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ANATOMICAL HOOKING LOCATION AND CONDITION OF ANIMALS CAPTURED WITH PELAGIC LONGLINES: THE GRAND BANKS EXPERIMENTS 2002–2003

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ABSTRACT

Experiments were conducted on the Grand Banks of the North Atlantic Ocean during 2002–2003 to evaluate the effect of circle hooks and mackerel bait on pelagic longline catches and bycatch, and compare the treatments to the industry standards at the time. Circle hooks were 18/0, and both non-offset and 10° offset were used as separate treatments and compared to the 9/0 J-hook control hooks with 10°–30° offset. Bait treatment was mackerel (*Scomber scombrus* Linnaeus, 1758), which was compared to the squid control (*Illex* spp.). We analyzed the effects of hook (one J- and two circle hooks), bait (mackerel and squid), temperature, soak time, and animal length on anatomical hooking location for seven fish species and two sea turtle species. We also analyzed the effects of the same variables, inclusive and exclusive of hooking location, on the odds of boating a dead fish. We found that hook was one of the most important variables in predicting anatomical hooking location, and that soak time and hook and/or anatomical hooking location were important in predicting the odds of observing a dead animal boatside. The importance of the other variables differed by species, and for several species no models were significant for predicting hooking location or for predicting observed mortality.

Throughout the last century, the growing human population and the demand for seafood have resulted in a dramatic increase in fishing effort, while technological advances have accelerated fishing power, raising concern about the sustainability of harvest and the integrity of the ocean's ecosystems today (Valdemarsen 2001, Pauly et al. 2005). The incidental capture of animals that are either unwanted or are required to be discarded in fisheries (bycatch) is an important aspect of marine conservation (Alverson et al. 1994, Lewison et al. 2011). There are three means of reducing the impact of a fishery on bycatch: reduce the number of animals (1) interacting with the gear (cryptic) or (2) captured on gear (observed), and (3) increase their post-release survival. Circle hooks have been advanced as a means of both reducing bycatch and increasing the post-release survival of bycatch (Prince et al. 2002, Cooke and Suski 2004, Watson et al. 2005, Gilman et al. 2006, Lyle et al. 2007, Ward et al. 2009). Circle hooks also are believed to increase the quality and hence the value of the marketed seafood product, but as noted by Serafy et al. (2012a), has yet to be demonstrated.

In 2002–2003, the National Marine Fisheries Service together with the Blue Waters Fishermen's Association conducted experiments on the fishing grounds of the Grand Banks in the North Atlantic. The purpose of these experiments was to investigate the effect of circle hooks on the catch rate of loggerhead (*Caretta caretta,* see Table 1 for species authorities) and leatherback (*Dermochelys coriacea*) sea turtles, and also on the catch of target species, usually swordfish (*Xiphias gladius*). The 2002 results were analyzed quickly to support rule-making, and were published relatively soon after the completion of the experiments (Watson et al. 2005). They focused narrowly on the catch rates of the two sea turtle species and four fish species. In the 2002 experiment, the tested circle hooks greatly reduced the bycatch of both sea turtle species over the standard J-hook, and also decreased the proportion of deeply ingested hooks—considered to be the most lethal (Ryder et al. 2006)—in loggerhead sea turtles. Furthermore, with the appropriate hook and bait combination, the catch of the swordfish in cool waters was not diminished. The 2002 results, combined with the unpublished 2003 results, culminated in the mandatory requirement of United States (US) pelagic longline fishermen in both the Atlantic fishery and in the Hawaii-based shallow set fishery to use circle hooks (US Department of Commerce 2004a,b).

The comparison of catch rates of target and bycatch species for the combined 2002–2003 Grand Banks experiments are reported by Foster et al. (2012). Their study expands the number of species analyzed over that presented by Watson et al. (2005) and explores a year effect. Our study is a companion paper to Foster et al. (2012), and focuses on the condition of both target and bycatch species in the same experiments by evaluating the effects of hook, bait, sea surface temperature, soak time, and animal length on the anatomical hooking location and observed boatside mortality of animals captured during 2002–2003 experiments.

METHODS

SAMPLING

The sampling methods are summarized here, but see Watson et al. (2005) and Foster et al. (2012) for details. Commercial pelagic longline fishing vessels were contracted to fish on the Grand Banks in the North Atlantic Ocean, 2002–2003. Two types of hooks were alternated along the mainline, using only one type of bait per set. For the purposes of the present study, we only are using data from two treatment circle hooks and from the control J-hooks because sampling effort for other treatment hooks tested in 2003 was low (Foster et al. 2012). The control hooks used were Mustad 9/0 #7698 RD, Mustad 9/0 #76801, Eagle Claw 9/0 #9016 and #9015, and Lindgren-Pittman SW 9/0; the Lindgren-Pittman J-hook, the model most frequently used by the fleet, had 10° offset and a minimum hook width of 4.2 cm; the remaining control hooks had offsets of 20°–30° and a minimum hook width of 3.9 cm. Hook offset is the angle of the barb's deviation from the shaft (Swimmer et al. 2010). The vessels had the freedom to choose their control hooks (J-20). The treatment hooks were Lindgren-Pittman 18/0 forged stainless steel circle hooks, one with 0° offset (C-0) and one with 10° offset (C-10). The minimum hook width for the 18/0 circle hooks was about 5.0 cm. Bait was squid (*Illex* spp.), the control, and mackerel (*Scomber scombrus* Linnaeus, 1758), the treatment. The non-offset circle hook (C-0) was not baited with mackerel due to the difficulty of baiting whole fish on non-offset hooks. Vessels alternated among the experimental set configurations. In 2002, there were three set configurations, each involving the control J-hook (J-20 and C-0 and squid; J-20 and C-10 and squid; J-20 and C-10 and mackerel). In 2003, there were four set configurations, but only one directly compared two of the hooks used in our analysis (J-20 and C-0 and squid). For each of the remaining three configurations, only one hook was of interest: two configurations involved C-10 baited with mackerel, and one involved C-0 baited with squid. To minimize gear-induced variability, fishing gear was standardized both among vessels [odd number of hooks between floats (3 or 5), gangions longer than float lines, green lightsticks on every hook, leaded swivels on all gangions, consistent bait size, restrictions on time gear was deployed] and within a vessel's trip (hook spacing between floats, leader length and size, and mainline, buoy line and leader colors, and placement of lightsticks and leaded swivels). Within these constraints, captains chose the fishing locations, trip lengths, total number of hooks fished on a set, etc.

