Fisheries Research 164 (2015) 231–237

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Hooking locations in sea turtles incidentally captured by artisanal longline fisheries in the Eastern Pacific Ocean

María L. Parga[a], Maite Pons[b], Sandra Andraka[c,*], Liliana Rendón[d], Takahisa Mituhasi[e], Martín Hall[f], Lucas Pacheco[g], Alvaro Segura[h], Michael Osmond[i], Nick Vogel[f]

[a] SUBMON, C/Rabassa 49-51, 08024 Barcelona, Spain
[b] Centro de Investigación y Conservación marina (CICMAR), Giannattasio km. 30.5 El Pinar, Canelones CP 15008, Uruguay
[c] WWF, Latin America and the Caribbean Program, 400 m sur Plaza del Sol, San Francisco de Dos Ríos, PO Box 629-2350, San José, Costa Rica
[d] Escuela de Pesca del Pacífico Oriental/WWF, Calle 34 Av. Flavio Reyes, Manta, Ecuador
[e] Overseas Fishery Cooperation Foundation of Japan, Minato-ku, Tokyo 107-0052, Japan
[f] Inter-American Tropical Tuna Commission (IATTC), 8901 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA
[g] WWF, Panama Office, 235 Building, 1st Floor, Ciudad del Saber, Clayton CP 08160-7168, Panama
[h] WWF, Costa Rica Office, Barrio los Yoses, Avenida 14, Calle 37, San Francisco de Dos Ríos, PO Box 629-2350, San José, Costa Rica
[i] WWF US, 2081 Landings Drive, Mountain View, CA 9404, USA

ARTICLE INFO

Article history:
Received 24 April 2013
Received in revised form 21 October 2014
Accepted 17 November 2014
Handling Editor Dr. P. He

Keywords:
Hook type
Hook size
Bait
Olive ridley
Surface longline

ABSTRACT

Bycatch by longline fisheries, especially by artisanal small-scale fisheries, is one of the main conservation problems for some sea turtle populations around the world. Since 2004, a network of professionals under the “Eastern Pacific Regional Sea Turtle Bycatch Program” have been working with artisanal longline fishers in the Eastern Pacific Ocean (EPO) to reduce sea turtle bycatch and related mortality. Trials assessing circle hooks of different sizes and shapes, and different baits, have been conducted to determine the effectiveness in the reduction of sea turtle bycatch and changes in hooking location. In this paper, information from 1823 olive ridley sea turtles incidentally captured in the EPO were analyzed to assess how hook type (J, tuna hooks or circle hooks), hook size, bait type (squid or fish), turtle size and target species (tunas, sharks or mahi-mahi) affect hooking location on sea turtles. This were modeled with a Classification and Regression Tree using hooking location as a multinomial variable response (for 6 categories of hooking locations); and also as a binomial response (swallowed vs. non-swallowed) using a Generalized Linear Mixed Model (GLMM). Hook type and size, plus bait type, were the most important factors affecting hooking location, while turtle size and target species did not have any significant effect. J-hooks and tuna hooks had a much greater probability of being swallowed than circle hooks. In addition, as the hook size increased, the likelihood of swallowing it decreased. The use of fish bait in combination with larger circle hooks tended to produce higher proportions of external hookings. An increase in external or lower mandible hookings is preferred since these locations are assumed to be less dangerous for the animal’s post-release survival, and because hooks and attached gear are easier to remove by well-trained fishermen.

1. Introduction

Bycatch is one of the most important issues affecting global fisheries management today (Hall et al., 2000; Soykan et al., 2008; Gilman, 2011). This problem becomes particularly sensitive when the non-target species incidentally caught are long-lived animals, have low reproductive rates and are threatened or endangered (Dayton et al., 1995; Lewison et al., 2004). This is the case of sea turtles when they interact with longline fisheries, one of the main causes for the decline of some sea turtle populations in the world (Camiñas et al., 2003; Deflorio et al., 2005; Gilman et al., 2006; Casale et al., 2007; Brazner and McMillan, 2008; Alessandro and Antonello, 2010).

Several studies have been conducted in a number of longline fisheries around the world assessing different measures to reduce the incidental capture of sea turtles (Bolten and Bjorndal, 2003;

---

* Corresponding author. Tel.: +506 83650845.
E-mail address: sandrakag@gmail.com
E-mail addresses: mariluz@submon.org (M.L. Parga), pons.maite@cicmar.org (M. Pons), sandrakag@gmail.com (S. Andraka), lilianarendonm@hotmail.com (L. Rendón), mituhasi@fish.kagoshima-u.ac.jp (T. Mituhasi), mhall@iattc.org (M. Hall), lucasrovira@yahoo.es (L. Pacheco), alvaro.segurah@gmail.com (A. Segura), michael.osmond@wwfus.org (M. Osmond), nvogel@iattc.org (N. Vogel).

http://dx.doi.org/10.1016/j.fishres.2014.11.012
0165-7836/

Shiode et al., 2005; Swimmer et al., 2005, 2010; Gilman et al., 2006; Baez et al., 2007; Wang et al., 2007; Brazner and McMillan, 2008). Of these, changes in bait type, and in the size, type and shape of hook seem to be the most promising (Largacha et al., 2005; Watson et al., 2005; Gilman et al., 2006; Gilman et al., 2007; Read, 2007; Brazner and McMillan, 2008; Sales et al., 2010). In particular, the use of mackerel bait in combination with large (size 18/0) circle hooks has been shown to reduce incidental capture of sea turtles by up to 90% in longline fisheries of the Western Atlantic and Hawaii (Watson et al., 2005; Gilman et al., 2007). However, due to differences in longline fisheries at regional and local levels, mitigation measures cannot always be readily adopted, and research needs to be conducted in each region and fishery before mitigation measures can be implemented in management plans (Gilman, 2011; Andraka et al., 2013). Furthermore, a thorough understanding of the socio-economic and political drivers of the region is essential to ensure the success of any proposed mitigation measure.

