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SHORT COMMUNICATION

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A dawn peak in the occurrence of 'knifing behaviour' in blue sharks

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Abstract

Background: Knifing is a behaviour whereby a shark swims directly at the surface with its dorsal fin out of the water. While this behaviour has been reported in a number of species, information on the frequency and timing of such behaviour could provide insights on how sharks use the ocean–atmosphere interface.

Findings: Our analysis of the timing of the reception of satellite (Argos) messages from SPOT-tagged blue sharks has revealed important insights on knifing behaviour in one of the ocean's most abundant large predators. We found that knifing behaviour was common in all tagged sharks and occurred during 54–76 % of days tracked, with a mean (and SD) of 4.7 ± 0.4 knifing events per day when observed. The frequency of knifing behaviour increased during the dawn period in all sharks and was supported by analysis of high-resolution depth data from a recovered archival tag. One shark also had a pronounced peak in knifing activity at dusk.

Conclusions: We suggest that blue sharks may be using surface waters during twilight periods to maximise foraging opportunities. Light conditions at dawn are consistent with surface-dwelling prey being both more dispersed and silhouetted by ambient light conditions, making individual prey more visible. The application of this analysis to other species of sharks may provide further insights on knifing behaviour.

Keywords: *Prionace*, Argos, Satellite tracking, Surfacing behaviour, SPOTs, PSATs

Background and aims

A review of the literature shows a large amount of work focusing on the depth preferences of oceanic sharks [1–4]. Despite limited examples in the literature where sharks are recorded spending considerable time in surface waters or are described as surface orientated [5–7], the behaviour whereby sharks 'knife' their dorsal fin through the water's surface (hereafter termed knifing behaviour) is largely unreported outside of the planktivorous sharks [8]. Tracking studies on blue sharks suggest that this species displays knifing behaviour regularly, as smart position only tags (SPOTs) successfully transmit multiple locations throughout the day [9, 10] and pop-up satellite archival tags (PSATs) have described distinct surface-orientated behaviours [7].

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Here, we use an intrinsic feature of all shark satellite tracking studies that utilise the advanced research and global observation satellite (Argos) system and SPOT tags; namely, the timing and frequency of satellite locations received is dependent on the shark's dorsal fin breaking the surface. Therefore, this present study aimed to quantify the timing and degree of knifing behaviour by blue sharks using a novel analysis of Argos data.

Methods

Five sharks were fitted with Argos-linked satellite tags between 2010 and 2013 ~20 km south of Cork, Ireland. Two were tagged with PSAT (MK10, Wildlife Computers, Redmond, WA, USA) in September 2010 (shark A) and September 2012 (shark B). Three sharks (sharks C, D, and E) were fitted with Smart Position Only Tags (SPOT, Wildlife Computers), one in September 2012 and two in September 2013 (see Table 1; Additional file 1: Supplementary Material for attachment protocols and tag configurations).

Table 1 Shark summary data

Shark ID	A	B	C	D	E	Mean values (±SD)
Length of shark (fork length and total length in cm)	150, 180	118, 140	167, 205	134, 163	138, 167	–
Sex of shark	F	SJ	M	M	F	–
Date tagged	17/9/10	7/9/12	19/9/12	25/9/13	25/9/13	–
Number of days tracked	120	70	212	314	74	200.0 (±120.4)
Number of days knifing events were recorded	–	–	162	191	40	131.0 (±80.1)
% of days knifing events were recorded	–	–	76.4	60.8	54.1	63.8 (±11.4)
Number of knifing events recorded	–	–	807	921	170	632.7 (±404.7)
Daily rate of knifing events (excl. of days when no knifing events were recorded)	–	–	5.0	4.8	4.3	4.7 (±0.4)
Maximum number of knifing events recorded (per day)	–	–	26	13	11	16.7 (±8.1)
Longest duration (days) no knifing events were detected	–	–	9	27	9	15.0 (±10.4)

PSATs were attached to sharks A and B, and SPOTS were attached to sharks C–E

F female, *M* male, *SJ* small juvenile

Argos messages (uplinks) occur when a SPOT tag breaks the water surface and successfully transmits to a satellite. SPOT tags were configured to transmit up to 250 transmissions a day with a 45-s delay between transmissions, resulting in a string of messages if the tag remained above the surface. Each string of messages (and associated location) was considered a 'knifing event'.

