



Predation of satellite-tagged juvenile loggerhead turtles *Caretta caretta* in the Northwest Atlantic Ocean

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ABSTRACT: We present evidence of predator interactions with 8 juvenile loggerhead sea turtles *Caretta caretta* equipped with pop-up satellite archival transmitting tags (PSATs) following incidental capture in the Northwest Atlantic. Ingestion of PSATs occurred up to 5 mo after tagging and was identified by an abrupt change in depth distribution, a stabilization and/or increase in ambient temperature and a marked drop in light levels to near zero, with cessation of diel light level cycling. In some cases, following expulsion from the digestive tract of predators, positively buoyant PSATs descended to the sea floor or beyond the programmed release depth threshold (1800 m), indicating that they remained tethered to the indigestible carapaces of turtles and that the entire turtle was originally consumed. PSAT data, combined with the sudden termination of satellite uplinks from 2 loggerheads also equipped with platform transmitting terminals, provided additional evidence of whole-turtle predation. PSAT data indicated that both endothermic and ectothermic sharks ingested tags. Based on PSAT-logged temperature data, dive patterns and geographic distribution, the following shark species were considered as candidate predators: white, porbeagle, shortfin mako, tiger and blue. This study represents the first analysis of data collected by loggerhead turtle PSATs inside predators. The results expand the list of shark species known to prey on large juvenile loggerheads and point to the importance of acknowledging predation as an important source of mortality for loggerhead turtles in the Northwest Atlantic Ocean.

KEY WORDS: Loggerhead turtle · Predation · Shark · PSAT · Pop-up · Tether

1. INTRODUCTION

Application of electronic tags to wildlife facilitates studying behaviour *in situ* and is commonly used to remotely monitor movements and collect environmental data. A diverse suite of biologging instruments now exist, from archival data recorders equipped with sensors to measure depth, temperature and salinity, to satellite-linked transmitters which facilitate long-term terrestrial and marine animal tracking. While deployment of biotelemetry instru-

mentation has contributed much to our understanding of organismal biology, there can be associated costs to tagged animals. Enhanced risk of predation as a result of tagging is one of the least studied topics in the tagging literature (Jepsen et al. 2015). With fish, additional drag from tethered tags may decrease the ability of prey to escape, or the shape, colour and movement of these instruments may increase visibility to predators (Jepsen et al. 2015), potentially functioning as lures. Animals other than fish also experience tagging effects, such as king penguins *Aptenodytes*

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patagonicus tagged with flipper bands which have a significantly higher mortality rate than untagged individuals, linked, in part, to reduced swimming efficiency (Saraux et al. 2011). Ultimately, fitness-related effects and predation susceptibility are normally positively correlated. For example, Ross & McCormick (1981) showed that externally radio-tagged fish were more vulnerable to predation than controls. However, there are exceptions: Janak et al. (2012) reported no difference in predator avoidance between untagged and externally tagged juvenile chinook salmon *Oncorhynchus tshawytscha*.

Pop-up satellite archival transmitting tags (PSATs) present an option for studying mortality of marine animals, including post-release mortality of species targeted in recreational fisheries and those incidentally caught in commercial fisheries (e.g. Sasso & Epperly 2007, Tracey et al. 2016, Orbesen et al. 2019, Schaefer et al. 2019). These tethered tags can also reveal evidence of predation. However, distinguishing natural predation from tag-related predation can be challenging (Cosgrove et al. 2015, Jepsen et al. 2015). Studies have reported predation of PSATs on American eels *Anguilla rostrata* (Béguer-Pon et al. 2012), Atlantic salmon *Salmo salar* and chinook salmon (Lacroix 2014, Seitz et al. 2019, Strøm et al. 2019), tuna (*Thunnus alalunga*, *T. maccoyii*) (Cosgrove et al. 2015, Tracey et al. 2016), opah *Lampris guttatus* and white marlin *Tetrapturus albidus* (Kerstetter et al. 2004). In most cases, ingestion of the tag is presumed to be incidental, accompanying predation of the tagged animal itself; however, it is also possible that the tag itself may be independently targeted and consumed (Rogers et al. 2017).

