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Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator

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Overfishing is a primary cause of population declines for many shark species of conservation concern. However, means of obtaining information on fishery interactions and mortality, necessary for the development of successful conservation strategies, are often fisheries-dependent and of questionable quality for many species of commercially exploited pelagic sharks. We used satellite telemetry as a fisheries-independent tool to document fisheries interactions, and quantify fishing mortality of the highly migratory shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic Ocean. Forty satellite-tagged shortfin mako sharks tracked over 3 years entered the Exclusive Economic Zones of 19 countries and were harvested in fisheries of five countries, with 30% of tagged sharks harvested. Our tagging-derived estimates of instantaneous fishing mortality rates ($F = 0.19-0.56$) were 10-fold higher than previous estimates from fisheries-dependent data (approx. 0.015–0.024), suggesting data used in stock assessments may considerably underestimate fishing mortality. Additionally, our estimates of F were greater than those associated with maximum sustainable yield, suggesting a state of overfishing. This information has direct application to evaluations of stock status and for effective management of populations, and thus satellite tagging studies have potential to provide more accurate estimates of fishing mortality and survival than traditional fisheries-dependent methodology.

1. Background

Worldwide, populations of many shark species have experienced significant declines, primarily attributed to increased fisheries exploitation [1]. Although some shark species are targeted commercially, many are captured incidentally as bycatch, which is often poorly quantified. A suite of generally k-selected life-history traits (i.e. slow growth, late age at maturity, low fecundity) typical of larger-bodied sharks yields slow population growth rates, making rebounding from even moderate levels of exploitation difficult, and rendering many species especially vulnerable to over-exploitation [2]. As upper trophic level predators, sharks can exert considerable top-down functional forces in marine ecosystems, leading to concerns about the potential impacts their removal may trigger on the stability of marine communities [3–6].

Successful fisheries management and conservation are dependent on accurate estimates of population parameters, including survival from total mortality and the specific effect of fishing mortality. Because of their wide distributions, propensity to travel long distances and use of remote offshore environments, these parameters are particularly difficult to measure for highly mobile pelagic shark species. Conventional tagging studies provide a possible means to quantify survival of pelagic species via mark–recapture methods. Agency-run tagging programmes, such as the NOAA NMFS Cooperative Shark Tagging Program, have deployed thousands of tags over several decades. Although these programmes have provided important information on movements and distributions of sharks, only recently have these data been used to quantitatively estimate survival for the few species with sufficient tag returns [7,8]. A major limitation of using conventional mark–recapture studies to estimate mortality and survival is that such programmes rely on voluntary cooperation of fishers to report captures of tagged animals. Several studies have demonstrated that substantial numbers of tagged fishes of various species captured in commercial fisheries are not reported, and that tags may be shed prior to recapture, resulting in underestimated mortality of tagged fish if not properly accounted for [9,10]. Additionally, it may take many years to accumulate a sufficient sample size of tag reports to support such analyses, further limiting the applicability of such studies. Owing to this and other limitations, stock assessments of pelagic sharks conducted by organizations such as the International Commission for the Conservation of Atlantic Tunas (ICCAT) have not incorporated tag–recapture data, and instead rely on catch or effort information from the different fleets to estimate fishing mortality.

In studies of terrestrial wildlife, survival rates and sources of mortality are often estimated using telemetry [11], where the fates of individuals within a population are determined by frequent and regular monitoring over time. The application of telemetry-based methods to estimate these critical population parameters for exploited shark populations would be advantageous by overcoming many of the limitations associated with fisheries-dependent data collection. Although acoustic telemetry has been used for estimating natural and fishing mortality of juvenile coastal sharks [12–14], the primary use of telemetry in survival studies of sharks has been for estimating post-release survival [15–18]. Satellite telemetry is now a standard tool for studying behaviour and ecology of pelagic sharks, with potential applications for estimates of mortality and survival. Two types of tags are commonly used in satellite telemetry studies on sharks, which could be expected to provide useful data for survival and cause-specific mortality studies: pop-up satellite archival tags (PSATs) are programmed to release from the animal after a given time period and relay archived light, depth and temperature data, whereas satellite-linked radio tags (SLRTs) communicate with satellite systems and triangulate a positional estimate each time the tag is exposed to air. The SLRT-style tags are often attached to a shark's dorsal fin and are particularly effective on species that frequent the surface. Advances in these technologies have resulted in tracking of individuals for durations exceeding 1 year [19–21].

