Fisheries Research 183 (2016) 210–221

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers

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ARTICLE INFO

Article history:
Received 29 September 2015
Received in revised form 31 May 2016
Accepted 5 June 2016
Handled by George A. Rose
Available online 23 June 2016

Keywords:
Accelerometer
Recreational fishing
Recovery period
Post-release mortality
Data logger

ABSTRACT

Recent declines in global fish stocks have raised questions regarding the sustainability of both extractive and catch-and-release fishing activities, and prompted efforts to quantify the total impact of fishing pressure. While at-vessel mortality rates are relatively easy to obtain, accurately assessing post-release mortality and sub-lethal behavioral effects has proven difficult. Acceleration data loggers (ADLs) represent a useful tool in post-release studies, but have yet to be fully utilized. The goal of this paper is to demonstrate the utility of ADLs in identifying mortality events, and to provide an example of recovery period quantification methods using acceleration-based swimming metrics. To illustrate the application of this method, we use sample data from blacktip sharks (*Carcharhinus limbatus*) captured and released in the Florida recreational shark fishery. Mortality events were inferred from stationary depth traces and the eventual cessation of all tailbeat activity, while posture information confirmed that the tag was still attached to the animal. We also detail how ADL data from surviving individuals were used to calculate 58 metrics of fine-scale swimming behavior. Using nonlinear mixed modeling, we found 19 of these metrics displayed a significant logistic relationship with time post-release, indicative of a recovery period. Calculated recovery periods ranged from 5.1 to 19.5 h, with a mean of 10.54 ± 3.78 h. The low cost of ADLs and their capacity for multiple deployments allows for relatively large sample sizes at a fraction of the cost of satellite tag studies. ADLs provide definitive evidence of post-release mortality, and also allow for the quantification of sub-lethal effects which can be used to measure the impact of different gear types or handling methods, even in species for which mortality events are rare.

1. Introduction

The creation and maintenance of sustainable fisheries are global challenges (Kleisner et al., 2013; Watson et al., 2013). In recent years, management initiatives that impose size restrictions and catch quotas have been considered positive steps toward conservation and sustainability (NMFS 2006; Morgan and Carlson, 2010; NOAA, 2010). However, these policies may increase bycatch (Ferretti et al., 2010; Lewison et al., 2004) and discards (Biery and Pauly, 2012; Gilman et al., 2008), and cannot be viewed as successful without a full evaluation of total fishing mortality (Molina and Cooke, 2012; Skomal, 2007; Skomal and Bernal, 2010). In fact, high bycatch mortality is often the factor preventing fisheries from being sustainable (Pelc et al., 2015). Although catch-and-release angling has been touted as a sustainable alternative to extractive fishing (Arlinghaus et al., 2007; Cooke et al., 2014), animals in these fisheries may be subjected to exhaustive exercise and stress before release, resulting in anaerobic respiration, elevated lactate levels, and respiratory acidosis (Skomal and Bernal, 2010). To better assess the ecological impacts of fishing (Hobday et al., 2011) and ensure sustainable harvest (Simpfendorfer et al., 2005), a combined assessment of immediate and post-release (cryptic) mortality is needed.

Abbreviations: ADL, acceleration data logger; VHF, very high frequency; ODBA, overall dynamic body acceleration; PSAT, pop-up satellite archival tag; VV, vertical velocity; TBAA, tailbeat acceleration amplitude; TBC, tailbeat cycle; LMM, linear mixed model; BIC, bayes information criteria; AIC, akaike information criteria.

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http://dx.doi.org/10.1016/j.fishres.2016.06.003
0165-7836/

In addition to documenting mortality, quantifying sub-lethal behavioral changes following the stress of capture may also provide critical information for resource managers. These effects have been shown to impact mating or foraging success in some species, with possible population- and ecosystem-level implications (Arlinghaus et al., 2007; reviewed by Lewin et al., 2006). For instance, longer recovery periods may lead to increasing susceptibility of depredation following release, and could impair energy intake causing temporary starvation or mortality (Donaldson et al., 2008; Olla et al., 1995). Stress from capture may also negatively impact the immune system, growth, and reproduction (see Lewin et al., 2006 for a review). Studies that have investigated post-release behavior have done so only at low resolution; e.g., inferring recovery time from brief acoustic tracks (Gurshin and Szedlmayer, 2004; Holts and Bedrofd, 1993), Crittercam deployments (Heithaus et al., 2002; Skomal et al., 2008), or from broad-scale changes in swimming depth in pelagic species that are unlikely to be detected in coastal species (Campana et al., 2009; Skomal, 2006).

While at-vessel mortality rates are relatively easy to obtain, quantifying post-release mortality and sub-lethal behavioral effects is more difficult. Previous studies have relied on proxies of stress such as blood stress chemistry (e.g., Brooks et al., 2011; Hyatt et al., 2011) and hormone levels (Barton, 2002), tag and recapture data (e.g., Francis, 1989; Hueter et al., 2006) or satellite and acoustic telemetry (e.g., Holts and Bedrofd, 1993; Hoolihan et al., 2011; Sepulveda et al., 2015; Skomal, 2006). Although the physiological proxies have revealed high inter-specific variability in the response to capture stress (Frick et al., 2010; Hyatt et al., 2011; Mandelman and Skomal, 2009; Marshall et al., 2012), very few studies have correlated these stress values to actual animal outcomes, and the ability of these proxies to predict post-release mortality or sub-lethal effects is largely untested. Tag-recapture studies require large sample sizes of frequently caught species and may take years of recapture data collection to provide an assessment (Hueter et al., 2006). While acoustic or satellite telemetry methods can be effective for assessing post-release mortality, cost limitations may result in small sample sizes, particularly in studies of highly mobile species. Additionally, these techniques may not be well suited for analyzing sub-lethal behavioral impacts of capture stress due to track duration or data resolution. For instance, active acoustic telemetry is labor-intensive, so track durations are often limited to a few hours (e.g., Gurshin and Szedlmayer, 2004; Holts and Bedrofd, 1993; Skomal and Chase, 2002), whereas passive acoustic telemetry requires that animals remain within the limited range of stationary receiver stations (e.g., Afonso and Hazin, 2014; Kneebone et al., 2013). Satellite tag studies typically cost 5–8 times more than those using acoustic tags (excluding boat and man hours), and infer mortality by comparing tag reporting rates between species (e.g., fin-mounted platform terminal transmitters, Gallagher et al., 2014) or more directly when a negatively buoyant animal sinks to the seafloor and remains there for a predetermined time limit assumed to indicate mortality (e.g., pop-up satellite archival tags; PSATs; Campana et al., 2009; Hoolihan et al., 2011; Moyes et al., 2006; Musyl et al., 2011; Sepulveda et al., 2015). All of these telemetry methods typically involve one-time use of each tag deployed, and some may confound mortality events with tag shedding or malfunction (e.g., when mortality is inferred from a lack of detection). At best, these technologies infer mortality from a lack of vertical and/or horizontal displacement, and do not incorporate data from the physical movement or posture of the animal.

