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PATHOLOGY AND DISTRIBUTION OF SEA TURTLES LANDED AS BYCATCH IN THE HAWAII-BASED NORTH PACIFIC PELAGIC LONGLINE FISHERY

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ABSTRACT: We examined the gross and microscopic pathology and distribution of sea turtles that were landed as bycatch from the Hawaii, USA–based pelagic longline fishery and known to be forced submerged. Olive ridley turtles (*Lepidochelys olivacea*) composed the majority of animals examined, and hook-induced perforation of the esophagus was the most common gross lesion followed by perforation of oral structures (tongue, canthus) and of flippers. Gross pathology in the lungs suggestive of drowning was seen in 23 of 71 turtles. Considering only the external gross findings, the pathologist and the observer on board the longline vessel agreed on hook-induced lesions only 60% of the time thereby illustrating the limitations of depending on external examination alone to implicate hooking interactions or drowning as potential cause of sea turtle mortality. When comparing histology of drowned turtles to a control group of nondrowned turtles, the former had significantly more pulmonary edema, hemorrhage, and sloughed columnar epithelium. These microscopic changes may prove useful to diagnose suspected drowning in sea turtles where history of hooking or netting interactions is unknown.

Key words: Drowning, fisheries, green turtle, longline, olive ridley turtle, pathology, pelagic.

INTRODUCTION

Interactions between sea turtles and fisheries continue to receive attention because of their potential adverse demographic impacts (Spotila et al., 2000; Lewison and Crowder, 2007). Longline fisheries have generated particular concern because of their documented bycatch of seabirds and sea turtles (Lewison et al., 2004). Significant effort has been made to estimate short- and long-term mortality of turtles interacting with longline fisheries using mathematical modeling combined with satellite telemetry (McCracken, 2000; Bjorndal et al., 2003; Hays et al., 2003; Chaloupka et al., 2004; Swimmer et al., 2006; Sasso and Epperly, 2007), but these methods have limitations. Satellite telemetry typically measures time to cessation of signals from the instrument (Chaloupka et al., 2004) and has not clarified whether hooking of turtles significantly adversely affects long-term survival (Swimmer et al., 2006; Sasso and Epperly, 2007). Because most turtles landed and released alive in the Hawaii, USA–based North Pacific pelagic longline fishery are immature, certain demographic data such as sex ratios, which would be of value to modelers, cannot be assessed (McCracken, 2000; Work and Balazs, 2002). Finally, satellite telemetry and observer data provide little insight into the health of the pelagic-phase sea turtles.

Necropsies of turtles caught in pelagic longline fisheries are the only reliable method to ascertain cause of death and to shed light on the health status of pelagic turtles. For example, Work and Balazs (2002) examined a limited sample of turtles from the Hawaii-based North Pacific pelagic longline fishery and found a skewed sex ratio for seven olive ridley turtles (*Lepidochelys olivacea*) and significant nonhook-related pathology in two immature leatherback turtles (*Dermochelys coriacea*).

The Hawaii-based North Pacific pelagic longline fishery mainly targets swordfish and tuna. The depths at which hooks are set appear to significantly influence bycatch of sea turtles, with more turtles caught in shallow fisheries than deep-set fisheries (Gilman et al., 2006). In Hawaii, the tuna fishery has deep-set hooks whereas, to be economically viable, the swordfish fishery sets their hooks relatively shallower. Because of the risk that the Hawaii-based swordfish longline fishery poses to sea turtles, this fishery is monitored by a variety of on-board observers of the National Marine Fisheries Service (NMFS) who are tasked, in part, with documenting bycatch of sea turtles (Gilman et al., 2006). Prior to being deployed at sea, these observers undergo an intensive multi-week training program. Most turtles caught in the Hawaii-based pelagic swordfish longline fishery are alive and released after hook removal; however, some are landed dead (McCracken, 2000). After careful documentation of the circumstances surrounding the death of the turtle by the observer, the turtle carcass is stored frozen until direct return to Honolulu where a complete necropsy is performed (Work and Balazs, 2002).

