ICES Journal of Marine Science, 2022, **79**, 2055–2068
DOI: 10.1093/icesjms/fsac137
Advance access publication date: 10 August 2022
Original Article

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

High-resolution post-release behaviour and recovery periods of two highly prized recreational sportfish: the blue marlin and sailfish

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High recreational catch rates of istiophorid billfishes in the eastern tropical Pacific (ETP) have led to substantial eco-tourism derived economic benefits for the countries in the region, prompting many countries to mandate catch-and-release practices for recreational anglers. Previous estimates of billfish post-release behaviours and recovery periods after these physiologically stressful capture events, however, vary widely depending on the type of tag used. Using high-resolution, multi-sensor biologging tags, we provide a fine-scale, detailed view of the behaviour and recovery periods of blue marlin (*Makaira nigricans*; $n = 9$) and sailfish (*Istiophorus platypterus,* Istiophoridae; $n = 9$) caught in a typical recreational fishery in the ETP. Angling times ranged from 4 to 90 min, and fish were monitored for periods of 6–70 h after release. Blue marlin showed a characteristic long, deep dive immediately after release, with significantly greater duration associated with longer fight times, a behaviour not typical for sailfish. Diving depths were, however, much shallower than those previously reported for both species due to the shallow thermocline and oxycline present in the ETP. Data from 40 derived metrics from acceleration (i.e. tailbeat period, amplitude, pitch, etc.) and physical parameters (i.e. depth, speed, temperature, oxygen saturation, etc.) used to quantify a recovery period suggest blue marlin and sailfish recover 9.0 ± 3.2 and 4.9 ± 2.8 h after release, respectively. Our high-resolution assessment of post-release behaviour suggests that these billfish are capable of rapid physiological recovery after capture in recreational fisheries, and that catch-and-release practices like those used here can be an effective approach to conserve and sustain billfish populations in the ETP. Predicted climate change caused shallowing of the oxygen minimum zone, however, would increase the vertical habitat compression present in this region, potentially prolonging or inhibiting recovery.

Keywords: biologging, billfish, large pelagic fishes, recovery period, recreational fishing, swimming kinematics.

Introduction

Recreational billfish fisheries have increased in popularity around the globe since the 1930's and provide considerable economic benefits via eco-tourism. Among avid offshore anglers, the eastern tropical Pacific (ETP) is widely considered to be one of the world's best fishing locations for istiophorid billfish (e.g. blue marlin *Makaira nigricans*, black marlin *Istiompax indica*, and sailfish *Istiophorus platypterus;* Istiophoridae). Many countries in the ETP either mandate or have programs in place to encourage catch-and-release practices for istiophorid billfish. Fortunately, data collected using acoustic tags and pop-up satellite tags document low rates of immediate and post-release mortality (mean 13.5%; 95% *CI*: 10.3–17.6%) for billfish (Musyl *et al.*, 2015). Capture on recreational gear, however, specifically subjects billfishes to exhaustive stress and exercise, the effects of which are exacerbated by direct injuries caused by the hook, contact with fishing vessel, and air exposure (e.g. Prince *et al.*, 2002; Graves and Horodysky, 2008; Schlenker *et al.*, 2016). These factors can subsequently result in physiological and behavioural responses that can negatively affect fish health, growth, reproduction, and escape response, and may ultimately influence stock dynamics (Lewin *et al.*, 2006; Cooke and Schramm, 2007; Donaldson *et al.*, 2008). Therefore, efforts focused on determining recovery periods and minimizing stress will inform the global recreational fishing industry for these two billfishes and add to basic biological data on billfish behaviour.

Fish stress and recovery time are not traditionally sought-after metrics for fisheries managers, but this could be due, in part, to the lack of availability of these numbers. In ecology, it is widely recognized that organismal physiology plays a role in population level demographics (Bergman *et al.*, 2019). As such, there is a growing push to integrate fish physiology with fishery science, which intersect at the behaviour of individuals within a population (Horodysky *et al.*, 2015; Killen *et al.*, 2016; McKenzie *et al.*, 2016; Lennox *et al.*, 2017). For example, armed with species-specific knowledge of behavioural traits and physiological tolerances after release from a fishing event, managers may be able to predict rates of post-release mortality based on environmental conditions (Horodysky *et al.*, 2015). Therefore, post-release behaviour and recovery time can shed light on the underlying physiological state of the individual and is an important component of assessing the success of catch-and-release as a management practice for billfish.

