Skubel *et al. Anim Biotelemetry* (2020) 8:34
https://doi.org/10.1186/s40317-020-00220-0

Animal Biotelemetry

METHODOLOGY Open Access

A scalable, satellite-transmitted data product for monitoring high-activity events in mobile aquatic animals

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Abstract

A growing number of studies are using accelerometers to examine activity level patterns in aquatic animals. However, given the amount of data generated from accelerometers, most of these studies use loggers that archive acceleration data, thus requiring physical recovery of the loggers or acoustic transmission from within a receiver array to obtain the data. These limitations have restricted the duration of tracking (ranging from hours to days) and/or type of species studied (e.g., relatively sessile species or those returning to predictable areas). To address these logistical challenges, we present and test a satellite-transmitted metric for the remote monitoring of changes in activity, measured via a pop-off satellite archival tag (PSAT) with an integrated accelerometer. Along with depth, temperature, and irradiance for geolocation, the PSAT transmits activity data as a time-series (ATS) with a user-programmable resolution. ATS is a count of high-activity events, relative to overall activity/mobility during a summary period. An algorithm is used to identify the high-activity events from accelerometer data and reports the data as a count per time-series interval. Summary statistics describing the data used to identify high-activity events accompany the activity time-series. In this study, we first tested the ATS activity metric through simulating PSAT output from accelerometer data logger archives, comparing ATS to vectorial dynamic body acceleration. Next, we deployed PSATs with ATS under captive conditions with cobia (*Rachycentron canadum*). Lastly, we deployed seven pop-off satellite archival tags (PSATs) able to collect and transmit ATS in the wild on adult sandbar sharks (*Carcharhinus plumbeus*). In the captive trials, we identified both resting and non-resting behavior for species and used logistic regression to compare ATS values with observed activity levels. In captive cobia, ATS was a significant predictor of observed activity levels. For 30-day wild deployments on sandbar sharks, satellites received 57.4–73.2% of the transmitted activity data. Of these ATS datapoints, between 21.9 and 41.2% of records had a concurrent set of temperature, depth, and light measurements. These results suggest that ATS is a practical metric for remotely monitoring and transmitting relative high-activity data in large-bodied aquatic species with variable activity levels, under changing environmental conditions, and across broad spatiotemporal scales.

Keywords: Biotelemetry, Biologging, Accelerometers, Activity, Sharks, Behavior, Activity levels, Satellite tags

Background

Interpretation of animal movement patterns has been a central focus of ecological studies and is a critical component of modern conservation research [1, 2]. Given the challenges of directly observing the movements and associated behaviors of marine and freshwater animals under natural conditions, researchers have used biologging and

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biotelemetry tools to monitor activity remotely. These methods provide a glimpse into the animals' behavior in wild environments, without the burden of human presence for observation [3].

Researchers have been increasingly integrating multiple sensors into tracking tools to provide additional information on how aquatic animals interact with their environments. Common combinations include tri-axial acceleration, temperature, and pressure (depth) sensors (e.g., [4, 5]). Similar combinations have been used to study where and when certain behaviors occur, such as mating or feeding [6–8]; to investigate biological drivers of movement patterns, such as circadian rhythms or behavioral thermoregulation [9, 10]; to identify impacts of human activity, such as post-release fishing mortality [11, 12] or provisioning for dive tourism [13]; and to measure field metabolic rates, infer thermal performance, and measure activity levels and their responses to environmental settings [14, 15].

In activity studies, accelerometers sample multiple axes at high frequencies, often measuring and logging at > 15 Hz, and up to 500 Hz [16–18]. The total amount of raw data recorded is therefore too large for transmission via satellite; as a result, researchers physically recover logging devices to obtain their raw data, or logging devices transmit their data from within an acoustic receiver array [18–20]. Tag recovery is logistically difficult for wide-ranging aquatic animals, such as elasmobranchs and large teleost fishes that do not return to locations where their recapture is predictable [21]. To maximize the probability of retrieving the loggers or having the data transmitted to an array, accelerometer applications are limited by tracking duration (e.g., from hours to days) and/or by the species studied (e.g., less mobile species or those returning to predictable areas) [19–23].

Study aims

Understanding how highly mobile or open-ocean animals respond to environmental variability, over multiple months, can give researchers evidence of animals', populations', or species' spatial and environmental preferences [24, 25]. Garnering such evidence can contribute to conservation planning and management, such as assessing climate change vulnerability or species use in protected and unprotected areas [25–27]. Following previous studies [28, 29] (Table 1), we aim to address this area of research by pairing a compressed metric of activity with environmental data (depth and temperature) and location data (geolocation). Specifically, we present a novel, satellite-transmittable, acceleration-derived metric of high-activity based on measurements obtained from pop-off satellite archival tags (PSAT). PSATs transmit this metric as an 'activity time-series' (ATS), which represents a count of high-activity events per a time-series interval, where an algorithm identifies high-activity events from accelerometer data. ATS is paired with an hourly measure of mobility (along x, y, and z-axes), and existing time-series data products for depth and temperature. The ATS-enabled PSAT can overcome the limited bandwidth of satellite transmission via Argos by processing the raw accelerometer data onboard the tag and only transmitting the ATS time-series with concurrent summary statistics of the raw data. Accordingly, this study had three primary objectives: (1) test the ATS data product under captive conditions to verify that it is a reasonable metric of high activity; (2) conduct wild deployments of ATS-PSATs to test their utility for measuring and transmitting ATS time-series data with corresponding mobility, depth, temperature, and light levels in highly migratory species; and (3) demonstrate the utility of the data obtained by comparing the ATS data product against other traditional accelerometer-derived measures of activity level (specifically, vectorial dynamic body acceleration, VeDBA).

Methods

PSAT tags

PSATs are positively buoyant devices that continuously log sensor data for a predetermined length of time. The tag then releases from the animal and floats at the surface where it transmits data to a receiving satellite in the Argos satellite network [30, 31]. These data commonly include temperature, depth, and light levels, which are used to approximate tag location during the deployment [32]. These concurrent time-series of environmental conditions contextualize the geospatial location of individual animals. There are two major drawbacks to data transmission via the Argos network: message size and satellite availability [33]. Data messages are limited in size and must be transmitted at a very small bandwidth (~ 32 bytes/message); this means that a researcher will need more messages to transmit more data. The Argos system comprises a network of polar-orbiting satellites; the availability of these satellites can vary both spatially and temporally. PSATs send messages to the satellites without acknowledgment of receipt, and corruption of messages is possible. To increase the likelihood that satellites receive the message correctly, manufacturers recommend sending each message multiple times. However, if attempting to transmit an extensive amount of data (e.g., three concurrent time-series), due to the above-mentioned issues, there may be some gaps in the data. To address this limitation, researchers can compress the data's dimensions, either by combining several data into one metric [34] or by recording events based on a predetermined algorithm which incorporates several streams of data [17, 28, 29], and/or compress the data temporally,

Table 1 Accelerometer-derived metrics of activity and/or behaviour for marine animals, including the targeted activity or behavior, equipment used, and example study or studies using the metric