Because of the circumstances surrounding forced submergence of sea turtles, the postmortem condition of the specimen is fresh, and turtles caught in pelagic longline fisheries provide a unique opportunity to document the morphologic changes associated with drowning in this group of animals. In human medicine, the diagnosis of drowning based on postmortem exam alone continues to provide significant challenges because of confounding factors such as decomposition and incomplete history surrounding discovery of the body (Timperman, 1972; Davis, 1986; Saukko and Knight, 2004; Lunetta and Modell, 2005). Furthermore, experimental models for this diagnosis are not completely satisfactory (Spitz and Silverman, 1969).

The organ most affected by drowning in humans is the lung, and although considerable data exist on the mechanisms and pathology of drowning in humans (Spitz and Silverman, 1969; Lauweryns, 1970; Timperman, 1972; Thompson, 1977; Davis, 1986; Saukko and Knight, 2004; Lunetta and Modell, 2005), similar data for animals, particularly marine fauna, are sparse (Knieriem and Hartmann, 2001). Systematically describing the gross and microscopic findings in sea turtles that died from drowning might be useful, particularly in instances where there is a weak or absent link between the presumed cause of drowning and the turtle. Hence, our objectives were to examine a 12-yr data set of necropsies done on sea turtles incidentally caught in the Hawaii-based North Pacific longline fishery to 1) evaluate their geographic and temporal distribution and 2) document the gross and microscopic morphologic changes in their lungs.

MATERIALS AND METHODS

Free-ranging marine turtles accidentally taken as bycatch (forced submergence) by the Hawaii-based North Pacific pelagic longline fishery between November 1996 and August 2008 were landed on commercial fishing vessels and evaluated for signs of life by observers employed by NMFS. Turtles that were judged to be dead by specific criteria (Balazs et al., 1995) were stored frozen (−20 C) and returned to Honolulu, Hawaii, USA, where we recorded weight to the nearest 0.1 kg and straight carapace length (SCL) to the nearest 0.1 cm. The spatial distribution of capture locations for turtles presented for necropsy was plotted by species using Arc Map 9.2 (ESRI, Redlands, California, USA). Turtles were classified as adult or immature based on SCL and gonad development. The cutoff measurements for adult condition of gonads was 82 cm for green turtles (NMFS and US Fish and Wildlife Service [USFWS], 1998a), 160 cm for leatherback turtles (NMFS and USFWS, 1998b), 90 cm for loggerhead turtles (NMFS and USFWS, 1998c), and 60 cm for olive ridley turtles (Zug et al., 2006).

Examinations of carcasses followed established protocols (Wolke and George, 1981; Work, 2002; Work and Balazs, 2002). Briefly, necropsies entailed a complete external and internal exam of all organ systems. Hooks encountered were classified as tuna, circle, offset tuna, or offset circle based on information provided by the on-board observer. Hooking in the turtle was classified as deep or light depending on whether the hook set beyond the glottis or rostral to the glottis, or set externally, respectively (Work and Balazs, 2002). Necropsy findings were categorized as those directly associated with longline activities (e.g., perforation, hemorrhage or pulmonary lesions) and those not directly associated with longline activities (e.g., old scars or presence of parasites). Lungs and airways were carefully examined for gross morphologic changes suggestive of drowning (Saukko and Knight, 2004; Lunetta and Modell, 2005), including presence of frothy material or seawater in bronchi or trachea, excessive fluid accumulations in small airways, or pleural effusion. Tissue samples including heart, lung, kidney, liver, spleen, brain, stomach, small intestines, skin, trachea, salt gland, gonad, thyroid, pancreas, and brain were fixed in 10% buffered formalin, sectioned at 5 µm, and stained with hematoxylin and eosin for microscopic examination.