In the Eastern Pacific Ocean (EPO), bycatch of marine turtles is a priority conservation issue in many longline, trawl and gillnet fisheries (FAO, 2004; Wallace et al., 2010). In 2004, the "Eastern Pacific Regional Sea Turtle Bycatch Program" (EPRSTBP), was started in Ecuador based on the successful experiments carried out by the National Oceanic and Atmospheric Administration (NOAA) that showed a significant sea turtle bycatch reduction using circle hooks and fish bait (Watson et al., 2005). The main objectives of the EPRSTBP were: (1) to assess the benefits of using circle hooks in artisanal longline fisheries in the EPO; (2) the voluntary adoption by longline fishers of measures to reduce sea turtle bycatch; and (3) the training of fishers in on-board best sea turtle handling and de-hooking techniques (Andraka et al., 2013).

Since 2004, an interdisciplinary team of professionals from regional fishery management organizations, non-governmental organizations, governmental institutions and the fishing industry, has conducted trials in artisanal longline fisheries in nine Eastern Pacific countries from Mexico to Peru. The trials were designed to assess circle hooks of different sizes, shapes and different bait types, with the aim of confirming their efficacy in reducing capture rates, and in changing the hooking location in captured turtles, a factor directly related to post-release mortality. Andraka et al. (2013) analyzed and discussed some of the results obtained in the trials performed in these countries regarding the impact of circle hooks in the capture rate of sea turtles and found that the results for target and non-target species were not consistent for all fisheries analyzed, although circle hooks did reduce sea turtle hooking rates in most of the cases.

In addition to reducing sea turtle bycatch rates, circle hooks have been promoted as an alternative to traditional J-hooks to minimize injury in sea turtles accidentally captured in pelagic longline fisheries (Watson et al., 2005; Piovano et al., 2009). Due to their shape, circle hooks tend to slide along the jaw and they lodge near the commissure of the mouth or externally instead of being swallowed (Epperly et al., 2012), allowing for potentially easier removal, especially by fishers trying to recover their hooks. This, in conjunction with adequate hauling methods (using a net, instead of hauling the animal by pulling the line) and handling and hook removal techniques, could effectively reduce sea turtle post-release mortality (Parga, 2012; Swimmer and Gilman, 2012).

Apart from hook type, there are a number of variables that have been suggested to alter the location of hooks in incidentally captured sea turtles. After studies in a laboratory setting using circle hooks, Stokes et al. (2011) suggested that hook size and bait type were the two variables that most significantly altered hook location in loggerhead sea turtles (*Caretta caretta*). Analyzing these variables plus hook type, in data gathered over ten years by National Marine Fisheries Service Atlantic fishery observers, Stokes et al. (2012) concluded that under normal fishery conditions, hook type seemed to be the only factor significantly affecting hooking location. Moreover, Epperly et al. (2012) had similar results in experiments conducted with pelagic longline fisheries in the North Atlantic Ocean, with J-hooks having a greater probability of being swallowed than circle hooks. However, the authors were unsure if this greater gut-hooking rate could be attributed to the hook type or due to the size, since J-hooks used were smaller than the circle hooks.

In the present study hook type (J-hooks, Japanese-style tuna hooks -from now on "tuna hooks"- and circle hooks), hook size, bait type and turtle size were analyzed as factors affecting hooking location on sea turtles in real fishing conditions, using data gathered from the EPO artisanal longline fisheries in the past 8 years (2004–2011). The variable "target species" was also considered, because the characteristics of longline configuration, areas and seasons change according to the target species of each fishing trip (see Andraka et al., 2013 for further details). The effect that these changes in hooking location may have on turtle mortality will also be discussed based on current knowledge, as well as measures that can be adopted to increase the probability of sea turtle post-release survival.

2. Material and methods

Data were collected between 2004 and 2011 by trained observers of the EPRSTBP during trials conducted on standard commercial fishing trips in the artisanal longline fisheries in the EPO. During this period, a total of 3,529,699 hooks in 8996 sets were observed between 19°S–16°N and 70°W–100°W. The surface longline fisheries of this area include fisheries targeting mahi-mahi, tunas or sharks, and use different types of hooks such as J-hooks, tuna hooks and circle hooks, described by Mituhasi and Hall (2011) and Andraka et al. (2013). During the trial, comparisons between J-hooks or tuna hooks vs. circle hooks (12/0 through 18/0) were performed. J-hooks or tuna hooks and circle hooks were placed in an alternating pattern along the longline. Further details on the experiments and fisheries characteristics, such as vessel size, fishing season, targets, hooks per set, among others, can be found in Andraka et al. (2013).

More than one type of bait was used in some of the longline sets; in many cases it was bait obtained opportunistically, and it was hard to control its use. Because there was no detailed information on bait type for each hook, for the purpose of this work only those sets using one type of bait were included in the analysis. Thus, 4838 sets were considered in the analysis from a total of 8996 observed by the EPRSTBP between 2004 and 2011. The bait types were pooled into two categories for further analysis: squid (mainly *Dosidicus gigas* but also *Illex* sp. and *Loligo* sp. were employed) and fish (mainly *Opisthonema* spp., *Scomber japonicus*, *Auxis* spp. and *Sardinops sagax*).

Observers collected the information using standardized forms, including details on type and size of the hook, bait, curve carapace length (CCL), hooking location and entanglement of sea turtles accidentally captured. The analysis was focused only on olive ridley sea turtles (*Lepidochelys olivacea*), as this species is by far the most frequently captured in the region (71% of all turtles caught; Andraka et al., 2013).