Metric	Identification	Target activity	Equipment	Frequency/timespan	Species	Ref
Calculated before data transmission (no device retrieval needed)						
PrCA (prey catch attempt)	Per-second change in acceleration greater than a (running average + threshold) value	Dive-foraging attempts via rapid head and body movements	Relay satellite tag	One dive sampled and summarized every 2.25 h at 16 Hz for up to 338 days	Wedell *(Leptonychotes weddellii)*[41] and southern elephant seals (*Mirounga leonine)*[31]	[28, 43]
KD (knockdown event)	Abrupt switch of PSAT from vertical to horizontal	Beginning of a swimming bout, mortality	PSAT	2-h summary of 1-Hz data/60 days	Pacific halibut (*Hippoglossus stenolepis*)	[29, 44]
Tilt (g)	Degree of PSAT tilt, from vertical to horizontal via z-axis	Swimming behavior (sustained or saltatory), mortality	PSAT	2-h summary of 1-Hz data/60 days	Pacific halibut (*Hippoglossus stenolepis*)	[29, 44]
ATS (activity time-series)	Per-second instances of mobility exceeding a dynamic high activity threshold	Relative high activity	PSAT	75-s and 1-h summaries of 1-Hz data/30 days	Sandbar sharks (*Carcharhinus plumbeus*)	[This study]
G	Vectorized acceleration along x, y, and z-axes	Diurnal activity	PSAT	3-min summaries of 1.5625-Hz data	Pacific sailfish (*Istiophorus platypterus*)	[34]
Calculated before device retrieval						
Burst acceleration events	Exceeds manually defined acceleration threshold	Escape behaviors	Accelerometer logger	500 Hz/18–45 h	Red seabream (*Pagrus major*) and yellowtail kingfish (*Seriola lalandi)*	[45]
Calculated after device retrieval						
Prey engulfment	Differential of acceleration > 1000 m/s	Feeding (raptorial and suction)	Accelerometer logger	200 and 333 Hz/timespan NA	Harbor seal (*Phoca vitulina*)	[19]
ODBA (overall dynamic body acceleration)	(Absolute acceleration along x, y, and z-axes) − (static acceleration due to gravity)	Energy expenditure (as acceleration around a center of mass)	Accelerometer logger	Moderate-to-high frequency (> 10 Hz)	NA	[46]

ATS is included for reference

by choosing a method to summarize data over a certain period [29]. We combined both strategies by combining three axes of acceleration into one metric, summarized and transmitted as a time-series (described below).

The PSATs in this study record pressure (depth) to 1700 m (±0.5 m resolution), temperature from − 40 to 60 °C (±0.05 °C resolution), and light levels from 5×10^{-12} to 5×10^{-2} W cm^{-2}, at 440 nm resolution. The devices' total length x width measured 124 × 38 mm, with a weight in air of 60 g (Wildlife Computers). This PSAT samples acceleration along the x, y, and z-axes (Ax, Ay, and Az) at 8 Hz for data processing and calculation of ATS, and then archives the processed data, along with raw sensor data every 1 s for storage, which researchers can access via download if they recover the tag.

The user chooses the time-series frequency and corresponding summary period span for MiniPAT tags. The summary period is used to parse the data into the time-series intervals, which the PSAT will transmit via satellite. This also provides a way to calculate summary statistics to describe the animal or environment over longer durations than the intervals themselves. In this study, the shortest possible time-series interval (75 s) was used to calculate ATS; however, MiniPAT time-series can be programmed for longer intervals. A longer period would cause less frequent calculations, but would extend the temporal coverage of the data. For example, a 75-s time-series uses a 1-h summary period, and a 10-min time-series uses an 8-h summary period. At the time of this study, the tag could record and transmit 75-s time-series data for activity, depth, and temperature, with additional light-level data for approximately 1 month (Additional file 1: Text and Additional file 1: Tables S1 and S2). All tag conditions are set ahead of deployment using the Wildlife Computers Tag Agent software.

We attached PSATs to the study animals via a tether to an umbrella dart embedded in the dorsal musculature, such that the tag trailed ~ 6 cm off the animals. Tethers comprised a stainless-steel cable sheathed in surgical tubing and covered by heat-shrunk plastic tubing. We used this attachment method so that the tags could detach from the animal, float to the surface, and transmit their data. Tags continuously transmit data through the Argos satellite network until they deplete their batteries. We note that most accelerometer experiments on fish usually affix the tag to the dorsal fin, permitting analysis for tri-axial acceleration to measure fine-scale fish pitch, roll, and tail-beat frequency. As the ATS-PSATs are tethered, permitting tag rotation, our application captures the total force exerted on the tag from fish movement. Accordingly, the summary metric is axis-independent and does not require differentiation among the *x*, *y*, and *z*-axes. As such, ATS is not intended to provide information on, or measure fine-scale fish pitch, roll, and tail-beat frequency, nor on specific behaviors such as feeding or hunting.

Activity metric

In this study, we broadly defined 'activity' as an animal's whole-body (locomotory activity) movement. We tested a filtered metric of high activity that can be applied across species and habitats and provide information about an animal's behavior without recovering the tag. Wildlife Computers (WC) (Wildlife Computers, Redmond, WA, USA), in consultation with the authorship team, developed the ATS metric and incorporated it into a WC MiniPAT tag. WC similarly records and formats all time-series data on their tags (e.g., at certain frequencies and over certain time spans), so the ATS metric was designed to operate within these parameters. After pre-programmed release from the animal, the PSAT begins a series of calculations (illustrated in Fig. 1):

1. 'Mobility': Mobility is the row-wise mean of the standard deviation (σ) of acceleration (A_x, A_y, and A_z are the x, y, and z-axes of acceleration), where σ is calculated over a 3-s moving window on the 8-Hz data that advances by 1-s increments, and then recorded for every 1 s:

$$\text{Mobility}_i = \frac{\sum_{i=1}^{24} \sigma\left(A_{xi} + A_{yi} + A_{zi}\right)}{24}.$$

2. 'High activity' (HA): for each summary period (e.g., 1 h), the Mobility vector is centered to a mean of 0. Any Mobility values occurring in the tail of this skewed distribution are identified as HA events. Records in the 'tail' are isolated by a dynamic threshold value, which is the absolute value of the minimum Mobility value of the centered distribution:

$$\text{HAthreshold}_{i:i+3559} = \left|\min\left(\text{cent}\left(\left(\varphi(\text{Mobility}_{\text{i:i+3599}})\right)\right)\right|$$

3. ATS: the number of HA events during each 1-h summary period is counted and split into time-series intervals (75 s). The count of HA events per 75-s interval is then transmitted via satellite as a time-series:

$$\text{ATS}_{[i:i+74]} = \sum_{i=1}^{75} M_i > \text{HAthreshold}_{i:i+74}.$$

Transmitted time-series data for these tags include the time-series data itself (ATS: high activity counts every 75 s) and 'Series Range' data (Additional file 1: Table S1). The Series Range data includes a set of metrics that describe the data used to calculate ATS over a

