AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2013)
Published online in Wiley Online Library
(wileyonlinelibrary.com). DOI: 10.1002/aqc.2396

Post-release mortality estimates of loggerhead sea turtles (Caretta caretta) *caught in pelagic longline fisheries based on satellite data and hooking location*

Y. SWIMMER[a,*], C. EMPEY CAMPORA[b], L. MCNAUGHTON[c], M. MUSYL[c,d] and M. PARGA[e]
[a]*National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, Hawaii, USA*
[b]*Biolintec Consulting, LLC, Kailua, Hawaii, USA*
[c]*Joint Institute for Marine and Atmospheric Research, University of Hawaii, Honolulu, Hawaii, USA*
[d]*Pelagic Research Group LLC, Honolulu, Hawaii, USA*
[e]*SUBMON, Barcelona, Spain*

ABSTRACT

1. There are few reliable estimates of post-release mortality for sea turtle species because of the many challenges and costs associated with tracking animals released at sea. In this study, the likelihood of sea turtle mortality as a result of interactions with longline fishing gear was estimated based on satellite telemetry data, such as the number of days an animal was successfully tracked, or days at liberty (DAL) and dive depth data, as well as anatomical hooking locations.
2. Pop-up satellite archival tags were deployed on 29 loggerhead sea turtles (*Caretta caretta*) caught by the North Pacific US-based pelagic longline fishery operating from California and Hawaii between 2002 and 2006. Loggerhead turtles were catagorized by observers as shallow-hooked (55%) if the animal was entangled in the line or the hook was in the flipper, jaw or mouth and could be removed, or deep-hooked (45%) if the hook was ingested and could not be removed. The vertical movements of turtles were used to infer potential mortalities.
3. Of the 25 tags that reported data, the DAL ranged from 3 to 243 days (mean = 68 days). The DAL was shorter (by nearly 50%) for shallow-hooked (mean = 48 days, range: 3 to 127) compared to deep-hooked turtles (mean = 94 days, range: 5 to 243), but these changes were not statistically significant ($P = 0.0658$).
4. Although aspects of these analyses may be considered speculative, these data provide empirical evidence to indicate that deep-hooking is not linked to shorter DAL.
5. DAL, anatomical hooking location, and gear removal were evaluated with inferences about the extent of injuries and rates of infection to estimate an overall post-release mortality rate of 28% (95% bootstrap CI: 16–52%).
6. This range of estimates is consistent with those used to shape some US fisheries management plans, suggesting that conservation goals are being achieved at the expected level and ideally striking a balance between the interests of industry and those of protected species.

Received 20 February 2013; Revised 25 June 2013; Accepted 05 August 2013

KEY WORDS: bycatch; telemetry; post-release mortality; sea turtles

*Correspondence to: Y. Swimmer, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, Hawaii 96822, USA. Email: yonat.swimmer@noaa.gov

INTRODUCTION

It is well established that loggerhead sea turtles (*Caretta caretta*) are vulnerable to incidental capture in shallow-set pelagic longline fisheries targeting swordfish (*Xiphias gladius*) or tunas (*Thunnus* spp.) (Wallace *et al*., 2010, 2013). These interactions have been documented in the Atlantic (Witzell, 1999; Kotas *et al*., 2004; Watson *et al*., 2005; Sales *et al*., 2010), Pacific (Lewison *et al*., 2004; Donoso and Dutton, 2010; Swimmer *et al*., 2010, 2011), and in the Mediterranean Sea (Camiñas *et al*., 2006; Piovano *et al*., 2009). Most loggerheads are alive when captured in shallow-set longline fishing gear (Swimmer *et al*., 2006, 2010, 2011; Casale, 2011), but it is widely assumed that a substantial number of animals die as a result of injuries caused by hooks or line entanglement following release (Lewison *et al*., 2004; Casale, 2011).

Despite being an essential component of risk assessment and hazard mitigation, there are few reliable estimates of post-release mortality for sea turtle species (Chaloupka *et al*., 2004a; Parker *et al*., 2005; Swimmer *et al*., 2006; Sasso and Epperly, 2007) owing to the many challenges and costs associated with tracking animals released at sea and identifying subsequent mortality events with sufficient statistical power. The uncertainty regarding post-release mortality estimates are complicated by the different types of injuries that an animal may sustain as a result of anatomical hook location, the level of stress induced by trauma, and the potential for greater vulnerability to predation during and after hooking. These challenges are further confounded by the difficult task of tracking turtles to definitively determine a mortality based on diving behaviour after their release.

Previous attempts to estimate post-release mortality have relied on observations of turtles over time in rescue centres after capture in longline gear. Recent mortality estimates have drawn on inferences from turtles tracked with telemetry devices, which are summarized in Table 1. Although advances in satellite telemetry have created opportunities to monitor animals post-release, there are limitations regarding data interpretation.

Estimating post-release mortality in sea turtles or other pelagic species often relies on a suite of assumptions (Moyes *et al*., 2006). Previous studies aimed at estimating the post-release mortality in turtles have employed platform terminal transmitters (PTTs) with the presumption that transmissions are indicative of a living animal, and cessation of transmission is the result of the animal dying and sinking or tag/battery malfunction. There are a number of reasons PTTs stop transmitting, including electronic malfunction, battery failure, biofouling, failure of the salt-water switch, or the transmitter itself detaching and sinking (Hays *et al*., 2004, 2007). As such, failure of electronic tags should not be considered synonymous with mortality (Goodyear, 2002; Chaloupka *et al*., 2004a, b; Hays *et al*., 2007; Musyl *et al*., 2011).