Microscopic changes in the lungs in bycatch turtles were compared to a control group of seven frozen green turtles (*Chelonia mydas*) collected as strandings in Hawaii in good to excellent postmortem condition that died of known causes not associated with drowning. The presence or absence of the following microscopic lesions in the lungs were evaluated for each species: foreign bodies, hemorrhage in airways, intramural hemorrhage, fibrin in airways, sloughed columnar epithelium, sloughed squamous edicular epithelium, airway edema, and airway collapse. In addition, airway changes (edema or collapse) were each subjectively assigned a score ranging from 1 (0–30% airways affected), 2 (31–60% airways affected), or 3 (>60% airways affected). All slides were read blind; the control drowning specimens were pooled. Anatomical nomenclature of pulmonary structures followed that of Solomon and Purton (1984) and Fleetwood and Munnel (1996).

The chi-square test was used to test the relationship between gross observations made by observers and those of the pathologist. The Kruskal-Wallis analysis of variance was used to compare the body-condition index and SCL of olive ridleys among years. Mean numeric scores for pulmonary changes (airway edema, airway collapse) were compared for the two most numerous species (olive ridleys and green turtles) using the Mann-Whitney rank sum test. Alpha for all statistical comparisons was 0.05 with a Bonferonni correction (alpha/n) according to the number (n) of comparisons made (Rice, 1989).

RESULTS

Between November 1996 and August 2008, we examined 58 olive ridley, eight green, three leatherback, and two loggerhead turtles (*Caretta caretta*; Table 1). On average, we necropsied six (SD=4) turtles per year; submissions were above average in 2002, 2004, 2006, and 2007 (Fig. 1). No dead turtles were landed on vessels in 1997. Green turtles were mostly distributed in the southern portions of the Northern Pacific, leatherbacks were more central, loggerheads had a more northerly distribution, and olive ridleys were the

TABLE 1. Numbers of turtles by sex, age, body condition, hook type, and set, for four species of turtles necropsied from the Hawaii-based North Pacific pelagic longline fishery.

	Green	Leatherback	Loggerhead	Olive ridley
Age				
Adult	0	0	0	21
Immature	8	3	2	37
Total	8	3	2	58
Sex				
Female	4	3	2	45
Male	4	0	0	13
Hook type				
Circle	1	0	0	2
Offset circle	1	0	0	6
Offset tuna	3	2	2	26
Tuna	0	0	0	8
Unknown	3	0	0	4
Hook set				
Deep	1	0	2	16
Light	7	2	0	42

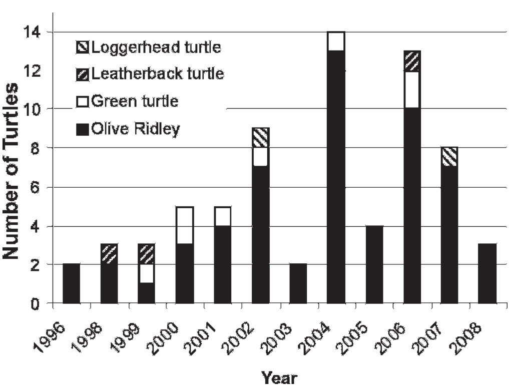

FIGURE 1. Number of turtles captured by the Hawaii-based North Pacific pelagic longline fishery and necropsied by year.

