TELEMETRY CASE REPORT

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Was my science project eaten? A novel approach to validate consumption of marine biologging instruments

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Abstract

Background: Biologging and tracking instruments provide valuable, remote surveillance on otherwise unobservable marine animals. Instruments can be consumed (ingested) by predators while collecting data, and if not identified, the retrieved dataset could be assigned to the incorrect individual and/or species. Consumption events of instruments, such as pop-up satellite archival tags and data loggers that record ambient light, are typically identified by negligible light levels and visual assessment of data records. However, when light-level data are not available (e.g., environments below the euphotic zone, instrument model), instrument consumption is not easily discernible. Instruments that record concurrent, time-series temperature and depth data provide detailed information on the ambient temperature in the water column. However, if the instrument is consumed, the temperature profile may dissociate from the depth profile, providing evidence and a means for detecting consumption.

Results: To quantify the dissociation between time-series depth and temperature profiles, we applied the cross-correlation function to evaluate the time delay and uncoupling between time-series depth and temperature profiles, suggestive of instrument consumption. Given that instruments may be consumed midway through the deployment duration, we extended the cross-correlation function to systematically slide across time-series profiles, sequentially considering subsets of data, to infer time of consumption. This method was applied to datasets from both deep-water (disphotic and aphotic) and epipelagic (euphotic) environments to evaluate instrument consumption. Results were dependent on ambient environment, data sampling rate, predator physiology, and function parameters.

Conclusions: Utilization of the cross-correlation function objectively indicates potential instrument consumption events without the bias induced by subjective methods such as visual assessment of tag-recorded data, and does not require the simultaneous collection of light-level data. This methodology aids in the appropriate biological interpretation of tag-recorded data, ensures that data are not attributed to the incorrect species, and can be used to authenticate data during the validation process. Additionally, it is particularly useful for contrasting datasets from comparable studies (i.e., same location and species) and is applicable across taxa and electronic biologging instrument variations.

Keywords: Cross-correlation function, Tag predation, Time series, Deep-water habitat, Biologging

Background

Biologging instruments are proven tools used to investigate migration, temperature selection, vertical habitat

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use, and post-release survivorship of marine fishes [1–4]. A variety of biologging instruments (hereafter referred to as BIs), such as data loggers, pop-up satellite archival tags (PSATs), and tri-axial accelerometers, are commonly employed to study marine animal behavior across all marine biomes [5–8]. Gathering time-series records on variables, such as ambient temperature, depth, acceleration, and swim speed, provides insight into the dynamics



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of animal behavior, allowing for inference of the functionality of behavioral patterns [9–14]. Additionally, instruments that record concurrent, time-series depth and temperature records enable the fine-scale assessment of vertical behavior in relation to ambient temperature [15, 16]. These approaches can therefore provide highly complex insight into three-dimensional animal behaviors, which is paramount in driving innovative management of marine resources.

Animals fitted with BIs are subject to multiple stressors during capture, handling, and release [3, 17–19], which can cause either direct mortality [17] or increase susceptibility to post-release predation [20, 21]. Therefore, the ability to detect incidences of predation in tracked animals has implications for accurate post-release survivorship estimates and is of direct conservation interest to resource managers [20]. Moreover, predation events are not necessarily associated with capture effects, and thus identifying instances of consumption helps delineate potential predator—prey interactions [22–28]. Consequently, identification of BI consumption, potentially indicating animal predation, is important to both the efficacy of ecological studies and development of contemporary management approaches.

Instances of BI consumption are commonly determined by a qualitative examination of instrumentrecorded data and, depending on the BI, evidenced by changes in behavioral patterns or tailbeat frequencies, elevated temperatures, temperature delays with respect to the depth profile, and negligible light levels [1, 22, 24-32]. Tag consumption may be obvious in some cases, such as when zero-valued light levels in epipelagic waters concurrent with elevated temperatures clearly indicate BI consumption by an endotherm [22]. However, depending on the BI model, its consumption may not be obvious, such as when a BI lacks a light-level sensor (or is too deep to record light levels) and the consumer is an ectotherm [21]. In these cases, BI-recorded data could represent the instrument consumer rather than the target species, resulting in the inaccurate interpretation. Despite the prevalence of BI consumption events identified in the literature [1, 22, 24–30], a standardized, quantitative approach for the assessment of consumption has not been presented. Therefore, a tractable mathematical approach to identify BI consumption across multiple habitats and a suite of predators (consumers) is warranted as a means of validating data prior to biological interpretation.