Shortfin mako sharks (*Isurus oxyrinchus*; hereafter, mako sharks) are among the pelagic shark species considered most vulnerable to exploitation [22]. As a long-lived species with low fecundity and late age at maturity, population recovery times are slow. Although mako sharks are only occasionally targeted in commercial fisheries, mako shark habitat use overlaps that of other commercially targeted taxa such as billfish and tunas, resulting in frequent capture as bycatch in these fisheries [23]. Mako sharks captured as bycatch are often retained due to the high market value of their meat [24], and even when released, mako sharks captured on pelagic longline gear exhibit low survival [18]. Given their vulnerable life-history traits and concerns about declining populations, mako sharks are categorized as Vulnerable globally by the International Union for the Conservation of Nature (IUCN) Red List [25], as Critically Endangered in the Mediterranean Sea [26], and are also listed under Appendix II (Unfavorable Conservation Status) of the United Nations Convention on the Conservation of Migratory Species of Wild Animals (CMS; http://www.cms.int/en/species/isurus-oxyrinchus). In the North Atlantic, the most recent stock assessment by ICCAT concluded that the population was not overfished and the probability of overfishing was low [27]. However, ICCAT also recognized discrepancies and high model uncertainty resulting from data deficiencies, and recommended a precautionary management approach until more reliable stock status estimates could be obtained. Among the key shortcomings identified in data availability were reliable estimates of fishing mortality. Thus robust fisheries-independent estimates of fishing mortality would represent a major contribution towards obtaining more reliable characterizations of stock status for mako shark populations.

As part of a separate study of mako shark movement ecology in the western North Atlantic Ocean using SLRTs, we found that in addition to tracking shark movements, we were able to identify fishing mortality events [28]. Here, we use an expanded dataset of SLRT-tracked mako sharks to describe fisheries interactions and provide the first fisheries-independent estimate of fishing mortality in the western North Atlantic. We compare our fisheries-independent estimates of fishing mortality to previous estimates for this population derived from stock assessments based on fisheries-dependent data sources, and discuss potential future applications of satellite telemetry to study survival of pelagic shark species.

2. Material and methods

(a) Tagging and movement analysis

We tagged mako sharks with SLRTs (SPOT5; Wildlife Computers, Redmond WA) during 2013–2015 at two locations: the Yucatán Peninsula in the vicinity of Isla Mujeres, Mexico (approx. 21.29° N, 86.29° W), and the northeast coast of the US, primarily in the vicinity of Ocean City, Maryland (approx. 38.10° N, 74.50° W). Tagging off the Yucatán Peninsula took place during March and April, and tagging off the US coast primarily took place in May, with the exception of three sharks tagged in June, August and September. All sharks were captured by rod and reel, and were either secured along the side of the boat or brought onboard for processing. When sharks were brought onboard the vessel, we covered their eyes with a wet towel to reduce stress, and placed a saltwater hose in the mouth to irrigate the gills. All sharks were sexed and fork length (FL) measured. We used FL and sex-specific growth curves for mako sharks in the North Atlantic [29] to estimate the age of each shark.

The SLRTs allow communication with the Argos satellite system when exposed to air, and were attached to the dorsal fin of each shark. Provided sufficient satellite communication is achieved, a location estimate of the shark is triangulated and remotely relayed to the researcher. Mako sharks spend considerable amounts of time at the surface [30], and such fin-mounted tags have proven to be effective tracking tools for this species [19,21,28]. We released all mako sharks immediately following processing, and all sharks swam away under their own power. Mako sharks which failed to report any locations, or which stopped reporting within 14 days of tagging with no evidence of harvest, were considered to represent either tag malfunction or tagging-related mortality and were excluded from analysis.

(b) Management jurisdictions

We used a continuous-time correlated random walk model (CTCRW) fitted using the package 'crawl' [31] in the R statistical computing environment [32] to account for location measurement error and obtain regular daily location estimates of each shark from the temporally irregular Argos locations. We intersected the resulting daily location estimates with a shapefile of global Exclusive Economic Zones (EEZs) in ArcMap (ESRI, Redlands, CA). This allowed us to identify the international jurisdictional boundaries mako sharks traversed during the study.