Post-release behaviour and recovery times have previously been estimated for istiophorid billfish, including blue

Received: April 5, 2022. **Revised:** July 5, 2022. **Accepted:** July 7, 2022

marlin and sailfish using acoustic telemetry and pop-up satellite archival tags (PSATs) (Jolley Jr and Irby Jr, 1979; Holland *et al.*, 1990; Block *et al.*, 1992a; Hoolihan *et al.*, 2011). Estimated recovery times have varied widely between studies, however, which may ultimately be due to differences in methodology and resolution of tag data. For example, blue marlin post-release recovery period estimates range from 4 to 6 h using active acoustic tracking (Holland *et al.*, 1990; Block *et al.*, 1992a) to 40 d using PSATs (Hoolihan *et al.*, 2011). Recovery period estimates appear correlated with tag type, suggesting data resolution is important and coarse-scale data typically produced by PSATs in past studies have not been detailed enough to accurately measure and define recovery period (Musyl *et al.*, 2015). Additionally, previous studies of post-release recovery time have relied on changes in fish depth or speed of a tracking vessel (a proxy for animal speed) as an indicator of recovery (Jolley Jr and Irby Jr, 1979; Holland *et al.*, 1990; Block *et al.*, 1992a; Hoolihan *et al.*, 2011; Musyl *et al.*, 2015). Yet, pelagic fish's depth use can be plastic depending on environmental conditions (Vaudo *et al.*, 2016; Carlisle *et al.*, 2017; Vaudo *et al.*, 2018), thus complicating determination of post-release recovery among studies. In addition, fish depth and heading metrics provide no information of body kinematics or swimming performance, which are known to be impacted by recreational fishing and that provide much more detailed estimates of recovery behaviour than depth information alone (Gleiss *et al.*, 2013; Whitney *et al.*, 2016).

Tri-axial accelerometry can be used to study the fine-scale swimming kinematics of fish not under direct observation by recording acceleration multiple times per second along three dimensions: the longitudinal body axis (surge), the dorso-ventral axis (heave), and transversely across the animal's body (sway) (Yoda *et al.*, 1999; Wilson *et al.*, 2008). Accelerometers have been applied to a variety of aquatic species to quantify a range of fine-scale behaviours (e.g. routine and burst swimming, resting, foraging, and mating), energetics and post-release recovery period (Myers and Hays, 2006; Whitney *et al.*, 2010; Gleiss *et al.*, 2011; Watanabe and Takahashi, 2013; Whitney *et al.*, 2016). More recently, other instruments have been incorporated with accelerometers to obtain additional fine-scale behavioural data: tri-axial magnetometers are added to enable calculation of the animal's heading (Williams *et al.*, 2017; Andrzejaczek *et al.*, 2019) and tri-axial gyroscopes to measure angular velocity of the animals' movements and turning. These can be combined with pressure (i.e. depth) and temperature sensors that gather data traditionally collected by other tag types to give a more complete picture of the animals' movements in relation to environmental cues.

The ETP is home to a unique combination of oceanographic features that contribute to a large, naturally occurring, hypoxic zone near the surface that can be several hundred meters thick (Prince and Goodyear, 2006; Karstensen *et al.*, 2008; Stramma *et al.*, 2012; Fiedler and Lavín, 2017). As a result, the water column features a narrow, productive surface layer of uniform temperature and oxygen saturation with a shallow, strong thermocline concomitant with the upper boundary of the oxygen minimum layer (i.e. oxycline). Together, these features cause vertical habitat compression, and are believed to increase the catchability of epipelagic fish, such as billfishes, in surface-based fisheries (Evans *et al.*, 1981; Prince and Goodyear, 2006; Prince *et al.*, 2010; Stramma *et al.*, 2012).