Sea turtles are regularly preyed upon by tiger sharks *Galeocerdo cuvier* (Witzell 1987, Lowe et al. 1996, Bornatowski et al. 2012, Lea et al. 2015). Other instances of sea turtle predation have been documented among bull sharks *Carcharhinus leucas* (Cliff & Dudley 1991, Heithaus et al. 2008) and white sharks *Carcharodon carcharias*, which are capable of swallowing whole loggerhead turtles *Caretta caretta* (ca. 60 cm) (Fergusson et al. 2000) and have teeth designed for cutting through hard objects (like turtle shells) with force (Long 1996). The shortfin mako shark *Isurus oxyrinchus* is another recognized predator of sea turtles, having been documented consuming a ~40 cm (curved carapace length) olive ridley turtle *Lepidochelys olivacea* (Carranza et al. 2006). Sea turtles are also consumed by marine mammals such as killer whales *Orcinus orca* and Mediterranean monk seals *Monachus monachus*, although such instances are uncommon (Fertl & Fulling 2007). Most

of the information on turtle–predator interactions is anecdotal, derived from predator stomach content analyses (Fergusson et al. 2000), or inferred from injury patterns consistent with predation (Long 1996, Archibald & James 2018). Probable predation has been mentioned in survivorship studies of sea turtles equipped with PSAT tags (Sasso et al. 2011, Maxwell et al. 2018), but instances of predation were not analysed or discussed in any detail.

Satellite-linked tags were attached to loggerhead turtles in Atlantic Canada as part of a broader study of loggerhead turtle biology and threats (authors' unpublished data). Sudden changes in depth, temperature and light data patterns in a subset of these tags near the end of tracking became apparent during a preliminary review of the data, consistent with potential ingestion by large marine predators, prompting further investigation. Here we present the results of detailed analyses of the corresponding tag data sets; describe predation events, tag retention times in predators and tag expulsion locations; and use depth and temperature data to identify probable predator species.

2. MATERIALS AND METHODS

2.1. Tagging

From 2011 to 2018, 62 juvenile loggerhead sea turtles that were incidentally captured in pelagic long-line fisheries targeting tunas and swordfish in Canadian waters were boarded with a dip net and tagged with PSATs (PAT-Mk10, Mini-PAT, or SPLASH323-B; Wildlife Computers), attached by a ~20 cm tether to the posterior margin of the carapace following the protocol of Epperly et al. (2007). Embedded hooks were not removed. PSATs continuously sampled and archived depth and temperature data at a 10 s sampling interval. To facilitate data transmission at the time of tag release via the Argos satellite-based location and data collection system (www.argos-system.org/), these data were then compressed into 6 h histogram summaries of time at depth (14 depth ranges spanning 0 to >200 m); maximum dive depth (14 depth ranges spanning 0 to >200 m); time at temperature (14 temperature ranges, spanning 8 to >32°C); and relative light level. Minimum and maximum temperatures observed at different depths in the 6 h binning period were also reported. A 6 h binning period provides sufficient resolution for differentiating between day and night cycles. Within each 6 h bin, the percentage of time spent at each depth, tem-

perature and light level range is collected. Such 6 h bins have been used to analyse diving behaviour of immature loggerheads in the Azores (Chambault et al. 2019). In the present study, tags were attached and scheduled to release after a programmed period ranging from 120 to 365 d. Release was also triggered if the tag spent 4 or 8 d (depending on programming) at a constant depth (± 1 m), or if it descended to a maximum depth threshold of 1800 m. At release, tags detached, floated to the surface and transmitted archived data to the Argos system, which continued to receive data and estimated tag locations through to tag battery failure. Data recovered through the Argos system were decoded using the tag manufacturer's data analysis program (Wildlife Computers).

To facilitate daily opportunistic acquisition of near real-time locations and tag sensor data through the Argos system, a subsample ($n = 7$) of turtles were also tagged with platform transmitting terminals (PTTs; Wildlife Computers) epoxied to the carapace. Unlike PSATs, which are programmed to transmit archived data only at pop-off, PTTs transmit (and thereby enable geolocation) throughout the tag deployment. When deployed with PSATs, PTTs can help validate tag predation events (i.e. time during which PSATs are in the gastrointestinal tracts of predators) and corroborate inference around whole turtle predation.

2.2. Evidence of predation

The average amount of time turtles spent at the surface and the maximum daily dive depth were examined across the time series histogram data of each tag to identify sudden changes in dive patterns and/or to detect abnormal behaviour, such as atypical (or biologically impossible) depth use, or increased/decreased time spent at the surface. Turtle fate was determined by examining the light, depth and temperature records. Mortality was identified when a turtle exhibited a change in diving behaviour followed by the turtle sinking and the tag remaining at a constant depth for 4–8 d (a programmed premature release criterion), or when the tag descended to 1800 m (a programmed premature release criterion), followed by the tag floating at the surface for 4–8 d. A predation event was evidenced by an abrupt change in dive depths and light levels, accompanied by temperature change.

In most cases of predation, it is challenging, if not impossible, to determine whether the entire turtle was predated, or just the tag was ingested. However, the PSAT itself is positively buoyant, allowing it to float to the surface upon release from the turtle,

whereas dead turtles are initially negatively buoyant. Therefore, if a PSAT sinks to the programmed release threshold depth after being expelled from the predator, this indicates that it is still attached to the carapace and that the tagged turtle was predated. In contrast, if the tag immediately floats to the surface upon expulsion from a predator it is not possible to conclude if the tagged turtle was initially ingested and the tag detached before it was expelled, or if only the tag was ingested and expelled.