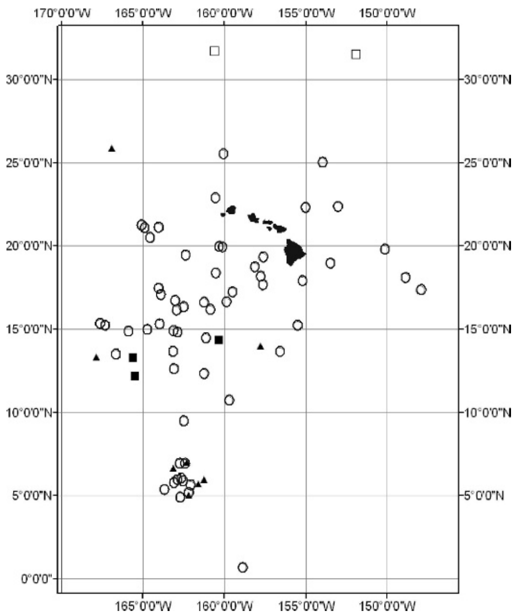

FIGURE 2. Plots of locations of olive ridley (circles), green (triangles), loggerhead (open squares), and leatherback turtles (dark squares) necropsied from the Hawaii-based North Pacific pelagic longline fishery and necropsied. The main Hawaiian Islands (black) are shown for perspective.

most widespread (Fig. 2). Immature turtles composed the majority of animals submitted for all species. Straight carapace length of olive ridleys did not differ significantly among years (data not shown). All animals were in fair to good body condition with adequate coelomic fat reserves.

Of the turtles with gross lesions, hook-induced perforation of the esophagus was most common (20/71) followed by perforation of oral structures (canthus, tongue; 14/71) and perforation of flippers (5/71). Twenty-three of 71 turtles (32%) had grossly visible lesions in the lungs or airways; of those 23, 15 had diffuse, red discoloration (three of which exuded large amounts of foam from small airways), five had large amounts of water in the trachea or bronchi, two had atelectactic lungs, and one had unilateral emphysema of the caudal left lung. Ancillary gross lesions associated with hooking included cloacal prolapse, reddening of the skin, or submandibular edema (seen in three turtles each) and internal hemorrhage in the coelomic cavity, lungs, muscles, pericardial sac, and liver (one turtle each). Sixty-five percent of olive ridleys and 50% of green turtles had one complete (or portions comprising a complete) recently ingested mackerel in the stomach; 8% of olive ridleys and 10% of green turtles had more than one mackerel in the stomach. One olive ridley had four mackerels in the stomach. The only other fish seen in stomach contents were small (1 cm) cowfish.

There was no significant agreement between anecdotal observer notes on hooking-induced lesions and necropsy findings on pathology. For example, of 65 cases where the longline observer noted a hook or entanglement in a turtle, the pathologist noted a lesion in the same area in only 39 (60%) of those cases. In contrast, in 36 cases where the pathologist noted a hook-induced lesion, the observer noted a similar finding in 32 (90%) of those cases. Finally, if the observer did not note any hook-induced lesions on a turtle, the pathologist agreed with this finding only 50% of the time. This lack of agreement did not differ whether hooking occurred in soft parts of the turtle where a lesion would presumably be more visible and hard parts where lesions may not be evident. For example, in 28 cases where observers and the pathologist disagreed, 22 (79%) were hookings in hard parts whereas in 43 cases where observers and the pathologist agreed, 20 (47%) were in hard parts; this was not statistically significant.

Compared to lungs of seven non-drowned turtles (Fig. 3A), lesions in the lungs of 71 drowned turtles were characterized by variable amounts of homogenous eosinophilic material within airways (edema), edicular septae, and perivascular connective tissues at times associated with collapse of airways (Fig. 3B). Small to moderate numbers of red cells or red cell fragments (hemorrhage) were within airways but much less commonly within