All vessels carried observers who identified every animal captured, condition when brought alongside the boat (alive vs dead; animals coded as "damaged," either from natural predation or anthropogenic cause, were censored from the analysis), the hook (J-20, C-0, and C-10 for the purpose of this analysis), and the nature of the interaction [entangled, externally-hooked (foul-hooked), mouth-hooked, deeply ingested (gut-hooked)]. Infrequently, the hook could not be determined because some animals were captured with more than one hook or because some animals only were entangled in the mainline; these data were excluded from the analysis. Boated animals were measured to the nearest cm [curved fork length (lower jaw) for swordfish and billfish, straight fork length for sharks (snout tip), tunas and other finfish (upper jaw), disk width for skates and rays, curved standard carapace lengths for sea turtles]. The lengths for animals not boated were estimated to the nearest 30 cm (approximately 1 ft). The observer also recorded the bait used for each set. Sea surface temperature (taken and analyzed as °F but later converted to °C for presentation here) and time were recorded for each end of a mainline section during setting of the gear and haulback; temperature was displayed on the vessel's equipment and the sensor was located on the hull, about a meter below the waterline. Soak time (min) and temperatures were estimated for each section of the mainline by averaging the soak times and temperatures for the beginning and end of each section.

Statistical Analyses

The log odds of a captured fish or sea turtle being gut-hooked (vs not gut-hooked) was modeled using a logistic regression model (Hosmer and Lemeshow 2000, Agresti 2007) with terms of hook, bait type, temperature, soak time, and animal length. Because mackerel bait never was used with the non-offset 18/0 circle hook (C-0), the hook by bait type interaction term was not included in the model. Temperature, soak time, and animal length were modeled as continuous covariates, with interpretations constrained to the range observed (Appendix 1). The odds ratio due to an increase of k units of the continuous variables can be computed as $(\text{odds ratio})^k$. Pairwise comparisons were made, keeping all other effects constant. For those species for which gut-hooking counts were very low for an adequate fit of the model, a different hooking location of interest with reasonable counts was modeled. Descriptive statistics are presented for species for which an adequate model could not be fit.

Anatomical hooking location was reported for almost all animals captured during these experiments, but that is not standard protocol for many observer programs, including that of the US Atlantic pelagic longline fleet (Keene et al. 2010). In the case of the US Atlantic program, hooking location usually is recorded only for the protected sea turtle species as a requirement of the Biological Opinion on the fishery (National Marine Fisheries Service 2004). Hence, in addition to analyzing the condition data taking into account anatomical hooking location, we also conducted the analysis without hooking location information so that commercial fishery observer data could be more easily compared to the experimental data (see Serafy et al. 2012b).

For each species, a logistic regression model was used to model the log odds of boarding a dead animal with the explanatory variables hook, hooking location, bait type, temperature, soak time, animal length, and hook by hooking location interaction. If the observed counts for a particular hooking location were very low and caused inadequate model fit, then that location was dropped to improve the model fit. If the hook by hooking location interaction was significant, then hooks were compared within hooking locations for significance (and vice versa) using appropriately constructed contrasts. The inference on main effects is not meaningful in the presence of interaction. If the interaction term was not significant, then it was dropped from the model and the model was refitted for inference on main effects. Pairwise comparisons were made keeping all other effects constant.

Models as described above also were fitted for each fish species without the terms of hooking location and hook by hooking location interaction.

Table 1. The most frequent taxa observed (captured on 18/0 circle hooks or 9/0 J-hooks or entangled on a gangion) during the 2002–2003 pelagic longline experiments on the Grand Banks.

Species and authority	Common name	Frequency	Percent
Prionace glauca (Linnaeus, 1758)	blue shark	22,000	50.0
Xiphias gladius Linnaeus, 1758	swordfish	16,372	37.2
Thunnus obesus (Lowe, 1839)	bigeye tuna	1,754	3.9
Lamna nasus (Bonnaterre, 1788)	porbeagle	898	2.0
Isurus oxyrinchus Rafinesque, 1810	shortfin mako	550	1.3
Thunnus alalunga (Bonnaterre, 1788)	albacore	547	1.2
Coryphaena spp.	dolphinfishes	285	0.6
Alepisaurus spp.	lancetfishes	277	0.6
Rajiformes	rays, skates	267	0.6
Thunnus thynnus (Linnaeus, 1758)	bluefin tuna	246	0.6
Dermochelys coriacea (Vandelli, 1761)	leatherback sea turtle	202	0.5
Caretta caretta (Linnaeus, 1758)	loggerhead sea turtle	167	0.4

RESULTS

During the 2002–2003 pelagic longline experiments on the Grand Banks, 67 trips were made by 13 vessels, accounting for 813,157 hooks of interest deployed in 999 sets. Fifty-one taxa comprising 43,963 individuals were reported captured on the hooks of interest. Twelve taxa accounted for 99% of all animals captured, with blue shark (*Prionace glauca*) and swordfish representing the majority of individuals (Table 1). Due to sample size constraints, we restricted the analyses to taxa representing at least 1% of the catch. In addition, we analyzed data for bluefin tuna (*Thunnus thynnus*) because it was being considered for listing as a protected species (US Department of Commerce 2011) and the two sea turtle species because they were protected species under the US Endangered Species Act. Thus, we report the results for a total of nine taxa.

ANATOMICAL HOOKING LOCATION

Most fishes were hooked in the mouth, some species more so than others (Fig. 1). A greater proportion of each of the fish species was gut-hooked on the J-hooks, when compared to circle hooks. In the case of the tuna species, the vast majority was mouth-hooked, regardless of hook. In contrast, most loggerhead sea turtles were gut-hooked on J-hooks and leatherback sea turtles mostly were hooked externally (foul-hooked) with all hooks.