(c) Harvest detection and fisheries interactions

Fishing mortality was identified directly from Argos data using similar clues used to detect fishing mortality of satellite-tracked marine turtles [33]; harvests were identified when a tag began consistently reporting from a static location on land, or when the transmitter began continuously tracking towards a coastal port, indicating that the SLRT was onboard a vessel. In several instances, contact with the fishers allowed us to confirm the fishery (gear type) in which the shark was captured. When it was not possible to contact the fishers to confirm gear type, we provisionally assigned the mortality to the most likely gear type based on our knowledge of fishery activity in the vicinity of capture, and the locations on land where the transmitter reported (e.g. commercial fishing port or fish processing centre). We defined a capture location as the last Argos location received before a tag began transmitting from land, or when a captured tag reported from onboard a fishing vessel, as the last location received before the vessel began directly tracking towards port (figure 1). Thus, for each fishing mortality event we were able to ascertain the approximate date and location of capture, the country of origin of the vessel, and the fishery, or most likely fishery, in which the animal was harvested.

(d) Survival analysis

We used known-fate models in MARK [34] to estimate annual harvest-specific survival probabilities, which we denote as S_F. Our estimates are harvest-specific because technological limitations of the SLRTs did not allow us to detect natural mortalities and distinguish them from instances of tag malfunction, which would be necessary to estimate total survival (S). Known-fate models are binomial models of survival through discrete time intervals. Tracked individuals known to be alive at the beginning of a sample interval either survive to the end of the interval or die during the interval. If contact is lost (e.g. in our study in the case of transmitter malfunction or undetected natural mortality) and fate is thus unknown at the end of the interval, the individual is censored from that interval. The model is formulated as a generalized linear model (GLM), which allows modelling survival as a function of individual-level covariates (e.g. size, age, sex). Estimates of survival across time intervals (for example, annual survival estimated from monthly sample intervals) can be calculated as the product of the survival likelihoods of each interval. Detailed information regarding model formulation and implementation can be found in the MARK software manual available at http://www.phidot.org/software/mark/docs/book/.

We estimated S_F over three-month intervals corresponding to the four meteorological seasons: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). Because of unbalanced sample sizes among years, and to ensure adequate sample sizes and mortality events in all sample intervals, we assumed S_F was constant among years, and individuals tracked for more than 1 year re-entered the analysis in the following year. We constructed four candidate models representing hypotheses regarding the potential effects of season and tagging location on S_F. The candidate models (i) held S_F constant across all seasons and tagging locations, (ii) allowed S_F to vary across seasons, (iii) allowed S_F to vary based on tagging location or (iv) allowed S_F to vary based on season and tagging locations. We ranked models using Akaike's information criterion adjusted for small sample sizes (AICc), and selected the most parsimonious model based on ΔAICc and AICc weights (w_i) [35]. We used the most parsimonious model to derive an estimate and associated 95% confidence interval (CI) of annual S_F. Models were run by calling MARK through the package 'RMark' [36] in R.

(e) Fishing mortality rate

Once S_F was estimated, the instantaneous fishing mortality rate (F) was calculated simply as $F = -\ln(S_F)$. We calculated a range of F based on the 95% CI of our estimate of annual S_F. Empirically derived ratios of the fishing mortality rate associated with maximum sustainable yield ($F_{\rm msy}$) and instantaneous natural mortality (M) have been postulated to range from approximately 0.41 to 0.50 for elasmobranchs [37,38]. We used these values and a recent estimate of M for mako sharks in the North Atlantic (0.075) [39] to calculate a range of approximate $F_{\rm msy}$ values of 0.031–0.038. We note that these values are approximations as they do not account for gear selectivity. We compared these $F_{\rm msy}$ values with our tagging-derived estimate of F to examine whether there is evidence that the stock is undergoing overfishing (i.e. $F > F_{\rm msy}$) and compared our results with those from the most recent ICCAT mako shark stock assessment [27].

We illustrate the influence of F on mako shark population size with a simple exponential population model of the form $N_t = N_0e^{rt}$ projected forward for one generation (approx. 26 years [22]), where N_0 is initial population size, t is years and r is the intrinsic rate of population increase. We calculated r through a Leslie matrix based on current life-history inputs [40]. Detailed descriptions of life-history inputs used are provided as the electronic supplementary material. We compared results with F corresponding to estimates derived from this study to recent stock assessment [27], tag-recapture data [7] and the case of no fishing mortality ($F = 0$).