Pop-up satellite archival tags (PSATs) are capable of providing depth, temperature, and geolocation data and can be programmed to release based on specified conditions and transmit data to satellites. Tags are specifically designed to be positively buoyant and are tethered to the animal so that they float to the surface after the tether is severed as programmed or shed. Data are not transmitted until the tag is at the surface. A major advantage of this type of tag is the ability to transmit stored data without the user having to physically retrieve the tag. PSATs can be equipped with other 'fail-safe' options that ideally allow an animal mortality to be differentiated from tag failure or a shed tag (Domeier *et al*., 2003; Sasso and Epperly, 2007; Musyl *et al*.,

Table 1. Estimates of sea turtle mortality from the literature

Author, year	Mortality rate	Comments	Methods
Aguilar *et al*., 1995	*c*. 20–30%		Captivity
Casale *et al*., 2008	65–82%	Some speculation based on floating turtles	Captivity
Hays *et al*., 2003	31%		PTT
Parker *et al*., 2005	20–40%	Depends on hook status	PTT
Chaloupka *et al*., 2004a	34% 8%	Deep hook shallow hook (within 1 week)	PTT
Swimmer *et al*., 2006	Unobserved (0%) within 6 weeks	Low rates in shallow gear	PSAT
Sasso and Epperly, 2007	19%	Depends on how much gear is removed	PSAT

2011), including tag release at a specific threshold depth that would indicate a sinking event as a result of mortality. Despite these features, PSATs and the interpretation of reported data can be problematic, as described in a comprehensive meta-analysis of more than 700 PSATs placed on 19 different species (Musyl *et al*., 2011). In this meta-analysis, the majority of PSATs (~80%) were shed before their programmed release date, suggesting that additional factors should be used to derive a realistic estimate of post-release mortality for any animal released to sea.

Hook location and the type of injury to the animal are proximate factors that may affect post-release survivorship (Parga, 2012). Recent testimony from a veterinary panel regarding post-release survivorship of turtles concluded that additional 'factors that may influence the survivability of an injury include environmental conditions, risk of predation, and general health prior to interaction' (B. Stacey, in Swimmer and Gilman, 2012). The time component for succumbing to injuries is critical and can be categorized into acute, sub-acute and delayed mortality, according to B. Stacey (in Swimmer and Gilman, 2012). Acute death can occur minutes to hours after situations such as forced submergence and severe trauma resulting in blood loss and loss of vital organ function. Sub-acute mortality can occur hours to days after an interaction as a result of severe injuries that are not immediately fatal, continued blood loss or failure to overcome hypoxic or exertional insults. Delayed mortality can occur weeks to months after the interaction and generally results from injuries such as plication and intussusception of the intestines due to ingestion of lines or secondary infections (B. Stacey, in Swimmer and Gilman, 2012).

In 2004, NOAA NMFS convened an expert working group to provide best estimates on post-interaction mortality rates based on the severity of the injury to the turtle and the amount of gear removed for both hardshell and leatherback turtles (Ryder *et al*., 2006). Based largely on non-empirical data, estimates for hardshell turtles ranged from 1% (for turtles hooked entangled in line with all gear removed) to 50% (for turtles that had ingested the hook with minimal line trailing) (Ryder *et al*., 2006). Estimates based upon hooking location (e.g. jaw vs. oesophagus) and the amount of line removed fall within this range.

Based on the previously described veterinary reports, the working hypothesis used to guide mortality inferences in this study was that post-release mortality should be roughly bimodal for deep-hooked turtles, with an increased risk of death near the interaction event and again weeks or months later to take into account a temporal component. For turtles that sustain injuries associated with entanglement and hookings whereby the hook can be readily removed, a relatively low risk of mortality was assumed at the time of the fisheries interaction based on expert opinion from sea turtle veterinarians (Swimmer and Gilman, 2012). In the proposed model, the mortality risk increases over time owing to the potential for a secondary infection (see Swimmer and Gilman, 2012). Figure 1 shows a hypothetical depiction of this hypothesis. The duration of the time component and the risk of mortality are undefined in the proposed model. However, it is well established that determination of an animal's fate after approximately 90 days is highly uncertain as a result of confounding variables regarding long-term health of the turtle and the functional life of the transmitter (Chaloupka *et al*., 2004a). In addition, longer time periods will invariably encompass the transition from fisheries-induced mortality to natural mortality.

This study reports the use of PSAT telemetry data, primarily days at liberty (DAL) and dive depth data, combined with an initial assessment of

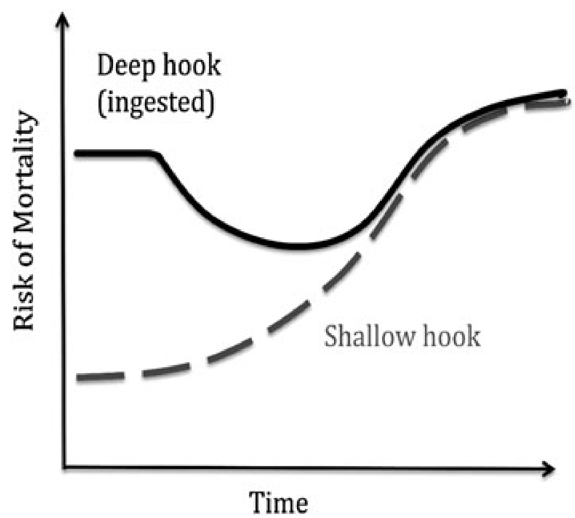

Figure 1. Hypothetical risk of mortality by injury type over time.

injuries (including hook type), to estimate the post-release fate of turtles following an interaction with longline gear. Hook type is considered, based on the assumption that injuries from circle hooks cause less injury than hookings from J-shaped or tuna hooks due to the placement of hooking (see reviews in Cooke and Suski, 2004; Read, 2007). On a circle hook, the point is perpendicular to the shank such that the point curves inward and is less exposed, whereas J- or tuna-style hooks have the point of the hook parallel to the shank (Cooke and Suski, 2004). Studies have shown that the use of J hooks increases the rate of gut-hooking in turtles compared with turtles captured on circle hooks (Epperly *et al.*, 2012), with a widely assumed lower risk of mortality associated with external hooking events.