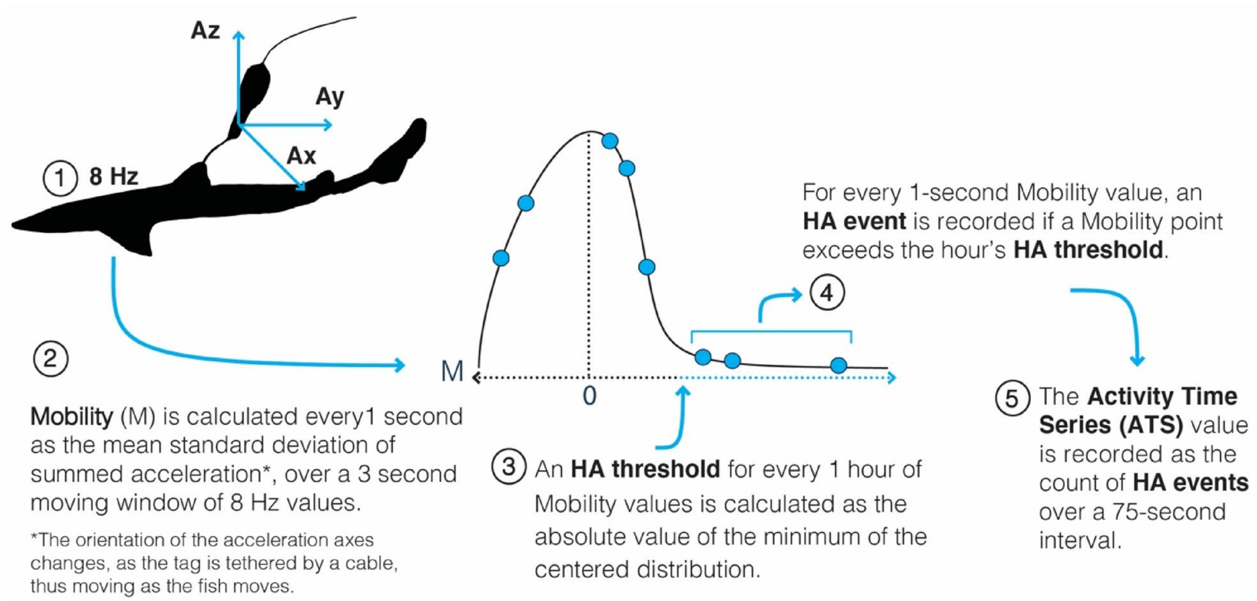

Fig. 1 A visual depiction of how the activity time-series (ATS) metric is calculated onboard the pop-off satellite tag (PSAT). (1) Tri-axial acceleration values are sensed at 8 Hz, and (2) are summarized as a single mobility (*M*) value (the mean standard deviation of the sum of Ax, Ay, and Az over a 3-s moving window). (3) The distribution of *M* over a set summary period is centered at zero, and a threshold value for HA events is established (the absolute value of the minimum of the centered distribution), such that (4) an *M* value greater than the threshold is considered a high-activity (HA) event. (5) The number of HA events is recorded over predetermined time-series (every 75 s) for transmission as ATS

1-h summary period; Series Range includes the mean and standard deviation of the Mobility vector that was used to find the High Activity (HA) events over each successive 1 h. The count of HA events (ATS) over the 1-h summary period is included with the 'Series' data.

The researcher can use ATS and its associated summary metrics (e.g., Mobility) to describe long-term and short-term activity patterns. The hourly mean and SD of Mobility provides a 'baseline' against which ATS events are determined. For example, a 1-h record of a reef fish swimming at a moderate, steady speed with no changes in acceleration would cause low ATS values, moderate 1-h mean Mobility, and low 1-h SD of Mobility. If the reef fish were to have several bouts of quicker swimming (e.g., evading a predator), there would be several instances of higher ATS data-points during the 1-h summary period, with higher SD in Mobility. Were this fish to rest on the bottom with a few movements over the hour, mean Mobility would be very low, although these few movements would be reflected in the ATS values.

Design considerations We note that our metric is a way to infer changes in activity from accelerometer data on a PSAT. It is not reflective of ODBA or VeDBA, and the inferences gained from it are also not equivalent to those of ODBA or VeDBA (Table 1). Rather, Mobility and ATS provide a metric of relatively high activity and when these active events occur, in a time-series format that corresponds to existing time-series metrics for temperature and depth. Given the metric, and individual variation both among and between species, the inference of a specific behavior is questionable and would likely not broadly apply.

ATS simulation

To contextualize and differentiate ATS from prior metrics of activity, we calculated VeDBA and ATS on the same set of archival data from tri-axial accelerometer loggers. We used two archives from wild deployments of accelerometer loggers, one at 50 Hz from a nurse shark (*Ginglymostoma cirratum;* OpenTag Motion OT3 Datalogger, Loggerhead Instruments. Sarasota, FL, USA), and one at 16 Hz from a gray reef shark (*Carcharhinus amblyrhynchos* [9], ORI400-D3GT logger, Little Leonardo Co., Tokyo, Japan). Archives were sub-sampled to 8 Hz to simulate data collected by ATS-PSATs. The sub-sampled 8-Hz data were then used to calculate ATS over 75-s periods. After removing the static component of acceleration from gravity using a Butterworth low-pass filter over a 3-s window, we calculated VeDBA ($VeDBA = \sqrt{A_x^2 + A_y^2 + A_z^2}$) at 8 Hz (using the packages "signal" and "tagtools" in R [35, 36]). We did not expect that ATS would mirror VeDBA, but that relatively high-activity events would occur at similar times. We identified relatively high-activity from VeDBA by applying a k-means clustering algorithm with four clusters (using "stats" in R [37]), then visually compared VeDBA clusters with simulated ATS. We did not conduct statistical tests, because we did not expect ATS and VeDBA to have similarities in their time-series—rather, we expected to see higher ATS values when there were sustained 'spikes' in VeDBA.

Captive trials

Animal tagging To test the performance of the ATS algorithm for measuring burst-activity, we deployed the tags on captive fish under both video and visual observation. We deployed tags on cobia (*Rachycentron canadum*), which allowed us to test the performance of ATS in a large, fast-moving teleost fish with heterogeneous activity levels. We also deployed the tags on a relatively slower moving fish with more homogenous activity levels (dogfish sharks, *Squalus acanthias*). However, after considering the video records, we deemed the small size of the animals (57–66 cm total length, TL) relative to the tags insufficiently representative of wild applications. We describe the tags' data output is alongside that of cobia in the supplementary electronic materials, however, did not use these data for further analysis.

We deployed ATS-PSATs over 5 days on four mature female cobia (103–112 cm TL, weight 8.16–9.07 kg) at the University of Miami's Experimental Hatchery (UMEH) facility in Miami, FL, USA). The tank housing the cobia was 20 m in diameter and 1.8 m in height and received a constant influx of ultraviolet flow-through seawater filtered down to 10 μm. We programmed the tags to release from the fish after 5 days. We then recovered the tags from the tanks so we could download the archived data for a comparison of raw data with the transmitted ATS product. We did not intend our captive deployments to test the transmission of ATS; rather, we sought to use the ATS archive for comparison with observed patterns in activity level.

Video observation To record cobia activity patterns, we mounted three GoPro cameras (two model HERO3 + and one model HERO4, GoPro, San Mateo, CA) around the tank (two downwards-facing, one lateral-facing). Cameras were deployed for two, 2-h periods each day (0900–1100 h, and 1500–1700 h) to capture a breadth of behaviors and activity levels based on research facility staff's prior knowledge (e.g., high activity associated with feeding events). Using the video footage, we first visually coded fish movements into 8 descriptive categories (Additional file 1: Table S3), and then sorted these into one of three activity levels, referred to as $\text{Activity}_{\text{obs}}$: rest, cruising, and quicker swimming. "Rest" was identified as the fish resting on the bottom of the tank; "cruising" as swimming not preceded by acceleration, or swimming following a 'deceleration'; and "quicker" as swimming following an acceleration. We assigned $\text{Activity}_{\text{obs}}$ for each 1 s of the video recording, for each fish, to correspond with the 1-s frequency of PSAT archives.

Analysis of captive trials To analyze the ability of ATS to reflect a *change* in activity level, we further condensed categories of $\text{Activity}_{\text{obs}}$ into two states: Resting and Not Resting. We used Bayesian logistic regression models with ATS as a predictor of $\text{Activity}_{\text{Obs}}$ using the 'arm' package in R [38]. We also ran a multinomial model to see if ATS could distinguish between additional behavior categories (resting, cruising, and quicker swimming), using the 'nnet' package in R [39].