In environments exhibiting well-defined temperature gradients, BI-recorded depth and ambient temperature variables are inherently coupled. However, if a BI is consumed, the time-series temperature profile may consistently lag behind the depth profile or arbitrarily dissociate

based on the thermal inertia of the BI consumer [1, 33, 34]. As a critical step in the data validation process, we present a novel approach using the well-established cross-correlation function [35, 36] to detect BI consumption of marine tracking instruments by quantifying the temporal dissociation between BI-recorded, time-series depth, and temperature profiles. Since this approach does not require ambient light data, it is applicable across taxa, including elusive deep-water species that may partly or fully reside below the euphotic zone where BIs consistently record inappreciable light levels.

Methods

Mathematical analysis

All analyses were performed in R (v. 2.15.3) [37]. To assess possible BI consumption, the temporal alignment between time-paired depth and temperature time-series profiles can be evaluated with the cross-correlation function (CCF) [35, 38]. The CCF measures the correlation between two time-series profiles for different lags (or shifts) of the time-series profiles relative to each other [36, 37] and is easily implemented with the built-in R "ccf" function [37] (Additional files 1, 2). Specifically, the CCF returns multiple correlation values, one for each integer-valued shift of the time series [36], and in order to summarize these results and obtain a coarse lag estimate, we identified the single lag associated with the largest correlation [35]. For example, if two profiles align exactly, then the maximum correlation would be 1, corresponding to a lag of 0. To ensure consistency, we routinely specify the depth profile as the "x" variable and the temperature profile as the "y" variable in the R "ccf" function [37]. In general, negative lag indicates that the temperature profile temporally lags behind the depth profile, and correspondingly, a positive lag indicates temperature is leading the depth profile. Additionally, the R "ccf" function requires specification of maximum lag to consider when evaluating the CCF [37].

The relationship between depth and temperature profiles may vary through time, especially if a BI is consumed midway through deployment, in which case, the section of tag-recorded data corresponding to the active fish may have different lag and correlation values relative to the section of data recorded while the tag was ingested by a predator. To account for this possible temporal dependence, we constructed a sliding CCF function that sequentially considers a sliding (or moving) set of records from the two time-series profiles [37] (Additional file 3). Specifically, the CCF is applied repeatedly to a sliding set of depth and temperature records (hereafter referred to as a window) with a step of one record between each application. The depth record at the center of each sliding window is assigned the CCF's maximum correlation

value and associated lag. The size of the sliding window (denoted as the window width and indicating the number of records) is arbitrary, and consequently, the sliding CCF should be evaluated for multiple window widths to ensure results are not an artifact of this variable. The sliding CCF does not begin on the first record, but rather starts at the record corresponding to half the width of the specified window width variable (Additional files 1, 2, 3).

Data description

In order to validate the CCF for detecting BI consumption, pop-up satellite archival tag (PSAT) data were collated from four independent datasets [19, 21, 39, 40] pertaining to five species of elasmobranchs: bluntnose sixgill shark (*Hexanchus griseus*), oceanic whitetip shark (*Carcharhinus longimanus*), Caribbean reef shark (*Carcharhinus perezi*), Cuban dogfish (*Squalus cubensis*), and gulper shark (*Centrophorus* spp.). All studies were conducted in The Bahamas, specifically, near Eleuthera and Cat Island, where temperature-at-depth records indicate monotonically varying temperature-versus-depth profiles in the water column [19, 41].

