1986). Second, our estimates constitute maximum survival values, which, as appropriate, should be combined with hook-specific post-release survival estimates (e.g., Kerstetter and Graves 2006b, Campana et al. 2009) when evaluating conservation benefits to bycatch organisms. Third, if the change in hook type was associated with changes in catchability, manifested as changes in catch rates of target or non-target species, it may have conflicting, and potentially negative, consequences for the fishery (Kaplan et al. 2007). Increases in catch rates of non-target species or decreases in catch rates of target species could both lead to a greater number of interactions with bycatch species. Determining how a change in hook type might affect catchability requires temporal overlap in hook utilization, again justifying a phasing-in of regulatory changes to allow for estimation of catchability effects.

Finally, beyond estimates of survival and catchability, there is also a need to obtain information on fishery compliance and seafood dealer and consumer behavior—poorly studied areas that are well beyond the scope of the present study. Where fishery observer and port agent infrastructure exists, better linkages between biological and

economic data collection may be attainable. For the marketed fishes, for example, directed studies deserve consideration whereby individual fish are tracked from their disposition upon gear retrieval through to the grade and price they ultimately fetch at the market. Further research in these areas is clearly warranted to assess the likelihood that the hooking survival levels and trends suggested in the present study are representative of the fisheries and of sufficient magnitude to translate into meaningful conservation and/or economic benefits.

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