Wild deployments

To test the ability and utility of the ATS-enabled PSATs to record and transmit ATS with corresponding environmental data from highly migratory species, we deployed seven ATS-PSATS on adult sandbar sharks (*Carcharhinus plumbeus*): two off the coast of Miami (Florida, USA) and five off the coast of Ocean City (Maryland, USA). Our goal was to receive full triplets of time-series data to match activity with depth and temperature data. In this study, we use these data to confirm the potential of ATS to monitor wild activity and do not infer beyond this. A more formal analysis of activity related to the environment will be forthcoming. We note that using different species for our wild and captive deployments was practical (i.e., having access to Cobia in a captive, observable setting, versus having no access to sandbar sharks in a captive setting) and did not interfere with the study goals; a strength of ATS is its adaptive threshold for HA events, rather than a pre-set threshold. The tags produced data suitable for analysis so long as the species were sufficiently large-bodied and varied in their activities. Rather than additional assessment or validation of ATS itself, we intended the wild deployments to test whether the ATS-PSATs work in a field-setting and whether the tags can collect activity data along with temperature and depth time-series.

PSAT deployments Sharks in Miami were caught as part of an ongoing survey using methods described in Calich et al. [40], then briefly restrained for tagging and measurement. Sharks in Maryland were caught using rod and reel before tagging, measurement, and release. PSATs were attached to the animals using a plastic umbrella dart inserted into the dorsal musculature, using a stainless-steel applicator. For Miami deployments, PSATS were test tags provided by the manufacturer with known weak attachment points at the tag release mechanism, so while we configured them for 30-day deployments, we expected a premature release for these 2 tags. For Maryland deployments, we programmed all five PSATS for a 30-day deployment. Besides instrumentation, each animal was sexed and measured for pre-caudal, fork, and total lengths [41].

Analysis of wild deployments We estimated the movement paths of the animals with the GPE3 state–space modeling tool in the Wildlife Computers Data Portal. GPE3 uses transmitted observations of irradiance (sunset and sunrise times), dive depth, and ambient surface temperature data, in combination with a diffusion-based movement model and known locations (from deployment location and known Argos locations), to estimate the most likely position of an animal at a given time. Before using GPE3, we removed observations from after the PSATs released from the animals (based on depth time-series showing a rapid ascent and subsequent residency at the surface) so that movement path calculation was only based on data from when the PSAT was on the animal.

Results

ATS simulation

Using archived accelerometer data from wild deployments on a nurse shark (20 min) and a gray reef shark (6 h), we calculated ATS, and VeDBA (Fig. 2). Visual examination showed similar timing for ATS (Fig. 2a, c), and changes in VeDBA (Fig. 2b, d). The reef shark's highest ATS values occurred within the first two hours

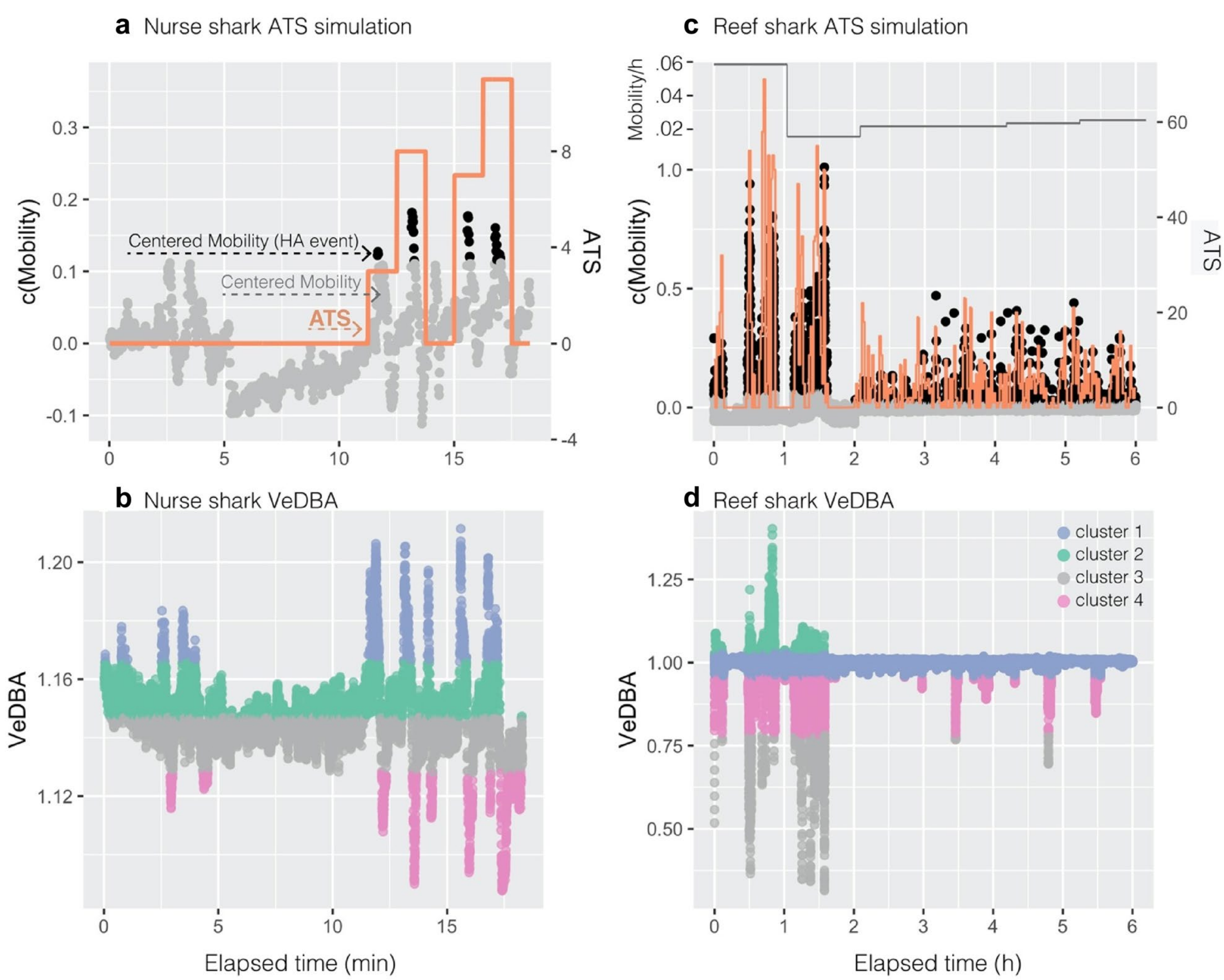

Fig. 2 A comparison of ATS and Mobility **a**, **c** with VeDBA **b, d**, calculated from two archived tri-axial accelerometry datasets. "High-Activity" (HA) events based on mobility are indicated by black points, which are counted over 75-s periods to calculate ATS (orange line). In **c**, a gray line indicates mean hourly mobility. VeDBA is colored by cluster, determined by a k-means clustering algorithm with a total of 4 clusters, to visualize different activity levels. ATS and Mobility are not meant to replicate VeDBA, but rather to indicate relative high activity over time

(Fig. 2c, d), when VeDBA was most frequently switching from low to high values. For the remainder of the 6-h time-series, ATS was lower, when VeDBA values were lower and showed fewer instances of switching to a relatively higher magnitude.

Captive deployments

PSAT deployments Of the four PSATs deployed on cobia, three tags dislodged prematurely from the fish after 1, 1.5, and 4.5 days, and one tag remained attached for the full 5 days. Video recording captured approximately 24 total hours of video for the tag that remained in place for the full 5 days (Additional file 1: Table S4 and S5, describes video recording durations for each tag).