In an effort to reduce the subjectivity of interpreting the data pertinent to each turtle's survival, a decision tree matrix was established that served as a guide and can potentially be modified for use in additional studies to incorporate multiple parameters in mortality estimates. The many uncertainties and limitations involved in presuming the fate of an animal at sea following release are also reviewed.

MATERIALS AND METHODS

Satellite telemetry

US National Marine Fisheries Service (NOAA NMFS) fishery observers operating from Long Beach, California and Honolulu, Hawaii were randomly assigned aboard US-based pelagic longline vessels operating in the North Pacific Ocean according to NMFS regulations. In general, vessels operating from California used primarily 9/0 J hooks, while Hawaii vessels were required to use 18/0 circle hooks after the fishery was re-opened in 2004. Table 3 lists probable hook type associated with the capture of each tagged turtle. The fishery is described in detail in Gilman *et al.* (2007). Observers were provided with PSATs to attach to hard-shelled sea turtles retrieved alive during longline operations. In total, 29 loggerheads were released alive during approximately 250 trips between December 2002 and March 2006. Turtles were brought onboard during haulback with the aid of dipnets. Each turtle was assigned a 'score' by the observer as follows: 'shallow-hooked' if the hook was lodged in the flipper, mouth, or jaw and was able to be removed or if the turtle was entangled in the line; and 'deep-hooked' if the hook was deep in the mouth and/or ingested such that it was not able to be removed (Figure 2). If the turtle was shallow-hooked, the hook was removed with de-hooking devices supplied by NOAA, as described in Epperly *et al.* (2004). If the turtle was deep-hooked, the hook was left in place and as much trailing line as possible was removed in accordance with veterinarian recommendations (Balazs *et al.*, 1995; Ryder *et al.*, 2006).

PSATs were attached via a tether to a baseplate epoxied to the carapace and designed to float if shed, as described by Swimmer *et al.* (2006). Ten PSATs from Wildlife Computers (WC; model PAT, Washington, USA) and 19 PSATs from Microwave Telemetry Inc. (MT; model PTT-100, Maryland, USA) were deployed. MT PSATs were programmed to record hourly pressure and temperature data for 243 days (8 months) and then detach and report these data to the ARGOS satellite service. The WC PSATs were programmed to record depth and temperature data every 60 s, and summarized hourly histograms and depth and temperature profiles were reported to ARGOS. The tags were equipped with a pressure release mechanism (RD 1500 from WC) that would sever the tether if the depth exceeded ~1200 m, which greatly exceeds the expected normal dive depth (150 m) of juvenile loggerheads in the North Pacific Ocean (Howell *et al.*, 2010). The PSATs were also programmed to detach and begin transmitting if there were no significant pressure changes (e.g. $\pm$ 10 m) for four consecutive days. This feature was set to activate if the PSAT was shed and floated at the surface or if the turtle died and sank to the seafloor in areas shallower than ~1200 m. In all cases, the first ARGOS satellite fix (with Location Class >1) was used to determine the pop-up location. DAL were recorded such that day zero represented the day of capture and release and the last day was 4 days before the initiation of transmission of data (e.g. temperature, depth, or location).

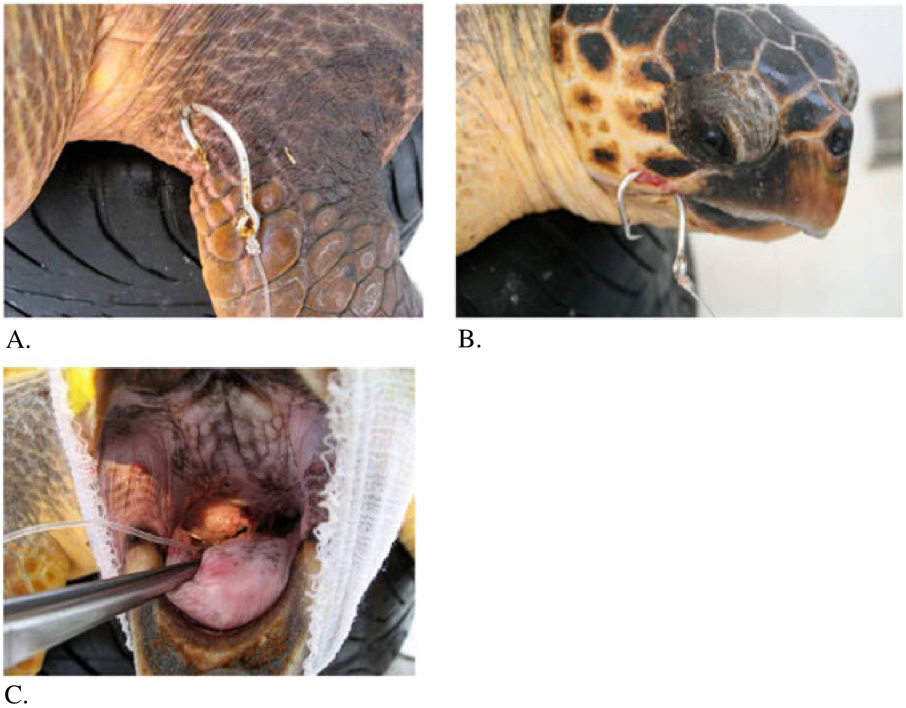

Figure 2. Photographs of shallow- and deep-hooked classifications for incidentally captured loggerhead turtles. (A) External (shallow) flipper hooking with removable hook. (B) External (shallow) jaw hooking with removable hook. (C) Internal (deep) hooking with a hook that is not removable.