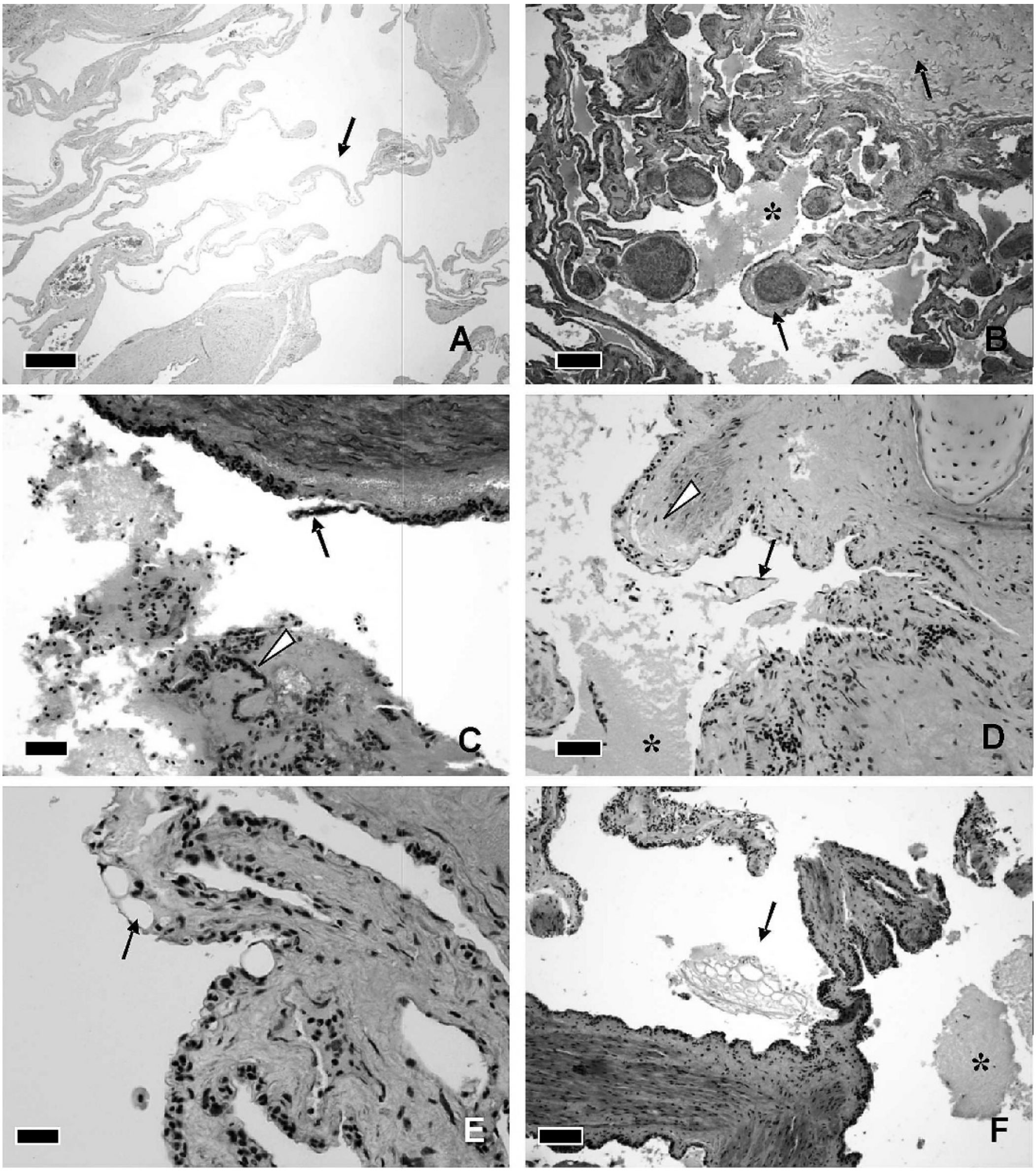

FIGURE 3. Lungs from green (A, D) and olive ridley (B, C, E, F) turtles. (A) Nondrowned turtle. Note spacious airways (ediculae) separated by interedicular septae consisting of smooth muscle, capillaries, and connective tissue. Bar=300 μm. (B) Drowned turtle. Note general collapse of airways, presence of eosinophilic material (asterisk) within airways, and marked infiltration of connective tissue spaces with similar eosinophilic material (arrows). Bar=100 μm. (C) Same turtle as B. Note columnar epithelium detaching from smooth muscle (arrow) and sheets of epithelium mixed with homogenous eosinophilic material and red cells within lumina of ediculae. Bar=50 μm. (D) Drowned turtle. Note sheets of squamous cells (black arrow) sloughing into lumen of ediculae mixed with clumps of homogenous eosinophilic material (asterisk). Similar material is dissecting between connective tissue spaces (white arrow). Bar=50 μm. (E) Drowned turtle. Note subepithelial vacuoles within interedicular septae (arrow). Bar=20 μm. (F) Drowned turtle. Note plant material within airway (arrow) and eosinophilic material in airway (asterisk). Bar=50 μm.