2.3. Predator classification

By comparing the tagging and tag release locations in the present study to known distributions of predator species and investigating any previous reports of these same predators consuming juvenile loggerheads, the number of potential predators was reduced. While most predators have the potential to consume a PSAT, only some have a large enough gape to consume all, or part of a turtle. Potential candidates in both cases are previously identified predators of sea turtles (white shark, tiger shark, bull shark, shortfin mako) (Carranza et al. 2006, Heithaus et al. 2008). Other sharks which have not been previously identified in predatory interactions with sea turtles include the porbeagle shark *Lamna nasus*, blue shark *Prionace glauca* and common thresher shark *Alopias vulpinus*. For details used to identify predators, see Table S1 at www.int-res.com/articles/suppl/n046p279_supp.pdf.

While PSAT temperature data normally reflect the ambient ocean temperature of the tagged turtle, in instances of tag ingestion, these data instead reflect the body temperature of the predator. Therefore, temperature data after ingestion (and before tag expulsion) were used as an indicator of the thermal physiology of the predator and were then applied to classify predators as probable ectothermic fish, endothermic fish or marine mammals. When the temperature of the tag did not differ from ambient, the predator was classified as an ectothermic fish (Seitz et al. 2019, Strøm et al. 2019). By contrast, a rapid increase in (and later sustained) ambient temperature following ingestion indicated an endothermic predator, but the extent to which this occurred helped differentiate marine mammals (i.e. temperature greater than $\sim 30^{\circ}\text{C}$; Melero et al. 2015) from endothermic fish.

As some marine predators exhibit strong diel vertical migration (DVM) patterns, the Wilcoxon test was used to determine if there were significant differences in day versus night mean maximum depth of

ingested PSATs. Depth distributions during day and night periods were also plotted to detect patterns associated with DVM. With the 6 h bin summaries, day was 06:00–18:00 h and night was 18:00–06:00 h. Consistent with related studies of other marine species (Béguer-Pon et al. 2012, Lacroix 2014, Cosgrove et al. 2015), the present analysis also adopted the use of thermal excess, or the difference between ambient water temperature and stomach temperature, to distinguish further between probable predators.

3. RESULTS

3.1. Evidence of predation

Data from 8 of 62 (0.13) PSATs deployed on juvenile loggerhead turtles were consistent with ingestion of the tag, or tagged turtle predation (Fig. 1). In each case, the predation event was identified by an abrupt change in depth distribution, a stabilization and/or increase in ambient temperature and, perhaps most telling, a marked drop in light levels plateauing near zero, indicating the cessation of diel light level cycling following ingestion (Fig. 1). Predation occurred between 8 and 135 d (mean \pm SD: 67.1 \pm 44.3 d) after tagging, and the predation event lasted between 3 and 44 d (16.9 \pm 12.3 d) (Table 1).

For all tags, the mean maximum temperature during the predation event was significantly different than the mean maximum temperature 2 wk leading up to predation (Table 2, Fig. 2). Prior to predation, tag data exhibited diel oscillations in light levels and temperature decreases when turtles dove to deeper depths. Changes in dive depths were also observed during the predation event, but the temperature record no longer changed with depth, even when dive depths were clearly much deeper than those made by live turtles (Fig. 1). The mean daily maximum depth of the predation event was significantly different from the mean daily maximum depth observed pre-predation for all tags, except 129589 and 148996 (Table 2). The percentage of time spent at the surface was lower during all predation events compared to pre-predation, and the difference was significant in 6 cases (Table 2; note that 1 tag had a sensor error that precluded calculation of surface time). There was some evidence of earlier (healed) interactions with sharks prior to PSAT deployments: fisheries observers recorded instances of shark bites on 3 juvenile loggerheads tagged in this study (Fig. S1).

Post predation, regular daily day and night light level fluctuations in PSAT data records resumed (Fig. 1). After being expelled from the predator, 6 PSATs (109810, 120011, 129589, 148991, 148996, 149004) floated to the surface (Fig. 1). Tag 109816 remained at 176 m for 8 d until the programmed premature release criterion related to constant depth was met, triggering the tag to detach and float to the surface (Fig. 1). Bottom depth registered by the tag was consistent with the bathymetric range in the corresponding area (Loder et al. 1992). Tag 148998 sank to the programmed release depth threshold of 1800 m before popping off (Fig. 1).