Hook was very important in predicting the probability that fish and loggerhead sea turtles were gut-hooked (vs not gut-hooked; i.e., all other locations combined) and also for predicting the probability of leatherback sea turtles being foul-hooked (Table 2). The details of the odds ratios for pairwise comparisons can be found in Table S1 in Online Supplemental Material. For all models with significant hook effects, keeping all other effects constant, the odds of gut-hooking on a J-hook always were significantly greater than the odds of gut-hooking on either of the 18/0 circle hooks. The odds of gut-hooking when comparing circle hooks with no offset to circle hooks with 10° offset were not significant except for swordfish. The hook effect was greatest for loggerhead sea turtles: the odds of being gut-hooked with a J-hook were 22.62 times the odds of being gut-hooked with a non-offset circle hook.

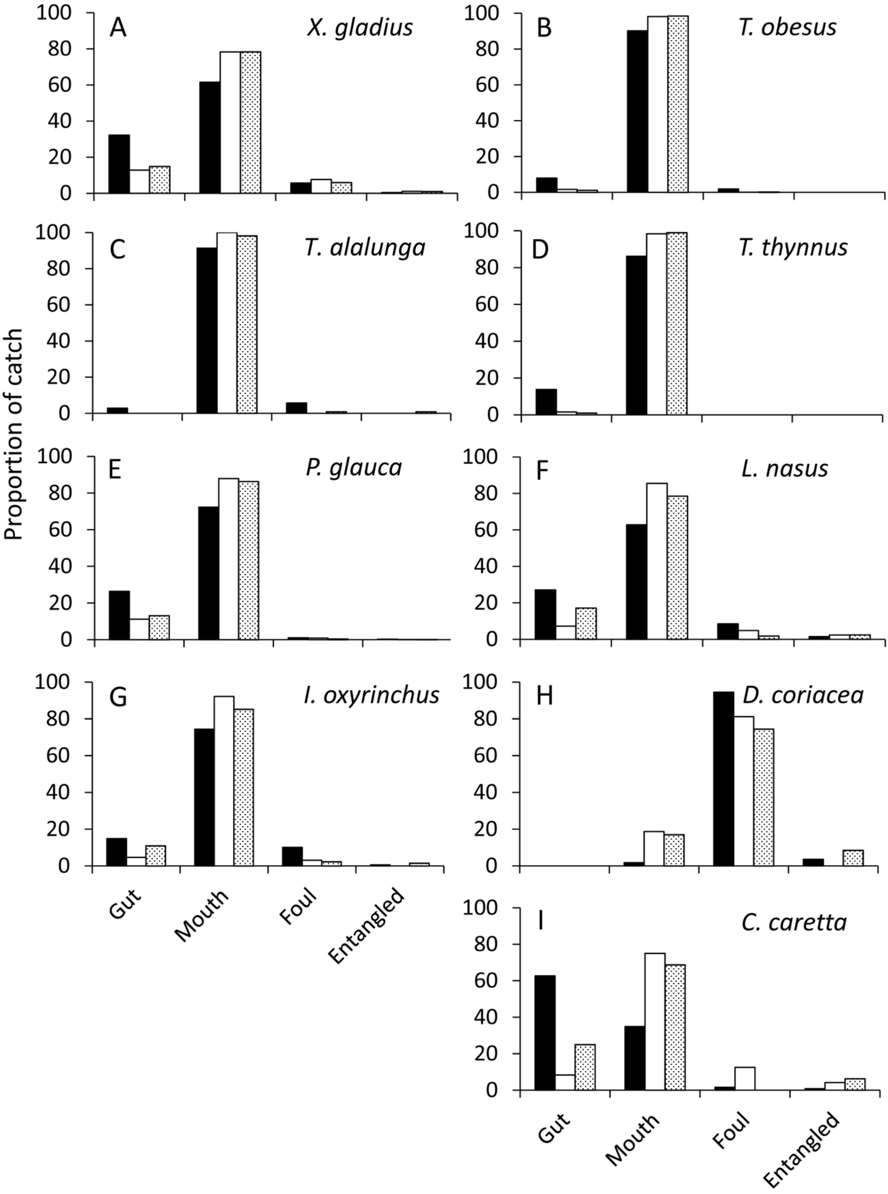

Figure 1. Hooking locations for (A) swordfish, (B,C,D) tunas, (E,F,G) sharks, and (H,I) sea turtles. The proportion of catch among hooking locations for a given species is shown for each hook style and offset. Dark shading is the 9/0 J-hook with 10°–30° offset, no shading is the 18/0 circle hook with no offset, and medium shading is the 18/0 circle hook with 10° offset.

Table 2. Summary of species-specific models for predicting the probability of an animal being gut-hooked (vs all other locations combined). For leatherback sea turtles (*Dermochelys coriacea*) only, the model predicts the probability of an animal being hooked externally (foul-hooked); "ns" indicates non-significant ($P \geq 0.05$) Wald chi-square values. The models for *Thunnus alalunga* and *Isurus oxyrinchus* were not significant and are not shown.

	Model terms				
Species	Hook	Bait	Mean section temperature	Mean section soak time	Animal length
Xiphias gladius	< 0.0001	< 0.0001	0.0025	ns	ns
Thunnus obesus	< 0.0001	ns	ns	ns	< 0.0001
Thunnus thynnus	0.0136	ns	ns	ns	ns
Prionacae glauca	< 0.0001	< 0.0001	ns	ns	< 0.0001
Lamna nasus	< 0.0001	0.0266	ns	ns	ns
Dermochelys coriacea	0.0084	ns	ns	ns	ns
Caretta caretta	< 0.0001	ns	0.0148	ns	0.0089

Mean section soak time was not a significant model effect for any species, but bait, mean section temperature, and animal length sometimes were important effects (Table 2). Baiting with squid rather than mackerel increased the odds of gut-hooking swordfish, but decreased the odds of gut-hooking blue sharks and porbeagles. The odds of gut-hooking decreased with increasing temperature for swordfish and loggerhead sea turtles. The odds of gut-hooking increased with increasing animal size for bigeye tuna, blue sharks, and loggerhead sea turtles.