A novel, relatively inexpensive method that shows great potential for studying post-release effects is accelerometry. Acceleration data loggers (ADLs) measure tri-axial acceleration, indicating fine-scale movement and body orientation, and provide high-resolution information on a tagged animal's behavior. ADLs have been applied to a wide range of aquatic species to quantify fine-scale details of swimming dynamics and identify specific behaviors (e.g., Gleiss et al., 2009, 2010; Kawabe et al., 2003; Nakamura et al., 2011; Whitney et al., 2007, 2010), and can also be used to study energy expenditure and metabolic rate based on an animal's overall dynamic body acceleration (ODBA; Gleiss et al., 2011; Whitney et al., 2012; Wilson et al., 2006). Because of the large amount of high-resolution swimming data obtainable with ADLs, they have the potential to provide not only definitive measures of mortality, but also detailed information regarding sub-lethal behavioral effects. ADLs have been applied to the study of captive-held bonefish after angling (Brownscombe et al., 2013), but have not been widely used to study post-release behavior in free-swimming animals.

The goal of this paper is to demonstrate the utility of ADLs in identifying mortality events and quantifying recovery periods using acceleration-based swimming metrics. To illustrate the application of this methodology in a real-world context, we use sample data from blacktip sharks (*Carcharhinus limbatus*) captured and released in the Florida recreational shark fishery. Specifically, we describe the definitive evidence of mortality provided by accelerometers and demonstrate a method to use fine-scale metrics of swimming performance to test empirically for and quantify a recovery period for this species.

2. Materials and methods

2.1. Model species and tagging

Blacktip sharks are found in tropical to sub-tropical waters, and are prevalent along the southeast U.S. coast (Castro, 1996) where they have been a main target of both recreational and commercial fisheries for decades (NMFS 2006). For this study, sharks were caught by rod and reel in and around Charlotte Harbor (26° 47′ 18″ N, 82° 7′ 23″ W) and Cape Canaveral (28° 19′ 8″ N 80° 20′ 6″ W), Florida between January 2011 and April 2013. Angled sharks were secured alongside the boat with the leader and a tail rope while still in the water, at which point they were quickly measured and blood sampled via caudal venipuncture as part of another study. Two holes were drilled into the first dorsal fin to allow attachment of a custom-designed data-logger package (Fig. 1; see Whitmore et al., 2016) containing a G6a ADL (CEFAS Ltd., Lowestoft UK) set to record tri-axial acceleration at 25 Hz, depth at 1 Hz, and temperature at 0.033 Hz, as well as a VHF transmitter (MM180B, Advanced Telemetry Services, Isanti, MN, USA) for package relocation and recovery. The entire tag-float package was approximately 7 × 11 cm in size and weighed 125 g in air (70 g positively buoyant in seawater; <0.5% body mass). The tag package was secured to the left side of the dorsal fin using monofilament or plastic cable ties and a galvanic timed release (International Fishing Devices Inc., Northland, New Zealand). The galvanic release dissolved in seawater after 1–7 days, releasing the tag package and allowing it to float to the surface for recovery. In an assessment of release timing accuracy, Whitmore et al. (2016) found an overall mean variance of 1% in actual GTR release time compared to expected time. Floating tag packages were detected using a hand-held VHF receiver (R45-20C, Advanced Telemetry Systems, USA), and retrieved by vessel (see Lear and Whitney 2016).

2.2. Data processing

We analyzed the ADL data using Igor Pro ver. 6.22 (Wavemetrics, Inc. Lake Osewego, OR, USA) and Ethographer (Sakamoto et al., 2009). As certain tags displayed large depth sensor drift over the deployment, a user-defined function was created to correct the depth trace by the minimum value (assumed to represent

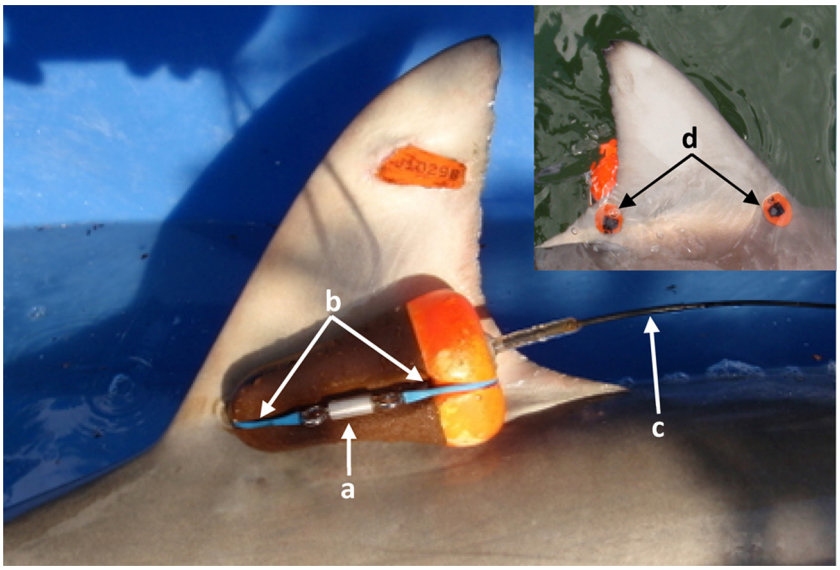

Fig. 1. Acceleration Data Logger and Very High Frequency (ADL/VHF) tag float package attached to the dorsal fin of a 121 cm pre-caudal length (160 cm total length) blacktip shark (a) 2-day galvanic release, (b) monofilament strap (encased in blue shrink-tubing), and (c) antenna of VHF transmitter protruding from top of float package, (d) the secured strap along the back of the fin. The logger is embedded on the opposite side of the tag float abutting the fin (not visible). The top of the float is painted orange to assist in tag package recovery at sea. The tag at the top of the fin is a roto-tag for identification purposes (from Whitmore et al., 2016).

depth = 0 m) every 60 min. The static component of the acceleration, which indicates body position, was determined using a 3 s box smoothing window, deemed appropriate considering the size of animals and their dominant tailbeat cycle of ~1 Hz (Shepard et al., 2008). This static component was then subtracted from raw acceleration to isolate the dynamic component, which represents animal movement. We also examined ODBA, which was calculated by summing the absolute value of the dynamic acceleration from all three axes (Wilson et al., 2006).

2.2.1. Mortality events

To identify mortality events, we looked for uncharacteristic swimming patterns. Similar to studies employing PSATs, we used a stationary depth trace as one indicator of mortality. However, we also had the benefit of acceleration data which showed when body movement ceased as additional confirmation of mortality. Since blacktip sharks are obligate ram ventilators (Carlson et al., 2004), cessation of swimming activity is likely to indicate distress and ultimately mortality. Additionally, representative data from known dead animals can be collected to serve as a reference point for inferring mortality events.

2.2.2. Recovery period

To analyze the depth data for the presence of a recovery period, we first smoothed the trace using a 10 s running mean. This revealed localized trends in diving behavior and enabled us to derive average Depth, Delta Depth (the change in depth over the course of a single vertical velocity phase; see below) and average Vertical Velocity (VV; calculated by taking the central difference of the smoothed depth over 1 s intervals). Based on VV, we separated the depth profile of the sharks into three VV phases: ascents, descents and level. Ascent and descent phases are defined as periods when VV exceeded an absolute value of 0.05 m/s for >10 s, and level swimming behavior as periods when the absolute value of VV was less than 0.05 m/s for >10 s. Each ascent period, descent period, or level swimming period was analyzed as a single event referred to henceforth as a VV phase. This manner of dividing the time series data enabled us to calculate the Number and Duration of VV Phases.