Low temperatures and dissolved oxygen concentrations have large negative physiological impacts on fish, including cardiac function and output (Brill *et al.*, 1998; Brown *et al.*, 2004; Pörtner and Knust, 2007). A fish's ability to survive and recover from a metabolically intense event such as capture and release would therefore be reduced or prolonged in low temperatures and/or dissolved oxygen concentrations. Due to the oceanographic conditions in the ETP and the high metabolic rate of regionally endothermic billfish caught and released in this region (Block, 1986; Idrisi *et al.*, 2003; Wegner *et al.*, 2010), these fish may be susceptible to extreme stress and may require prolonged recovery periods, putting these fish at greater risk of post-release mortality compared to other popular fishing destinations worldwide without a similarly shallow thermocline and oxycline. As such, billfish recovery behaviour in the ETP may provide a glimpse into the future of recreational billfish fisheries worldwide, as hypoxia-based habitat compression becomes widespread and oxygen minimum zones become increasingly shallow (Laffoley and Baxter, 2019; Leung *et al.*, 2019). Due to the lack of agreement of recovery times between previous studies and the importance of quantifying recreational fishery impact, we use a high-resolution biologging tag to determine the post-release recovery behaviour and period of blue marlin and sailfish in a catch-and-release fishery in the vertically compressed habitat of the ETP.

Methods

Tagging

We caught ten blue marlin and nine sailfish off the Pacific coast of southeast Panama via rod-and-reel and trolling high-speed lures or natural bait from September to November 2019. Each fish was brought alongside the vessel, assessed for physical trauma associated with hooking, and its weight estimated by an experienced captain. We attached a custom-designed biologging tag package to the dorsal musculature, just below the largest dorsal spine with two umbrella dart anchors. Once both anchors were securely imbedded in the muscle, the tag was firmly cinched against the fish's body using two galvanic timed releases (International Fishing Devices Inc., Northland, New Zealand) and a zip tie. The shape of the biologging tag was designed to be as hydrodynamic as possible, while also providing the necessary flotation for recovery. The tag consisted of an acceleration data logger (complete with tri-axial accelerometer, tri-axial magnetometer, and tri-axial gyroscope recording at 50 or 100 Hz), depth, temperature, and light sensors, and a small turbine-based fluid speed sensor all recording at 1 Hz (OpenTag 3.0, Loggerhead Instruments, Sarasota, FL, USA). The speed sensor was secured to the acceleration data logger and oriented such that the sensitive direction corresponds with the forward direction of movement (Gabaldon *et al.*, 2019). A small (12 mm diameter × 20 mm long) oxygen sensor (Micro Probe; OxyGuard, Farum, Denmark) that recorded dissolved oxygen concentration (% saturation) of the water at 1 Hz was also incorporated into the acceleration data logger (for details of the oxygen probe, see Coffey and Holland, 2015). The sensor has a manufacturer specified measuring range of 0–200% with accuracy within ±1% of the measured value. Finally, the tag package also contained a miniaturized video camera (68 mm × 21 mm × 22 mm; Little Leonardo, Tokyo, Japan) and a Smart Position and Temperature tag (SPOT-363A; Wildlife Computers, Redland, WA, USA) to aid in package recovery. The tag body was constructed of a high-density mixture of microballoons and resin to achieve desired buoyancy (Whitmore *et al.*, 2016). Tag package dimensions were 18 × 7 cm, increasing to 18 × 10.5 cm at the widest point with a weight of 335 g in air (see Supplementary Figure 1). Upon dissolution of the galvanic timed releases (selected for 1, 2, or 3 d after tagging), the tag package released from the fish, floated to the surface, and began transmitting its location via the SPOT tag and was tracked and retrieved at sea using a UHF handheld receiver (AOR AR8200, Fredericksburg, VA, USA).

Data processing

Depth

We smoothed depth data to a 10-s running mean to reduce small scale changes in vertical movements and examine localized trends in diving activity. Depth was then split into three swimming phases (“ascent”, “descent”, and “level”) using vertical velocity (VV), calculated as the difference between successive points of the smoothed depth data at 1 s intervals. Ascents and descents were categorized as periods where VV exceeded a magnitude of 0.05 $\mathrm{m\ s^{-1}}$ for more than 10 s; periods where this threshold was not exceeded were considered level swimming (Whitney *et al.*, 2016; Andrzejaczek *et al.*, 2019). Each period of ascent, descent, or level swimming was analysed as an individual event, allowing for calculation of the average VV of each phase, and the number and duration of ascent, descent, or level swimming phases as it related to time since fish release.