Although this method is applicable to data from any electronic BI providing concurrent, time-series depth and temperature records, all data analyzed in this study were recorded by X-Tags (Microwave Telemetry, Inc., Columbia, MD, USA; Additional file 4), and consisted of time-paired, time-series depth, temperature, and

light-level data at constant sampling rates (<5 min intervals). However, some datasets had temporal gaps (concurrent in both depth and temperature datasets), which were linearly interpolated for application of the CCF (Additional file 4).

Results

Example 1: CCF applied across species

We applied the cross-correlation function to a 5-day subset of time-paired depth and temperature data from multiple species tracked in The Bahamas (Table 1; Additional files 4 and 5). All active fish (n=5) exhibited a lag of either 0 or -1 (Table 1). The lag of -1 indicated that the temperature profile lags slightly behind the depth profile, presumably resulting from the conduction of heat through the tag to the temperature sensor. This inherent temperature delay would likely vary among BI models.

X-Tags attached to the oceanic whitetip shark (107797) and Caribbean reef shark (107800) registered light levels indicative of full light saturation during the deployment period, confirming that these tags were not consumed. The correlation (0.41) for the Caribbean reef shark (107800) dataset was considerably lower than the other active fish and is likely attributed to vertical habitat use in the mixed layer (Additional file 5), indicating that the CCF maximum correlation relates to the environment (i.e., temperature gradients) traversed by the fish. The remaining active tags (35545, 150491, and 154727) were deployed on deep-water species that use habitats below

Table 1 CCF results for both active fish and consumed tags

Fate	ID	Species	Deep-water (D) or epipelagic (E) species	Start of 5-day sequence	CCF maximum correlation	CCF lag	Sampling rate (s)
Active fish	35545	Bluntnose sixgill shark (Hexanchus griseus)	D	9/20/2010	0.99	0	286
	107797	Oceanic whitetip shark (Carcharhinus longimanus)	Е	5/22/2011	0.95	-1	120
	107800	Caribbean reef shark (Carcharhinus perezi)	Е	1/5/2012	0.41	-1	120
	150491	Cuban dogfish (Squalus cubensis)	D	10/8/2015	0.95	-1	133
	154727	Cuban dogfish (Squalus cubensis)	D	3/6/2016	0.96	-1	132
Consumed	65821	Bluntnose sixgill shark (Hexanchus griseus)	D	9/20/2010	0.85	-48	120
	103791	Gulper shark (Centrophorus spp.)	D	11/15/2010	0.45	-4	286
	103794	Gulper shark (Centrophorus spp.)	D	1/5/2011	0.64	-17	120
	115972	Caribbean reef shark (Carcharhinus perezi)	Е	7/10/2013	0.79	-82	120
	150489	Cuban dogfish (Squalus cubensis)	D	11/13/2015	0.95	-14	133

the euphotic zone where X-Tags register zero-valued light levels regardless of tag consumption. These tags surfaced immediately after initiation of the tag pop-off release mechanism (which causes the tag to detach from the fish and float to the surface; Additional file 4), providing additional evidence that the tags were not ingested (Table 1).

Next, we considered the results from the consumed datasets (n = 5). In the datasets collated from tagged gulper sharks (103791 and 103794), no light was registered, even though the predator spent the majority of time in the epipelagic zone (<200 m) where X-Tags typically record nonzero light levels, indicating tag consumption. The consumed Caribbean reef shark dataset (115972) demonstrated vertical habitat use in deep waters (400-1300 m) disjoint from other tracked Caribbean reef sharks [40], implying that this tag was consumed by a deep-water predator. Additionally, tags 115972 and 65821 did not surface when their release mechanisms were initiated, further suggesting these tags were ingested and consequently unable to surface. For Cuban dogfish (150489), a deep-water species occupying regions of the water column where an X-Tag only measures zero-valued light levels regardless of tag consumption, no further evidence suggests tag consumption besides the lag and correlation values (Table 1).