ATS as a predictor of activity We observed some variability in observed activity during the intervals being reported by ATS—for instance, between resting and cruising (Fig. 3a), and between cruising and quicker swimming (Fig. 3b). The time-series nature of ATS allows it to be adaptable throughout the deployment, which is evident from the range of ATS values for each $\text{Activity}_{\text{Obs}}$ level. For example, Fig. 3 shows increased mobility for cobia over two time periods; in Fig. 3a, the changes from 'resting' to *prolonged* durations of 'cruising' lead to the identification of more 'Active Events' via ATS than for the changes from 'cruising' to *short* durations of 'quicker swimming' in Fig. 3b. Our logistic regression model suggested that ATS was a significant predictor of $\text{Activity}_{\text{obs}}$ (coefficient estimate 0.322, standard error 0.002, *z*-test value 151.5, *p* value of the z statistic Pr $(>|z|)<0.001$; Additional file 1: Figures S1–S3) for the cobia, with the odds ratio of switching from resting to not resting when ATS increased was 1.38. A pseudo-Chi-square test for goodness of fit following Matthiopoulos et al. [42] returned a value greater than 0.05, indicating an acceptable model fit.

Wild deployments

PSAT deployment descriptions *Miami* We deployed the ATS-PSATs in July 2018 on two adult female sandbar sharks near Miami, FL (FL1 and FL2, Table 2 and Fig. 4). Both of the sharks were on the fishing gear for less than 30 min ahead of retrieval and tagging, and were in good condition upon release. The PSATs used in these two deployments released after 15 and 1 days for the sharks FL1 and FL2, respectively. As noted above, these tags were test tags, so we anticipated the premature release. Because of the short deployment duration, these tags transmitted near-complete datasets while floating at the surface: A shorter deployment resulted in fewer data collected and therefore fewer data messages to be transmitted for a complete dataset. Fewer data messages to be transmitted resulted in greater opportunity to transmit each message multiple times, and therefore increased the likelihood that satellites would receive each message without corruption. For these two tags, the majority (81.1 to 100%) of each activity, temperature, and depth time-series were transmitted and received; 61.7 (FL1) and 94.6% (FL2) contained the full 75-s time-series triplet (of activity, temperature, and depth). For ATS alone, 83.3 (FL1) and 94.6% (FL2) of

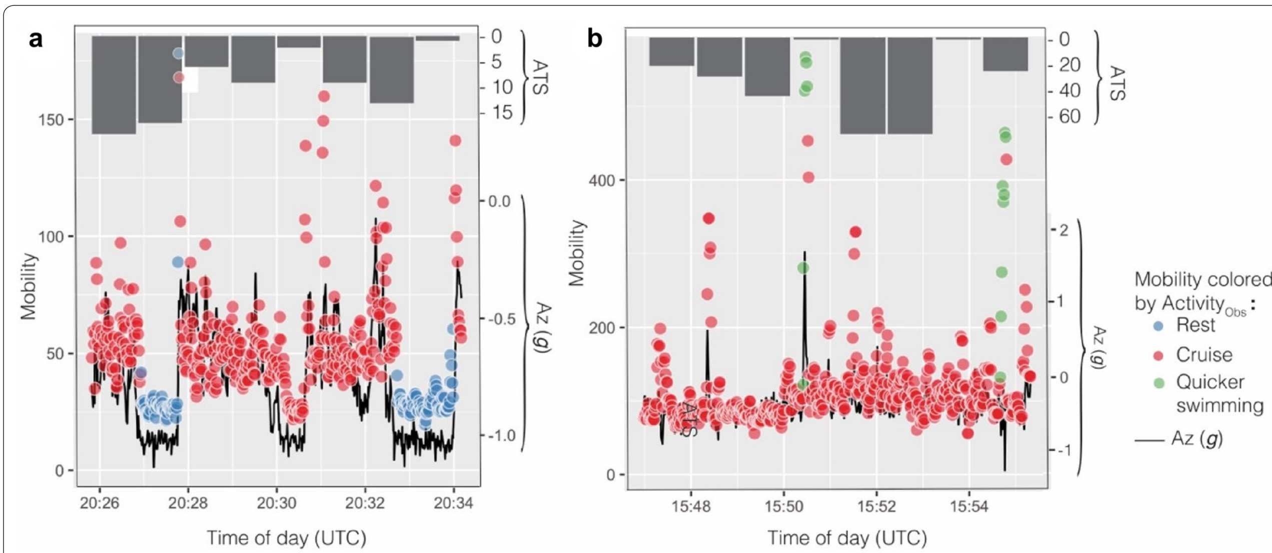

Fig. 3 For captive cobia CC2, 1-s mobility and Az, and 75-s ATS values over two 8-min periods. The gray bars indicate the count of ATS values, the black line indicates Az, and circles indicate mobility values (the mean standard deviation of the sum of Ax, Ay, and Az over a 3-s window). The color of each mobility data-point indicates which activity level was observed for that 1-s timepoint from video observation. Although one individual fish is displayed here, these patterns were similar across all data

Table 2 Animal size, sex, tagging location, deployment duration, and shark characteristics for the seven wild *Carcharhinus plumbeus* tagged with PSATs

Tagging					Shark characteristics				Movement summary	
ID	Date	Lat (DDs)	Lon (DDs)	Duration (days)	Sex	PCL (cm)	FL (cm)	TL (cm)	Distance (km)	Speed (km/day)
FL1	2018-07-22	25.64	− 80.09	14	F	160	178	214	582.21	19.42
FL2	2018-07-15	25.80	− 80.08	< 2	F	161	177	217	–	–
MD1	2018-09-19	38.22	− 75.03	30	M	105	115	152	241.41	7.91
MD2	2018-09-19	38.23	− 75.12	30	F	120	136	164	318.46	12.80
MD3	2018-09-19	38.22	− 75.12	30	F	122	132	163	789.12	26.05
MD4	2018-09-30	38.38	− 74.10	30	F	103	113	140	832.66	27.24
MD5	2018-10-04	38.25	− 74.08	30	F	105	115	142	260.34	8.59

Lat latitude, *Lon* longitude, *PCL* pre-caudal length, *TL* total length

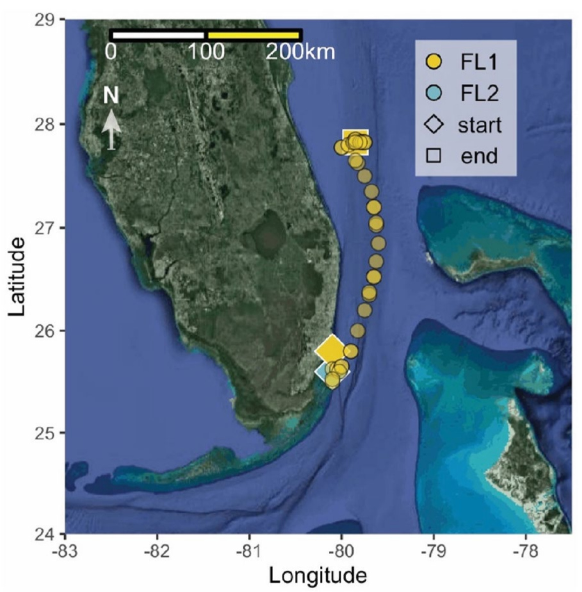

Fig. 4 Tagging locations, tag release locations, and geolocations for the two sandbar sharks tagged near Miami (Florida, USA). For shark FL2, only the location of tagging was available

both the time-series and range data were transmitted and received.

Ocean City, MD We successfully deployed ATS-PSATs on five sandbar sharks off the coast of Ocean City, Maryland, USA, in August 2018 (MD1–MD5 in Table 2 and Fig. 5). All sharks were in good condition upon release. Tags remained on the sharks for their pre-programmed 30-day duration. Each of the five tags transmitted the majority of each 75-s activity, temperature, and depth time-series (56.4–72.1%). Of the time-points covering the 30-day deployment, 22.2–41.2% contained the full 75-s time-series triplet (of activity, temperature, and depth). Additionally, 57.4–73.2% of the hourly *M* records were transmitted and received from MD sharks.