3.2. Turtle fates

In 4 turtles, it was evident that the entire turtle, not just the PSAT, was predated. Tags 109816 and 148998 sank before returning to the surface (Fig. 1). In each case, had only the tag been ingested, it would have floated to the surface upon being expelled. Instead, one turtle died and sank to a constant depth and the other descended to a threshold release depth of 1800 m (beyond the diving capacity of this species), which caused the tag to detach (Fig. 1). During the time these tags were sinking, and for 1 tag, the time it spent at constant depth, the temperature record was very cold (Fig. 1), indicating that the turtles were expelled from the predator.

The 2 loggerheads double-tagged with a PSAT and a PTT also presented strong evidence of predation involving the entire turtle. In both cases, the PTT ceased surface transmissions (was no longer detected by the Argos satellite system) the same day the PSAT data indicated predation had occurred. For the 4 other ingested tags, the fate of each corresponding turtle cannot be determined.

3.3. Predator classification

All tags released from turtles offshore, beyond the 1000 m isobath (Fig. 3). The temperature data from the PSATs suggest that they were consumed by ectothermic and endothermic fish. One tag did not exhibit a large increase in temperature; instead the temperature remained stable, consistent with ingestion by an ectothermic fish (129589; Fig. 1). Most of the tags exhibited an increase and stabilization in temperature, with temperature never exceeding 30°C (109810, 120011, 148991, 148998, 149004), suggesting ingestion by an endothermic predator (Fig. 1).

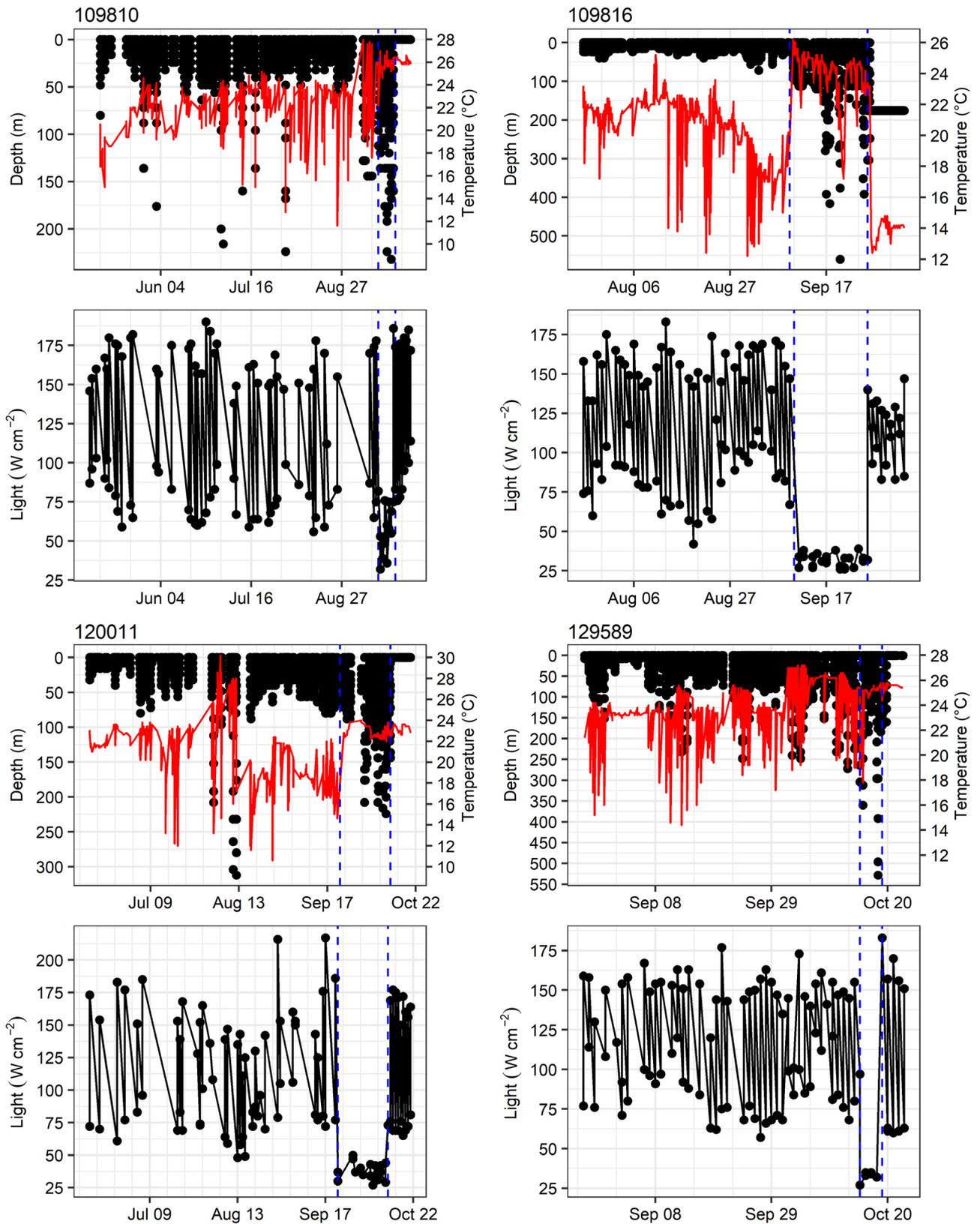


Fig. 1. Depth (black points) and temperature (red lines), and light levels recorded by pop-up satellite archival transmitting tags (PSATs) on 8 predated loggerhead turtles. Blue dashed vertical lines indicate the predation event