Mortality estimation

Mortalities were estimated based on days at liberty (DAL), type of hooking (e.g. shallow or deep), and depth profiles. Mortality was assumed to have occurred if the PSAT recorded a depth >1200 m, if it remained submerged at a constant depth for 4 days before transmitting, or if the final depth data reported were considered 'uncharacteristic' (i.e. greater than or equal to twice the mean depth recorded throughout the turtle's track). An inference as to the degree of damage caused by the hook and its effect on the turtle's health was recorded. Factors such as environmental conditions, risk of predation, and the general health of the animal before the interaction were assumed to be equal for all turtles. A matrix outlining various scenarios suggestive of mortality is shown in Table 2. The specific conditions used to derive the mortality estimates were as follows: (1) for DAL between 1 and 90 days, final depth data reported before scheduled tag release that was at least twice as deep as the mean depth recorded during the entire DAL (regardless of deep or

Table 2. Decision matrix with criteria used to infer mortality from a sample of tagged loggerhead sea turtles captured and released from longline fishing gear in the North Pacific Ocean

DAL	Deep hooked	Shallow hooked	Depth	Decision (inferred fate)	Tag #
1–90	--	--	2 × deeper than mean depth	Mortality	55667 44201
1–30	Yes (ingested)	No	--	Mortality	55675 55680 55670 29682
61–90	--	--	--	Mortality	13193
> 90	--	--	--	Assumed survival	

--Criteria not applicable to decision.

shallow hooking) was assumed to indicate a probable mortality; (2) for DAL between 1 and 30 days, a deep-hooked turtle was assumed to have experienced a mortality arising from acute injuries, such as gut perforation and acute coelomitis, severe blood loss or loss of vital organ function; (3) for DAL between 61 and 90 days, a mortality was assumed to be from secondary infection (regardless of deep or shallow hooking); and (4) for DAL greater than 90 days, survival was assumed regardless of the other parameters (Chaloupka *et al.*, 2004a).

Resampling techniques were used to construct 95% parametric bootstrap confidence intervals (with the assumption of a binomial distribution with 10 000 replicates) for post-release mortality estimates and PSAT reporting rates (Manly, 2007). Non-reporting tags were not used in this estimation of post-release mortality because of uncertainties regarding the cause of tag failure (Musyl *et al.*, 2011).

RESULTS

Tagging

Twenty-nine loggerhead turtles were brought onboard, tagged, and released alive. All of the turtles were large juveniles, with a curved carapace length ranging from 40 to 84 cm (mean = 63 cm). Hook position was classified as 'shallow' in 16 of the 29 turtles (55%) caught. In this group, two were entangled, seven were hooked in the flipper, and seven were hooked in the lower mouth or jaw. Hook position was classified as deep in 13 of the 29 turtles (45%) caught.

The DAL (defined as duration (days) from the day a turtle was tagged until first transmission minus the 4 days if final days indicated no change in depth) ranged from 3 to 243 days (mean = 68 days) for the 25 tags that reported. The DAL was shorter for shallow-hooked (mean = 48 days, range: 3 to 127 days) turtles compared to deep-hooked turtles (mean = 94 days, range: 5 to 243 days), but the difference was not significant ($t = 1.932$, two-tailed t-test $P = 0.0658$).

Nearly all (97%) of the PSATs detached and reported prematurely relative to their programmed release dates, which was not unexpected given past performance of PSATs across species (Musyl *et al.*, 2011). None of the PSATs reported depth data below 1200 m to indicate a sinking mortality event. Figure 3 includes three representative depth data profiles that are all suggestive of tag shedding as evidenced by the lack of a deep descent before tag release and initiation of transmission at the sea surface.

Deep-hooked loggerheads accounted for 41% of the PSAT instrumented turtles and were nine times more likely to be encountered by the California-based observer programme that used primarily 9/0 J hooks than the Hawaii-based programme using 18/0 circle hooks (log odds ratio = 2.27, $P < 0.005$). Hooking severity (shallow, deep), observer programme (California, Hawaii) and hook-type (J, circle) were, hence, all correlated or confounded risk factors.

Estimated mortalities based on the decision matrix

Of the 29 tags, four tags never reported (14%, 95% bootstrap CI: 3 to 28%), eight tags reported between 1 and 30 DAL (range: 3 to 30 days, 27%, CI: 10 to 45%), nine tags reported between 31 and 60 DAL (range: 35 to 60 days, 31%, CI: 14 to 48%), and two tags reported between 61 and 90 DAL (range: 69 to 85, 9%, CI: 0 to 17%). Six turtles had recorded tracking duration longer than 90 days (range: 95 to 243 days, 21%, CI: 7 to 34%).