3. Results

We tagged 46 mako sharks, of which we received sufficient data from 40 sharks tracked between March 2013 and May 2016 for our analyses; 14 sharks were tagged off the Yucatán Peninsula (8M, 6F) and 26 off the northeast coast of the USA (19M, 7F). Male sharks ranged in size from 117 to 198 cm FL, with estimated ages of 2.3–9.5 years [29]. Four males tagged off the Yucatán and three off the US east coast exceeded the size of approximately 50% maturity for males (185 cm FL) [29]; as such, it is likely that some of these individuals were mature or reaching maturity at the time of the study. Female sharks ranged from 122 to 252 cm FL, with estimated

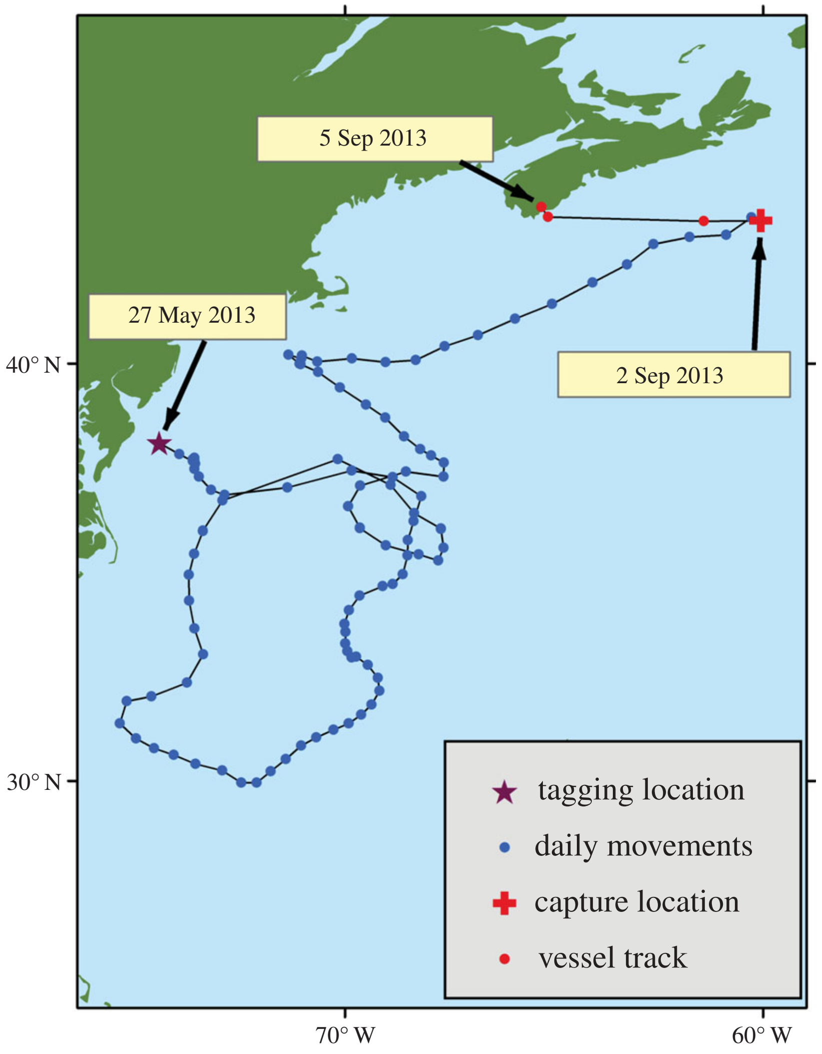

Figure 1. Example of location data from a harvested shortfin mako shark illustrating the movements of the shark, the date and approximate capture location, and the track of the vessel back to a port in Nova Scotia, Canada. (Online version in colour.)

ages of 3–15.4 years. All females were immature based on age and length at maturity estimates [29].