Fig. 1 continued on next page

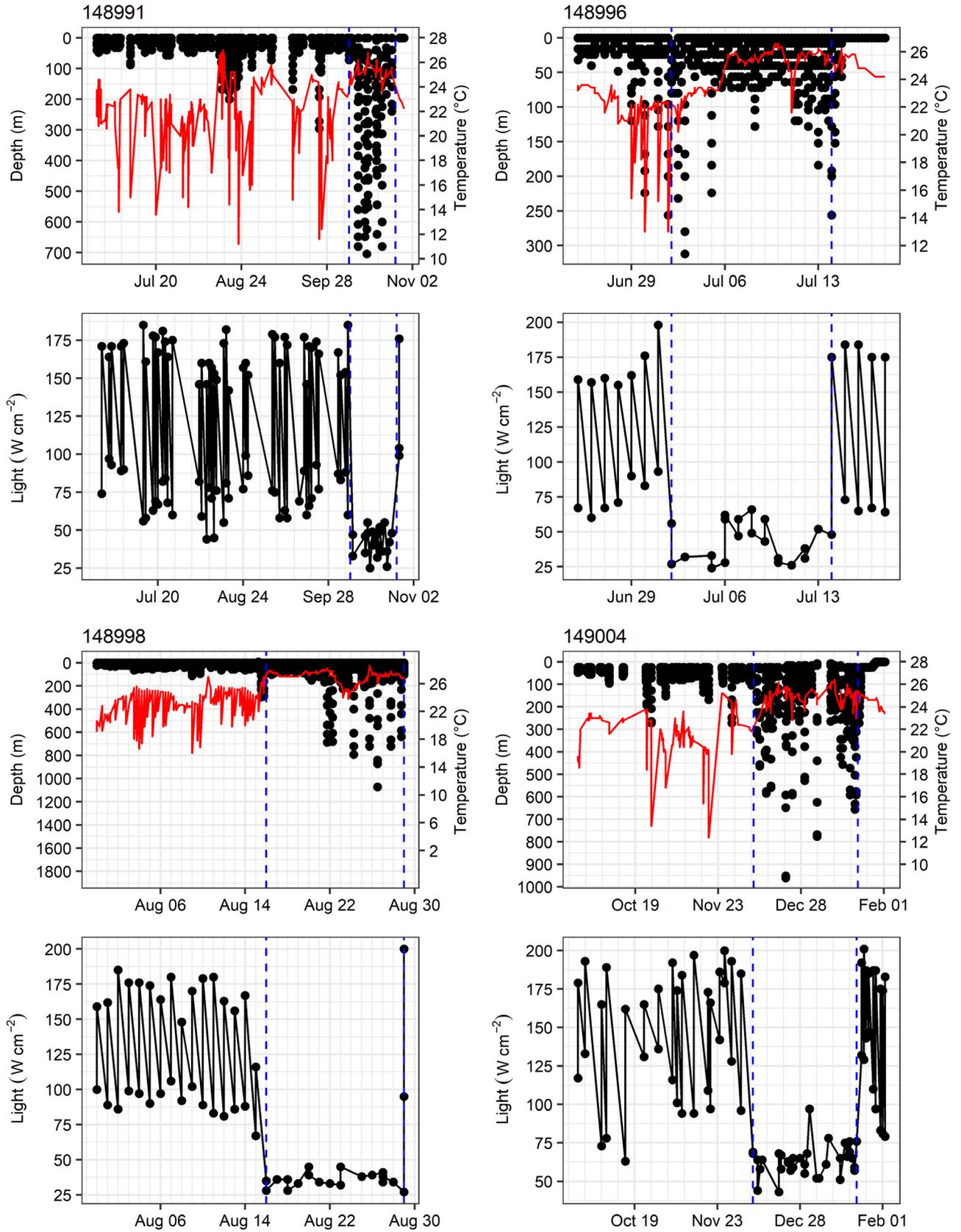


Fig. 1 (continued)

Table 1. Pop-up satellite archival transmitting tag (PSAT) types, curved carapace width (CCW) and curved carapace length (CCL) in cm, deployment date, release date, days since deployment to predation date, predation date and length of tag retention by the predator (d) for the loggerhead turtles in this study. Dates are month/day/year