Mixed effects models (using the lme4 package, with model checks using the LMERConvenienceFunctions package) in the R statistical framework were used to investigate the influence of time of day, proximity to dawn/dusk, and location on shark surfacing behaviour, with individual included as a random factor. A stepwise model selection process was undertaken using a combination of AIC values [11] and maximum likelihood ratio tests [12]. Patterns in knifing behaviour were validated by ruling out potential bias due to satellite coverage using *G* tests. Knifing events (0 m depth, $n = 271{,}503$) recorded by the recovered PSAT tag (shark B) were binned by hour into a frequency distribution to visualise patterns in the timing of knifing behaviour for comparative purposes.

Results

Sharks with SPOT tags were tracked for 74–314 days with a total of 1898 knifing events recorded (Table 1) (see Additional file 1: Figure S1). Surfacing events (knifing) of one message accounted for 32.2 % of the total number of events, 26.8 % of events had five messages or more (≥3.75 min duration) and 6.9 % of events had 10 messages or more suggesting a prolonged time spent at the surface (>7.5 min). Maximum knifing duration was ~12 min (based on 16 continuous messages detected by passing satellite and the tags programmed to transmit at the fast repetition rate of 45 s only and never to switch to the slow repetition rate of 90 s) (Additional file 1: Figure S2). For sharks C, D and E, knifing events were detected during 76.4, 60.8 and 54.1 % of tracked days. The mean number of knifing events per day (exclusive of days when no knifing events were recorded) was 4.7 ± 0.4 (Table 1), with the frequency of knifing events varying between individuals (Table 1) and location. It must be noted that the frequency of knifing events is likely much higher as the detection of such events depends on the coverage provided by the Argos system (a function of latitude and the angle of the satellite above the horizon) which is typically 20–25 %. Bad weather (i.e. large waves) may also prevent satellite tag transmissions from reaching a satellite.

Mixed effect models explained 36 % of the variability in shark knifing behaviour around dawn ($R^2 = 0.366$, $\chi^2_4 = 18.8732$, $p = < 0.001$) and 63 % around dusk ($R^2 = 0.637$, $\chi^2_4 = 39.743$, $p = < 0.001$). From Fig. 1 it is clear there is a post-dawn peak in knifing activity beginning around the time of civil sunrise (half hourly bins containing both day and night knifing events indicate that these are occurring around the transition from night to day). Examination of PSAT tag data showed that these two sharks spent 16.96 % (shark A) and 63.54 % (shark B) of their time in the top 5 m of water but failed to show any dawn or dusk peak in knifing activity because of the coarse resolution of binned data (Fig. 2). High-resolution archived depth data (every 10 s) from a recovered PSAT tag (shark B) also showed a clear dawn peak in knifing behaviour and a smaller peak at dusk (Fig. 3) despite the shark spending 59.93 % of its time in the top 1 m. This dawn peak in knifing behaviour was typically preceded by time spent in slightly deeper waters but with frequent surfacing events still present (Additional file 1: Figure S3). To determine if shark knifing behaviour was influenced by geography, we analysed the distribution of knifing events both on and off the continental shelf (defined as waters <200 m in depth) for sharks C and D, which