2.1. Statistical analysis

Hooking locations were pooled into categories as follows: 'External': hooks on flippers, tail, carapace and neck; 'Tongue': hooks lodged in the tongue or glottis; and 'Swallowed': deep in the mouth, independently of whether the shank was visible or not. 'Lower jaw', 'Upper jaw' and 'Jaw joint' were not grouped, and each

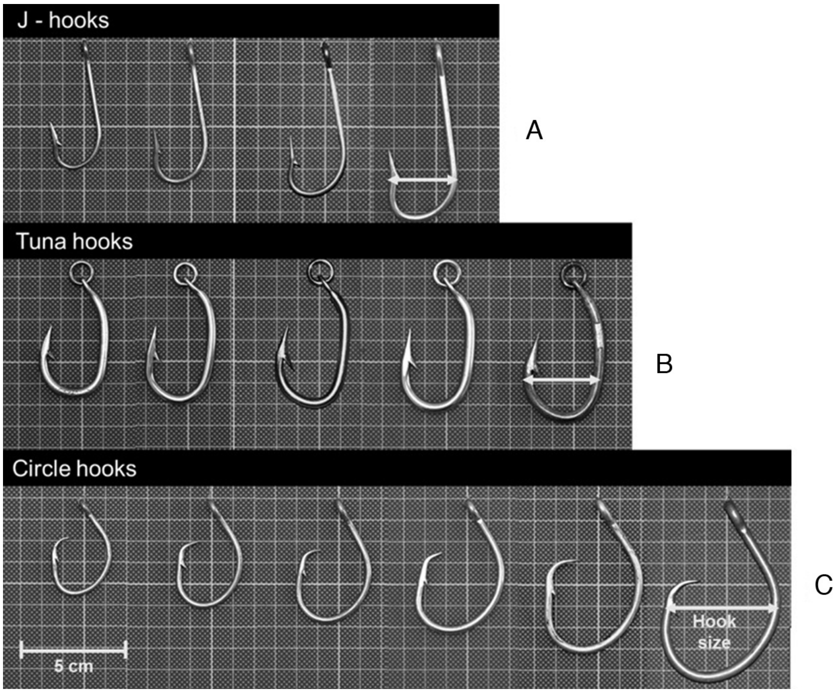

Fig. 1. Main hook types and sizes used in the EPO artisanal longline fisheries. (A) J-hooks; (B) tuna hooks and (C) circle hooks. Circle hooks varied between 12/0 (left) and 18/0 (right). The arrows indicate the total width used for the analysis.

was considered a separate category, as it has been suggested that they present different severity of injury on sea turtles (Ryder et al., 2006; Parga, 2012). Also, entangled turtles were not considered unless hooked.

Different independent variables were used to model hooking location in olive ridley sea turtles: hook type (J-hooks, tuna hooks and circle hooks), bait type (squid or fish), hook size (mm), CCL (cm) and target species (tunas, sharks or mahi-mahi, *Coryphaena hippurus*). Hook types and size range used are illustrated in Fig. 1. These hooks include the most representative hooks employed by the surface longline fleets in the EPO. Hook size was measured as the total width between the shank and the lower end of the hook barb (Fig. 1). These measurements were directly taken from the hook illustrations in the hook catalogue by Mituhasi and Hall (2011) in which the images are produced in the true size (1:1 scale) and hooks are positioned as if hanging in a longline in a commercial fishing trip. Hook size and CCL were modeled as continuous variables and each variable were divided by their mean to adjust both to the same scale.

Most of the hooks used in these fisheries have 0°, 5° or 10° offsets. However, the presence of offset in the hooks was not considered in this study because the information was partial and considerably reduced the number of data available for the analysis. In support of this assumption, Swimmer et al. (2010) found in the Costa Rican surface longline fishery that 14/0 circle hooks with 10° offset did not show difference in hooking location in relation to the same hooks without offset.

The hooking locations (dependent variable) from olive ridley sea turtles were analyzed using two different approximations. First, a multinomial variable response (for each of the 6 categories of hooking locations) was modeled by a Classification and Regression Tree (CART) (Breiman et al., 1984). This method is a binary splitting method, which partitions recursively the data set into disjoint subgroups. Because our response variable was categorical, we performed a classification tree so the category assigned to each leaf or terminal node is the class most probable beyond which no further decisions (or splits) can be made. To construct the optimal tree, two steps were used: the first one involved growing a maximal tree and the second "pruned" it to get the best sub-optimal tree. This sub-optimal tree is one that explains the greater relative error through the simplest model.

This type of models are flexible enough to handle complex problems with multiple interacting elements making them ideal for modeling ecological systems (Olden et al., 2008). The best advantage is their representation in form of a binary tree which makes a complex model easy to interpret.

Finally, a Generalized Linear Mixed Model (GLMM) with a Binomial error distribution was used to assess the influence of different variables on hooking locations (hook swallowed vs. non-swallowed). In contrast to the previous model, which assumes a multinomial error distribution, the response variable in this model assumes a binomial response. The GLMM are an extension of Generalized Linear Model (GLM), with the addition of random effects to the linear predictor (McCulloch and Searle, 2001). Factors considered as random effects were used to minimize the risk that the detected effects resulted in systematic biases caused by variables that are not explicitly considered in the design. In our study we used the country as a random effect, as it was expected that factors related to the longline fisheries in each country were highly correlated.