TABLE 2. Number of instances pulmonary lesions were observed in controls ($n=7$) versus drowned ($n=71$) comprising pooled olive ridley ($n=58$) versus green ($n=8$), leatherback ($n=3$), and loggerhead ($n=2$) turtles incidentally caught in the Hawaii-based North Pacific pelagic longline fishery.

	Green turtle	Leatherback turtle	Loggerhead turtle	Olive ridley	Control	Drown	Control (%)	Drowned (%)
Tissue changes								
Intramural edema	6	2	2	37	0	47	0	64
Intramural hemorrhage	0	1	0	1	0	2	0	3
Airway changes								
Airway edema	8	1	2	53	0	64	0	88
Fibrin in airways	4	1	0	27	0	32	0	44
Sloughed bronchiolar epithelium	3	0	1	20	0	24	0	33
Airway hemorrhage	5	2	1	37	1	45	14	62
Collapsed airways	4	1	0	8	0	13	0	18
Sloughed edicular epithelium	4	0	0	5	2	9	29	12
Subepithelial vacuolation	0	0	0	2	0	2	0	3
Foreign bodies	0	0	0	3	0	3	0	4

edicular septae and perivascular connective tissues. Occasional clumps of fibrin were present within airways as were variably sized clumps of columnar epithelium characterized by a cuboidal ciliated cell with a large nucleus and basophilic cytoplasm (Fig. 3C). Sloughed squamous edicular epithelium was less common and exemplified by squamous to fusiform cells found isolated or in sheets, either floating or associated with edicular septae (Fig. 3D). Variably sized subepithelial vacuoles were present in ediculae (Fig. 3E). Foreign bodies were rarely seen and comprised isolated clumps of material with cell walls (plant material of unknown origin) and unidentified basophilic round structures (Fig. 3F). Edema of the airways associated with hemorrhage and sloughed columnar epithelium were the most common microscopic findings in lungs of drowned turtles. In nondrowned control turtles, mild airway hemorrhage was seen but was less frequent than for drowned turtles. Sloughed squamous edicular epithelium was more commonly seen in nondrowned turtles (Table 2). Overall mean (SD) scores for airway edema or collapse for drowned turtles were 1.4 (0.8) and 0.3 (0.8), respectively. No significant difference was seen between olive ridley and green turtles in mean severity scores for tissue or airway edema or airway collapse (data not shown). Incidental microscopic findings in longline turtles included mild inflammatory cell infiltrates in the stomach, skin, lungs, liver, kidney, and spleen not associated with organisms. We saw no evidence of massive internal hemorrhage secondary to hook perforation.

DISCUSSION

Peak numbers of olive ridley turtle carcass submissions occurred in 2002, 2004, 2006, and 2007. Although our study was not designed to answer why this occurred, we speculate that fishing effort, seasonality, or fishing methods may have been the cause. In 2001, the Hawaii-based North Pacific pelagic longline shallow-set swordfish fishery was closed because of evidence that shallow-set hooks led to more loggerhead turtles being caught (Gilman et al., 2006). This left the deep-set fishery operational, and may have had the unintended result of increasing bycatch of olive ridleys that tend to dive deeper than loggerhead turtles (Polovina et al., 2003). However, this would not explain the decrease in numbers in intervening years. The geographic distribution of sea turtles is most likely explained by foraging activities linked with currents that often overlap longline fishing areas (Polovina et al., 2000; Polovina et al., 2004).