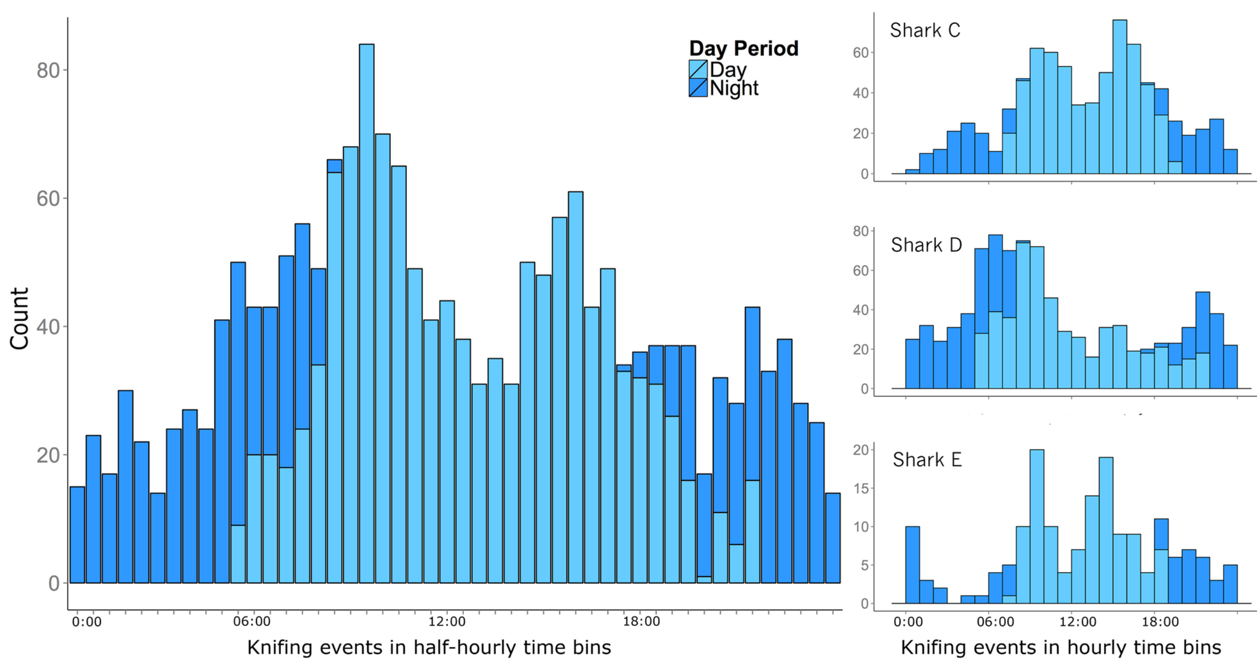

Fig. 1 The distribution of knifing events binned by half-hour slots (*main figure*, all sharks). *Inserts* show the distribution of knifing events binned by hour slots for individual sharks (sharks C–E). Day and night were calculated by determining whether the event preceded dawn or dusk and was corrected for by location and time of year

both spent considerable time in the Celtic Sea ($n = 66$ and 99 locations, respectively) and in the deeper waters of the Bay of Biscay ($n = 49$ and 39 locations, respectively). Shark E was omitted from analysis as there were too few off-shelf locations for meaningful comparison. The distribution of knifing events on and off the continental shelf was no different for both sharks (*G* test, both $p > 0.1$) indicating that the timing of knifing behaviour was consistent across broad geographical features.

Discussion

Analysis of Argos messages demonstrated that blue sharks frequently swim at the surface with their dorsal fin out of the water (knifing), often for durations exceeding seven and a half minutes. A mixed effects model showed that 'proximity to dawn' explained 36 % of the variability in shark knifing behaviour between midnight and midday, with a post-dawn peak evident in knifing behaviour (Fig. 1). Despite a dusk peak in knifing behaviour being evident for shark C, the mixed effects model using 'proximity to dusk' found no corresponding peak in knifing behaviour across all sharks around dusk. We are confident that the pattern in knifing behaviour was not influenced unduly by bias in satellite coverage or tag setup and transmission frequency (Additional file 1: Figures S4, S5). The observed pattern of knifing behaviour was further supported by high-resolution time at depth data from a recovered PSAT (Fig. 3). While surface orientated behaviour has previously been documented for blue sharks [7, 9], for example, a study in the Northeast Atlantic found that blue sharks can spend large periods of their time 'at or near the surface' [7]; the authors do not specify knifing behaviour. Here we specifically highlight the frequency and timing of knifing behaviour that has not been reported in previous studies, likely due to a combination of coarse resolution of binned depth data in PSAT tags (Fig. 2), and/or a broader focus on other behaviours such as diel vertical migration [13] or spatial ecology [10].

Surface-oriented behaviour more generally (top 20 m of water) has been observed in many species of teleosts and elasmobranchs, and has been linked with various hypotheses including thermal recovery after deep diving [14], navigation/orientation [3, 15] and optimal foraging [8]. For deep-diving fish species, surfacing periods are likely linked with thermoregulation [14, 16], with surfacing behaviour resulting in elevated body temperatures that enable animals to spend longer periods at depth or speed up physiological processes. All three sharks tagged with SPOT tags showed an increase in knifing activity at dawn, a time inconsistent with a thermal recovery. The recovered PSAT tag data revealed very little difference (<0.2 °C) in the mean temperature experienced during