Main factors and interaction terms were used for each combination of fixed variables, except for the interaction between hook size and hook type, because the range of sizes by category of hook-type exhibited little overlap (see Fig. 1). Hook size range between 22 and 33 mm in J-hooks, 29 and 35 mm in tuna hooks, and 30 and 54 mm in circle hooks.

To select the optimal model that explained a significant portion of the observed variance in hooking location, a forward stepwise approach was used, where each factor and interaction are tested one by one from a null model (with no explanatory variables). The final model was evaluated according to the Akaike Information Criteria (AIC) and by the Bayesian Information Criteria (BIC). The

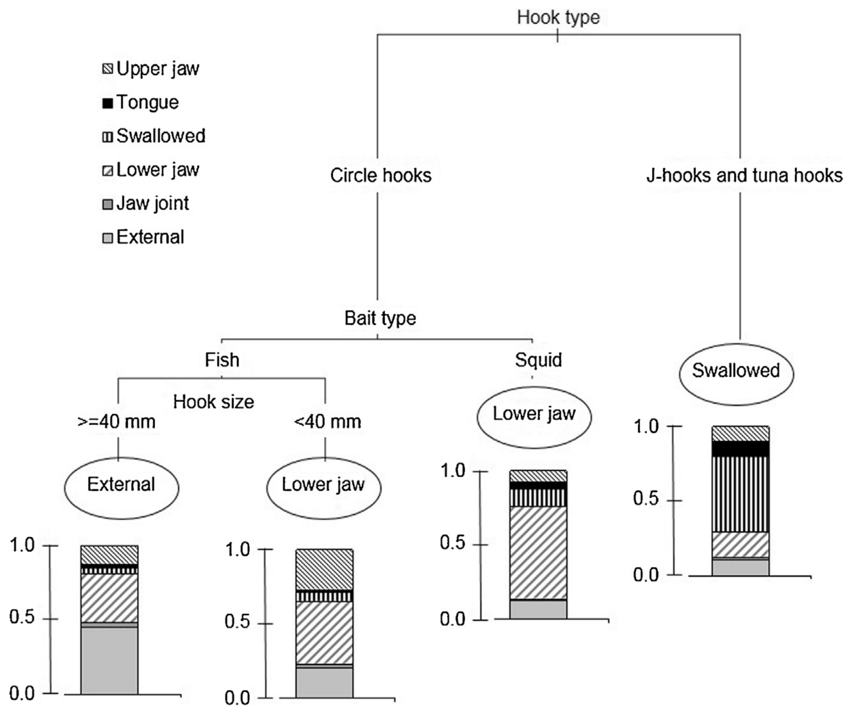

Fig. 2. Classification tree of olive ridley sea turtles hooking locations. Each node shows the split variable and in the branches the split criteria. In the leaves or terminal nodes of the tree a bar-plot is showed with the proportion of hooking locations in each leaf. The category in each terminal node corresponds to the dominant hooking location.

significance of the estimated parameters in the final model was evaluated using the Wald statistic (McCullagh and Nelder, 1989; Crawley, 2007).

The base comparison level (contrast) for each factor in the model was J-hook for hook type, fish for bait type and tuna fishery for target; and is referred as the intercept of the model in the significance table.

3. Results

A total of 1823 olive ridley sea turtles were analyzed in the present study. The mean CCL was 60.4 ± 7.3 cm, ranging from 25 to 85 cm, although 95% of turtles were between 45 and 70 cm CCL. In general, most olive ridley sea turtles were hooked in the lower jaw (44.7%), followed by swallowed hooks (17.9%) and external hookings (17.7%). The other categories, tongue, upper jaw and jaw joint, involved the remainder 19.7%.

3.1. CART

The resultant maximal tree generated by the CART model had five terminal nodes. Nevertheless, the tree with four nodes explained the same amount of relative error (84%, Appendix A), so this tree was selected as the best sub-optimal model (Fig. 2). In the "leaves" or terminal nodes of the tree the most frequently hooking locations can be observed: swallowed, lower jaw and external. The terminal nodes had a mixture of hook locations where one of them occurs in a greater proportion (see the bar-plots in Fig. 2). The first node, "the root", took the hook type as split variable, separating circle hooks on the left side and J-hooks and tuna hooks on the right (Fig. 2). The latest are grouped into a clear terminal node dominated in 50% by swallowed hooks, suggesting that tuna and J-hooks tend to be swallowed in a greater proportion than circle hooks. Although J-hooks and tuna hooks were analyzed as two different categories, they were classified together as one group in the CART model (Fig. 2). On the other hand, the hook location of circle hooks depends on the bait type. Circle hooks baited with squid tend to lodge around the lower jaw in 62% of the turtles hooked. However, hook locations of circle hooks baited with fish depend on the hook size. That is, circle hooks larger than 40 mm (15/0, 16/0 and 18/0) and baited with fish produced a high proportion (46%) of external hooking, while smaller circle hooks (12/0, 13/0 y 14/0) also baited with fish produced mostly hookings in the lower jaw (43%). The target and CCL were not considered significant split variables in the CART model.

3.2. Binomial model

The model with the lower AIC and BIC values was: logit (swallowed) = hook type + hook size + bait type + CCL (Appendix B). Any of the interactions considered, as well as the target, were not selected in the optimal model. The factors that explained a significant proportion of the observed variability to meet criteria for inclusion in the model were hook type and hook size ($p < 0.01$), followed by bait type ($p = 0.05$, Table 1). Both circle and tuna hooks reduced the proportion of hooks being swallowed by olive ridley sea turtles in relation to J-hooks. Tuna hooks reduced 2.5 times the proportion of swallowed hooks compared with J-hooks (odds = 0.40) and circle hooks reduce this probability 6 times (odds = 0.17, Table 1). In addition, hook size showed a significant and negative slope (−2.45, $p < 0.01$), suggesting that as hook size

Table 1
Estimated coefficients for the binomial GLMM with its standard error (S.E.), statistical significance (*p*) and odds ratio. The intercept for these variables are J-hook for hook type, and fish for bait type. CCL: turtles curve carapace length.