Based upon the injuries inferred from the hook data and DAL, it is inferred that four (55675, 55680, 55670, and 29682; see Table 3) of the eight turtles tagged in the group that reported between 1 and 30 DAL may have died as a result of their injuries. All of these turtles were deep-hooked and released to sea with hooks remaining in their digestive tracts. The tags on turtles 55675 and 55680 had less than 8 DAL, which is consistent with mortalities as a result of acute injuries as described previously. Turtles 55670 and 29682 had 26 and 30 DAL, respectively, and were both deep-hooked (ingested). These were included as possible mortalities based on the decision matrix criteria owing to the potential for acute injury. Because the shallow-hooked turtles in this DAL group were superficially hooked and the hooks were always removed, it is highly unlikely that any of them incurred infections that led to death within this

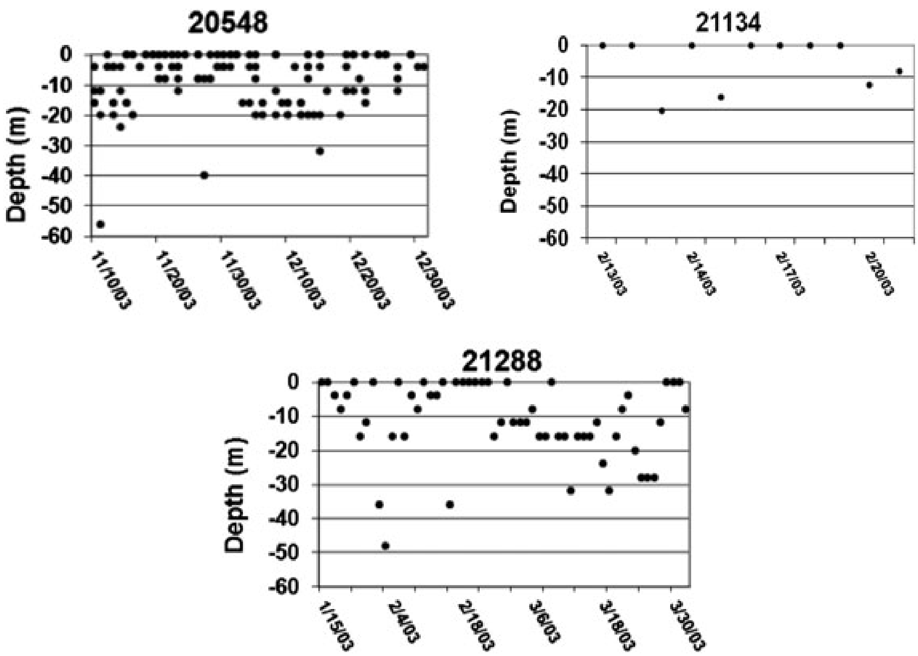

Figure 3. Depth data from three individual loggerhead turtles representative of the tagged group (n = 25) of turtles with PSATs that transmitted data. All suggest early PSAT shedding as evidenced by the lack of a deep descent immediately before tag release and initiation of transmissions at the sea surface

short time frame, unless the animal was unhealthy at the time of hooking. Based on the best available information for the turtles with between 1 and 30 DAL (n = 8), an estimated four individuals may have died in this time frame, with an estimated mortality rate of 50% (CI: 0–75%).

A total of nine turtles were reported between 31 and 60 DAL (Table 3). PSAT depth data indicated that all of these turtles generally remained within the top 40 m, with occasional deeper dives to approximately 60 m (Figure 3), with one exception. The turtle with tag 55667 (Figure 4) had been superficially shallow-hooked in the flipper. The mean depth of this turtle throughout the track was 9.4 m. This turtle had a final descent reported at over 190 m (35 DAL), which reflected a difference more than two times the turtle's mean depth. A liberal interpretation of the dive data alone (i.e. final reported descent at least twice as deep as the mean depth during DAL) compared with the other tracks presented in this group suggests a mortality occurred, yet it is unlikely to be a direct result of the external light injury sustained by the fishery interaction. There is an extremely low probability (based upon reports of turtles monitored in captivity over time; Parga, pers. comm.) that an external wound would develop into a secondary infection and cause septicaemia (whole body infection) during a 2-month time frame. Given the relatively shallow nature of the longline set (~60 m) and the ability of the hooked turtles to tow the branchline up to reach the surface to breathe and bask near the surface, the potential for hypoxia during longline haulback was ruled out. All of the other turtles in this DAL group were assumed to survive. Summarizing, the depth and DAL data suggest that one mortality occurred during this time frame, providing an estimated 11% mortality rate (CI: 0 to 33%).

There were only two turtles with a DAL between 61 and 90 days, and both were identified as probable mortalities. Data from tag 44201 suggest that this turtle died and sank 69 days after the longline interaction. Although the turtle did not sink to the preset 1200 m depth required for release, the depth and telemetry data indicate that the turtle made an uncharacteristically deeper and colder dive than usual just before the tag's release, which was interpreted as a probable sinking event (Figure 4). Before the final recorded depth >160 m, this turtle had remained within the top 60 m during the 69 day tracking period. This animal

Table 3. Details from 29 loggerhead sea turtles (*Caretta caretta*) incidentally caught in longline fishing gear and released alive. Days at liberty is the period between release and 4 days after transmission was first received from the tag. Observer programmes were from Hawaii or California. Tag types were Microwave Telemetry (MT) or Wildlife Computers (WC)