The SLRTs were successful in providing long-duration tracks. Track durations averaged 358 days (range: 81–754) for mako sharks that ceased reporting prior to the end of the study and were not harvested, with 11 tracks of non-harvested makos exceeding 1 year. Four mako sharks were still actively reporting locations as of the end of the study (31 May 2016), with tracking durations of 374, 375, 379 and 415 days, respectively. Mako sharks ranged widely throughout the western North Atlantic Ocean, although there was little spatial overlap between sharks from each respective tagging location (figure 2). Sharks traversed EEZs under the sovereignty of 19 countries during the study period (figure 2).

Overall, we identified 12 mako sharks (30%) harvested by fishers: four (28.6%) sharks tagged off the Yucatán and eight (30.8%) sharks tagged off the US east coast. Mako sharks were harvested by vessels from five countries, namely Canada (4), the USA (3), Mexico (3), Spain (1) and Cuba (1) (figure 2). We estimate that 10 sharks (83.3%) were harvested by pelagic longliners based on contact with the fishers after capture (six harvests), or our knowledge of fishery activity in the vicinity of where the shark was captured and the locations on land where the transmitter reported (four harvests). One shark was harvested by a sport fisher off New York, USA, and one in a bottom trawler off Maryland, USA. Harvests occurred during all seasons in both tagging regions.

The model that held survival constant across seasons and tagging regions was the most supported, with the lowest AICc value and 56% of the combined model weight (w_i; table 1). Confidence limits for all season and tagging region parameters in the remaining models crossed 0, suggesting they were uninformative, and confidence intervals of derived estimates of S_F overlapped considerably as well (see electronic supplementary material, table S2 and figure S1). Therefore, we used the model that held survival constant across time and region to derive an estimate of annual $S_F = 0.72$ (95% CI: 0.57–0.83). This can be interpreted as a mako shark in the western North Atlantic having an approximately 72% probability of surviving a year and not being harvested by a fisher. The 95% CI estimates of S_F yielded a range of $F = 0.19–0.56$, which is 5–18 times greater than estimates of F_{msy} (0.031–0.038). As fishing mortality estimates exceeded those associated with maximum sustainable yield ($F > F_{\text{msy}}$), this suggests a state of overfishing of mako sharks in the western North Atlantic.

In the absence of fishing mortality ($F = 0$; applied across all age groups), the population is expected to grow at an instantaneous rate of $0.037\ \text{yr}^{-1}$, whereas population growth decreases to $0.017\ \text{yr}^{-1}$ when $F \approx 0.02$ as estimated in the 2012 assessment [27]. The population decreases when

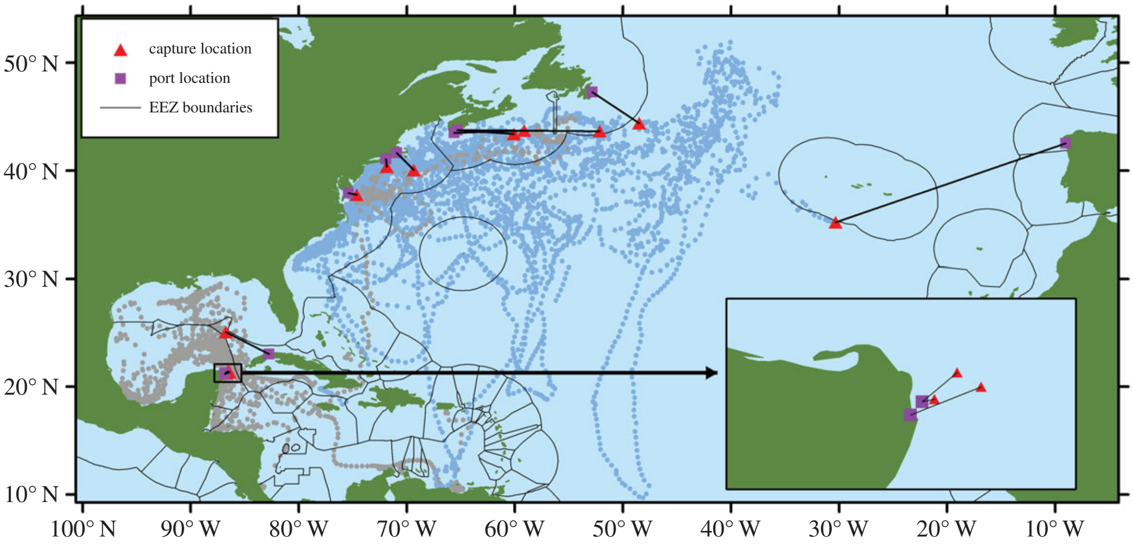

Figure 2. Daily locations of shortfin mako sharks tagged off the US coast (blue dots) and Yucatán Peninsula (grey dots) during March 2013 – May 2016. Capture and landing port locations of harvested sharks are indicated, as are boundaries of Exclusive Economic Zones (EEZs). (Online version in colour.)