	Estimate	S.E.	*p*	Odds ratio
Intercept	1.31	0.86	0.129	
Hook type: circle hook	−1.80	0.29	<0.01*	0.17
Hook type: tuna hook	−0.91	0.31	<0.01*	0.40
Hook size	−2.45	0.77	<0.01*	0.09
Bait type: squid	0.54	0.28	<0.01*	1.71
CCL	0.47	0.59	0.43	1.60

* Correspond to *p*-values that are statistically significant.

increased the frequency of a sea turtle swallowing it decreased. Moreover, hooks baited with squid were swallowed 1.7 times more than hooks baited with fish (odds = 1.71, Table 1). Although CCL was not significant, the positive slope (0.47) suggests that as sea turtle size increases the frequency of a sea turtle swallowing a hook increases.

4. Discussion

The results of the present study suggest that the use of circle hooks under real fishing conditions in the EPO shallow-set artisanal longline fisheries has great conservation potential, especially since fishermen in this region will try to remove all hooks from captured turtles before releasing them. In this situation, hooks in the mouth or external make it less likely for fishermen to cause further injury when removing the hook. Circle hooks resulted in fewer swallowed hooks compared with the traditional J-hook and tuna hook, therefore offering a more practical option to attempt hook removal. In addition, a high proportion of external hookings, which can be assumed to be less dangerous, were produced with larger circle hooks (sizes 16/0 and 18/0). Pacheco (2013), in the Panamanian mahi-mahi longline fishery, also found that larger circle hooks (15/0) produce a significant greater proportion of external hooking than smaller circle hooks (13/0 and 14/0).

As in other parts of the world (Bolten and Bjorndal, 2003; Watson et al., 2005; De la Serna et al., 2006; Gilman et al., 2006; Minami et al., 2006; Gilman et al., 2007; Read, 2007; Brazner and McMillan, 2008), the type of hook proved to be the most important factor affecting the chances of a turtle swallowing it. However, because most J-hooks and tuna hooks used in the EPO are slightly smaller than circle hooks, a confounding effect of hook type on a potential hook size could be produced in the GLMM as was suggested also by Epperly et al. (2012) and Stokes et al. (2012). Nevertheless, CART analysis confirmed that a difference in hooking location exists between small and large circle hooks (Fig. 2). Smaller circle hooks, less than 40 mm, comparable with the size of J-hooks and tuna hooks, presented a higher proportion of hooks located in the mouth in comparison to same size of J-hooks. This means that for the same size, circle hooks tended to lodge in the mouth rather than being swallowed. The point of a circle hook tends to be bent toward the shank, less exposed, likely reducing the chance (more so in the non-offset hooks) of being lodged in a tubular-like structure as the esophagus, even if the turtle swallows it. In contrast, the point of J-hooks is very exposed, and gets lodged easily (MLP pers. obs.). Probably both circle and J-hooks of the same size potentially have the same chance of getting swallowed, but only J-hooks end up getting lodged in the esophagus, while circle hooks tend to slip out of the esophagus and only get hooked in the mandible, when the point gets lodged as it rotates while getting out of the mouth (Stokes et al., 2012). However, this is impossible to confirm at sea, since by the time turtles are recovered, the hook is already lodged.

The results also confirmed that the use of squid as bait significantly increases the probability of hooks being swallowed compared to hooks baited with fish. This is mainly related to the way in which turtles approach and ingest the bait, taking it entirely in 1–2 bites if it is squid, or tearing it to pieces if it is a sardine or mackerel (Watson et al., 2004; Stokes et al., 2011; Serafy et al., 2012). Moreover, the use of large circle hooks (15/0, 16/0 and 18/0) used in combination with fish bait produced a higher proportion of external hookings.

An increase in hooks lodged externally or in the lower mandible is generally preferred, both because these hooking locations are assumed to be less dangerous for the animal's post-release survival, but more so because it is easier to attempt removal of both hooks and the attached gear, potentially further reducing post-release mortality (Ryder et al., 2006; Swimmer and Gilman, 2012). According to the information collected by the EPRSTBP observers during the 8 years of study, only 3.7% of all externally hooked turtles and 1.15% of turtles hooked in the mouth were released with the hook still lodged. In contrast, from all turtles with swallowed hooks assisted by the EPO surface longline fishery observers, about one third were released with the hook still inside, although the line was cut short in all cases. However, one should bear in mind that a change in hook location is only beneficial if fishers are willing to handle turtles and remove the hooks, and if they receive the necessary tools and training on best practices (Parga, 2012; Swimmer et al., 2013). Therefore, such a change in fishing gear should always be accompanied by a sound management plan including trained fishery observers, and intensive awareness and training sessions for fishers. Removing a hook from a turtle's mouth is no easy task, and no fisher should be expected to do it without proper training and adequate tools. Because of their shape, circle hooks may be more difficult to remove than J-hooks in some cases (Gilman et al., 2007; Piovano et al., 2009; Alessandro and Antonello, 2010; Parga, 2012; Yokota et al., 2012), and the possibility of causing further injuries is quite significant if not done carefully.