Tag #	Observer programme	Tag type	CCL (cm)	Tagging date	Days at liberty	Shallow or Deep (*inferred mortality)	Probable hook type (18/0 circle or 9/0 J)	Hooking details, hook removed Y/N?
13107	Hawaii	MT	74.5	29 Apr 02	3	Shallow	J	Jaw hooked, Y
55663	Hawaii	MT	62.0	19 Jan 06	4	Shallow	Circle	Flipper hooked, Y
55675	Hawaii	MT	66.0	17 Dec 05	5	Deep*	Circle	Ingested hook, N
55680	Hawaii	MT	61.0	30 Jan 06	7	Deep*	Circle	Ingested hook, N
55661	Hawaii	MT	64.5	10 Jan 06	13	Shallow	Circle	Shallow Jaw hooked, Y
55670	Hawaii	MT	84.0	5 Mar 06	26	Deep*	Circle	Ingested hook, N
55681	Hawaii	MT	61.0	24 Feb 05	30	Shallow	Circle	Shallow jaw hooked, Y
29682	Calif	WC	58.5	9 Nov 03	30	Deep*	J	Ingested hook, N
55667	Hawaii	MT	73.5	17 Mar 06	35	Shallow*	Circle	Flipper hooked, Y
55669	Hawaii	MT	59.0	14 Mar 06	42	Shallow	Circle	Shallow jaw hooked, Y
55678	Hawaii	MT	61.5	23 Feb 05	47	Shallow	Circle	Flipper hooked, Y
20548	Calif	WC	57.0	10 Nov 03	51	Shallow	J	Shallow mouth hooked, Y
55671	Hawaii	MT	58.0	18 Feb 05	53	Shallow	Circle	Entangled in line, Y
55659	Hawaii	MT	66.0	21 Feb 05	54	Shallow	Circle	Entangled in line, Y
20544	Calif	WC	67.5	27 Jan 04	55	Shallow	J	Flipper hooked, Y
21134	Calif	WC	40.0	13 Feb 03	55	Deep	J	Ingested hook, N
55668	Hawaii	MT	59.5	7 Jan 06	60	Shallow	Circle	Flipper hooked, Y
44201	Calif	MT	61.0	6 Jan 04	69	Deep*	J	Ingested hook, N
13193	Calif	WC	61.5	28 Jan 04	85	Deep*	J	Ingested hook, N
55662	Hawaii	MT	60.5	15 Nov 05	95	Shallow	Circle	Shallow jaw hooked, Y
44195	Hawaii	MT	60.5	17 Feb 05	127	Shallow	Circle	Flipper hooked, Y
22052	Calif	WC	65.5	11 Feb 03	148	Deep	J	Ingested hook, N
44193	Calif	MT	52.5	7 Jan 04	177	Deep	J	Ingested hook, N
21288	Calif	WC	62.0	15 Jan 03	192	Deep	J	Ingested hook, N
44196	Calif	MT	66.0	11 Jan 04	243	Deep	J	Ingested hook, N
22269	Calif	WC	64.5	2 Dec 02	--	Shallow	J	Flipper hooked, Y
21119	Calif	WC	73.0	4 Feb 04	--	Deep	J	Ingested hook, N
20780	Calif	WC	62.0	5 Feb 04	--	Deep	J	Ingested hook, N
46565	Hawaii	MT	54.0	27 Jan 05	--	Shallow	Circle	Shallow jaw hooked, Y

-- Non-reporting tags.

had ingested the hook, which was not removed before release, rendering it more likely to have died from injuries incurred during the fisheries interaction. The turtle with tag 13193 was deep-hooked (ingested), indicating an increased likelihood of death because of a secondary infection. A subjective interpretation of DAL, anatomical hooking and depth data suggest that mortality occurred for two turtles between 61 and 90 days post-release, reflecting an estimated 100% mortality rate.

Six transmitters reported DAL longer than 90 days (range: 91 to 243 days). Two tags with the shortest DALs in this group were superficially shallow-hooked, with the hooks removed before the turtles' release.

Overall, seven out of 25 turtles may have died after their release to sea, resulting in an overall mortality estimate of 28% (CI:16 to 52%). This represents a mortality rate only slightly higher than that assumed for natural survival, which is approximately 15–19% based on projection model estimates of annual survival for adult female North-west Atlantic loggerheads (0.8091 to 0.85, 95% CI = 0.77–0.84) (TEWG, 2009).

DISCUSSION

By combining PSAT depth and DAL data with anatomical hooking location, hook removal, and inferred injury from hooks that remained in the turtle, the post-release mortality of sea turtles is estimated to be 28% from 25 reporting tags. In the present study, 55% (6/11) of the deep-hooked turtles and 7% (1/14) of the shallow-hooked turtles were estimated to have died as a result of a fisheries interaction. The 28% mortality estimate from the present study should not be considered representative of the US Pacific longline fishery for swordfish, which has a lower estimated mortality rate owing to a lower incidence of deep-hooking and a higher rate of gear removal than for the