Depth and temperature trends To demonstrate the 'triplet' of measurements, we show the 75-s resolution time-series for activity, temperature, depth, over the entire deployment for sharks FL1 (Fig. 6) near Florida, and MD1 (Fig. 7) near Maryland. Summary data for all 7 deployments (Table 3) shows a higher mean temperature over the deployments in FL (26.7 ± 2.2 °C for FL sharks vs 22.5 ± 1.8 °C for MD sharks) and a broader temperature range (12.3–30.8 °C for FL sharks vs 10.4–26.1 °C for MD sharks). Depth range was broadest over the deployments in FL (0-213 m for FL sharks vs 0.5-127 m for MD sharks). Mobility values had a similar range between regions (28–63 for FL sharks vs 29–63 for MD sharks), with higher mean mobility values for deployments in MD (37.54 ± 8.98 for FL sharks vs 51.75 ± 11.8 for MD sharks).

Discussion

The simulated activity metric compared with VeDBA

As we anticipated, our simulation of ATS from accelerometer data loggers reflected the timing of switches to relatively high values in the VeDBA time-series (Fig. 2). Over the six hours of data from the reef shark, the ATS time-series showed a decrease that mirrored decreasing VeDBA values over the same time span.

Evaluations of the activity metric based on captive trials

For the captive trials, ATS was a significant predictor of $\text{Activity}_{\text{Obs}}$. The results of our logistic regression model had an odds ratio greater than one, indicating that as ATS increases, the switch from resting to not resting will occur more often than not (e.g., 1.38 times more likely). Our multinomial model's results showed that ATS was a good predictor of multiple activity levels, with the transitions from both resting to cruising and resting to

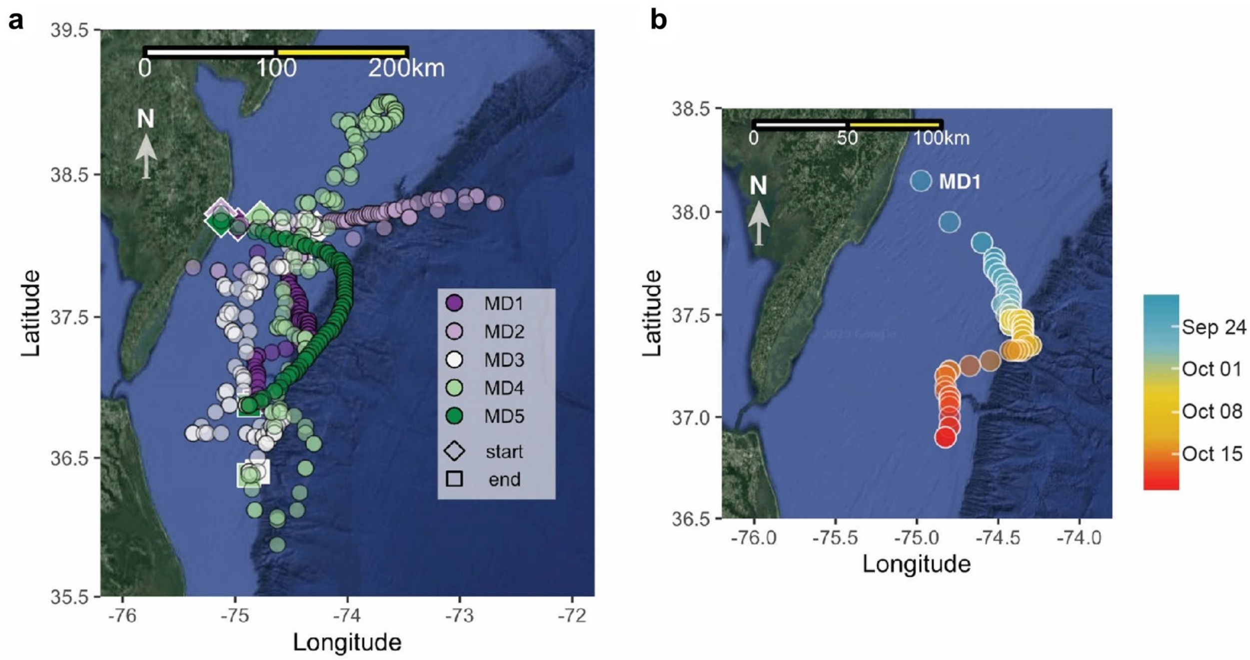

Fig. 5 **a** Tagging locations, tag release locations, and geolocations for the five sandbar sharks tagged near Ocean City (Maryland, USA), and **b** geolocations for shark MD1, with locations colored by date

quick swimming being significant. Cobias' variability in $Activity_{obs}$ likely explains the ability of the model to predict changes in their activity from ATS; we observed the fish resting, cruising, and swimming quickly around their tank, and displaying a significant change in activity during feeding events. This suggests that ATS can identify large changes in variable activity patterns. The detection of this variability in cobia suggests that ATS could play a role in detecting differences in activity among individual sharks, which researchers could relate to life history characteristics (size, sex, reproductive stage) or environmental conditions.

Our results are in line with other studies. Accelerometers recording at 5 Hz sufficed to capture swimming and resting behaviors in lemon sharks (*Negaprion brevirostris* [25]). In sailfish, satellite-transmitted metric of acceleration data (the standard deviation of *g*, where *g* is the square root of the sum of acceleration over 3 min) was successfully used to characterize general activity patterns [26]. Despite a longer summary period of 3 min, versus the 75 s in this study, the authors detected diel periodicity in relative activity levels.

The activity metric in wild deployments

In FL, the short deployment duration enabled a high proportion of data transmission and reception, providing a detailed look at post-release behavior. For shark FL1, linking the estimated movement path with the activity data suggests a relatively low activity for the first 8–9 days of the track. During this time, the shark moved steadily northwards, followed by periods of higher activity behavior for the remaining 4 days of the track (Fig. 7a-b) when the shark remained in a localized area (Fig. 5).

In MD, the longer deployments provided a broader perspective of activity levels, temperature, depth, and spatial movements. For instance, shark MD1 moved directly southwest for ~ 6 days after tag deployment, heading towards the continental shelf (Fig. 5). As the shark approached the edge of the shelf, there were more clustered locations for ~ 14 days. Next, the shark moved back to the continental shelf, and then southwards for the remainder of the 31-day track. There were three time periods of sustained higher Mobility and increased ATS values during the track (Fig. 7a, b): post-release (Sept. 20), once the shark moved off the shelf, and when it conducted a series of deeper dives in a localized area (Oct. 6–7 and Oct. 11–12; Fig. 6d). Additionally, MD1 Mobility values appeared higher at night than during the day prior.

Limitations

The time-series nature of ATS renders it low resolution when compared with recovering a full archive of accelerometer data. As a result, fine-scale behaviors such as burst acceleration events may be obscured if they occur on very short timescales. Further, we could not account for the influence of water flow on tag movement. This