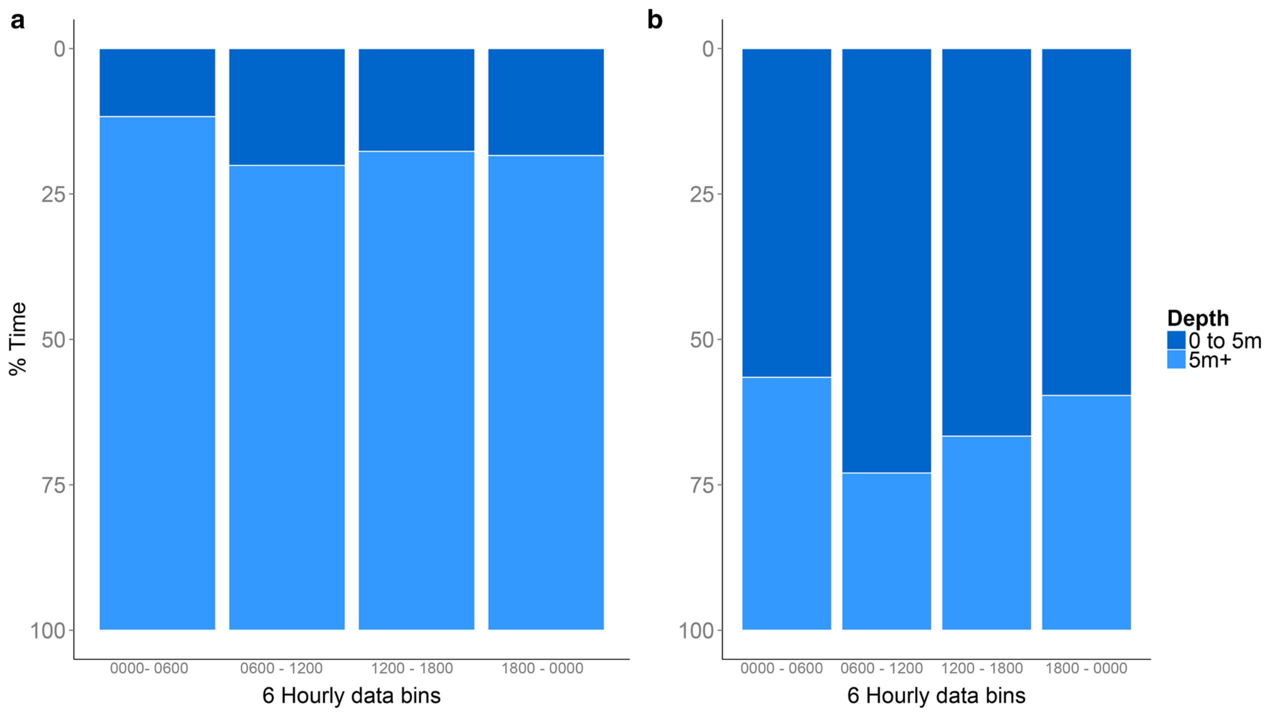

Fig. 2 Frequency distribution of depths occupied by blue sharks by time of day (from PSAT tag data). Depth data are binned into 6-h intervals. **a** Shark A was tagged in September 2010 and was at liberty for 120 days, and **b** shark B was tagged in September 2012 and was at liberty for 70 days. The coarse resolution of this data makes it difficult to discern patterns in knifing events

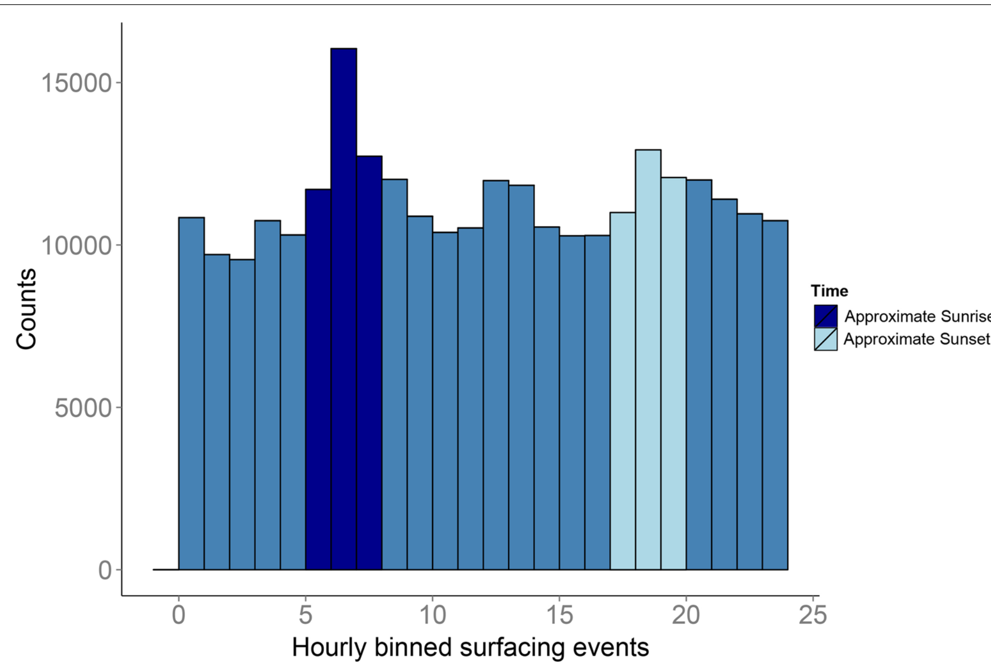

Fig. 3 The frequency distribution of 271,503 depth readings of knifing events (0 m depth) binned into time of day from the recovered PSAT tag (shark B). The *figure* illustrates a clear peak of knifing events at or near dawn and a smaller secondary peak around dusk