Table 1. Model selection results of candidate models used to model survival from fishing mortality (S_F) of satellite-tagged shortfin mako sharks in the western North Atlantic Ocean, March 2013 – May 2016.

model[a]	K	AICc	ΔAICc	w_i
S_F (.)	1	85.8	0.00	0.56
S_F (location)	2	87.8	2.02	0.20
S_F (season)	4	88.2	2.36	0.17
S_F (location + season)	5	90.3	4.46	0.07

[a] Models allow S_F to remain constant (.), or vary by season or tagging location (Yucatán Peninsula or US east coast). We report the number of estimable parameters (K), Akaike's information criterion adjusted for small sample size (AICc), difference in AICc relative to smallest value (ΔAICc) and Akaike weights (w_i).

$F = 0.10$ as reported in Wood *et al.* [7] ($r = -0.069$) based on tag–recapture data, and declines precipitously when $F = 0.328$ ($r = -0.361$), corresponding to $S_F = 0.72$ estimated in our study (figure 3).

4. Discussion

Using satellite telemetry, we were able to document harvest events and quantify fisheries interactions of mako sharks in the western North Atlantic ocean. This included the number of individuals harvested, the spatial distribution of harvest events, the countries responsible for harvests and the relative contribution of different gear types to total harvest. Furthermore, to our knowledge this study represents the first use of satellite telemetry to quantify fishing mortality (F) of an exploited shark in a fisheries-independent manner.

As expected for the species, the majority of harvests were attributed to longline fisheries; however, we also observed harvests in bottom trawl and sport fisheries. Mako sharks are a popular sport fish and are occasionally recorded in bottom trawls [41,42], although the relative mortality associated with these fisheries is assumed to be dwarfed by that of longlines [41]. The ability to quantify the contribution of individual fisheries independent of reporting by fishers is an appealing aspect of satellite telemetry. Similarly, with 40 individuals we recorded harvests by fishers from five countries from both the western and eastern North Atlantic, and recorded mako sharks travelling through the EEZs of 19 sovereign nations as well as international waters, underscoring the critical need for coordinated international management efforts.

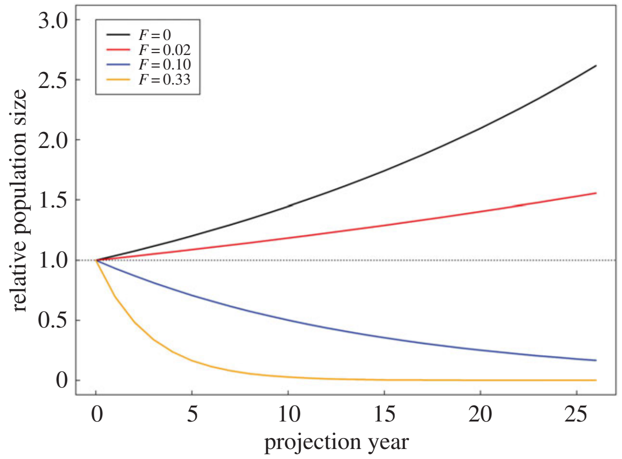

Figure 3. Effect of assuming different levels of F ($F = 0$; $F = 0.02$, 2012 ICCAT stock assessment; $F = 0.10$, tag–recapture data; and $F = 0.33$, present study) when projecting a hypothetical shortfin mako population forward one generation (approx. 26 years) using a simple exponential population model. (Online version in colour.)

We discovered high levels of fishing mortality, with 30% of our sample known to have been harvested by fishers. Notably, estimates of F derived from survival models in our study (0.19–0.56) were considerably higher than estimates available for mako sharks in the North Atlantic based on stock assessments that rely heavily on fisheries data. The 2012 ICCAT stock assessment estimated F on the order of approximately 0.015–0.024 with Bayesian surplus and catch-free age-structured production models. Based on 27 years of conventional tag-return data in which 5813 tags were deployed and 654 (11%) tags were subsequently recovered, Wood *et al.* [7] estimated F at approximately 0.10. Wood *et al.* [7] computed F by subtracting M from the total instantaneous mortality rate

(Z). As M was obtained based on life-history invariant estimators which likely overestimated M [39], F was also thus underestimated.