Turtle size was not significantly related to the probability of a hook being swallowed. Stokes et al. (2011) found in loggerhead sea turtles (*C. caretta*) a significant difference in the chances of a larger turtle attempting to swallow a hook when comparing turtles of 65 cm vs. turtles of 45 cm straight carapace length (SCL). This difference, however, was not as important when comparing turtles over 55 cm SCL, suggesting that turtles over this size have a similar potential to ingest hooks of sizes between 14/0 and 20/0, the ones used in their study. Most of the loggerhead sea turtles involved in another analysis by Stokes et al. (2012) were also over 55 cm SCL, and again turtle size did not influence hooking location. Olive Ridley turtles captured during fishing trials in the EPO had an average curved carapace length (CCL) of 60.4, which for this species is considered an adult size (Zug et al., 2006). Since this species is smaller than loggerhead sea turtles, it may well be that the differences observed by Stokes et al. (2011) do not appear when the size ranges are restricted. In any case this comparison between loggerhead and olive ridley turtles should be taken with precaution, since mouth morphometry could potentially also play a significant role in interpreting both results.

Regarding the change in hooking location in the multinomial model, three main locations were considered: external, lower jaw or swallowed. Other areas such as upper jaw, tongue or corner of mouth were not statistical significantly affected by the change in hook type, size, or bait. The most probable reason for this is that those hooking locations are rare, and the amount of information in these categories was not large enough to get evidence of factors affecting these hooking locations.

When considering if a mouth hook is better or worse for a turtle than a swallowed hook, another factor to consider is the socio-economic reality of the fishery and the region involved, and its attitude toward an incidentally hooked turtle. In parts of the world where hooks are expensive and fishers cannot afford to lose them, a hook lodged in the mouth is preferable to a hook that is swallowed (Casale and Cannavò, 2003; Hall et al., 2012), since its removal is less likely to be fatal. On the contrary, if fishers are not willing to haul turtles on board and remove the hooks (Guglielmi et al., 2000), then it might be more beneficial for the turtle, due to its unique anatomy and physiology, to have the hook lodged in its esophagus rather than in the mouth, as long as all the trailing line is cut as short as possible (Parga, 2012). In fact, studies have already shown that a swallowed hook, if well handled, does not necessarily mean a higher post-release mortality (Mangel et al., 2011; Swimmer et al., 2013).

In order to better understand the effect of hooking location on sea turtle post-release survival, it is essential to incorporate into the observer programs the collection of specific data about the interaction. In longline fisheries of the EPO, standardized forms including detailed information on hooking location and a description of the hook removal process including pre- and post-removal pictures, would largely contribute to define the effectiveness of circle hooks and other mitigation measures (such as correct handling and release techniques).

In conclusion, the results of this study confirm that in the EPO region the combination of large circle hooks and fish bait increases external and mouth hooking on sea turtles, facilitating complete gear removal. For those fisheries in which the use of large circle hooks would greatly reduce target captures (e.g. Ecuadorian mahi-mahi fisheries, see Andraka et al., 2013), the use of small circle hooks is a possible alternative to maintain a high rate of mouth and external hookings. This change to circle hooks should always be accompanied by the implementation of training sessions for fishers and fishery observers in the best turtle handling and release techniques. In order to expand the use of circle hooks in the EPO region, governments should guarantee the availability of circle hooks at competitive prices in each country, and fishery authorities should implement regulatory measures in the use of tools to handle and release turtles. For the EPO region, the use of measures and techniques to reduce sea turtles bycatch and post-release mortality should be presented to fishers as a chance to improve fishing practices and access international, environmentally sensitive markets. Moreover, before adopting circle hooks, managers should consider the effects of the change on target species or other bycatches (Serafy et al., 2012).

Acknowledgements

The authors would like to thank all the observers for their efforts helping produce the database. Thank you also to all the fishers from the region that have cooperated with us and trusted us, fisheries organizations and country fisheries agencies from Mexico, Guatemala, El Salvador, Nicaragua, Costar Rica, Panama, Colombia, Ecuador and Peru. The authors would also like to acknowledge the long list of organizations that have supported this project with funds, technical advice, or in many other ways, which includes: WWF Latin American Program (Mexico, Central America, Colombia and Peru), WWF National Offices (WWF Netherlands and WWF US) and WWF International, particularly to Robin Davies, Carol Phua, Carlos Drews, Moises Mug, Samuel Amorós, Michael Valqui, and other fisheries staff; other key collaborators and member of the team—Manuel Parrales, Erick Villagrán, Sara Pérez, Celina de Paz and Salvador Siu; Fauna and Flora International Nicaragua Program—Velkiss Gadea, Alejandro Cotto and José Urteaga; the Western Pacific Regional Fishery Management Council-Kitty Simonds; NOAA NMFS personnel—Jeffrey Seminoff, Charlie Bergmann, Chris Boggs and many others; the Inter-American Tropical Tuna Commission staff; the State Department USA-US–AID; the Overseas Fishery Cooperation Foundation-Japan; MUSTAD; the Walton Family Foundation, and other donors and foundations that trusted and supported our work. A very special thank you to the *Nationale Postkode Loterij* for supporting all the analysis carried out for this work.

Appendix A.

Relative error (differences between the observed and predicted values) in relation to the size of the tree. The tree with four terminal nodes explain almost the same amount of error than the tree with five. Thus, the tree with less number of terminal nodes was selected as the best sub-optimal tree.

Appendix B.

Analyses of alternative Binomial GLMM for hooking location on olive ridley sea turtle. DF: degrees of freedom; AIC: Akaike Information Criteria; BIC: Bayesian information criteria; *p*: *p*-value of Chi square test between two consecutive models. Highlighted is the final model selected.

Appendix C. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.11.012.

References

Alessandro, L., Antonello, S., 2010. An overview of loggerhead sea turtle (*Caretta caretta*) bycatch and technical mitigation measures in the Mediterranean Sea. Rev. Fish. Biol. Fish. 20, 141–161.