The depth trace and the static and dynamic components of acceleration were used to generate metrics of swimming performance (see Whitney et al., 2012 and references therein). From the static component, we derived body Pitch and Roll angles. From the dynamic component of acceleration, we used a continuous wavelet transformation of the sway axis in Ethographer to calculate Tailbeat Acceleration Amplitude (TBAA, a proxy measure of the amplitude of the acceleration waves; Sakamoto et al., 2009), and Tailbeat Cycle (TBC, the duration of a single tailbeat cycle, the inverse of tailbeat frequency). ODBA was derived from the dynamic components of all three measures of acceleration, and visual analysis noted spikes of activity (ODBA Bursts), which were subsequently defined as any time ODBA exceeded a threshold value of 1*g* (units of gravity; $1g = 9.8\ m/s^2$) for any duration.

Because our study species is negatively buoyant (Baldridge, 1970), a shark swimming toward the surface (negative VV) will have to work harder than sharks swimming toward the bottom (positive VV), given it swims at the same speed (Gleiss et al., 2011). Therefore, in addition to analyzing each acceleration-based metric over total deployment, we also conducted separate analyses over each VV phase. Overall, we were able to systematically calculate 58 metrics from 12 categories (Table 1). These metrics were summarized hourly, and were then further evaluated for indication of a recovery period.

2.3. Statistical analysis

We built several models using the nlme (Pinheiro et al., 2016) and mgcv (Wood, 2011) packages in R (version 2.15) to investigate relationships between time post-release and the hourly values of metrics from the initial analysis (Table 1). Since the experimental design incorporated repeated measures on multiple individuals, statistical analyses treated individual as a random effect. First, we regressed each metric against hour post-release using linear mixed models (LMM). Each of these models was compared to a null model that did not include hour post-release. All model comparison was performed using Bayes Information Criterion (BIC), as it favors simpler models compared to the Akaike Information Criteria (Kass and Raftery, 1995). Our candidate model was deemed to be significantly better with a $\Delta BIC > 10$ (Table 1). This threshold was selected as highly conservative to limit type I error during repeated analysis (Burnham and Anderson, 2002). Many of the metrics exhibited non-

Table 1
Fine-scale swimming behavior metrics from acceleration data-loggers (ADLs) that have been calculated for each hour and evaluated for indication of a recovery period in blacktip sharks. Model fit (ΔBIC) is shown for linear and additive models with hour post release. Metrics with significant change over time in both the linear and additive models are marked with (Bold). These parameters were used in the NLMM stage of analyses.

Variable	Units	Description	Linear ΔBIC	Additive ΔBIC
Depth-Avg	m	Average depth	−3.5	−101.3
Depth-Min	m	Minimum depth	6.6	−6.6
Depth-Max	m	Maximum depth	6.7	−10.0
Depth-Avg Ascent	m	Average depth during all ascents	6.6	−53.6
Depth-Avg Descent	m	Average depth during al descents	8.1	−40.9
Depth- Avg Level	**m**	**Average depth during all level phases**	**−10.0**	**−102.9**
Duration Ascending	**s**	**Total number of seconds ascending**	**−17.3**	**−61.4**
Duration Descending	s	Total number of seconds descending	−78.1	1.0
Duration Level	**s**	**Total number of seconds level**	**−44.5**	**−18.6**
Dive Depth-Avg Min Ascent	m	Average minimum depth of ascents	6.6	−85.2
Dive Depth-Avg Max Ascent	m	Average maximum depth of ascents	−1.8	−17.2
Dive Depth-Avg Avg Ascent	m	Average of the average depth of each ascent	6.6	−49.4
Dive Depth-Avg Min Descent	m	Average minimum depth of descents	6.0	−88.3
Dive Depth-Avg Max Descent	m	Average maximum depth of descents	−3.8	−6.2
Dive Depth-Avg Avg Descent	m	Average of the average depth of each descent	6.6	−42.0
Dive Depth-Avg Min Level	m	Average minimum depth of level phases	4.7	−34.5
Dive Depth-Avg Max Level	m	Average maximum depth of level phases	6.6	−60.3
Dive Depth-Avg Avg Level	m	Average of the average depth of each level phase	7.1	−51.3
Number of Ascents	**n**	**Number of ascents**	**−42.6**	**−14.7**
Number of Descents	**n**	**Number of descents**	**−31.6**	**−30.1**
Number of Level	**n**	**Number of level phases**	**−39.0**	**−55.6**
Delta Depth-Avg Ascent	**m**	**Average change in depth of ascents**	**−68.5**	**−68.7**
Delta Depth-Avg Descent	**m**	**Average change in depth of descents**	**−69.7**	**−104.6**
Delta Depth-Avg Level	**m**	**Average change in depth of level phases**	**−24.2**	**−115.0**
VV-Avg	m/s	Average VV	6.6	6.4
VV-Min	**m/s**	**Minimum VV (the fastest ascent)**	**−75.4**	**−59.3**
VV-Max	**m/s**	**Maximum VV (the fastest descent)**	**−58.4**	**−94.1**
VV-Avg Ascent	m/s	Average VV during ascents	−21.2	−4.5
VV-Avg Min Ascent	**m/s**	**Minimum VV during ascents**	**−62.5**	**−66.3**
VV-Avg Descent	**m/s**	**Average VV during descents**	**−211.8**	**−247.1**
VV-Avg Max Descent Max	**m/s**	**Maximum VV during descents**	**−76.7**	**−105.6**
VV-Avg Level	m/s	Average VV during level phases	−4.7	−27.9
TBAA-Avg	**g**	**Average tailbeat amplitude**	**−38.0**	**−64.5**
TBAA-Avg Ascent	g	Average tailbeat amplitude of ascents	5.1	−21.8
TBAA-Avg Descent	g	Average tailbeat amplitude of descents	−4.1	5.7
TBAA-Avg Level	**g**	**Average tailbeat amplitude of level phases**	**−72.2**	**−92.4**
TBC-Avg	**s**	**Average cycle**	**−340.7**	**−249.5**
TBC-Avg Ascent	**s**	**Average cycle of ascents**	**−172.1**	**−185.4**
TBC-Avg Descent	**s**	**Average cycle of descent**	**−296.6**	**−181.4**
TBC-Avg Level	**s**	**Average cycle of level phases**	**−274.5**	**−269.1**
ODBA-Avg	g	Average ODBA	4.6	−91.7
ODBA-Max	**g**	**Maximum ODBA**	**−160.9**	**−31.2**
ODBA-Avg Ascent	**g**	**Average ODBA of ascents**	**−14.8**	**−22.6**
ODBA-Max Ascent	**g**	**Maximum ODBA of ascents**	**−110.2**	**−29.3**
ODBA-Avg Descent	**g**	**Average ODBA of descents**	**−24.5**	**−29.3**
ODBA-Max Descent	g	Maximum ODBA of descents	−21.8	−0.3
ODBA-Avg Level	g	Average ODBA of level phases	1.3	−103.5
ODBA-Max Level	**g**	**Maximum ODBA of level phases**	**−102.1**	**−41.7**
ODBA Bursts-Seconds Total	**s**	**Number of seconds for which ODBA > 1**	**−156.4**	**−21.0**
ODBA Bursts- Seconds Ascent	**s**	**Number of seconds for which ODBA > 1 during ascents**	**−86.5**	**−10.3**
ODBA Bursts- Seconds Descent	s	Number of seconds for which ODBA > 1 during descents	−26.3	−0.1
ODBA Bursts- Seconds level	s	Number of seconds for which ODBA > 1 during level phases	−66.7	−8.8
Pitch-Avg Ascent	deg	Average pitch during ascents	−19.7	6.5
Pitch-Avg Descent	deg	Average pitch during descents	−9.8	3.3
Pitch-Avg level	deg	Average pitch during level phases	0.2	−31.9
Roll-Avg Ascent	deg	Average roll during ascents	−15.2	2.7
Roll-Avg Descent	deg	Average roll during descents	−7.6	4.3
Roll-Avg Level	deg	Average roll during level phases	2.8	5.7

linear relationships and were subsequently fitted using generalized additive mixed models (GAMM; Table 1). was All metrics were then run through a GAMM with a smoother around hour post release. GAMMs were compared to the LMM to determine the significance of the nonlinear component which was determined by a ΔBIC > 10.