The models for albacore and shortfin mako were not significant for predicting gut-hooking. We also fit models for mouth-hooking (vs all other locations) for these two species: the model was significant only for shortfin mako, with hook being the only significant effect ($P = 0.0029$). The odds of mouth-hooking on the J-hook were significantly less ($P = 0.0028$) when compared to the 10° offset circle hook (odds ratio 0.428, CI: 0.246–0.746); the odds of mouth-hooking on the J-hook were not significant ($P = 0.0593$) when compared to the non-offset circle hook (odds ratio = 0.364, CI: 0.128–1.040).

Condition

Swordfish experienced the highest mortality; the majority were dead when brought alongside the vessel (Table 3). In contrast, all sea turtles of both species were released alive. Hence, sea turtles were excluded from the analysis of effects on observed boatside mortality.

Animal Condition Taking into Account Anatomical Hooking Location.— Anatomical hooking location, and to a lesser extent hook, were important variables in predicting whether a fish was likely to be boated dead (Table 4). Soak time was a significant variable for all species and temperature was significant for all species except the shortfin mako. Bait was important only for swordfish. Animal length was important for bigeye tuna and blue shark. The details of the odds ratios for pairwise comparisons can be found in Table S2 in Online Supplemental Material.

In the case of swordfish and blue shark, the interaction term of the hook by hooking location was significant (Table 5). Hence, one must consider anatomical hooking location when comparing hooks for these two species, and vice versa. Keeping all other effects constant, the odds of boating a dead animal on a J-hook were 22% greater for swordfish and 16% greater for blue shark than the odds of boating a dead fish

Table 3. Percent of animals that were alive when brought alongside the vessel, by hook style and offset, excluding animals reported as damaged, animals for which hook type could not be determined, and animals that were entangled in the mainline only.

Species (*n*)	9/0 J-hook, 10°–30° offset	18/0 circle hook, no offset	18/0 circle hook, 10° offset
Xiphias gladius (16,191)	28.1	33.4	35.9
Thunnus obesus (1,719)	71.4	78.7	73.0
Thunnus alalunga (538)	38.1	35.6	33.9
Thunnus thynnus (243)	46.2	58.5	60.2
Prionace glauca (21,684)	77.4	80.1	81.2
Lamna nasus (866)	70.0	68.4	70.5
Isurus oxyrinchus (543)	73.5	78.7	76.3
Dermochelys coriacea (177)	100.0	100.0	100.0
Caretta caretta (166)	100.0	100.0	100.0

on an offset circle hook when the animal was hooked in the mouth. The odds of boating a dead swordfish captured on a J-hook and hooked in the mouth or foul-hooked also were greater (1.16 times and 2.25 times, respectively) than the odds of boating an animal dead on a non-offset circle hook. For all three hooks, the odds of boating either species dead was 2.70–4.54 times greater if the animal was hooked in the gut compared to mouth-hooked. Also, for swordfish, the odds of boating a dead animal when gut-hooked were 1.96–4.48 times greater than if it was foul-hooked. For both species, the odds of boating a dead fish increased with increasing water temperature and soak time (Table 5).

Sometimes the results for swordfish and blue sharks differed. For example when comparing the two circle hooks, the odds of boating a dead foul-hooked swordfish on an offset circle hook were 2.14 times greater. However, the reverse was true for blue sharks, where the odds of boating a dead foul-hooked shark on the non-offset circle hook were 3.84 times greater. The odds of boating a blue shark decreased as animal length increased (odds ratio = 0.993, CI: 0.992–0.995); for swordfish, length was not significant ($P = 0.0979$) and the direction of the trend (odds ratio = 1.001, CI: 1.000–1.002) was opposite that for blue shark.

The models for albacore and for bluefin tuna were not significant and the interaction term of hook by hooking location was not significant in the models for bigeye

Table 4. Summary of species-specific models, including hooking location as an effect, when animals were dead at boarding. Probabilities are for the Wald chi-square for each model term; "ns" indicates not significant ($P \geq 0.05$). The models for albacore and bluefin tuna were not significant and are not shown. Significant interaction terms preclude evaluation of main effects because these could not be evaluated separately.

	Model terms						
Species	Hook	Hooking location	Interaction of hook type by location	Bait	Mean section temperature	Mean section soak time	Animal length
Xiphias gladius			< 0.0001	< 0.0001	< 0.0001	< 0.0001	ns (0.0979)
Thunnus obesus	0.0287	< 0.0001	ns	ns	0.0304	< 0.0001	0.0188
Prionacae glauca			0.0242	ns	< 0.0001	< 0.0001	< 0.0001
Lamna nasus	ns	< 0.0001	ns	ns	0.0049	< 0.0001	ns
Isurus oxyrinchus	ns	< 0.0001	ns	ns	ns	0.0050	ns

Table 5. Summary of species-specific models, excluding hooking location as an effect, when animals were dead at boarding. Probabilities are for the Wald chi-square for each model term; "ns" indicates not significant ($P \geq 0.05$). The models for albacore and bluefin tuna were not significant and are not shown. Note that animal length is only marginally non-significant for swordfish.