Andraka, S., Mug, M., Hall, M., Pons, M., Pacheco, L., Parrales, M., Rendón, L., Parga, M.L., Mituhasi, T., Segura, A., Ortega, D., Villagrán, E., Pérez, S., de Paz, C., Siu, S., Gadea, V., Caicedo, J., Zapata, L.A., Martínez, J., Guerrero, P., Valqui, M., Voguel, N., 2013. Circle hooks: developing better fishing practices in the artisanal longline fisheries in the Eastern Pacific Ocean. Biol. Conserv. 160, 214–223.

Baez, J.C., Real, R., García-Soto, C., De la Serna, J.M., Macías, D., Camiñas, J.A., 2007. Loggerhead sea turtle bycatch depends on distance to the coast, independent of fishing effort: implications for conservation and fisheries management. Mar. Ecol. Prog. Ser. 338, 249–256.

Bolten, A., Bjorndal, K., 2003. Experiment to evaluate gear modification on rates of sea turtle bycatch in the swordfish longline fishery in the Azores—phase 2. In: Final Project Report submitted to the US National Marine Fisheries Service. Archie Carr Center for Sea Turtle Research, University of Florida, Gainesville, FL.

Brazner, J.C., McMillan, J., 2008. Loggerhead turtle (*Caretta caretta*) bycatch in Canadian pelagic longline fisheries: relative importance in the western North Atlantic and opportunities for mitigation. Fish. Res. 91, 310–324.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Chapman and Hall, New York, NY.

Camiñas, J.A., Valeiras, J., De La Serna, J.M., 2003. Spanish surface longline gear types and effects on marine turtles in the western Mediterranean Sea. In: Margaritoulis, D., Demetropoulos, A. (Eds.), Proceedings of the First Mediterranean Conference on Marine Turtles. Barcelona Convention–Bern Convention–Bonn Convention. Nicosia, Cyprus, pp. 88–93.

Casale, P., Cannavò, G., 2003. When a turtle is worth a hook. Mar. Turtle Newslett. 101, 28.

Casale, P., Cattarino, L., Freggi, D., Rocco, M., Argano, R., 2007. Incidental catch of marine turtles by Italian trawlers and longliners in the central Mediterranean. Aquat. Conserv: Mar. Freshwater Ecosyst. 17, 686–701.

Crawley, M.J., 2007. The R Book. John Wiley & Sons Ltd, England.

Dayton, P.K., Thrush, S.F., Agardy, M.T., Hofman, R.J., 1995. Environmental effects of marine fishing. Aquat. Conserv: Mar. Freshwater Ecosyst. 5, 205–232.

Deflorio, M., Aprea, A., Corriero, A., Santamaria, N., De Metrio, G., 2005. Incidental captures of sea turtles by swordfish and albacore longlines in the Ionian Sea. Fish. Sci. 71, 1010–1018.

De la Serna, J.M., Ortiz de Urbina, J.M., García, S., 2006. Resultados de la acción piloto (RAI—AP—52/2004) de pesca experimental con palangre de superficie dirigido al pez espada en el Mediterráneo occidental. In: DOC.CRS—2006/163. IEO, Málaga, Spain.

Epperly, S.P., Watson, J.W., Foster, D.G., Shah, A.K., 2012. Anatomical hooking location and condition of animals captured with pelagic longlines: the Grand Banks experiments 2002–2003. Bull. Mar. Sci. 88, 513–527.

FAO, 2004. Expert consultation on interactions between sea turtles and fisheries within an ecosystem context. In: FAO Fisheries Report No. 738. Food and Agriculture Organization of the United Nations, Rome.

Gilman, E., Zollett, 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, 1–22.

Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P., Kinan-Kelly, I., 2007. Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. Biol. Conserv. 139, 19–28.

Gilman, E., 2011. Bycatch governance and best practice mitigation technology in global tuna fisheries. Mar. Policy. 35, 590–609.

Guglielmi, P., Di Natale, A., Pelusi, P., 2000. Effetti della pesca col palangaro derivante sui grandi pelagici e sulle specie accessorie nel Mediterraneo centrale. In: Rapporto al Ministero per le Politiche Agricole e Forestali. DGPA, Roma.

Hall, M.A., Alverson, D.L., Metuzals, K.I., 2000. By-catch: problems and solutions. Mar. Pollut. Bull. 41, 204–219.

Hall, M.A., Swimmer, Y., Parga, M.L., 2012. No "silver bullets" but plenty of options: working with artisanal fishers in the Eastern Pacific to reduce incidental sea turtle mortality in longline fisheries. In: Seminoff, J.A., Wallace, B.P. (Eds.), Sea Turtles of the Eastern Pacific: Advances in Research and Conservation. University of Arizona Press, Tucson, AZ, pp. 136–153.

Largacha, E., Parrales, M., Rendon, L., Velasquez, V., Orozco, M., Hall, M., 2005. Working with the Ecuadorian Fishing Community to Reduce the Mortality of Sea Turtles in Longlines: The First Year March 2004–March 2005. Western Pacific Regional Fishery Management Council, Honolulu, HI.

Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol. Evol. 19, 598–604.

Mangel, J.C., Alfaro-Shigueto, J., Witt, M.J., Dutton, P.H., Seminoff, J.A., Godley, B.J., 2011. Post-capture movements of loggerhead turtles in the southeastern Pacific Ocean assessed by satellite tracking. Mar. Ecol. Prog. Ser. 433, 261–272.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, second ed. Chapman & Hall, London.

McCulloch, C., Searle, S., 2001. Linear and mixed models. In: Generalized, Linear and Mixed Models. John Wiley & Sons, Brisbane.