ID	Tag type	CCW	CCL	Deployment date – release date	Days since deployment	Predation date	Retention (d)
109810	PAT	63.0	64.0	05/01/2012 – 09/28/2012	135	09/13/2012	8
109816	PAT	53.5	57.3	07/25/2012 – 10/04/2012	46	09/09/2012	16
120011	PAT	65.0	65.0	06/14/2012 – 10/20/2012	100	09/22/2012	20
129589	PAT	71.4	69.2	08/25/2014 – 10/23/2014	51	10/15/2014	3
148991	Mini-PAT and PTT	64.0	69.0	06/25/2015 – 10/31/2015	104	10/07/2015	19
148996	Mini-PAT and PTT	70.0	70.0	06/24/2015 – 07/18/2015	8	07/02/2015	12
148998	Mini-PAT	60.5	61.5	07/29/2017 – 08/29/2017	18	08/16/2017	13
149004	PAT	68.0	69.0	09/24/2015 – 02/01/2016	75	12/08/2015	44

Tag 109816 exhibited a large increase in temperature, but there were still fluctuations ranging from 18 to 25°C (Fig. 1). Tag 148996 did not show an increase in temperature until 4 d into the predation event, and there was one 4°C drop in temperature on the ninth day of predation (Fig. 1).

DVM patterns were not evident for 6 of the 8 predation events. The difference in mean depth between day and night was significant for 2 of the ingested tags, but the pattern was not the same. 148996 made deeper dives at night and 149004 made deeper dives during the day (Table S2, Fig. S2).

3.4. Turtle behaviour pre-predation

To identify potential effects of the fishery interaction that may enhance susceptibility to predation among the turtles considered here, their pre-predation surfacing was compared to that of loggerheads that did not interact with fisheries (control turtles; Sasso & Epperly 2007). Prior to predation, tagged turtles did not spend more time at the surface than control turtles. The mean percent time spent at surface ranged from 11.69 to 54.14% (mean: $36.7 \pm 15.04\%$; Table 2).

4. DISCUSSION

4.1. Tag effects

The use of tethered tags, like the PSATs deployed in this study, have been linked to predation of different species. External tags can interfere with the streamlined body shape of many marine animals and increase drag, ultimately reducing swimming per-

formance, or they can become biofouled (e.g. barnacle growth), which may increase drag further and potentially lead to increased predation risk (Thorstad et al. 2013). It is also possible that the shape and towing characteristics of PSATs could potentially function like a lure, attracting some predators. The tagging of sea turtles with electronic tags is generally associated with minimal impacts, including fitness costs. There have been cases of necrosis and mild microbial growth at the attachment site of towed electronic tags on sea turtles (Epperly et al. 2007), and energetic costs have been identified for satellite tags attached to the carapace (Jones et al. 2013). Tethered tags cause drag, resulting in turtles making shorter movements and fewer course changes (Senko et al. 2019), but there has been no evidence of the impact of telemetry devices on the reproduction, growth or survival of sea turtles (Omeyer et al. 2019). The present results suggest that loggerhead sea turtles equipped with PSATs in the Northwest Atlantic could potentially experience increased predation risk.

4.2. Fisheries effects

There was no behavioural evidence to indicate that any of the 8 turtles considered here were compromised by the original fishery interaction that led to their capture, or by subsequent handling or tagging (Fig. 1). Capture, tagging and handling effects are also refuted by the long period of time that elapsed between the bycatch event and the time of predation (between 8 and 135 d). Prior to predation, the turtles in this study did not spend more time at the surface compared to control turtles from other studies (41–52% time spent at surface; Sasso & Epperly 2007).

thaus & Frid 2003, Heithaus 2013). The behaviour of the 8 turtles considered here (Table 2) suggests that associated predation risk was not heightened by increased surface activity.

4.3. Turtle fates

With the exception of the 2 PSATs that sank (initiating their premature release) and the 2 double-tagged turtles (equipped with PSATs and PTTs), it is not possible to discern whether only the tag itself was ingested, or if the tagged turtle was predated. Rogers et al. (2017) presented a similar case where it was impossible to determine whether school sharks were consumed by predators with tags attached, or if only the PSATs were consumed.