	Model terms				
Species	Hook	Bait	Mean section temperature	Mean section soak time	Animal length
Xiphias gladius	< 0.0001	< 0.0001	< 0.0001	< 0.0001	ns (0.0554)
Thunnus obesus	0.0053	ns	0.0403	< 0.0001	0.0033
Prionacae glauca	< 0.0001	ns	< 0.0001	< 0.0001	< 0.0001
Lamna nasus	ns	ns	0.0130	< 0.0001	ns
Isurus oxyrinchus	ns	0.0489	ns	0.0028	ns

tuna, porbeagle, and shortfin mako (Table 5). Due to the very small number of shortfin mako ($n = 5$) that were entangled, those observations were omitted from the analysis; no bluefin tuna were entangled. The odds of boating a dead bigeye tuna on the offset circle hook were greater than the odds of boating a dead bigeye tuna on either the J-hook (15%) or non-offset circle hook (52%); the mortality odds were 32% greater for the J-hook than the non-offset circle hook. For bigeye tuna, porbeagle, and shortfin mako, gut-hooking was 2.37–5.18 times more lethal than mouth-hooking and mortality increased with soak time. For shortfin mako, foul-hooking was 4.58 times more lethal than mouth-hooking. For bigeye tuna, the odds of boating a dead fish increased with increasing temperature, but decreased with increasing temperature for the porbeagle. Animal length was significant only for bigeye tuna, with mortality increasing with length.

Animal Condition Not Accounting for Anatomical Hooking Location.—Soak time was a significant explanatory variable for predicting the odds of an animal being boated dead for all species (Table 5). The effect was similar among species; odds ratios were 1.001–1.002 per minute increase and multiplicative. Temperature was significant for all species except the shortfin mako. For swordfish, bigeye tuna, and blue shark, keeping all other effects constant, the odds of boating a dead animal increased with increasing temperature (odds ratios = 1.026–1.050 for the first 0.6 °C), but the odds decreased with increasing temperature for porbeagle (odds ratio = 0.928 for the first 0.6 °C). The details of the odds ratios for pairwise comparisons can be found in Table S3 in Online Supplemental Material.

Hook was significant for predicting mortalities for swordfish, bigeye tuna, and blue shark (Table 5). For all three species, keeping all other effects constant, the odds of boating a dead fish were 22%–48% greater if caught on a J-hook than if caught on a non-offset circle hook, and were also significantly greater for swordfish (29%) and blue shark (28%) when compared to the offset circle hook. For swordfish and bigeye tuna, the odds of mortality were 14%–50% greater if caught on an offset circle hook compared to a non-offset circle hook.

Animal length was a significant explanatory variable for bigeye tuna and blue shark, but not for swordfish ($P = 0.0554$; Table 5). As size increased, the odds of boating a dead swordfish or bigeye tuna increased (odds ratio = 1.001–1.010 cm^{-1}), but the odds of boating a dead blue shark decreased (odds ratio = 0.994 cm^{-1}). Bait was significant only for swordfish, with the odds of boating a dead swordfish 32% greater on squid than on mackerel.

Discussion

Hook and often circle hook offset significantly affected the location in which an animal was hooked for all species analyzed, except for albacore and shortfin mako for which the multiple regression models were not significant. A greater proportion of animals captured on the 9/0 J-hook compared to the circle hooks had deeply ingested the hook, which is usually the most lethal location (Ryder et al. 2006, Lyle et al. 2007, Grixti et al. 2008). With the exceptions of albacore and bluefin tuna, for which the regression models were not significant, anatomical hooking location, sometimes in interaction with hook, was important in predicting the probability of an animal being boated dead, and these results are consistent with the findings of other studies (e.g., Alós et al. 2008, 2009). Interestingly, while mean section soak time and temperature seldom were significant effects in the models predicting hooking location, they were significant in predicting boatside mortality, with only one exception (temperature was not significant for shortfin mako mortality).

It is not clear whether the greater gut-hooking rate of the J-hook, and consequently the higher observed boatside mortality associated with that hook, is due to the style (J- vs circle) or size of the hook, or differences in hook offset, or all. Circle hooks are thought to increase the probability of mouth-hooking. Animals attack a baited hook in different ways, from gulping it to tearing at the bait. It is believed that initially a circle hook with little or no offset does not engage (e.g., the point does not penetrate tissue), even if swallowed. As the animal pulls away from the gangion and turns, it is believed that the circle hook is pulled outward and rotates, catching in the corner of the jaw. Many studies have reported circle hooks to have a lower gut-hooking rate than J-hooks, and consequently a higher survival rate, whether observed at boatside or post-release (see reviews in Cooke and Suski 2004 and in Gilman et al. 2006; Beckwith and Rand 2005, Kerstetter and Graves 2006, Sales et al. 2010). In the Grand Banks experiments, we found the probability of boating a dead bigeye tuna or, for some hooking locations, a dead swordfish or blue shark, increased if the animal was captured on a J-hook. While some studies, including ours (e.g., *Lamna nasus* and *Isurus oxyrinchus;* Tables 4, 5), have not found significant differences in gut-hooking or survival rates between hook styles for selected species (see Cook and Suski 2004 for review; Mapleston et al. 2008, Ward et al. 2009, Curran and Bigelow 2011), studies reporting an increase in gut-hooking or a greater lethality with circle hooks are rare (Cooke et al. 2003, Curran and Bigelow 2011).

Hook size is an important factor, as hook selectivity for species and individual size is well documented (Anonymous 1963). Hook size also may affect anatomical hooking location; larger hooks may be less likely to be swallowed but more likely to foul-hook. In controlled laboratory experiments using captive-reared loggerhead sea turtles, the frequency of attempts to swallow hooks decreased as the width (35.7–62.1 mm) of a modified hook increased (Stokes et al. 2011). The loggerheads captured in our experiments, however, were of a size (mean 61 cm CCL, see Appendix 1) capable of swallowing the control and treatment hooks of the Grand Banks experiments equally well (Stokes et al. 2011). Hook style and size is confounded in the Grand Banks experiments because the minimum width of experimental circle hooks was approximately 1 cm wider than the width of the control J-hooks. A greater proportion of J-hooks, which were smaller, were swallowed, which is what we would expect based on hook size alone.