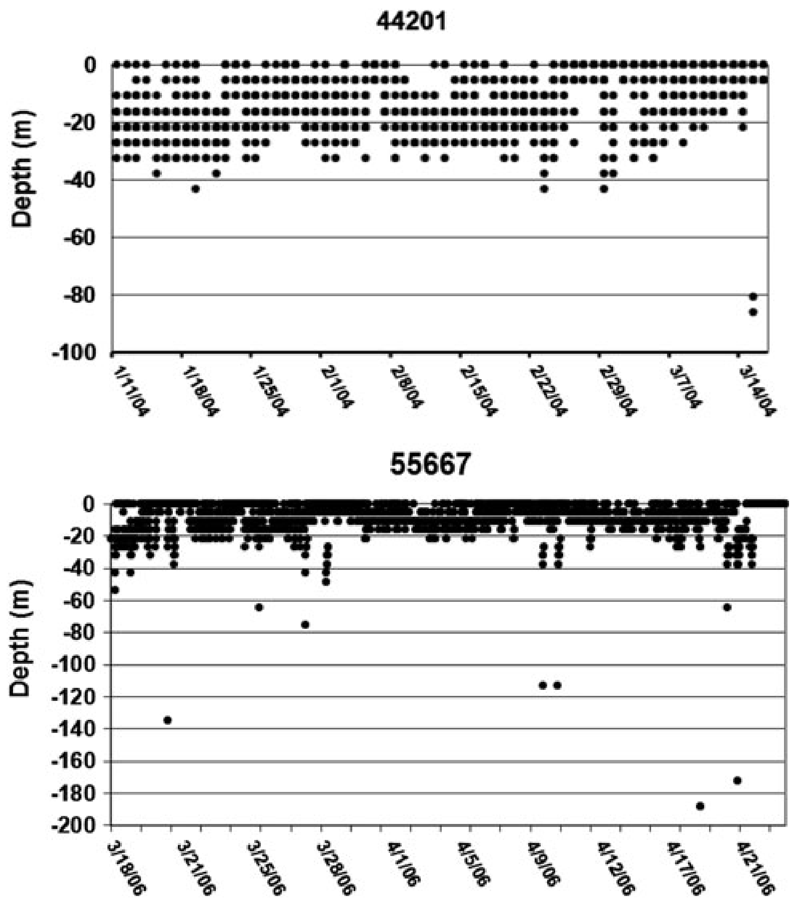

Figure 4. Depth data for tags 44201 and 55667, which reflect estimated mortality events because the final depth data reported was more than twice as deep as the mean depth during the days at liberty.

turtles used in this study (NMFS, 2012). Despite the promise of fail-safe mechanisms in the use of PSATs, we have no means to confirm that the prematurely detached tags indeed reflect mortality. This estimated rate does not account for differences in shallow or deep hooking, but rather was compiled from turtles with a range of interaction types, such as simple entanglement and release from line and hooking events, that resulted in turtles released with the hook remaining in their digestive system. These values are within the wide range reported in the NOAA NMFS guidance document for estimating post-release mortality of sea turtles released from longline gear, which is based largely on expert opinion combined with limited empirical data (Ryder *et al*., 2006). Specifically, post-release mortality estimates for hard-shell turtles range from 5% (for turtles entangled in the line with all gear removed) to 85% (for turtles that ingested the hook with the line trailing) (Ryder *et al*., 2006). The estimates provided herein are at the low end of the estimates, but are inclusive of all injury types. In addition, given that the turtles were handled and released with the utmost care and caution, these estimates may reflect post-release survival in a best-case scenario.

Estimates in this study are comparable with other estimates derived from a combination of methods. Based on size and age estimates for a number of global pelagic longline fisheries, Wallace *et al*. (2008) reported estimates of post-release mortality with information on turtle reproductive values to be between 0% and 42%. The estimated post-release mortality attributable to gear-induced injury for 40 PTT instrumented loggerheads caught on J hooks in the Hawaii-based pelagic swordfish longline fishery was 34% (CI: 22–45%) for deep-hooked turtles and 8% (95% CI: 0–21%) for shallow-hooked turtles within 1 week of post-release (Chaloupka *et al.*, 2004a).

Sasso and Epperly (2007) used 25 PSAT tagged loggerhead turtles in the North Atlantic to infer post-release mortalities in three groups (one in a control group and two released from longline gear). All turtles were shallow-hooked, although the hook type was not described. Only one loggerhead was inferred to have died post-release within 90 days, a time period which has previously been postulated to reduce confounding gear-induced mortality with natural mortality (Chaloupka *et al.*, 2004a). Similarly, only one shallow-hooked loggerhead was inferred to have died in the present study. Swimmer *et al.* (2006) deployed 14 PSAT tags on olive ridley sea turtles caught in eastern tropical Pacific longline fisheries and based on depth data inferred no mortalities attributable to gear-induced injury. In a recent study of juvenile loggerhead turtles tracked off the coast of Peru after their capture and release from longline fishing gear, Mangel *et al.* (2011) did not observe any differences in the habitat use or track duration of turtles as a function of injury score.

Based on the overall poor retention of tags and lack of clear descent depth data suggestive of mortality in the majority of cases, it is inferred that tag attachment failures and PSAT detachment malfunctions, which unfortunately cannot be distinguished, probably accounted for most of the detachments in this study. Musyl *et al.* (2011) identified potential PSAT failure modes in a 'fault tree' that summarized the potential sources of attachment and reporting failures. Given the prevalence of premature PSAT reporting among various taxonomic groups, all of this information must be considered when estimating the actual fate of an animal.

The pathological data and type of hooking injury were interpreted based on indications that it was highly unlikely that a previously healthy turtle would die from a lesion caused by a flipper hooking or light jaw hooking within an immediate time frame (i.e. less than 30 days). If an infection occurred in response to hooking, it is more likely that the turtle would die after several weeks or months. The potential for mortality during a longer post-release time frame is confounded by many factors, including secondary infections from the fishing event, natural mortality, and an increased potential for tag malfunction, which is known to increase in proportion to the duration of DAL (Hays *et al.*, 2007; Musyl *et al.*, 2011). In addition, there is the potential that a turtle may become subsequently hooked in fishing gear, which was not evaluated in this study. However, the horizontal data did not suggest differences in swim speeds that would have suggested a turtle was riding on a boat and not powering its own movements.