In smaller fish like salmon, which can readily be consumed whole by most marine predators and where PSAT tethers are short and close to the body, it is easier to clarify if it is only the tag, or the fish and the tag, that are consumed. If the fish is active until predation and the PSAT data indicate extended time in the predator, then it is assumed that the fish and the attached PSAT were predated (and the PSAT will be retained until some degree of digestion has occurred), but if the PSAT depth record indicates a detached and floating tag before predation, then it is assumed that only the tag was consumed and expelled thereafter (Lacroix 2014). It is not possible to assume the same criteria for juvenile loggerhead turtles because PSATs are towed from a longer tether which is attached to the rear margin of the carapace. Therefore it is possible for only the tag to be bitten off the turtle. For the 4 predated tagged turtles, it is not possible to conclude if the turtle was wholly consumed, or if a portion of the carapace with the tag attached was bitten off. Loggerhead turtles, including several in this study, regularly present with injuries consistent with shark predation (e.g. bite out of the carapace or flipper). This demonstrates that while not always wholly consumed, they are still targeted by predators (e.g. Fig. S1). Loggerhead sea turtles of the same size class in this study have been found intact inside white sharks (Fergusson et al. 2000), but there have been no other reported instances of whole loggerhead turtle ingestion.

4.4. Predator identification

Strøm et al. (2019) observed evidence of predation on Atlantic salmon by 3 types of predators, pointing

to the large difference in temperature ranges for ectothermic fish (below 20°C), endothermic fish (fluctuating around 20–25°C) and marine mammals (close to 40°C). The stomach temperatures recorded by ingested PSATs in this study were not warm enough to indicate marine mammals, as none rose above 30°C (Melero et al. 2015). PSAT temperature data suggest that the most probable predators of tagged juvenile loggerhead turtles in the areas where predation events occurred were endothermic and ectothermic fish. Ectothermic predator candidates for the tags in this study are the tiger shark and blue shark, while potential endothermic predators are the porbeagle shark, shortfin mako, white shark and thresher shark. Bull sharks are not included among the predators considered here because their coastal distribution (Brunnschweiler et al. 2010) does not coincide with the tag pop-off locations (Fig. 3).

The body temperature of ectothermic fish does not differ markedly from ambient (e.g. nurse sharks; Papastamatiou & Lowe 2005). They cannot maintain constant body temperature across broad thermal regimes, although the body size of certain predators can cause some degree of stasis or delayed change in temperature (Kerstetter et al. 2004, Lacroix 2014). If a PSAT is consumed by an ectotherm, the temperature observed prior to predation would be similar to that observed during the predation event. This has been reported for chinook salmon (Seitz et al. 2019) and Atlantic salmon (Strøm et al. 2019). In the present study, one tag (129589) did not show an increase in temperature following predation, but there was a general stabilization of temperature. In this case, the temperature of the tag during the predation event was lower than it was during the 2 wk leading up to predation.

In large-bodied ectothermic fish like many sharks (e.g. tiger shark), the internal temperature of the animal as it descends into deep water may not immediately reflect the ambient temperature at depth, as a high body volume to surface area ratio and physiological mechanisms promote low thermal inertia. Therefore, large ectothermic marine predators are likely to maintain relatively warm stomach temperature, a remnant of time spent in warmer surface waters, unless they are ingesting cold food or water at depth (Meyer & Holland 2012). Infrequent feeding may also serve to maintain body temperature at a fairly constant level in some sharks (Cortés & Gruber 1990). In the case of tag 129589, the corresponding predator dove much deeper than the turtle (in excess of 500 m versus 250 m), with no observed decrease in temperature, even after 3 d of deep diving. Potential ectothermic predators consistent with some of the PSAT tem-

perature records in this study include the blue shark and the tiger shark, the latter being more probable given that it is a known predator of sea turtles.

In other cases, PSAT temperature data suggested that predators ingesting tags were endothermic. Béguyer-Pon et al. (2012) and Lacroix (2014) focused on predation of American eels and Atlantic salmon, respectively. Based on vertical migration data and temperature data from PSATs, they surmised that porbeagle sharks were likely predators. Porbeagle sharks exhibit a great thermal excess (Carey & Teal 1969, Carey et al. 1971), and their stomach temperature rapidly recovers post-feeding (Lacroix 2014). In some of the present PSAT data sets, temperature fluctuations are evident during the predation event (e.g. 109816). This is not unusual for endothermic fish. White shark-ingested PSATs show temperature drops, which may be attributed to an influx of cold-bodied prey into the stomach (Kerstetter et al. 2004). As white sharks can be satiated for ~15 d with a meal of 30 kg of blubber (Semmens et al. 2013), temperature flux may not always regularly occur.

To further distinguish between endothermic predators, depth data should also be considered. DVM patterns of sharks are apparent in PSAT data from studies of other predated fish species. For example, tags reached deeper depth strata during the day when porbeagle sharks were identified as probable predators of American eels and Atlantic salmon (Béguyer-Pon et al. 2012, Lacroix 2014). In this study, we observed few DVM patterns among the 8 PSAT data sets. While the mean maximum depth was deeper during the day for 4 tags, tag 149004 was the only PSAT where this difference was significant and DVM patterns were apparent (Fig. S2), suggesting that the associated predator could be a porbeagle shark, a species which exhibits distinct day–night depth distributions (Saunders et al. 2011). Additional evidence implicating the porbeagle shark as a probable predator in this case comes from the temperature record of tag 149004 during predation and the deep dives (>1000 m) that were registered (porbeagles are among the deepest-diving pelagic sharks; Campana et al. 2011).