Several of the metrics appeared to have an asymptotic relationship with hour post release. If metrics had a significant change over time, as determined by a ΔBIC > 10 for both the LMM and GAMM models, the metric was included for further analysis to quantify the potential asymptotic relationship. To quantify the nonlinear relationship between each metric and hour post-release we used nonlinear mixed models (NLMM). The metric was fit with either a four-parameter logistic curve (Eq.(1)) or an asymptotic regression model (Eq. (2)):

$$\text{Metric} = A + \frac{B - A}{1 + e^{\frac{\text{Hour Post Release} - \text{xmid}}{\text{Scal}}}} \quad (1)$$

$$\text{Metric} = \text{Asym} + \frac{RO - \text{Asym}}{e^{e^{\text{lrc}}} + \text{Hour Post Release}} \quad (2)$$

In the four parameter logistic curve (Eq. (1)) A and B are the lower and upper asymptotes of the model, *xmid* is the inflection and mid-

point of the logistic function, and *scal* is the scaling factor of the graph which determines the time between *xmid* and the asymptote. For the asymptotic regression (Eq. (2)) *Asym* represents the asymptote, while *RO* is the initial value at time zero ($t = 0$; herein referred to Hour 0), and *lrc* is the rate constant that controls the speed at which the metric reaches the upper asymptote. Sequential models were run for each metric with random term structures that incorporated individual variability into the upper asymptote, the halfway point, and the scale. This structure allows for flexibility in how individual sharks recover, accounting for variability within the population. However, if the NLMM did not converge, the individual random effects terms were removed and the models were run until convergence.

For metrics that displayed a recovery period, time to recovery was calculated as the time at which the metric reached 80% of the difference between the initial post-release value and the fully recovered value (right asymptote in the equations). By definition, the recovered value can never fully reach the asymptote and using an 80% threshold allowed us to calculate a specific recovery time using consistent methodology across parameters. Incorporation of individual as a random effect also enabled us to estimate recovery values for each animal tagged.

Correlations were calculated between individual recovery periods from different metrics to determine the degree of agreement between metrics. In addition, hierarchical clustering was used to find the degree of similarity between different metrics, with significance determined by multiscale bootstrap analysis with a significance determined with an alpha of 0.05 (R package pvclust; Suzuki and Shimodaira, 2015). Comparisons of metrics during different VV phases were conducted using mixed models in the nlme package with significance being determined by an analysis of variance (ANOVA). Unless otherwise noted, significance was determined at alpha of 0.05. All reported values are presented as mean ± SD. Recovery period analyses were limited to the first 48 h after release to maintain an adequate sample size.

3. Results

We used data from 20 blacktip sharks (mean precaudal length 108.6 ± 12.8 cm) providing a total of 626 h of acceleration data. This was a subset of data from a larger study on post-release mortality in this species. We achieved a tag-float package recovery rate of 100% over deployment durations ranging from 7.1 to 71.7 h (26.8 ± 22.1 h), despite some animals moving up to 35.2 (10.9 ± 10.4 km) away from their point of capture (see Whitmore et al., 2016 for details on package recovery). Surviving sharks often exhibited repetitive oscillations or "yo-yo" diving behavior between the surface and various depths (Fig. 2) but there was substantial variability in dive patterns. Maximum dive depths varied from 5 to 15 m between individuals, and likely represented the local seafloor depth for each shark. A LMM revealed no overall change in average hourly depth over time post-release. Immediately after release, sharks typically displayed rapid, high amplitude tailbeats. During this period, they actively swam during descents (determined by TBAA, TBC, and ODBA). However, as time progressed, sharks' tailbeats slowed and became less forceful, indicated by a decrease in TBC and TBAA. As this change occurred, sharks were observed to spend more time engaging in bursts of activity and quick movements, indicated by an increase in frequency of ODBA Bursts.

3.1. Mortality

Three individuals exhibited unique behaviors which led us to presume mortality. The similarities in the acceleration and depth traces between these three individuals enabled us to draft a set of characteristics that can be used to infer mortality events. Depth and ADL data analysis showed that these moribund sharks initially displayed behavior similar to surviving animals. However, within two hours of release, moribund individuals descended to the bottom and ceased body movement. Once on the sea floor, individuals made sporadic attempts to swim, which were characterized by powerful tailbeats (Fig. 3). These bouts of activity lasted 1–17 s, and occurred 3–13 times for each moribund individual. Regardless of these attempts, these individuals ceased all body movement within 1 h after first coming to rest on the bottom, and at that point were presumed dead. Each of these animals maintained equilibrium and rested on the bottom in an upright position for several hours after death confirming that tag-float packages were still properly fixed to the animals rather than having snagged on debris and detached prematurely.

3.2. Changes in swimming behavior over time

Subsequent analyses were limited to 17 surviving individuals. Of the 58 metrics derived from the ADL data, 27 displayed a significant nonlinear relationship with time after release determined by the GAMMs (Table 1). However, NLMMs did not converge for all 27 of these metrics. Only 19 metrics showed a significant relationship with time after release predicted by the nonlinear model, indicating a recovery period (Table 2). These metrics came from six categories: Delta Depth, VV, TBAA, TBC, ODBA, and ODBA Bursts. The remaining categories (Pitch, Roll, Number of Phases, Duration, and Depth) did not show clear evidence of a behavioral change indicative of a recovery period within our study period.

3.2.1. Delta depth

Delta Depth is a metric of the vertical displacement of each VV phase. In the first hour after release, individuals displayed consistent ascents and descents of deep depths, which became shallower as individuals recovered. While Delta Depth for ascents and descents in the first hour post-release were similar (3.51 ± 0.47 m and 3.41 ± 0.57 m respectively), Delta Depth during ascents showed a 37% decrease after a recovery period of 19.5 h, while during descents, it decreased by 59% from the value at Hour 0 over a 16.5 h recovery period (see Table 2).

3.2.2. Vertical velocity (VV)

Vertical velocity is a metric of the rate of depth change. Individuals maintained a consistent average VV during ascents (0.16 ± 0.03 m/s) throughout the monitoring period. However, average VV during descents decreased by 45% over a recovery period of 13.8 h (Fig. 4a; Table 2). There were also interesting patterns regarding hourly maximum and minimum VV values. Keeping in mind that VV is directional, VV during both descents and ascents decreased. This means descents slowed, while ascent velocity increased. The overall maximum VV, as well as the maximum VV during descents, decreased by 59% and 54% from the value at Hour 0 over 8.0 and 9.3 h recovery periods respectively, nearly converging at recovery values of 0.66 and 0.60 m/s. In contrast, the overall minimum VV and minimum VV during ascents decreased by 530% and 583% over recovery periods of 5.5 h and 5.1 h, to −1.08 and −1.00 m/s respectively (Table 2).