The exact role of hook shape on post-release mortality in turtles is unknown, however, a lower mortality rate has generally been assumed for turtles caught on circle hooks primarily because of the increased probability of a superficial hooking compared with deeper hookings more often associated with J hooks. There is a greater potential that a gut-hooked animal would suffer more severe injuries or a punctured vital organ, such as the stomach, heart, large vessels or the bronchi, in the turtles caught on J hooks. In this study, deep-hooked loggerheads were considerably more likely to be encountered by the California-based observer programme that uses 9/0 J hooks than by the Hawaii-based programme using 18/0 circle hooks. However, interpretations related to effects of hook type alone are limited because of their confounding effects with observer programme and associated fishery specifics between California and Hawaii fleets, as well as hooking type (deep vs. shallow). As an aside, the opportunity to breathe is the reason for very high survival rates of turtles caught in shallow set fisheries (Swimmer *et al.*, 2006), which was similar in this study in that no turtles were retrieved dead at haulback.

A limitation in this study is the term 'deep hooked' for injury category, as this is simply too broad from which to draw meaningful inferences or predictions, especially when sample sizes are also limited. Detailed categorization, such as location of hook point within body or mouth cavity may not be possible on board, but this limitation should be addressed. From a veterinary standpoint, the prognosis for an animal with a hook lodged mid-oesophagus or in the stomach is probably worse than with a hook lodged in a location distant from critical organs owing to the increased potential to perforate the stomach and cause coelomitis or perforate the heart, large vessels or trachea. A hook could perforate the stomach and cause coelomitis, perforate the heart, large vessels or trachea, or might pass through the intestines without causing problems. Onboard observers should more precisely differentiate where the hook is located to predict the degree of injury and likelihood of survival. Specifically, a more useful designation could be to record whether or not the shank can be seen when the mouth is fully open and the neck extended, or if it cannot be seen at all. Such observations and recordings could improve the accuracy estimates of the post-release mortality of turtles.

Recent research studies have aimed to overcome the challenges associated with post-release analyses and provide more confident estimates of survival of turtles after interactions with fishing gear. Despite these attempts, it remains extremely difficult to identify a post-interaction mortality with a high degree of certainty given a limited sample size. Differentiating the effects of tag failure or injury/death and speculating on the fate of a turtle based on its condition at release is subjective. Continued investment in the research and development of methods to improve credibility of estimates of turtle post-release mortality may be a priority for fisheries managers, yet it is unlikely that technological advances or increased funding would become available to greatly improve mortality estimation, and as such, degrees of uncertainty will remain a component to this type of work. In the interim, a turtle's rate of post-release survivorship can be greatly improved by use of safe-handling gear, such as dip nets, line cutters, de-hooking tools, followed by a gentle release to sea – all these measures can minimize a turtle's level of injury and increase probability of survival, thereby reducing the impacts of fisheries on sea turtle populations. These goals can be accomplished through outreach and education aimed directly at people such as boat captains, crew and on-board observers who handle turtles directly.

In this study, several approaches were combined to infer turtle mortality as a result of an interaction with longline fishing gear. The number of days at liberty in combination with anatomical hooking location, gear retained, and inferred injury was used to make reasonable estimates based on an understanding of hard-shell sea turtle physiology and function. Other limitations to this study include a small sample size, apparent frequent premature tag release, lack of definitive time frames regarding the effects of acute injury or secondary infection, and speculative assessment of these effects. We understand and acknowledge that estimation of post-release survival relies on multiple assumptions. However, this type of integrative, holistic approach may be required in order to assess the fate of released turtles based on limited data.

Additional variables to incorporate in this type of study include measures of stress in sea turtles after their interactions with fishing gear. For example, physiological stress, such as elevated levels of corticosterone and disruptions in blood biochemistry due to hypoxia and forced submergence, has previously been observed for sea turtles caught in fishing gear, such as trawls (Berkson, 1966) and gillnets (Snoddy *et al*., 2009). In the future, biochemical correlates of morbidity and mortality combined with tagging and anatomical hooking descriptions may provide more detailed assessments of survival. Additional assessments should include factors regarding handling. Specifically, the 'safe handling' of turtles, including the use of dip nets and line cutters to remove as much line as possible from a hooked or entangled turtle, can play a critical role in the eventual fate of turtles post-release. Meeting the goal of improving the probability of survival of turtles post-release to sea relies upon well-integrated and consistent fisheries policies and training both on local and global scales. In addition to fishery management plans in US waters, regional fisheries management organizations oversee the management of fisheries that are not confined to waters of a single nation. Among their tasks is to mitigate adverse effects of bycatch and discards (Gilman *et al*., 2012). As such, mandating measures to improve sea turtle survival rates, such as implementation of regional observer programmes and a requirement to maintain safe-handling gear on board, are useful steps towards minimizing marine ecosystem impacts of commercial fishing.

ACKNOWLEDGEMENTS

We thank the fisheries observers, coordinators, vessel owners and crew involved in this project. We are also grateful to C. Boggs, L. Nakamura, D. Lau and J. Sibert for extensive technical and administrative assistance. This project was funded by the University of Hawaii Pelagic Fisheries Research Program (Grant #658847) and the Pacific Islands Fisheries Science Center (NOAA, US National Marine Fisheries Service). All research was conducted in accordance with the protocols and handling guidelines set forth by the University of Hawaii Animal Care and Use Committee (IACUC Protocol #00-037-2). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA of any of its subdivisions.

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