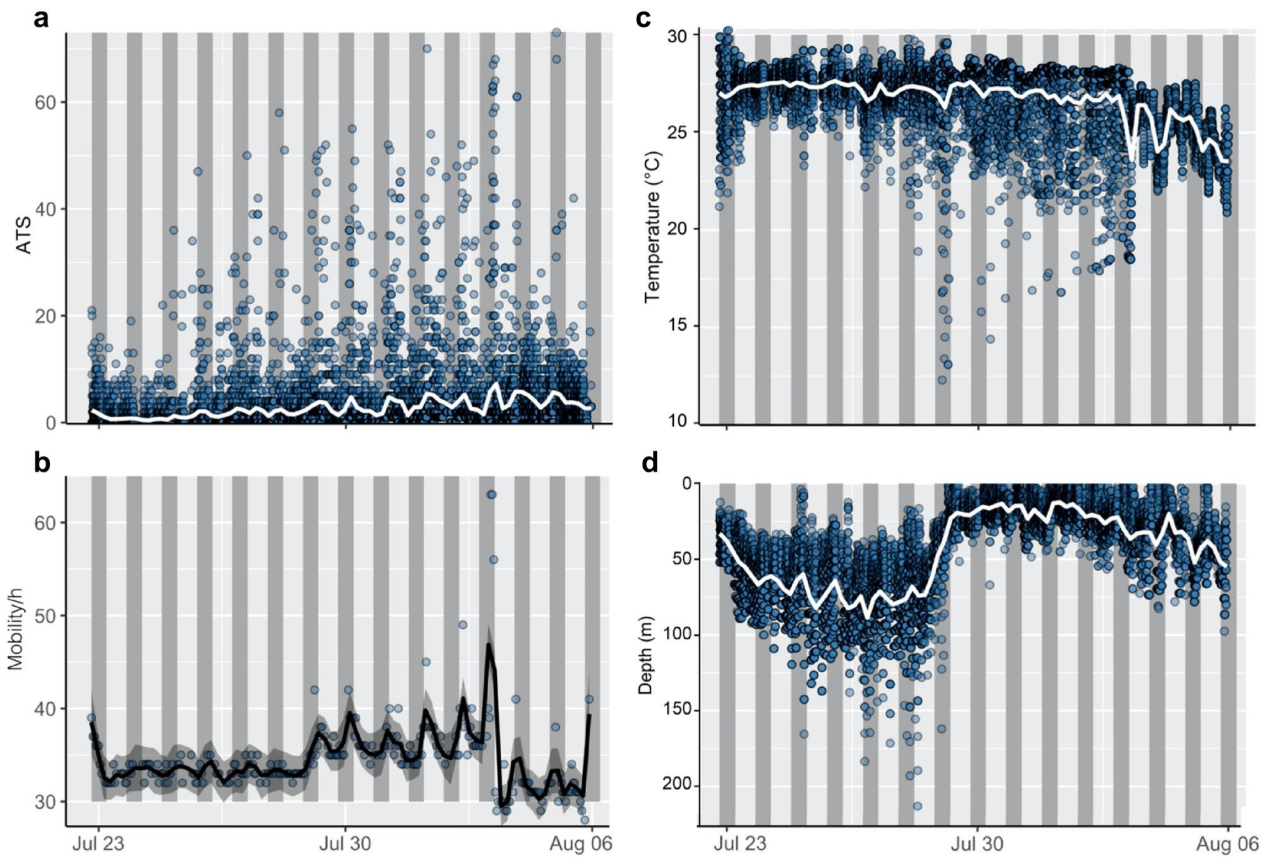

Fig. 6 For shark FL1, **a** 75-s ATS (activity time-series), **b** 1-h Mobility, and **c** depth at 75-s frequency, and **d** mean mobility over 1 h, for the 30-day deployment. Blue circles indicate time-series datapoints, and the thick white or black line represents a smoothed time-series using the loess method at a 5% span. Shaded gray rectangles indicate sunset to sunrise (20:00 to 06:30)

was most limiting in captive testing, as cobia were smaller relative to the PSATs, compared with the sandbar sharks. Lastly, the results from the captive trials suggest that while this metric is suitable for teleost fish with variable levels of activity, benthic fish with homogenous activity levels (e.g., smooth dogfish sharks) may not be practical candidates.

The 1-s archived values of mobility from the cobia (Fig. 3) suggest some considerations for inference. First, the summary period for ATS may have a lag effect because the duration of an activity may not fully occur within one time-series interval (Fig. 2a). Consequently, the summary period and time-series interval should be chosen wisely, ideally using prior knowledge of the study species. Second, short durations of high-mobility values did not appear to have a strong effect on ATS for cobia (Fig. 3b). However, the lag effect was not apparent in our simulation of ATS on archived data from wild deployments of accelerometer loggers (Fig. 2a, c); this may be due to greater variation in activity levels observed for the archived data (nurse sharks and gray reef sharks), such that relatively high-activity was more pronounced for those species for the cobia.

Lastly, in this study, our ATS-PSATS were limited to 1-month deployments for our choice of tag settings (e.g., 75-s time-series intervals). For future ATS-PSAT deployments, developers have extended this recording period to 3 months, with the accelerometer now able to sample at 10 Hz.

Conclusions

In summary, we tested a novel satellite-transmitted metric of activity in captive and wild settings, to approximate coarse activity levels in free-ranging aquatic animals. This metric is intended to measure relative changes in activity levels over a sufficient length of time to capture variability across a range of environmental conditions, which can transmitted via satellite. This metric is not intended to replace the high-resolution data collection and analysis from recoverable devices which permit a more detailed description of behavior and an absolute measure of activity level at a specific time point. In captive animals, the

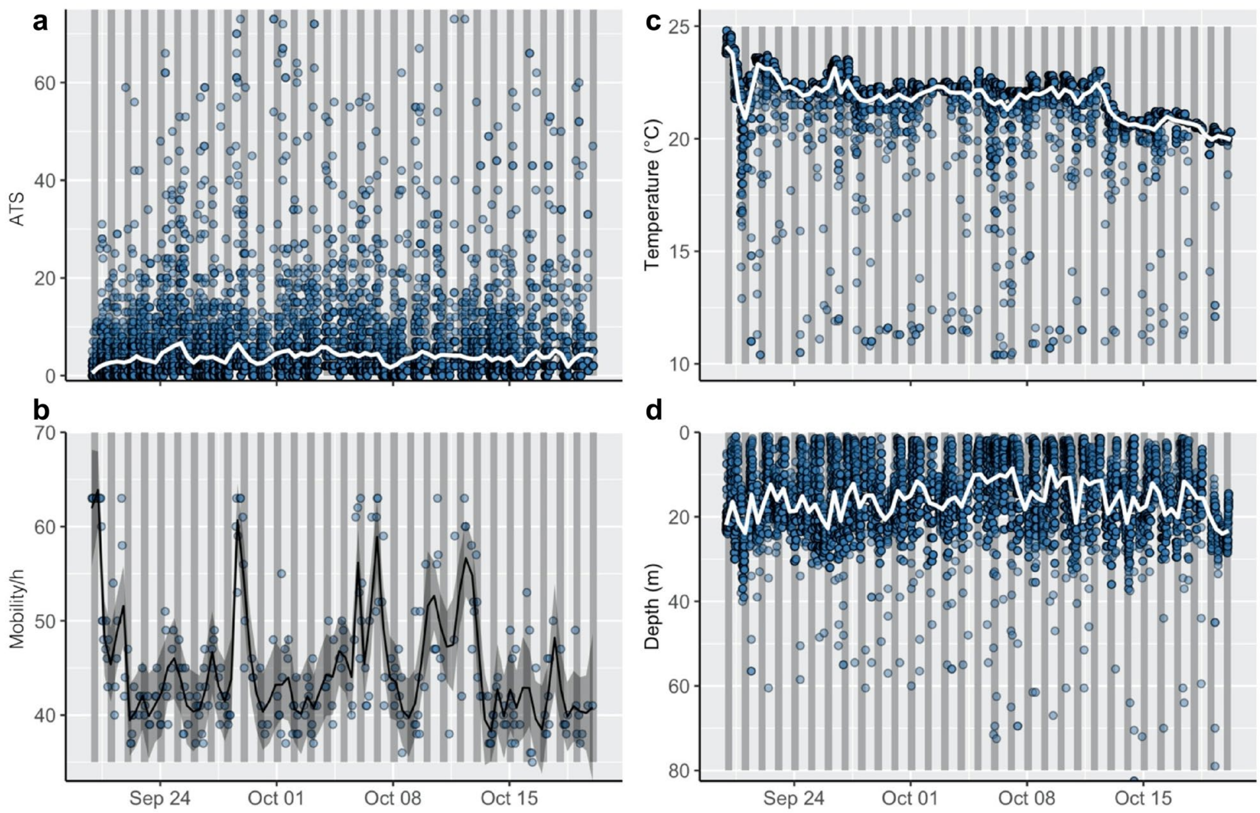

Fig. 7 For shark MD1, **a** 75-s ATS (activity time-series), **b** 1-h Mobility, and **c** depth at 75-s frequency, and **d** mean mobility over 1 h, for the 30-day deployment. Blue circles indicate time-series datapoints, and the thick white or black line represents a smoothed time-series using the loess method at a 5% span. Shaded gray rectangles indicate sunset to sunrise (20:00 to 06:30)