Hook offset is believed to increase the probability that the hook's point will penetrate tissue immediately after the bait is taken, but there is debate about what constitutes minor (thus insignificant effect) vs major offset (thus significant effect). For many comparisons in the Grand Banks experiments, there were no differences between the two circle hooks (0° and 10° offsets). However, when there was a significant difference, the odds of gut-hooking and the odds of boating a dead fish both were greater for the offset circle hook, with foul-hooked blue shark the only exception. We found significant differences between the non-offset and 10º offset circle hooks for swordfish anatomical hooking location and, for foul-hooked and entangled swordfish, significant differences in mortality. There also were significant differences in survival between the two circle hooks for bigeye tuna, with higher mortality realized for the offset hooks. Some circle hooks with offsets may have similar effects as J-hooks. Prince et al. (2002) reported that billfish captured on circle hooks with offsets <4° had lower incidence of bleeding than billfish captured on circle hooks with 15° offset, defined by the authors as a severe offset. Bleeding on the severely offset hook was comparable to the incidence of bleeding observed with J-hooks. Swimmer et al. (2010) compared circle hooks with no offset and 10° offset, and found no significant difference in hooking locations between the two hooks for cheloniid sea turtles. Interestingly, Carruthers et al. (2009) compared hooking locations among animals captured on non-offset J-hooks (36–41 mm hook width), 20°–30° offset J-hooks (36–41 mm hook width), and a non-offset circle hook (50 mm hook width) and found no significant difference among hooks for anatomical hooking locations for loggerhead sea turtles, but found a significant difference for sharks. In contrast, we found significant differences between the J-hooks (with 10°–30° offsets) and circle hooks (with 0° and 10° offsets) in both anatomical hooking location and survival for many species.

For some species encountered in the Grand Banks experiments, bait also affected anatomical hooking location and survival: we report that the odds of gut-hooking and the odds of mortality for swordfish were higher with squid bait. In contrast, the odds of gut-hooking in the blue shark and shortfin mako were higher with mackerel bait. In controlled lab experiments with loggerhead sea turtles, bait was a significant effect in sea turtles' attempts to swallow the hook (Stokes et al. 2011). The authors found that the odds of swallowing the hook were higher when the hook was baited with squid than when baited with a Spanish sardine (*Sardinella aurita* Valenciennes, 1847). They also found a significant effect of baiting technique: the odds of swallowing the hook were higher when bait was threaded on the hook than when the hook was single-baited. We found no bait effect on hooking location for loggerheads in the Grand Banks experiments, a result consistent with an analysis of data for the entire US Atlantic fleet (Stokes et al. 2012). However, we note that baiting techniques were not controlled in the Grand Banks experiments nor were they recorded in the commercial fishery database, and thus the methods were mixed, further confounding the results of both studies.

Continuous variables often were also important for predicting the boatside mortality observed in the Grand Banks experiments. For all fish species with significant models, longer soak time increased the odds of boating a dead fish. The odds ratios for all species were similar: 0.1%–0.2% for the first minute increase in soak time (6%–12% for a 60 min increase in soak time). For most species, water temperature contributed to the prediction of mortality, but the direction of the response was not consistent. For porbeagle, mortality decreased with temperature (odds ratio for the first 0.6 °C increase is 0.911), whereas for swordfish, blue shark, and bigeye tuna, mortality increased with increasing temperature (odds ratio for the first 0.6 °C increase ranged from 1.031 to 1.054). Infrequently, animal length was a significant factor, and, like temperature, the response varied in direction among species. Mortality was significantly lower for larger blue sharks (odds ratio = 0.993 for the first centimeter increase), but was significantly higher for larger bigeye tuna (odds ratio = 1.008 for the first centimeter increase). In an analysis of Canadian pelagic longline bycatch data from an area in proximity to our study, Carruthers et al. (2009) found that longer soak times increased the likelihood of bycatch mortality and that length was a significant predictor of mortality for discarded swordfish, but length did not significantly affect the odds of survival for discarded blue shark. Temperature was not included in their models.

The mortality information presented in the present study represents only the immediate boatside mortality. Additional mortality is expected after live animals are released, and that mortality likely will be influenced by several factors including species, animal size and condition, water temperature, anatomical hooking location, and handling. Understanding post-release mortality is the focus of many studies (e.g., Horodysky and Graves 2005, Millard et al. 2005, Lyle et al. 2007, Sasso and Epperly 2007, Grixti et al. 2008) as it has important implications for stock assessments. Animals discarded dead and animals that are released alive but later die due to the gear interaction must be accounted for in population assessments, separate from animals marketed.

While the Grand Banks experiments attracted interest worldwide due to the demonstrated potential to reduce bycatch, especially for sea turtles, without impacting the catch of primary target species, concern was raised about the applicability of the results to other areas, and the major regional fisheries management organizations encouraged further research (ICCAT 2005, IOTC 2005, IATTC 2007). Subsequently, many experiments have been conducted across the oceans, testing a variety of hook styles, hook sizes, hook offsets, and baits, with varied results that are not easily compared (e.g., Yokota et al. 2006, Piovano et al. 2009, Ward et al. 2009, Sales et al. 2010, Swimmer et al. 2010, Curran and Bigelow 2011), thus reinforcing the need to evaluate the effects individually among separate regions, for target and bycatch species. The mixed results also point to the need for researchers to be explicit when designing experiments and reporting results, specifically identifying hook dimensions, hook offset, species and size of bait tested, and baiting method, and to examine each of these factors in their analysis, rather than pooling data. Furthermore, the importance of anatomical hooking location in predicting boatside mortalilty, and likely effect on post-release mortality (Horodysky and Graves 2005, Ryder et al. 2006) suggests that observer programs should be encouraged to include hooking location information among the data collected for scientific analysis.

The Grand Banks experiments demonstrated that changes in terminal gear and/or bait, perhaps in conjunction with soak time, water temperature, and animal size, not only affect catchability (Foster et al. 2012), but also boatside condition (present study) for a number of species. The 2004 regulations requiring circle hooks and whole bait in the US Atlantic fishery and the Hawaii-based shallow-set fishery changed both these factors for the US fisheries in ways that have potential to alter stock assessment results. Consequently, these changes need to be considered in future assessments to reduce bias and uncertainty in the management quantities estimated (see Cass-Calay et al. 2012).

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Literature Cited

Agresti A. 2007. An introduction to categorical data analysis. Wiley, New York. http://dx.doi.org/10.1002/0470114754

Alós J, Cerdà M, Deudero S, Grau AM. 2008. Influence of hook size and type on short-term mortality, hooking location and size selectivity in a Spanish recreational fishery. J Appl Ichthyol. 24:658–663.