Our study is unique in that we were able to estimate F directly from observations of harvest events within a population of continuously monitored individuals. Such direct estimates should be more accurate than those derived from stock assessments, which estimate F based on often incomplete or unreliable catch or effort information from the different fleets. Assuming our sample is truly representative (i.e. individuals in this study were not more susceptible to harvest than unmarked sharks of the same age/size class), our results suggest that mako sharks in the western North Atlantic are experiencing greater fishing mortality than previously inferred from fisheries-dependent data sources. These observations broadly coincide with other studies suggesting that available fisheries data underestimate true human-induced mortality of shark populations [43].

Our fishing mortality estimates were 5–18 times greater than those associated with maximum sustainable yield (F_{msy}), implying the North Atlantic stock of mako sharks is currently experiencing overfishing (i.e. $F > F_{\mathrm{msy}}$). Thus, if the level of fishing mortality we observed is representative of the western North Atlantic population, it is likely to be unsustainable (figure 3). Furthermore, the fact that our harvested sample consisted primarily of immature individuals is concerning because populations of slow-growing, low-productivity shark species are most negatively impacted by high mortality in juvenile age classes, as reduced recruitment into the adult population slows population growth rates [2]. Additionally, despite the high levels we observed, it is possible that we are still underestimating fishing mortality to some degree because some fishers may have destroyed or discarded tags at sea and never reported the capture. In such cases, we would not have been able to detect the harvest event. We refrain from making a definitive claim regarding the status of the mako shark stock in the western North Atlantic, and caution that interpretation of our results must consider that our estimates of F_{msy} did not account for gear selectivity, and that we tracked sharks within a relatively narrow size/age class. Still, the discrepancy between our estimates of F and those derived previously from tag–recapture [7] or stock assessment [27] highlights the need for further assessments of mortality in this population.

Given the technological limitations of the tags we used, which only reported locations when exposed to air, we were not able to detect natural mortalities. This was sufficient for our goal of quantifying F; however, we were unable to estimate total survival because the survival probabilities we report (S_F) refer to survival from fishing mortality only. It is difficult to speculate how prevalent natural mortality was in our study, but we believe it is unlikely total survival, $S = e^{-(M+F)}$, would be much lower than the S_F we estimated for several reasons. Evidence suggests natural mortalities were rare as tracking durations of non-harvested sharks in our study were often as long as, or longer than, the predicted manufacturer tag longevity based on battery size and tag programming, indicating battery drain may have been the primary cause of lost contact rather than shark mortality. Interestingly, our estimate of annual S_F (0.72; 95% CI: 0.57–0.83), which only accounts for survival from harvest, is lower than S (0.79; 95% CI: 0.71–0.87) reported by Wood *et al*. [7], which accounted for all forms of mortality.

We found no strong evidence for an effect of season or tagging region on S_F. Simulations suggest our sample size should have been sufficient to detect regional differences when effect sizes were moderate to large (i.e. 25–50% regional difference in S_F); however, it is possible that smaller effects may have gone undetected (see the electronic supplementary material). Fishing effort is not evenly distributed at large scales in the north Atlantic [23], and it is likely that some degree of spatial variation in harvest mortality also exists. Larger sample sizes and carefully designed studies will help elucidate such effects in the future, and have important implications if there exists strong spatial structuring of the Atlantic mako shark population. For example, if immature makos show strong fidelity to high-productivity coastal regions, as recent evidence suggests [19,21,28], then this segment of the population may have lower S_F than mature cohorts as a result of greater exposure to fishing pressure. This would limit recruitment into the breeding cohort, subsequently limiting population growth and recovery potential. The stock structure of mako sharks in the Atlantic is currently not well resolved, and future fisheries-independent studies of mako shark movements and fishing mortality will be important in developing focused management actions.