Example 2: application of the sliding CCF

We validated the sliding CCF based on data from tag 103794, which was originally deployed on a gulper shark (Table 1). Throughout deployment, this tag recorded zero-valued light levels, even though present in euphotic waters (<200 m). Coupled with the unusually shallow habitat use for a deep-water species, these observations indicated this tag was consumed. In this example, we only considered the lag determined by the sliding CCF. The sliding CCF was evaluated twice for window widths of 100 and 500 records (corresponding to approximately 3.3 and 16.7 h, respectively), and the depth profile was colored by the resulting sliding CCF-determined lag values (Fig. 1). For the smaller window width (100 records), there was more variability in the lag throughout deployment (demonstrated by variable colors; Fig. 1a). However, for the larger window width (500 records), the lag values were more uniform across the time series (demonstrated by consistently blue points; Fig. 1b). Consequently, the sliding CCF suggested tag consumption.

Example 3: sliding CCF for comparing datasets and effect of sampling rate

Two X-Tags (35545 and 65821) were deployed on bluntnose sixgill sharks on the same day and at the same location (Additional file 4). The sampling rates of these two datasets differed (4.75 and 2 min), and consequently, we

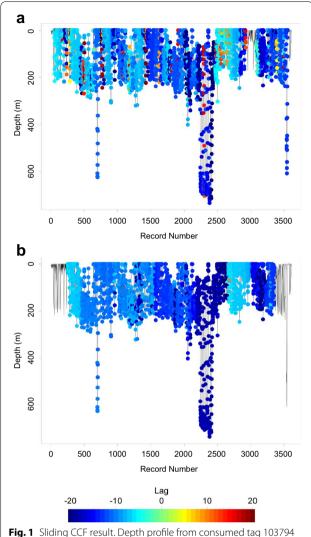


Fig. 1 Sliding CCF result. Depth profile from consumed tag 103794 colored by the lag identified with the sliding CCF for window widths of **a** 100 records (3.3 h) and **b** 500 records (16.7 h)

subsampled the 2-min profile to create a 4-min profile, for a more comparable dataset. Based on visual comparison, the depth and temperature profiles from 35545 (4.75 min sampling rate) closely aligned (Fig. 2a), but profiles from tag 65821 (4-min sampling rate) appeared to be misaligned, such that the temperature profile is shifted to the right relative to the depth profile (Fig. 2b).

Considering the first 10 days of data obtained from each tag, the sliding CCF results (Fig. 3) indicated considerable lags in 65821 (represented by blue points; Fig. 3a) not observed in 35545 (represented by green points; Fig. 3a). Additionally, the dataset from tag 35545 exhibited high correlation (dark red points; Fig. 3b) unlike 65821 which demonstrated lower and more variable correlation values (yellow, orange, and red points;

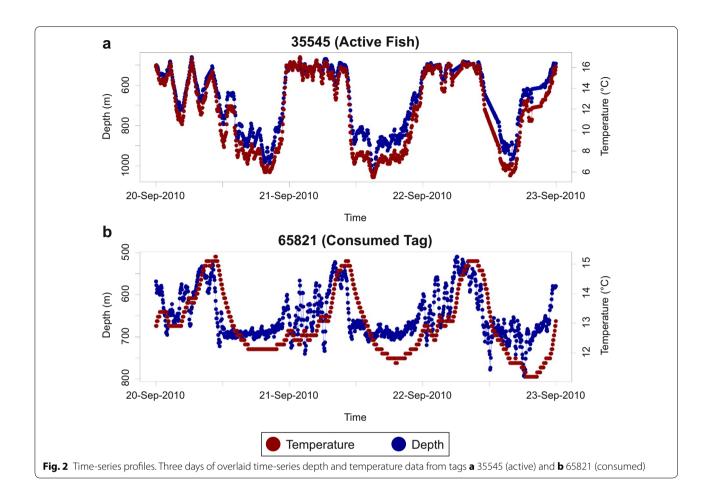


Fig. 3b). This comparison between datasets suggests that tag 65821 was consumed while tag 35545 collected data from an active fish.