Tags 120011, 109816 and 148996 exhibited deeper depths at night, with the latter 2 tags indicating likely predation of the tagged turtle. A probable predator in this case is the white shark, a species known to change its diving patterns based on behavioural mode rather than closely corresponding to diel cycles (Weng et al. 2007). White sharks also have a mouth gape large enough to consume whole juvenile loggerhead turtles of the size range tagged in this study (Fergusson et al. 2000).

Shortfin mako sharks do not consistently show clear diel patterns in diving, but mean depth of dives is generally deeper during the day (Abascal et al. 2011). DVM has also been observed in this species and is believed to be prey driven (Loefer et al. 2005). Shortfin mako sharks exhibit thermal excess that can range from around 2–4°C (Carey et al. 1971, Sepulveda et al. 2004) to 7–13°C above ambient (Carey & Teal 1969). Thresher sharks usually only have a thermal excess of around 4°C (Carey et al. 1971) and also exhibit DVM patterns (Weng & Block 2004, Cartamil et al. 2010). The thermal excess observed for 3 PSATs with deeper maximum depths recorded during the day (109810, 148991 and 148998; Table S2) falls approximately within the range of shortfin makos, and data sets corresponding to the latter 2 tags also reveal evidence of the tagged turtle being ingested. In these cases, shortfin mako is the most likely candidate predator because the species is known to consume sea turtles (Carranza et al. 2006). However, the possibility remains that the corresponding predators are white sharks, based on the previous discussion of dive patterns. Both shortfin mako and white sharks have broad depth distributions (Loefer et al. 2005, Weng et al. 2007), with maximum depths recorded ranging from 800 to 1000 m (Nasby-Lucas et al. 2009, Vaudo et al. 2016).

A limitation to the present study is that the PSAT depth data summarize behaviour over 6 h collection periods, a contrast to the 15–30 min periods used for predation studies of other taxa (Béguyer-Pon et al. 2012, Lacroix 2014, Seitz et al. 2019). This difference in resolution impacts detection of diel-mediated dive patterns at fine scales. However, at the present 6 h resolution, it was still possible to define day (06:00–18:00 h) and night (18:00–06:00 h) more broadly. Tags 148996 and 149004 revealed the strongest patterns of DVM in the sample, with deeper dives consistently occurring at night (tag 148996), and during the day (tag 149004) (Fig. S2).

PSAT retention time within the predator varied in this study from 3 to 44 d. Previous studies of predation of other species reported PSATs retained from 4–6 d to >1 mo (Strøm et al. 2019), 1–10 d (Seitz et al. 2019) and 10 and 27 d (Rogers et al. 2017). Ectothermic sharks in captivity exhibit ingested tag retention times of 5–12 d (Papastamatiou et al. 2007). Most of the retention times for ingested PSATs in the present study match what has been previously reported in other predation studies, with the exception of the one tag that remained 44 d inside the predator. While sharks have the ability to swallow many things, not all objects fully pass through the gastrointestinal

tract, and in these cases sharks normally evert the stomach to expel indigestible material (Brunnenschweiler et al. 2011), a process which can occur long after items are consumed. Therefore, the longer PSAT retention times observed here may be associated with stomach eversion, as regular digestion normally occurs within days instead of weeks (Stillwell & Kohler 1982, Medved 1985).

5. CONCLUSIONS

In the present study, predation of satellite-tagged sea turtles was identified for the first time using depth, temperature and light level data collected before and during predation events. The corresponding results show that tiger sharks and white sharks, both previously identified predators of sea turtles, targeted loggerheads tagged with PSATs across a broad area of the Northwest Atlantic. Additionally, new potential predators of juvenile loggerheads were identified, including the shortfin mako, porbeagle and blue shark. Evidence for predation of tagged turtles was not conclusive in all cases; however, two turtles double-tagged (PTT and PSAT) yielded additional data that helped confirm predation events. Therefore, the use of double-tagging in future studies of sea turtle mortality is strongly recommended. While PTTs represent the most common type of satellite-linked tag applied to sea turtles, such instruments provide little if any data that can be used to confirm mortality events. Moreover, when mortality is presumed in studies using PTTs, the causes are normally ambiguous (Chaloupka et al. 2004), and could include a variety of anthropogenic and natural factors (e.g. direct harvest, fisheries interactions, boat strikes, disease, etc.). The present results show that predation may be an underestimated fate for juvenile loggerhead turtles equipped with tethered electronic tags and, importantly, represents some of the mortality that might otherwise be misattributed to fisheries interactions.

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