(a) Future studies

The known-fate modelling approach we used has been widely adopted in studies of terrestrial wildlife monitored via telemetry [44–46]; however, to our knowledge application to pelagic vertebrates has been limited to sea turtles [47]. Like many contemporary approaches to modelling survival of wildlife [11], known-fate models are appealing because of the ability to model survival probability as a function of individual covariates (e.g. location, time of year, sex or age-class), and to employ information-theoretic approaches to compare relative support of hypotheses regarding the influence of covariates on survival. Furthermore, because annual survival probabilities are the products of the survival likelihoods of each sample interval, it is possible to derive annual survival estimates from tags with deployment lengths less than 1 year, provided enough individuals are tracked within each respective sample interval. This may be particularly useful for studies using PSATs, which often do not last as long as fin-mounted SLRTs. Known-fate models quantify survival in discrete time, and we note that similarly powerful methods of modelling wildlife survival in continuous time that incorporate individual covariates and allow for information-theoretic model selection are available, such as proportional hazard models [11]. The appropriate statistical approach will depend on specific study objectives and data availability.

For management and conservation purposes, knowledge of the relative contributions of both natural and human-induced causes to total mortality is important. At present, we are not aware of any studies that provide direct measures of natural mortality for pelagic shark populations. For pelagic and other sharks, M is generally calculated through life-history-invariant methods based on life-history characteristics, such as maximum age and parameters of size-at-age curves (e.g. [48,49]). While life-history-invariant methods are efficient in that they do not require large amounts of data, the estimates they provide are of unknown precision

[50]. As empirical management benchmarks such as F_{msy} can be generated relative to these estimates of *M*, it would be advantageous to have some independent measure of natural mortality. Incorporation of PSATs into future studies may prove fruitful in this regard. PSATs archive time-series data of depth and temperature, and thus mortality can be inferred from records that indicate constant depth for extended periods of time (in most tags this scenario will trigger the pop-off mechanism). PSATs have been used to measure post-release survival of shark species [15–18] with the focus on survival over relatively short time periods (days to weeks). However, with slight modifications to study design and analysis it is feasible to use these tags to also generate annual survival estimates. An additional benefit of PSATs is that the depth data from the tags could be combined with information on depth and spatial distribution of fishing effort to derive selectivity in stock assessments, as demonstrated by Carvalho *et al*. [51].

The benefit of telemetry-based studies in constructing effective conservation and management plans will be most realized in their ability to contribute to, or be directly incorporated into, stock assessments. In the most basic scenario, independent, telemetry-derived parameter estimates (e.g. *F* or *M*) may be used to improve stock assessment models, for example by generating informative priors for Bayesian models. Beyond this, harvest and survival data, along with the associated movement data, could be incorporated directly into integrated spatially explicit assessment models, and used to test hypotheses about population dynamics and structure [52]. Although electronic tagging data have been used for capture–recapture and population dynamics models [53,54], estimates of *F* and *M* derived directly from satellite telemetry data are still lacking for sharks and other pelagic fishes. Given the widespread use of satellite telemetry to study the ecology of sharks, we suggest attention be given to using these data to explicitly address fundamental questions of survival and mortality.

5. Conclusion

Our study illustrates how the use of satellite telemetry to track individual sharks in a population is a potentially time-efficient way to gather useful fisheries interaction data. By tracking 40 mako sharks over a 3-year period we were able to capture a wealth of information regarding the distribution of harvests and the associated fisheries and countries involved. Significantly, we were able to quantify *F* in a fisheries-independent manner, a metric with direct application to stock assessment and stock status evaluation. Importantly, the fishing mortality rates we observed were well above those previously reported for mako sharks in the North Atlantic, calling into question the sustainability of current fishing pressure on this population. This, combined with movements across multiple international management jurisdictions and the documentation of harvest by multiple countries, underscores the importance of coordinated international management to ensure the long-term sustainability of mako sharks in the North Atlantic.

Ethics. This study was conducted under NSU IACUC control # 064-398-15-0203.

Data accessibility. Mako shark tagging and harvest data are available from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.h9f3c) [55].

Authors' contributions. M.E.B, E.C., J.J.V, B.M.W. and M.Sh. conceived the study. M.E.B and E.C. developed and carried out analyses. M.E.B, J.J.V, G.C.M.H., M.Sa. B.M.W. and M.Sh. conducted fieldwork. M.E.B wrote the paper with extensive contributions from E.C., J.J.V., B.M.W. and M.Sh. All authors provided input on the paper.

Competing interests. We have no competing interests.

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