Alós J, Palmer M, Grau AM. 2009. Mortality of *Diplodus annularis* and *Lithognathus mormyrus* released by recreational anglers: implications for recreational fisheries management. Fish Manage Ecol. 16:298–305. http://dx.doi.org/10.1111/j.1365-2400.2009.00675.x

Alverson DL, Freeberg MH, Murawski SA, Pope JG. 1994. A global assessment of fisheries and discards. FAO Fish Tech Pap 339. Available at: http://www.fao.org/DOCREP/003/T4890E/T4890E00.HTM

Anonymous. 1963. The selectivity of fishing gear. Intern Comm Northw Atl Fish Spec Publl. 5:1–225.

Beckwith GH, Rand PS. 2005. Large circle hooks and short leaders with fixed weights reduce the incidence of deep hooking in angled adult red drum. Fish Res. 71:115–120. http://dx.doi.org/10.1016/j.fishres.2004.08.023

Carruthers EH, Schneider DC, Neilson JD. 2009. Estimating the odds of survival and identifying mitigation opportunities for common bycatch in pelagic longline fisheries. Biol Conserv. 142:2620–2630. http://dx.doi.org/10.1016/j.biocon.2009.06.010

Cass-Calay SL, Walter JF, Schirripa MJ. 2012. Using a stock assessment framework to examine circle hooks: exploring changes in catchability and implications for management. Bull Mar Sci. 88:745–754. http://dx.doi.org/10.5343/bms.2011.1070

Cooke SJ, Suski CD. 2004. Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? Aquat Conserv: Mar Freshwat Ecosyst. 14:299–326. http://dx.doi.org/10.1002/aqc.614

Cooke SJ, Suski CD, Barthel BL, Ostrand KG, Tufts BL, Philipp DP. 2003. Injury and mortality induced by four hook types on bluegill and pumpkinseed. N Amer J Fish Manage. 23:883–893. http://dx.doi.org/10.1577/M02-096

Curran D, Bigelow K. 2011. Effects of circle hooks on pelagic catches in the Hawaii-based tuna longline fishery. Fish Res. 109:265–275. http://dx.doi.org/10.1016/j.fishres.2011.02.013

Foster DG, Epperly SP, Shah A, Watson J. 2012. Evaluation of hook and bait type on the catch rates of target and bycatch species in the Western North Atlantic Ocean pelagic longline fishery. Bull Mar Sci. 88:529–545. http://dx.doi.org/10.5343/bms.2011.1081

Gilman E, Beverly S, Nakano H, Davis K, Shiode D, Dalzell P, Kinan I. 2006. Reducing sea turtle by-catch in pelagic longline fisheries. Fish Fish. 7:2–23. http://dx.doi.org/10.1111/j.1467-2979.2006.00196.x

Grixti D, Conron SD, Morison A, Jones PL. 2008. Estimating post-release survival and the influential factors for recreationally caught black bream (*Acanthopagrus butcheri*) in the Glenelg River, southeastern Australia. Fish Res. 92:303–313. http://dx.doi.org/10.1016/j.fishres.2008.01.014

Horodysky AJ, Graves JE. 2005. Application of pop-up satellite archival tag technology to estimate post-release survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank ("J") hooks in the western North Atlantic recreational fishery. Fish Bull. 103:84–96.

Hosmer DW, Lemeshow S. 2000. Applied logistic regression. Wiley, New York. http://dx.doi.org/10.1002/0471722146

IOTC (Indian Ocean Tuna Commission). 2005. Recommendation 05/08. Available at: http://www.iotc.org/files/CMM/Recommendation%2005-08.pdf

ICCAT (International Commission for the Conservation of Atlantic Tunas). 2005. Resolution 05-08. Available at: http://www.ofdc.org.tw/fishserv/File/Rule/ICCAT_Resolutions_E/05-08.pdf

IATTC (Inter-American Tropical Tuna Commission). 2007. Resolution C03-10. Available at: http://www.iattc.org/PDFFiles2/Resolutions/C-07-03-Sea-turtles.pdf

Keene KF, Beerkircher LR, Lee DW. 2010. SEFSC pelagic observer program data summary for 2005 and 2006. NOAA Tech Mem. NMFS-SEFSC. 603:1–23.

Kerstetter DW, Graves JE. 2006. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish Res. 80:239–250. http://dx.doi.org/10.1016/j.fishres.2006.03.032

Lewison RL, Soykan CU, Cox T, Peckham H, Pilcher N, LeBoeuf N, McDonald S, Moore J, Safina C, Crowder LB. 2011. Ingredients for addressing the challenges of fisheries bycatch. Bull Mar Sci. 87:235–250. http://dx.doi.org/10.5343/bms.2010.1062

Lyle JM, Moltschaniwskj NA, Morton AJ, Brown IW, Mayer D. 2007. Effects of hooking damage and hook type on post-release survival of sand flathead (*Platycephalus bassensis*). Mar Freshwat Res. 58:445–453. http://dx.doi.org/10.1071/MF06233

Mapleston A, Welch D, Begg GA, McLennan M, Mayer D, Brown I. 2008. Effect of changes in hook pattern and size on catch rate, hooking location, injury and bleeding for a number of tropical reef fish species. Fish Res. 91:203–211. http://dx.doi.org/10.1016/j.fishres.2007.11.026

Millard MJ, Mohler JW, Kahnle A, Cosman A. 2005. Mortality associated with catch-and-release angling of striped bass in the Hudson River. N Am J Fish Manage. 25:1533–1541. http://dx.doi.org/10.1577/M04-175.1

National Marine Fisheries Service. 2004. Endangered Species Act – Section 7 Consultation Biological Opinion. Reinitiation of consultation on the Atlantic pelagic longline fishery for highly migratory species. NMFS Southeast Regional Office, St. Petersburg, FL. Available at: http://www.nmfs.noaa.gov/sfa/hms/Protected%20Resources/June_1_2004_Biological_Opinion.pdf

Pauly D, Watson R, Alter J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Phil Trans R Soc B. 360:5–12. PMid:15713585. PMCid:1636108. http://dx.doi.org/10.1098/rstb.2004.1574

Piovano S, Swimmer Y, Giacoma C. 2009. Are circle hooks effective in reducing incidental captures of loggerhead sea turtles in a Mediterannean longline fishery? Aquat Conserv: Mar Freshwat Ecosyst. 19:779–785. http://dx.doi.org/10.1002/aqc.1021

Prince ED, Ortiz M, Venizelos A. 2002. A comparison of circle hook and "J" hook performance in recreational catch-and-release fisheries for billfish. Am Fis Soc Symp. 30:66–79.