3.2.3. Tailbeat acceleration amplitude (TBAA)

A proxy measure of the amplitude of the acceleration waves, TBAA directly measures one component of swimming behavior. Throughout the monitoring period, two aspects of TBAA decreased (see Fig. 4b), indicating tailbeats became less forceful as the animal recovered. Average TBAA decreased by 26% over a 13.1 h recovery period, and TBAA during level phases decreased by 32% from the

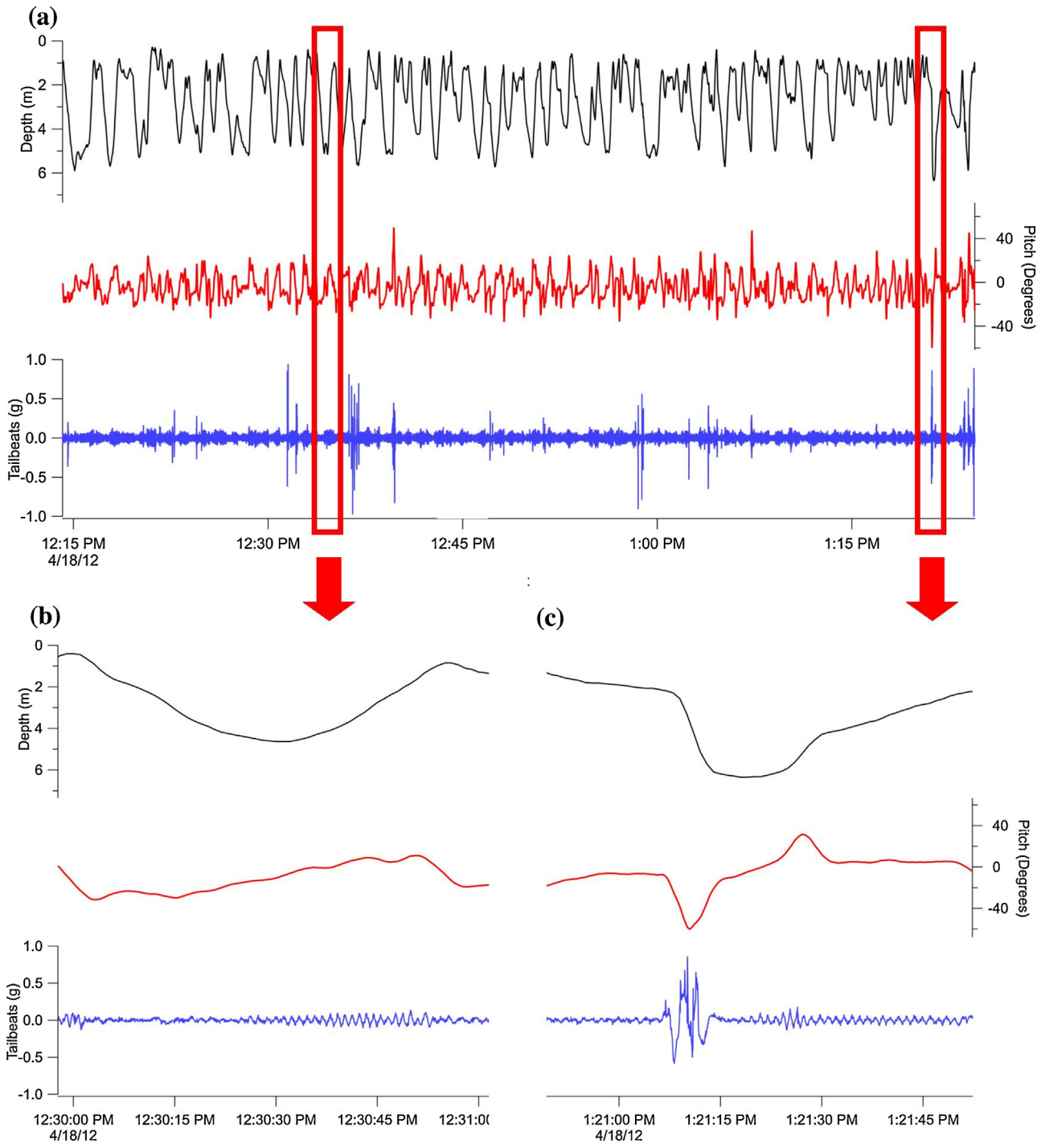

Fig. 2. Life of a shark: Depth, body pitch, and tailbeat acceleration of a surviving blacktip shark post-release in a recreational fishery. (a) The animal swims normally with an oscillating "yo-yo" diving pattern, (b), The shark often exhibits a decrease in tailbeat acceleration amplitude (TBAA) on descents, and an increase in TBAA on ascents, due to its negative buoyancy. (c) Burst swimming events are noted by a spike in TBAA (which contributes to Overall Dynamic Body Acceleration [ODBA].

Hour 0 value over a 13.9 h recovery period (Table 2). Over the entire monitoring period, TBAA during ascents (0.06 ± 0.02 g) was significantly higher than TBAA during descents (0.04 ± 0.01 g; ANOVA, $F_{1,1385} = 2063$, $p < 0.001$), reflecting more forceful and regular tailbeats during ascents compared to descents.

3.2.4. Tailbeat cycle (TBC)

The TBC metric refers to the time taken to complete a single oscillation of the tail. Overall, the TBC metric reveals increasingly slow tailbeats as the animal recovered. Average TBC increased by 78.1% over a 9 h period (Fig. 4c; Table 2). TBC during all three VV phases increased significantly over time, although by varying degrees. While TBC during ascents, descents, and level phases were similar the first hour post-release (0.87 ± 0.08 s, 0.96 ± 0.23 s, and 0.87 ± 0.11 s respectively), our model revealed TBC during ascents increased by 71% of the Hour 0 value after a 10.8 h recovery period, TBC during descents increased by 189% after an 10.2 h recovery