night versus day and that the warmest waters experienced were typically during midday to afternoon (Additional file 1: Figure S6). Navigation may also play a part in surface swimming in sharks, with use of celestial cues hypothesised as a reason for a white shark (*Carcharodon carcharias*) swimming just below the surface (0–0.5 m) for 61 % of its time in oceanic waters [5]. Indeed, many animals use the sun as a primary compass in conjunction with a map sense [17], and therefore, the observed increased frequency of knifing near dawn (and dusk for shark C) may be a good way of defining direction.

Perhaps the most parsimonious explanation for increased knifing post-dawn is that blue sharks are feeding on increased prey densities at the surface around dawn, or are taking advantage of the changing light conditions to surprise attack prey silhouetted at the surface. For example, a 13-year study at Seal Island, South Africa, observed white sharks making 61 nonconsumptive strikes on seabirds [18]. Remarkably, most of these strikes occurred within an hour of dawn, consistent with our post-dawn peak [18]. In the same area, studies of white shark predatory interactions with Cape fur seals (*Arctocephalus pusillus pusillus*) found that predatory success was highest during low light levels occurring at dawn [19]. For blue sharks, such surface orientated 'curiosity' could result in a meal. Several studies have reported blue sharks consuming birds [20, 21] and lumpsucker fish (*Cyclopterus lumpus*), a fish associated with rafting seaweed [22]. Support also exists for blue sharks profiting from increased densities of surface-dwelling prey at dawn. A study on blue shark diet near Santa Catalina Island, California, found that northern anchovies (*Engraulis mordax*) were the most abundant prey item and that predation most likely occurred in predawn hours when anchovy schools dispersed into a thin surface scattering layer [23]. Success rates of sharks feeding on schools may be lower than when targeting single prey (e.g. predator confusion effect, [24, 25]), so a combination of non-aggregated anchovy in surface waters and dawn light silhouetting them against the surface may provide increased foraging opportunities and explain the increased knifing behaviour at this time. The increase in knifing behaviour observed in one shark (shark C) at dusk is also likely to be related to similar processes occurring around dawn.

In conclusion, our novel analysis of the timing of Argos messages has provided important insights on the frequency and timing of knifing behaviour in blue sharks. Similarly, a new study evaluated predator–prey interactions between tiger sharks (*Galeocerdo cuvier*) and loggerhead turtles (*Caretta caretta*) by testing for differences in their surfacing behaviour (derived from the frequency of Argos messages received from satellite tags, as in our study) in and out of home range overlap areas [26]. The wider implications of our study are that blue sharks may be more vulnerable to bycatch from surface longlines during the twilight periods. Furthermore, the application of this method to larger datasets and other species (i.e. fin-mounted SPOT tags have been successfully deployed on at least five other species [2]) is likely to increase our understanding of the ecology and behaviour of wide-ranging marine predators.

Additional file

Additional file 1: Figure S1. Complete tracks of three blue sharks satellite tagged with SPOT tags off southern Ireland (closed star is approximate tagging location for all sharks). **Figure S2.** The frequency distribution for the number of knifing events detected through the Argos satellite system per satellite pass. **Figure S3.** a) The mean depth of Shark B for every 10 s of a 24 h clock (averaged over the entire tracking period of 70 days) (data from recovered PSAT). b) and c) are examples of depth versus time traces for two randomly chosen days (20/10/2012 and 01/11/2012). **Figure S4.** Hourly binned satellite passes for a period when an individual was resident in the Celtic sea (left panel) and the distribution of knifing events from the Shark D at this time (right panel). **Figure S5.** Distribution of counts of 'time of last transmissions' from a SPOT tag (Shark D) during July 2014. **Figure S6.** Temperature depth plot for Shark B (from recovered PSAT) showing that there was very little difference in the mean temperatures experienced by this shark during night and day (<2 °C).

Authors' contributions
TKD, LAH and MJ conceived of the study. LAH, TKD and DH conducted the fieldwork. AB, MJ and TKD performed the data analyses. TKD, MJ and AB wrote the manuscript with contributions from LAH and DH. All authors read and approved the final manuscript.

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Compliance with ethical guidelines

Competing interests
The authors declare that they have no competing interests.

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