Minami, H., Yokota, K., Kiyota, M., 2006. Effect of circle hooks and feasibility of dehooking devices to reduce incidental mortality of sea turtles in the Japanese longline fishery. In: WCPFC-SC2-2006/EB WP-9. Scientific Committee of the Western Central Pacific Fisheries Commission, Manila, Philippines.

Mituhasi, T., Hall, M., 2011. Hooks Used in Artisanal Longline Fisheries of the Eastern Pacific Ocean. Inter-American Tropical Tuna Commission, La Jolla, CA.

Olden, J.D., Lawler, J.J., Poff, N.L., 2008. Machine learning methods without tears: a primer for ecologists. Q. Rev. Biol. 83, 171–193.

Pacheco, L., 2013. La pesca con palangre pelágico en el pacifico panameño. In: Aspectos operativos de la selectividad de los anzuelos y repercusiones en la captura incidental de tortugas marinas, ⟨http://rua.ua.es/dspace/bitstream/10045/36118/1/Tesis%20m%C3%-A1ster%20Lucas%20Pacheco.pdf⟩ (last accessed on Thursday 8th of May, 2014).

Parga, M.L., 2012. Hooks and sea turtles: a veterinary's perspective. Bull. Mar. Sci. 88, 731–741.

Piovano, S., Swimmer, Y., Giacoma, C., 2009. Are circle hooks effective in reducing incidental captures of loggerhead sea turtles in a Mediterranean longline fishery? Aquat. Conserv: Mar. Freshwater Ecosyst. 19, 779–785.

Read, A.J., 2007. Do circle hooks reduce the mortality of sea turtles in pelagic longlines? A review of recent experiments. Biol. Conserv. 135, 155–169.

Ryder, C.E., Conant, T.A., Schroeder, B.A., 2006. Report of the workshop on marine turtle longline post-interaction mortality. In: NOAA Technical Memorandum NMFS-F/OPR-29. US Dep. Commerce.

Sales, G., Giffoni, B.B., Fiedler, F.N., Azevedo, V.G., Kotas, J.E., 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. Freshwater Ecosyst. 20, 428–436.

Serafy, J.E., Cooke, S.J., Diaz, G.A., Graves, J.E., Hall, M., Shivji, M., Swimmer, Y., 2012. Circle hooks in commercial, recreational, and artisanal fisheries: research status and needs for improved conservation and management. Bull. Mar. Sci. 88, 371–391.

Shiode, D., Hu, F., Shiga, M., Yokota, K., Tokai, T., 2005. Midwater float system for standardizing hook depths on tuna longlines to reduce sea turtle by-catch. Fish. Sci. 71, 1182–1184.

Soykan, C.U., Moore, J.E., Žydelis, R., Crowder, L.B., Safina, C., Lewison, R.L., 2008. Why study bycatch? An introduction to the theme section on fisheries bycatch. Endang. Species Res. 5, 91–102.

Stokes, L.W., Hataway, D., Epperly, S.P., Shah, A.K., Bergmann, C.E., Watson, J.W., Higgins, B.M., 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.

Stokes, L.W., Epperly, S.P., McCarthy, K.J., 2012. Relationship between hook type and hooking location in sea turtles incidentally captured in the United States Atlantic Pelagic longline fishery. Bull. Mar. Sci. 88, 703–718.

Swimmer, Y., Arauz, R., Higgins, B., McNaughton, L., McCracken, M., Ballestero, J., Brill, R., 2005. Food color and marine turtle feeding behavior: can blue bait reduce turtle bycatch in commercial fisheries? Mar. Ecol. Prog. Ser. 295, 273–278.

Swimmer, Y., Arauz, R., Wang, J., Suter, J., Musyl, M., Bolaños, A., López, 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. Freshwater Ecosyst. 20, 445–451.

Swimmer, Y., Gilman, E., 2012. Report of the sea turtle longline fishery post-release mortality workshop. In: Convened via Webinar, 15–16 November 2011, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, HI.

Swimmer, Y., Empey Campora, C., Mcnaughton, L., Musyl, M., Parga, M., 2013. Post-release mortality estimates of loggerhead sea turtles *(Caretta caretta)* caught in pelagic longline fisheries based on satellite data and hooking location. Aquat. Conserv: Mar. Freshwater Ecosyst., http://dx.doi.org/10.1002/aqc.2396.

Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., Bjorkland, R.K., Finkbeiner, E.M., Helmbrecht, S., Crowder, L., 2010. Global patterns of marine turtle bycatch. Conserv. Lett. 3, 1–12.

Wang, J.H., Boles, L.C., Higgins, B., Lohmann, K.J., 2007. Behavioral responses of sea turtles to lightsticks used in longline fisheries. Anim. Conserv. 10, 176–182.

Watson, J., Foster, D., Epperly, S., Shah, A., 2004. Experiments in the Western Atlantic Northeast distant waters to evaluate sea turtle mitigation measures in the pelagic longline fishery. In: Report on Experiments Conducted in 2001–2003. US National Marine Fisheries Service, Pascagoula, MS.

Watson, J., Epperly, S., Shah, A., Foster, D., 2005. Fishing methods to reduce sea turtle mortality associated with pelagic longlines. Can. J. Fish. Aquat. Sci. 62, 965–981.

Yokota, K., Mituhasi, T., Minami, H., Kiyota, M., 2012. Perspectives on the morphological elements of circle hooks and their performance in pelagic longline fisheries. Bull. Mar. Sci. 88, 623–629.

Zug, G.R., Chaloupka, M., Balazs, G.H., 2006. Age and growth in olive ridley seaturtles (*Lepidochelys olivacea*) from the North-central Pacific: a skeletochronological analysis. Mar. Ecol. 27, 263–270.