Table 3 Temperature, depth, and activity time-series (ATS), and mobility trends across all five sharks, and all sharks analyzed together, based on 75-s transmitted values

ID	Temperature (°C)		Depth (m)		ATS		Mobility	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
FL1	27.02 ± 1.94	12.3–30.9	39.1 ± 30.5	0.5–213	3 ± 6	0–73	35.92 ± 7.01	28–63
FL2	25.45 ± 2.67	15.8–30.2	13.1 ± 21.7	0–142	4 ± 5	0–48	37.90 ± 9.75	31–50
All FL	26.71 ± 2.19	12.3–30.9	34.21 ± 30.77	0–213	–	–	37.54 ± 8.98	28–63
MD1	21.77 ± 1.40	10.4–24.8	15.72 ± 7.98	1–82.5	3.78 ± 7.05	0–73	45.24 ± 7.27	35–63
MD2	23.96 ± 0.53	22.2–25.3	8.70 ± 3.75	1–19	3.02 ± 4.86	0–63	60.84 ± 7.78	30–63
MD3	22.11 ± 1.60	13.4–25.8	13.80 ± 11.10	0.5–91.5	4.49 ± 6.41	0–73	49.52 ± 11.56	31–63
MD4	20.63 ± 1.27	11.8–24.1	16.71 ± 13.00	0.5–127	3.10 ± 5.68	0–73	62 ± 2.28	50–63
MD5	24.10 ± 1.05	13.4–26.1	11.20 ± 4.66	1.5–46	5.67 ± 7.60	0–73	40.58 ± 9.74	34–44
All MD	22.54 ± 1.77	10.4–26.1	13.13 ± 9.36	0.5–127.0	–	–	51.75 ± 11.8	29–63

SD indicates standard deviation, range indicates minimum to maximum values, and IQR indicates the interquartile range (25–75th percentiles). ATS is not given across all sharks, as the values are calculated relative to the individual sharks' mobility measurements within 75 s. Mobility is recorded hourly

ATS, recorded as a 75-s time-series of acceleration at 8 Hz, was used to predict visually observed behaviors in cobia, a large teleost fish. Wild deployments in Maryland and Florida (USA) produced a concurrent time-series record of activity, temperature, and depth. This suggests the potential for interpreting relative activity in the context of an animals' environment. These data may also be useful for studying the post-release recovery from fishery interactions over periods of weeks to months, depending upon tag settings.

We particularly recommend this metric in settings where researchers cannot feasibly retrieve biologging devices. The most successful research applications would target animals that are both relatively large (e.g., fish > 1.5 m total length) and undergo considerable variability in activity (e.g., from resting to moving, or from slow to fast swimming speeds). Although the frequency of the logged activity metric tested here (75 s) is too low to capture more fine-scale behaviors, we believe this metric is measured at a sufficient frequency (8 Hz) ahead of filtering to be a proxy for the distribution of general activity level across time and space. The combination of ATS, and environmental data over longer periods provides a unique opportunity for investigating the effects of temperature on activity, diel activity patterns, activity patterns near habitat features (e.g., coral reefs versus pelagic areas), and/or comparisons of high-activity events among individuals and species. This is the first transmittable metric of continuous whole-body activity available on a PSAT-style tag, and our results suggest that this activity metric could provide another dimension (relatively high-activity) to studies of long-range aquatic animal movements.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40317-020-00220-0.

Additional file 1: Text. Methodology for the deployment of PSATs on dogfish sharks (*Squalus acanthias*). **Figure S1.** An example of camera output used for activity level description and classification, of captive cobia **a** and dogfish **b**. **Figure S2.** Frequency distribution of archival values from captive deployments, for mobility (**a**, **b**) and activity time-series (ATS) (**c**, **d**), for all animals of each species. Each panel includes mean, standard deviation, and range. **Figure S3.** A logistic curve based on the results of our binary logistic regression for $Activity_{Obs} \sim ATS$. Teal circles represent observations of ATS, classified as either resting (0) or not resting (1). **Table S1**. Data products generated by the Wildlife Computers miniPAT pop-off satellite tag (PSAT). **Table S2.** Estimated deployment durations for the Wildlife Computers miniPAT pop-off satellite tag (PSAT) incorporating the ATS metric, depending on the length of the summary period (75 to 600 s). Percentages represent the probability of receiving 1 message, and a triplet of messages, sent 10, 20, and 30 times. **Table S3.** Description of observed behavior states from video recordings of captive cobia and dogfish. States were also observed in combination (e.g., quick swimming while rolling/righting). **Table S4**. Animal characteristics for captive trials, and temporal tag and video coverage of fish activity. Tag detachment was based on visual observation of detachment where possible or estimated from depth and activity time-series (ATS) records downloaded from tags, as the point in time where depth and ATS remained constant. Captive dogfish (Squalus acanthias) are indicated as CD, and captive cobia (Rachycentron canadum) as CC. **Table S5.** The number of 1 s labeled visual observations from video-recording of captive fish behavior, and the proportion of each behavior (%) with respect to total observations for the species.

Abbreviations

PSAT: Pop-off satellite archival tag; miniPAT: Wildlife Computers-brand PSAT; ATS: Activity time-series, a count of relatively high-activity events per time-series interval; Mobility: Raw accelerometer measurements summarized as the mean standard deviation of the sum of Ax, Ay, and Az; $Activity_{Obs}$: Visually observed activity.

Acknowledgements

For their assistance in captive trials, we thank the staff and student volunteers of the University of Miami Experimental Hatchery, particularly R. Hoenig, J. Florentino, and S. Mathur, the University of Miami Shark Research and Conservation Program, and the University of New England Department of Marine Science. Thank you to Austin Gallagher from Beneath the Waves Inc and his team, for deploying PSATS on sandbar sharks off Maryland. Thanks to Gaétan Richard for the initial development of the activity algorithm and providing feedback on our adaptation for use on a PSAT. We acknowledge that this research was performed on ancestral Tequesta and Seminole territories.

Authors' contributions

RS, NH, and YP conceived the ideas and designed methodology for testing the algorithm; RS, HJV, and NH collected the data; RS analyzed the data and led the writing of the manuscript, and KW adapted and integrated the ATS algorithm for use on a PSAT, and assisted with data analysis for captive trials. All authors contributed critically to the drafts. All authors read and approved the final manuscript.

Funding

RS is supported by an NSERC PGS-D scholarship from the Government of Canada, a UM Fellowship from the University of Miami, and a Guy Harvey Scholarship from Florida Sea Grant and the Guy Harvey Ocean Foundation. This study was supported by a University of Miami Provost Grant.

Availability of data and materials

The datasets and code produced during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures in studies involving animals were performed following ethical standards of the institution at which the studies were conducted (the University of Miami Institutional Animal Care and Use Committee (IACUC), Protocol Numbers [15–238], and the University of New England IACUC Protocol Number 051518-001).

Consent for publication

Not applicable.

Competing interests

Authors declare no competing interests.

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Received: 26 February 2020 Accepted: 17 October 2020
Published online: 22 November 2020

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