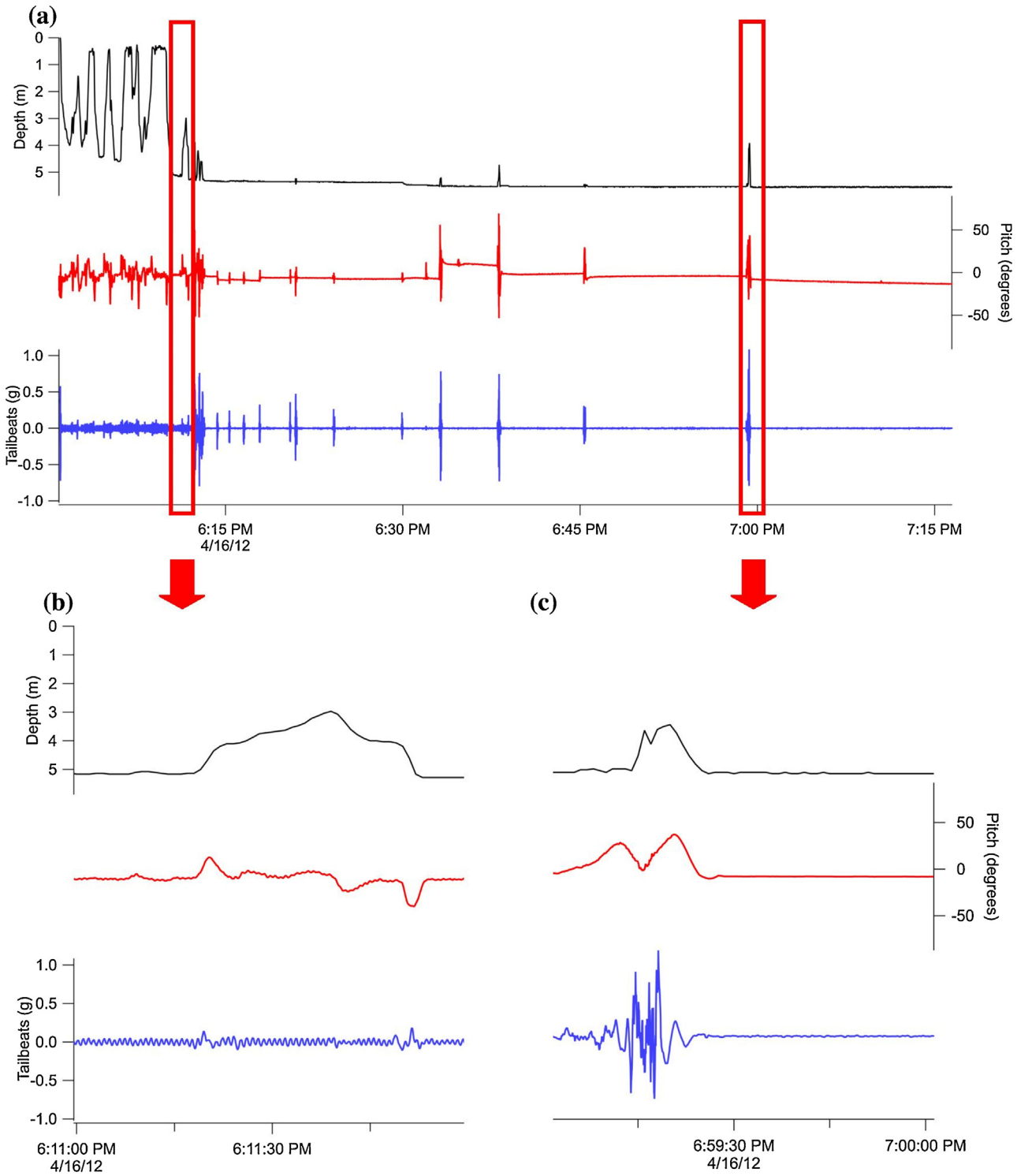

Fig. 3. Death of a shark: Depth, body pitch, and tailbeat acceleration of a dying blacktip shark post-release in a recreational fishery. (a) The animal begins swimming normally with an oscillating dive pattern for several minutes before (b) descending to the bottom where it continues tailbeating and briefly recovers. (c) Tailbeats then largely cease for the next several minutes as the animal lies on the bottom, with sporadic attempts to recover with a few, high amplitude tailbeats every few minutes until all activity ceases approximately one hour after release.

period, and TBC during level phases increased by 60% after an 11.5 h recovery period (Table 2).

3.2.5. ODBA

The ODBA metric measures overall body movement and is a proxy of activity-specific energy expenditure. The overall average ODBA did not change significantly over time post-release. However, once ODBA was separated by VV phase, it was revealed that ODBA during ascents and descents change in opposite ways, with increasing activity during ascents and decreasing activity during descents. ODBA during ascents increased by 49% over a 5.8 h recovery period, whereas ODBA during descents decreased by 21% over a 13.0 h recovery period (Table 2).

Maximum ODBA also increased significantly over time post-release, showing animals exhibited more forceful bursts of activity as they recovered. Overall maximum ODBA increased 191% over

Table 2
All metrics that displayed a significant change over time indicative of recovery period.

Category	Metric	Value at Hour 0	Recovery Value	Percent Change	Hour Recovered
Delta Depth (m)	Avg Ascent	3.673	2.324	−36.727	19.5
	Avg Descent	4.035	1.957	−51.499	16.5
VV (m/s)	Avg Descent	0.215	0.119	−44.651	13.8
	Max Overall	1.617	0.659	−59.246	8.0
	Max Descent	1.402	0.640	−54.351	9.3
	Min Overall	−0.171	−1.077	529.825	5.5
	Min Ascent	−0.151	−1.035	585.430	5.1
TBAA (g)	Avg Overall	0.051	0.038	−25.490	13.1
	Avg Level	0.051	0.035	−31.373	13.9
TBC (s)	Avg Overall	0.858	1.528	78.089	9.0
	Avg Ascent	0.742	1.272	71.429	10.8
	Avg Descent	0.739	2.136	189.039	10.2
	Avg Level	0.894	1.430	59.955	11.5
ODBA (g)	Avg Ascent	0.087	0.130	49.425	5.8
	Avg Descent	0.106	0.083	−21.698	13.0
	Max Overall	1.425	4.150	191.228	7.2
	Max Ascent	0.865	2.902	235.491	8.4
	Max Level	1.114	3.115	179.623	9.1
ODBA Bursts (n)	Overall	16.541	168.103	916.281	10.6

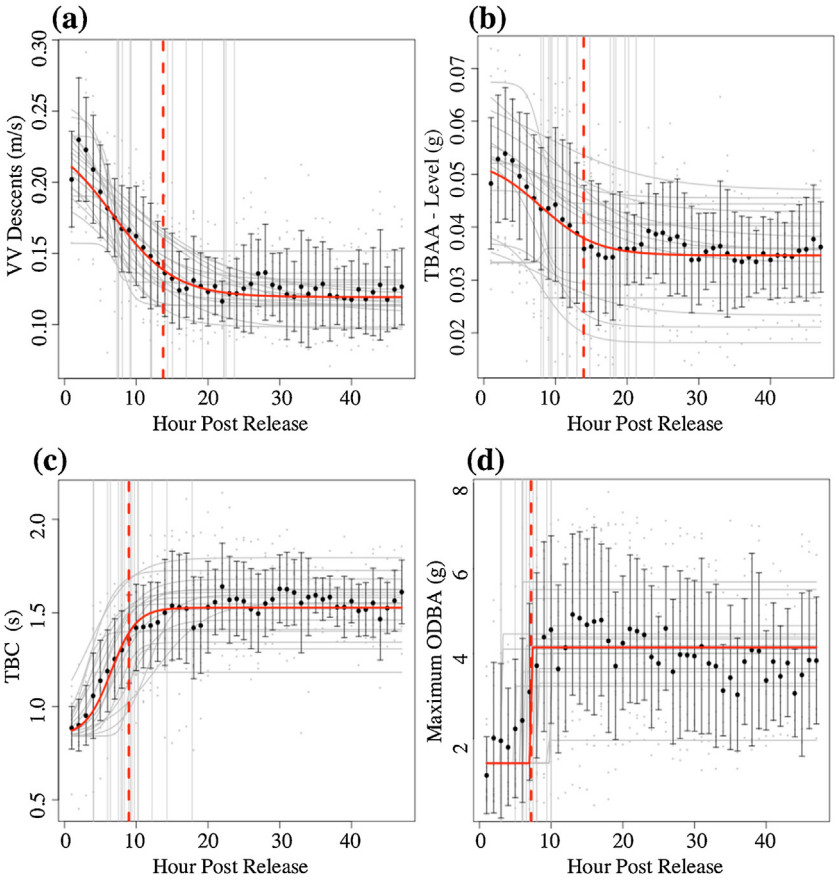

Fig. 4. Recovery periods in blacktip sharks after being caught and released by recreational fishermen. Shown are hourly means of (a) Vertical Velocity during Descents, (b) Level Swimming Tailbeat Acceleration Amplitude (TBAA), (c) overall Tailbeat Cycle (TBC), and (d) maximum Overall Dynamic Body Acceleration (ODBA) per hour. Gray lines and dots represent individual hourly means and regressions, with black dots and standard deviation bars representing means across individuals. The solid red line is the combined regression, with the red dashed line denoting the point at which this metric reached its 80% threshold and was considered to be recovered.

a 7.2 h recovery period (Fig. 4d), while maximum ODBA during ascents and level phases increased 236% and 180% over 8.2 h and 9.1 h recovery periods respectively.