Ryder CE, Conant TA, Schroeder BA. 2006. Report of the workshop on marine turtle longline post-interaction mortality. Bethesda, Maryland, USA, 15–16 January, 2004. US Department of Commerce, NOAA Tech Mem NMFS-OPR-29. 40 p.

Sales G, Giffoni BB, Fiedler FN, Azevedo VG, Kotas JE, Swimmer Y, Bugoni L. 2010. Circle hook effectiveness for the mitigation of sea turtle bycatch and capture of target species in a Brazilian pelagic longline fishery. Aquat Conserv: Mar Freshwat Ecosyst. 20:428–436. http://dx.doi.org/10.1002/aqc.1106

Sasso CR, Epperly SP. 2007. Survival of pelagic juvenile loggerhead turtles in the open ocean. Wildl Manage. 71(6):1830–1835. http://dx.doi.org/10.2193/2006-448

Serafy JE, Cooke SJ, Diaz GA, Graves J, Hall M, Shivji M, Swimmer Y. 2012a. Circle hooks in commercial, recreational, and artisanal fisheries: research status and needs for improved conservation and management. Bull Mar Sci. 88:371–391. http://dx.doi.org/10.5343/bms.2012.1038

Serafy JE, Obesen ES, Snodgrass DJG, Beerkircher LR, Walter JF. 2012b. Hooking survival of fishes captured by the United States Atlantic pelagic longline fishery: impact of the 2004 circle hook rule. Bull Mar Sci. 88:605–621. http://dx.doi.org/10.5343/bms.2011.1080

Stokes LW, Epperly SP, McCarthy K. 2012. Sea turtle incidental bycatch in the United States Atlantic pelagic longline fishery: investigating the role of circle hooks in hooking location. Bull Mar Sci. 88:703–718. http://dx.doi.org/10.5343/bms.2011.1074

Stokes LW, Hataway D, Epperly SP, Shah AK, Bergmann CE, Watson JW, Higgins BM. 2011. Hook ingestion rates in loggerhead sea turtles *Caretta caretta* as a function of animal size, hook size, and bait. Endang Species Res. 14:1–11. http://dx.doi.org/10.3354/esr00339

Swimmer Y, Arauz R, Wang J, Suter J, Musyl M, Bolaños A, Lópes A. 2010. Comparing the effects of offset and non-offset circle hooks on catch rates of fish and sea turtles in a shallow longline fishery. Aquat Conserv: Mar Freshwat Res Ecosyst. 20:445–451. http://dx.doi.org/10.1002/aqc.1108

US Department of Commerce. 2004a. Fisheries off west coast states and in the western Pacific; western Pacific pelagic fisheries; pelagic longline fishing restrictions, seasonal area closure, limit on swordfish fishing effort, gear restrictions, and other sea turtle take mitigation measures. Fed Regist. 69:17,329–17,354.

US Department of Commerce. 2004b. Atlantic highly migratory species (HMS); pelagic longline fishery. Fed Regist. 69:40,734–40,758.

US Department of Commerce. 2011. Listing endangered and threatened wildlife and plants; 90-day finding on a petition to list Atlantic bluefin tuna as threatened or endangered under the Endangered Species Act. Fed Registr. 75:57,431–57,436.

Valdemarsen JJ. 2001. Technological trends in capture fisheries. Ocean Coast Manage. 44:635–651. http://dx.doi.org/10.1016/S0964-5691(01)00073-4

Ward P, Epe S, Kreutz D, Lawrence E, Robins C, Sands A. 2009. The effects of circle hooks on bycatch and target catches in Australia's pelagic longline fishery. Fish Res. 97:253–262. http://dx.doi.org/10.1016/j.fishres.2009.02.009

Watson JW, Epperly SP, Shah AK, Foster DG. 2005. Fishing methods to reduce sea turtle mortality associated with pelagic longlines. Can J Fish Aquat Sci. 62:965–981. http://dx.doi.org/10.1139/f05-004

Yokota K, Kiyota M, Minami H. 2006. Shark catch in a pelagic longline fishery: comparison of circle and tuna hooks. Fish Res. 81:337–341. http://dx.doi.org/10.1016/j.fishres.2006.08.006

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Appendix 1. Descriptive statistics for continuous variables, by species. Fork length (FL) = straight for all fishes except swordfish (curved); carapace length (CLL) curved for both sea turtles.

	Temperature (°C)			Soak time (min)			FL or CCL (cm)		
Species	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Swordfish, *Xiphius gladius*	11	17	24	274	804	2,805	45	162	290
Bigeye tuna, *Thunnus obesus*	11	17	22	312	823	1,612	60	125	199
Albacore, *Thunnus alalunga*	12	18	20	312	850	1,584	60	93	199
Bluefin tuna, *Thunnus thynnus*	12	16	20	304	804	1,468	62	188	282
Blue shark, *Prionacae glauca*	11	17	24	241	794	2,805	34	135	360
Porbeagle, *Lamna nasus*	12	16	22	298	814	1,420	50	89	200
Shortfin mako, *Isurus oxyrinchus*	12	18	24	360	799	1,449	30	133	269
Leatherback sea turtle, *Dermochelys coriacea*	11	18	24	356	790	1,506	100	157	210
Loggerhead sea turtle, *Caretta caretta*	16	18	24	438	894	1,499	35	61	76