As in previous studies (Work and Balazs, 2002), the majority of sea turtles that were landed dead in the Hawaii-based pelagic longline fishery were immature. This may reflect the life history of the species in that the pelagic phase is dominated by immature turtles (Bjorndal et al., 2003), whereas adults predominate in the benthic phase (near nesting beaches and foraging grounds). Alternatively, it may mean that immature turtles are disproportionately susceptible to being hooked and landed on longline boats, although in the case of loggerheads, larger animals predominate (Watson et al., 2005). Green turtles are able to withstand prolonged periods of submergence (Berkson, 1966), but will suffer pulmonary collapse at pressures greater or equal to 19 atmospheres (Berkson, 1967). Lutcavage and Lutz (1991) hypothesized that in loggerheads, aerobic respiration limits were longer for voluntary versus forced dives and that immature turtles may have a lower tolerance than adults to conditions of forced submergence.

In contrast to earlier studies in which 7/7 olive ridley sea turtles were females (Work and Balazs, 2002), we saw a sex ratio approaching 1:1 for olive ridley turtles. This finding probably reflects the larger sample size of this study. The sex ratio of green turtles found in this study corroborates that of Wibbels et al. (1993) who found a sex ratio close to 1:1 in benthic, immature Hawaiian green turtles as determined by testosterone assays and close to 1:1 in stranded green turtles in Hawaii as determined by necropsy (Chaloupka et al., 2008). In contrast, Limpus et al. (1994), using fiberoptic examination of gonads, found a female-biased sex ratio in green turtles in eastern Australia. Little data exist on natural sex ratios of olive ridley turtles, so it is difficult to compare findings from this study with those of experimental studies.

Presence of airway edema and froth exuding from the airways along with waterlogging are common gross findings in drowned humans; however, these findings are not universal. Lunetta et al. (2002) found external foam in only 17% of drowning cases and foam in lung airways in 46%. In contrast, in our study, airway frothing was rarely seen on necropsy in turtles and never documented by the on-board observer. This may be due in part to postmortem dissipation of foam (Auer and Mottonen, 1998), although this would not explain the presence of foam in airways of three turtles. At necropsy, seawater was found in the airways of five (7%) turtles and frothy edema in three (4%). Wolke and George (1981) noted that, although suggestive, froth in the lungs and airways of sea turtles should not be considered diagnostic of drowning. Thus, it appears that gross findings in the lungs of sea turtles may not be as useful as in humans for diagnosis of drowning. Perhaps sea turtles are more prone to "dry lung," or drowning secondary to laryngospasm that prevents entry of liquids into the lungs; reflex cardiac arrest; or reabsorption of fluids from the lung into the circulation (Lunetta et al., 2002; Lunetta and Modell, 2005). In humans, dry-lung drowning manifests in 10–15% of cases (Lunetta and Modell, 2005).

In terrestrial mammals, the microscopic hallmarks of drowning in the lungs include intra-alveolar edema with thinning, distension, and rupture of interalveolar septae (Timperman, 1972; Lunetta and Modell, 2005). In marine mammals, the changes are similar; however, the degree of rupture of interalveolar septae is not as severe, presumably because the lungs of marine mammals have a stronger pleura and more cartilage support (Knieriem and Hartmann, 2001). Marine turtles showed lesions that were similar to those described for marine mammals, except that rupture of tissues was not observed. Like Knieriem and Hartmann (2001), we suspect anatomy plays a role. Unlike mammals that have alveoli, reptilian lungs have ediculae bordered by smooth muscle and connective tissue sandwiched between two capillary walls (Solomon and Purton, 1984). This particular lung morphology and the great elasticity of the tissues probably prevent the mechanical tissue damage to the respiratory walls seen in mammals. The respiratory anatomy of sea turtles, consisting of large amounts of solid tissues and a great blood supply (Valente et al., 2007), may also explain the extensive tissue edema seen in drowned turtles. Disagreement exists on the value of histopathology for diagnosing drowning in humans (Saukko and Knight, 2004), so the wisest application of the findings of this study in sea turtles would be to validate them in blind trials when cases of drowning are suspected, particularly where legal action may be necessary.