3.2.6. *ODBA bursts*

ODBA Bursts, a metric of bouts of high activity, followed a similar pattern as maximum ODBA, increasing as the animal recovered. In the first hour after release, individuals displayed few seconds of Bursts per hour (6.86 ± 18.34); yet after a 10.6 h recovery period, the seconds of Burst activity per hour increased by 916% (Table 2).

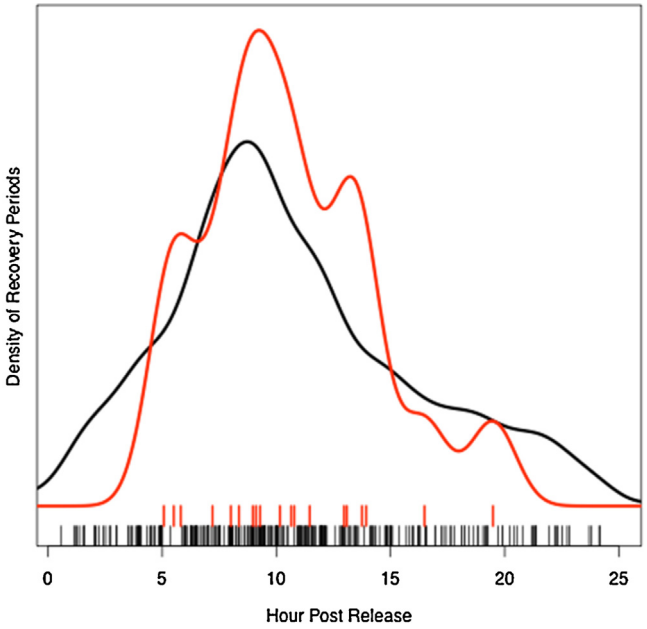

Fig. 5. A density plot of recovery periods calculated from all 19 metrics for the 17 surviving individuals (black), and combined recovery periods for each metric (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Recovery periods

Although each metric analyzed achieved 80% of its asymptote (recovered value) at a slightly different time, each recovery period was less than 20.0 h after release. The highest density of recovery periods occurs at 9.2 h (Fig. 5). VV during ascents produced the shortest estimated times to recovery (5.1 h), while both ascent and descent Delta Depth displayed the longest time to recovery (19.5 and 16.5 h respectively). When all significant metrics were incorporated, the mean recovery period for the study population was 10.54 + 3.78 h.

3.3.1. Individual recovery periods

The random effect component of the NLMM enabled us to determine individual recovery values, by allowing the coefficient for each individual to vary from the population, assuming a normal distribution. The highest density of recovery periods calculated for each individual occurred at 8.7 h after release, with a mean recovery period of 11.0 ± 2.6 h. Recovery periods from different metrics were variable within an individual, with an average standard deviation of 5.8 ± 1.9 h. In addition, the distribution of values was variable, with recovery periods for each metric occurring between 1 and 48 h post-release for any individual (Fig. 5).

Hierarchical clustering of the metrics was performed based on the estimated individual recovery periods for each shark. Metrics based on the depth (VV and Delta Depth) largely clustered separately from recovery periods based on swimming behavior generated from acceleration data ($p = 0.04$).

4. Discussion

Understanding how individual fish respond to capture events is critical to assessing how populations are impacted by fishing activities. Here, we demonstrate a novel method for post-release response studies, providing the first detailed methodology on how high-resolution acceleration and depth data can be used to quantify post-release mortality and sub-lethal behavioral effects that can be applied to both commercial and recreational fisheries.

4.1. Identifying mortality events

As many post-release studies have small sample sizes, imprecise or inaccurate assessment of individual mortalities can impact the overall estimated post-release mortality rate for a species. Additionally, inferring mortality rates from depth data, lack of horizontal displacement, or from non-reporting tags may be confounded by a number of logistical and behavioral issues (Moyes et al., 2006; Musyl et al., 2011). The fine-scale movement data provided by ADLs offer additional context and clarity in interpreting and identifying mortality events (e.g., Fig. 3). Indeed, for species capable of resting on the seafloor, a stationary depth trace may not be an accurate proxy for mortality, and the movement data provided by ADLs could allow for investigations on a broader range of taxa than are appropriate for other tagging methods. Additionally, the ability to recover tags and re-use them can allow for increased sample sizes, further improving post-release mortality estimates (Lear and Whitney 2016). Based on our findings, we propose that ADLs can be used to fill knowledge gaps regarding post-release mortality and sub-lethal behavioral effects in a wide variety of coastal taxa.

4.2. Recovery period

As sub-lethal effects may alter behavior, growth, or reproduction, a thorough understanding of how animals respond to capture events is critical when evaluating ecosystem-wide impacts of fishing activities (Wilson et al., 2014). Additionally, by measuring sub-lethal effects, fisheries managers may be able to elucidate differences in handling and fishing practices and implement regulations that minimize animal stress, even in species where post-release mortality is relatively rare and difficult to quantify.

Our use of ADLs enabled us to obtain information on the sub-lethal effects of catch-and-release fishing, such as relatively fast tailbeats (short TBC) with high TBAA immediately after release. These coincided with large, consistent vertical movements. During this time, individuals actively beat their tails during descents. However, over the course of an individual's recovery period, TBAA decreased and TBC increased, meaning tailbeats were slower and less forceful. Individuals increased gliding during descents, as evidenced by a decrease in both descent ODBA and descent VV. Diving behaviors became more variable, with shorter ascents and descents, and individuals began to exhibit increased bouts of high activity behaviors. This is evidenced by an increase in Ascent VV, various ODBA values, and ODBA Bursts.

Combined analysis across all metrics revealed an 10.54 +/− 3.78 h recovery period for the blacktip sharks in this study, which is similar to values published for other shark species studied in captivity (Kneebone et al., 2013; Spargo, 2001). Whereas different metrics are bound to produce different estimates of recovery period, accelerometry eliminates complications from holding animals in captivity and also provides higher-resolution behavioral information than conventional telemetry, allowing recovery to be assessed from the physical movements of the animal instead of their horizontal or vertical displacement.

Metrics derived from acceleration data (TBAA and TBC) often displayed more definite signs of a recovery period than those derived from depth (VV and Delta Depth), which displayed higher variability. For instance, depth measurements produced both the fastest (VV) and the slowest recovery periods (Delta Depth). In contrast, acceleration-based metrics provided recovery periods more similar to one another as displayed by hierarchical clustering. The underlying mechanisms driving the differences in recovery periods from various metrics are still not fully understood, but the range seen in depth-derived metrics may be linked to the fact that depth alone does not fully encompass swimming behavior. Depth is a more coarse measurement of animal activity than acceleration

(Gleiss et al., 2013), and thus relying exclusively on depth data from PSATs for determining post-release recovery periods may not be as accurate as the method presented here.