In addition, we assessed how the maximum correlation and corresponding lag in the (non-sliding) CCF were dependent on sampling rate by sequentially doubling the sampling interval. For tag 65821, we considered CCF results for sampling rates between 1 and 60 min on 1-min intervals (Additional file 4), while for tag 35545, we considered CCF results for sampling rates incremented by 4.75 up to 62 min. The correlation remained consistent across sampling rates (Fig. 4a). As expected, lag followed a logarithmic curve for the consumed tag; specifically, data records collected on 1-min intervals indicated a maximum lag of -165, while data records collected on 60-min intervals indicated a maximum lag of -3 (Fig. 4b). Comparatively, the lag from the active fish was 0 despite the varying sampling rate.

Discussion

The application of the CCF and sliding CCF is a simple, systematic method for comparing time-series depth and temperature profiles and provides a novel approach to

infer biologging infer BI consumption. When a BI is consumed by a predator, recorded temperature records dissociate from the concurrently recorded depth records. For example, internal stomach temperatures of endothermic species, such as Atlantic bluefin tunas (Thunnus thynnus) and mako sharks (Isurus oxyrinchus), remain elevated and relatively invariable despite fluctuating depth and ambient temperatures [33, 42]. In contrast, internal temperatures from ectotherms such as blue sharks (Prionace glauca) and dusky sharks (Carcharhinus obscurus) change, although not instantaneously or linearly, in response to ambient temperature [33, 43]. The CCF provides a means of assessing the degree of uncoupling through a systematic shift (considerable lag) and/or arbitrary disassociation (low correlation) between depth and temperature profiles, over a wide range of BI consumer taxa. The sliding CCF extends this result to consider how the depth-temperature association changes through time, which is particularly useful if a BI is consumed midway through a deployment mission.

Application of this technique is also useful for assessing BI consumption in deep-water (>200 m) species that reside where inappreciable light levels disguise BI

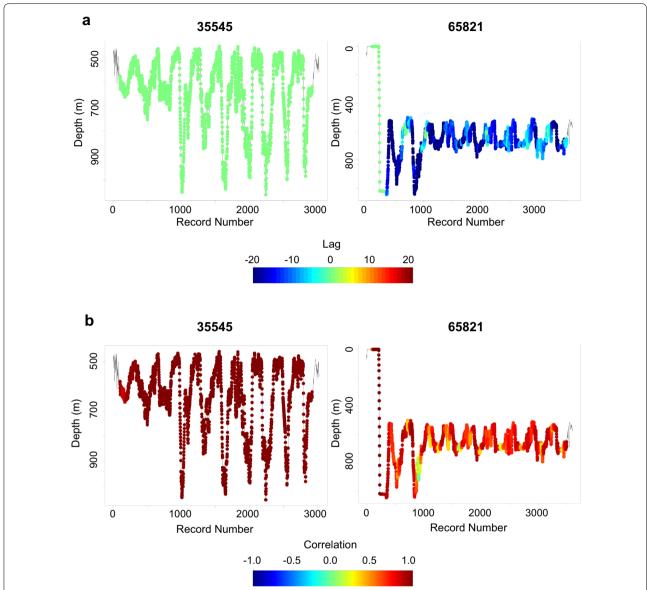
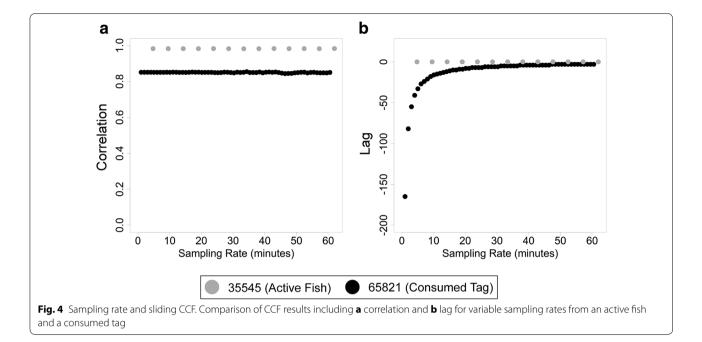