Other lesions in turtles (sloughing of columnar epithelium) have not been documented in mammals and may reflect the mechanics of water inhalation in sea turtles' lungs. Collapse of airways may be a result of pressures to which animals are subjected; the target depths of hooks on which these turtles were caught ranged from 50 m to 200 m. In contrast to humans suspected of drowning, we saw no diatoms in any of the lungs of drowned turtles. In humans, the presence of diatoms as a diagnostic marker of drowning has a mixed record, with some investigators advocating its use and others not (Timperman, 1972; Davis, 1986; Pachar and Cameron, 1993). In the case of turtles, diatoms seem to hold no value in diagnosis of drowning; however, to definitively assess this would require the use of more comprehensive methods to examine organs for diatoms, such as digestion and quantification (Lunetta and Modell, 2005). Even so, the utility of doing this is questionable in an animal that lives its entire life in a diatom-rich environment; sorting out whether diatoms are antemortem or postmortem in such a situation would be challenging.

Based on our comparative observations of lungs in sea turtles that were frozen but known not to have drowned, and the postmortem condition of turtles examined in this study (good to excellent), we think it is highly unlikely that the changes we documented in drowned sea turtles were postmortem decomposition or preservation artifacts due to freezing. Sloughed squamous edicular epithelium may be one such artifact as this was found more commonly in nondrowned turtles. Other lesions were considered minor or described elsewhere (Work and Balazs, 2002). Evidence of infection with vascular flukes was rare (Work et al., 2005) and no evidence of fibropapillomatosis (tumors) was seen (Work et al., 2004). Although an ideal test for comparing drowned to nondrowned turtles would involve examination of freshly preserved nonfrozen samples from pelagic turtles found dead from causes other than drowning, the limitations of the situation outlined in this study (pelagic longlines, vast distances from diagnostic facilities) make this unrealistic.

The lack of agreement between the gross external finding by the pathologist and the observations of the on-board observer highlight the limitations of external observations alone to document hooking interactions in sea turtles. This problem has been well documented in humans where the diagnosis of drowning is made by a combination of a careful documentation of history surrounding the death along with postmortem and laboratory examination (Timperman, 1972; Davis, 1986). In the case of sea turtles, the sensitivity of a gross external examination only to confirm hooking interaction and drowning (i.e., probability that the pathologist noted a lesion that the observer noted as a lesion) was only 60%. In contrast, the predictive value of pathologic exams (i.e., probability that the observer noted a lesion that the pathologist noted) was high (90%). Statistically, this was regardless of whether turtles were hooked in hard parts only.

The presence of one to multiple recently ingested mackerel in stomachs of green and olive ridley turtles has two possible explanations. First, some turtles of these two species are habituated to foraging on multiple longline baited hooks that are each typically baited with a single mackerel. Fish baits tend to come off the hook when foraged upon by sea turtles (Gilman et al., 2006). Alternatively, turtles scavenge bait that may have been incidentally thrown overboard. Pelagic-phase green and olive ridley turtles are known to naturally feed mainly on pyrosomes and small crustaceans (NMFS and USFWS, 1998a; Parker and Balazs, 2005). These organisms, in addition to barnacles, cowfish, and pelagic snails composed a majority of the stomach contents of olive ridley and green turtles in this study.

As in human medicine, the diagnosis of drowning in sea turtles is made through a combination of careful history and postmortem examination. In cases where evident gross lesions are present, pathology, with its high predictive value, will help confirm the diagnosis. Histopathology can bolster this diagnosis because a significant percentage (>50%) of turtles that suffer drowning will also manifest edema, hemorrhage, and sloughed columnar epithelium in the airways. Thus, for turtles in good postmortem condition, observer documentation concomitant with gross and microscopic pathology should give a fairly robust confirmation of drowning associated with hook-and-line and net interactions.

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