4.2.1. Evaluation of swimming metrics

Examination of metrics used to calculate recovery period can also be correlated to existing knowledge concerning stress and physiology. For example, exhaustive anaerobic exercise and the resulting blood acidemia associated with fighting on the line incur oxygen debt that has to be repaid following release (Brill et al., 2008). This is manifested by increased oxygen consumption and, as a result, a smaller scope for activity (Wilson et al., 2014). Thus, as the time post-release increases, the animal would be expected to display increasing capacity to perform high intensity activities, which we observed in the increase of ODBA Bursts over time. Additionally, in the data collected here, ascent TBAA is much higher than descent TBAA, and ascent TBC is shorter duration than descent TBC, showing that sharks beat their tail harder and faster while ascending than while descending. This is likely due to their lack of a swim bladder and negative buoyancy (Baldridge, 1970; Gleiss et al., 2015), which makes ascending more work than descending (Gleiss et al., 2011; Nakamura et al., 2011; Weihs, 1977). Thus individuals chose to exert additional energy performing low-cost behaviors (such as descents) during recovery, possibly to increase water flow over the gills, but not in high-cost behaviors (such as ascents; Gleiss et al., 2011). This trend may explain why tiger sharks captured on hook and line for tag attachment showed largely active descents after being released (Heithaus et al., 2002; Nakamura et al., 2011), whereas whale sharks (*Rhincodon typus*) and white sharks (*Carcharodon carcharias*) that were equipped while free-swimming (and thus not subjected to capture stress) exclusively performed gliding descents (Gleiss et al., 2011).

4.3. Applications

Here we have demonstrated the ability of ADLs to provide definitive estimates of post-release mortality in a coastal fish, and we posit that this method can be used in studies on a wide variety of targeted and bycaught species. ADLs have already been applied to studies of fishes such as Japanese flounder (*Paralichthys olivaceus*), salmon (*Oncorhynchus keta*), sturgeon (*Acipenser sinensis*), and dolphinfish (*Coryphaena hippurus*) among others, demonstrating their applicability to fishes other than elasmobranchs (Kawabe et al., 2003; Tsuda et al., 2006; Watanabe et al., 2008; Furukawa et al., 2011 respectively). However, this method is not without its limitations. Since ADLs must be firmly fixed to an animal to accurately record swimming movements, they cannot be quickly and easily attached with a pole-applicator without handling the animal, as can be done with satellite and acoustic tags in some cases. This increased handling time could lead to increased post-release mortality, although Campana et al. (2015) found no difference between post-release mortality in mako sharks (*Isurus oxyrinchus*) pole-tagged in the water versus boat-landed, and quick, secure attachment of ADLs is available for some species (Gleiss et al., 2009; Chapple et al., 2015).

The need to recover the tag package to retrieve its data is likely the largest constraint of the method presented here. This requires the use of a float package (which must be purchased or custom-made), which means that, like PSATs, it may not be applicable to smaller species. The need for recovery also increases time and labor costs, and limits deployment duration in studies of pelagic or highly mobile species. Although packages can be detected by a VHF receiver from up to 25 km away once they float to the surface, detection range is variable depending on air and sea conditions (Lear and Whitney 2016).We achieved 100% package recovery over periods of up to 72 h at large. Even when accounting for recovery costs and the one-time cost of the VHF receiver equipment (~$1000), the ADL method is still 1/4th to 1/8th the cost (per shark) of using satellite tags (Lear and Whitney 2016). This economy is due not only to the purchase price differential between ADLs and satellite tags, but also the ability to re-use ADLs repeatedly after recovery (see Lear and Whitney 2016 for a more detailed discussion).

While we demonstrated the ability to detect post-release mortality using this method, the relatively short monitoring period may not record delayed mortality events. However, recent studies on large coastal sharks using long-term monitoring PSAT tags show that post-release mortality occurs within the first 12 h after release (e.g. Skomal, 2006; Marshall, 2015) while others cite periods of 1–3 d (reviewed by Skomal 2007; Brill et al., 2008; Campana et al., 2009; Frick et al., 2010; Skomal and Bernal 2010), meaning our deployment lengths are largely sufficient to examine post-release mortality. Long-term mortality (e.g. days to weeks after release) is often related to injuries sustained during capture, such as gut-hooking or trailing gear, rather than physiological stress (e.g., Sepulveda et al., 2015). Caution should therefore be exercised when applying this method to species that are often gut-hooked or are released with fishing gear attached.

Care should also be taken when interpreting individual recovery periods and model fits, as there can be large variability between specific metrics as well as between consecutive hours within a metric for a specific individual. This emphasizes the need to use multiple metrics when assessing recovery period, and to use caution when interpreting recovery periods based on coarse metrics such as depth and temperature (e.g., Campana et al., 2009; Hoolihan et al., 2011), until the drivers behind each metric's changes are better understood. Differences in maturity, time since feeding, or intrinsic physiological and behavioral differences may contribute to the range of individual recovery times observed here (Virani and Rees, 2000). The variation observed between individual recovery times points to the complexity of the system we studied, and further emphasizes the need for robust sample sizes and data analysis techniques that account for intraspecific variability.

Increasingly popular and low-cost alternatives to tagging methods include biological indicators such as Reflex Action Mortality Predictors (RAMP; Davis 2007) and blood biochemistry analysis. RAMP studies have demonstrated a significant decrease in reflex response as the severity of stress events increases in teleosts (Brownscombe et al., 2013; Raby et al., 2012), and capture stress has been shown to have significant effects on lactate, pH, and other parameters (Brooks et al., 2011; Hoffmayer and Parsons, 2001; Hyatt et al., 2011; Mandelman and Skomal, 2009; Marshall et al., 2012; Skomal and Chase, 2002; Skomal and Mandelman, 2012). However, for these data to have meaning for fisheries management, they must first be correlated with actual animal outcomes (Skomal, 2007). We have demonstrated that ADLs represent a viable method of determining post-release mortality and sub-lethal behavioral effects, and assert that they are a cost-efficient means to validate these alternative methods.

Additionally, while mortality estimates have historically been the main target of post-release studies, by providing data on recovery period and sub-lethal effects of capture, ADLs may also be able to elucidate differences in the impact of various handling practices and gear types. For example, this method would be useful in comparing the differential impacts of circle- and J-hooks, or various soak times in longline fisheries.

4.4. Conclusions

Here, we have demonstrated how accelerometers can more definitively infer mortality events than previous technologies, and how to use a series of models to elucidate recovery periods based on quantitative swimming metrics, showing this technology's appli-

cability in post-release mortality studies of coastal species. While the use of ADLs is complicated by the need to physically recover the tag to obtain the data, our 100% tag recovery rate demonstrated the feasibility of using accelerometers to study even highly migratory species over short periods. ADLs are a fraction of the cost of satellite tags and can be deployed multiple times, facilitating larger samples sizes and more robust mortality estimates.

Our methods provide an example of how recovery periods based on swimming metrics can provide insights into the physiological impacts of capture. While responses are likely to be highly species-specific, these analytical techniques can be applied to elucidate important post-release information for a variety of species. This novel technology has the potential to facilitate conservation and sustainable fisheries management by accurately assessing the impact of recreational and commercial fishing activities on coastal fish species.

Acknowledgements

This study would not have been possible without the expertise, hard work, and dedication of Captain Robert Moore. We also thank Dr. John Carlson, and Captains Gregg and Dusty Rapp for their help and support. Jack Morris was essential to the success of all fieldwork. John Tyminski provided extensive help with fieldwork and other logistics, as did Dr. Heather Marshall. Many thanks to Dr. Kathy Heym, Susan Coy, Virginia Wright-Placeres, and Kimberly Casey (Florida Aquarium) who provided support in equipment maintenance and accounting. We also thank numerous interns and volunteers who helped with this work. This study was funded by the NOAA/NMFS Cooperative Research Program, grant #NA11NMF4540120. All work was done under FWC permit #SAL-11-0041-SRP and approved under Mote Marine Laboratory Institutional Animal Care and Use Committee (IACUC) #13-11-NW2 as well as the Florida Aquarium IACUC. This report serves as Sea Research Foundation publication No. 255.

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