Fig. 3 Comparing datasets with sliding CCF. Depth profiles from 35545 and 65821 colored by the **a** lag and **b** correlation determined by the sliding CCF (sliding window width = 200 records)

consumption by ectothermic predators. The prevalence of tagging studies on deep-water taxa remains low, however has increased in recent years due to the technological development of sampling gears [19]. For these species, the exacerbation of capture, handling, and tagging effects through photic, thermal, and barometric stress increase their at-vessel and post-release mortality [19]. Therefore, as scientists extend study efforts into habitats where BI consumption is not easily identified, the CCF could serve as a useful and routine tool to identify previously unrealized BI consumption events [21]. Beyond applicability

to deep-water habitats, this method is also suitable for depth and temperature data loggers that do not record light levels. For example, research using accelerometer data loggers, which also record time-series depth and temperature records, obtain high-resolution data to assess short-term recovery periods and post-release mortality [44, 45]. Application of the CCF or sliding CCF could reveal post-release tag consumption events, potentially unrealized without available light levels.

The CCF and sliding CCF results were dependent on data sampling rate, ambient temperature gradients,



consumer physiology, and, in the case of the sliding CCF, the window width variable. Correspondingly, we did not identify a universal lag or correlation threshold indicative of BI consumption, and therefore, it is critical that CCF results are interpreted in the context of the environment and study species. This method is only applicable across vertical habitats exhibiting a temperature profile that monotonically and continuously varies with depth, and is not appropriate in locations without considerable temperature gradients, such as the nearly constant depth-versus-temperature profile of the Mediterranean Sea in the winter [28, 46]. Furthermore, this technique is applicable to animals that traverse through the temperature gradients of the water column and, therefore, may not be suitable for benthic or vertically stationary species [47], or species that may follow isotherms (e.g., great hammerhead sharks, Sphyrna mokarran) [48]. We recommend using the CCF to compare similar datasets, such as data from multiple conspecifics at the same study site. Comparison of CCF outputs could indicate a typical lag or correlation for that environment or species, and further, a dissimilar result (i.e., a considerable lag or low correlation) might highlight possible BI consumption [21]. Additionally, we recommend evaluating the sliding CCF for multiple window widths (as completed in Example 2) and standardizing the sampling rate between datasets when making comparisons (as completed in Example 3). Lastly, the CCF requires time-series records, and thus, this method cannot be applied to static binned or summarized data.

Conclusions

The CCF and sliding CCF are simple and effective tools for inferring tag consumption, and we suggest evaluating all concurrent time-series depth and temperature datasets for which light levels are unavailable with the CCF and/or sliding CCF to assess for tag consumption during the data validation process. Furthermore, this method is especially effective for contrasting datasets from the comparable studies (i.e., same location and species) and is broadly applicable across varying taxa, BI models, and study locations. While this method does not indicate that a tracked animal was consumed, but rather the tag itself was consumed, its implementation is valuable to the correct biological interpretation of tag-recorded data.

Additional files

Additional file 1. Cross-correlation function tutorial in R.

Additional file 2. Time-series depth and temperature records from X-Tag 65821.

Additional file 3. Sliding CCF function R code.

Additional file 4. Tag and study details.

Additional file 5. Example 1 data and results.

Abbreviations

Authors' contributions

LAH, LKBJ, RDG, AB, SW, EJB, and ONS completed field work and contributed corresponding data. ERT and RPH developed the application of the CCF and sliding CCF to detect tag consumption. ERT performed the analysis. ERT and

ONS wrote the paper with significant contributions from LAH, LKBJ, and RPH. All authors read and approved the final manuscript.

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Competing interests

ERT, RPH, LAH, and LKBJ are employed by the manufacturer of the X-Tags used in this study, but this had no bearing on data analysis or interpretation of the results.

Availability of data and materials

The R code for the sliding CCF (Sliding_CCF_Function.r) is provided as Additional file 3, and example data (65821_ExampleData.txt) are provided in Additional file 2.

Ethics approval

Research was conducted under permits MAF/FIS/17 and MAF/FIS/34 from the Bahamian Department of Marine Resources, and animal sampling followed guidelines of the Association for the Study of Animal Behavior and Animal Behavior Society.

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