Speed

We calibrated the turbine with water velocity by placing the completed tag package into a 90-L Loligo swim tunnel respirometer with a flowmeter. Calibration resulted in a measured linear relationship of $\mathrm{m\ s^{-1}} = 0.022 \times \mathrm{rotations\ s^{-1}} + 0.25$ ($R^2 = 0.99$, $p < 0.0001$). It was found that the turbine requires a minimum flow speed of ~0.25 $\mathrm{m\ s^{-1}}$ to turn, therefore, after the calibration step any calculated speed of ≤ 0.25 $\mathrm{m\ s^{-1}}$ was set to zero. In addition, speed could not be estimated for some deployments because the tag attachment angle prevented water from consistently moving over the speed sensor in the desired orientation, so speed data were removed for those fish.

Oxygen

Not all tags used in this study had oxygen sensors incorporated into the acceleration data logger. As a result, four blue marlin and four sailfish did not have accompanying oxygen data. To assign oxygen data to all fish, we created *in situ* % dissolved oxygen and depth profiles from each fish carrying an oxygen sensor, and the mean % oxygen saturation was calculated at 0.5-m-depth intervals. Because all tag deployments occurred over the same spatial and temporal scale, and % oxygen saturation variability was low across depths and deployments (average *SD* = 4.35%), the mean % oxygen values were assigned to the corresponding depths of fish without oxygen readings.

Tri-axial sensors

We analysed acceleration, gyroscopic, and magnetometer data using Igor Pro v. 8.0.4.2 (Wavemetrics, Inc. Lake Oswego, OR, USA) with the Ethographer extension (Sakamoto *et al.*, 2009), R (R Core Team, 2019), or a combination of the two. We calculated the static component of the acceleration, which indicates body position from changes due to gravity, using a 3-s box smoothing window on the raw acceleration data (Shepard *et al.*, 2008). Tag attachment angle on each fish was corrected by rotating the raw acceleration data so that the x and y axis had a mean of 0. Body pitch (angle) was then calculated from the surge axis (anterior–posterior) of the static component. The static component of each axis was then subtracted from their respective raw acceleration value to isolate the dynamic component, which represents the movement due to the fish. From this dynamic component, ODBA (overall dynamic body acceleration) was calculated by summing the absolute value of the dynamic acceleration from all three axes (Wilson *et al.*, 2006). Because it has been shown to produce the clearest tailbeat signal (Andrzejaczek *et al.*, 2019), we used the sway (lateral) axis of the angular velocity data (i.e. gyroscope) to calculate the tailbeat amplitude (TBA) and tailbeat period (TBP) using a continuous wavelet transformation with Ethographer (Sakamoto *et al.*, 2009). As such, all further mention of “tailbeat” is indicative of the lateral sway of angular velocity. Finally, a compass heading was calculated from the magnetometer data using the *magHead* function in the gRumble R package (https://github.com/MBayOtolith/gRumble).

Recovery behaviour

It has been previously observed that blue marlin in other geographic regions dive to the upper layers of the thermocline upon release and remain there for an extended period (Holland *et al.*, 1990; Block *et al.*, 1992a). To quantify this initial dive behaviour and determine how fight time may have affected the dive, we regressed the duration of the initial dive (min) against the fight time (min). Dive duration was calculated as the time elapsed from the first dive below 10 m lasting at least 20 s, until the fish returned to 10 m. Each variable was log transformed prior to regression so that the residuals of the model approximated a normal distribution.

We used heading data to calculate the circular mean and *SD* of movement for each fish over the duration of the tracking period, as well as the mean resultant length, $\bar{R}$, as a measure of the concentration of unimodal circular data in 15 min time windows using the circular R package (Pewsey *et al.*, 2013; Cremers and Klugkist, 2018). When $\bar{R}$ is close to or equal to one, values in that time window are closely clustered around the mean direction and are highly directional, and as $\bar{R}$ approaches zero, values are spread more evenly between 0 and 360°, indicative of a tortuous path. The circular mean and *SD* were compared within species using a Watson–Williams test, and between species using a Watson’s two sample test of homogeneity, with significance determined at the $p < 0.05$ level. $\bar{R}$ was used as a continuous time series variable to determine if path tortuosity changed over the course of the tracking period using the methods outlined below.

Recovery period

We summarized metrics of depth, speed, static, and dynamic components of acceleration, angular velocity, and heading hourly and evaluated them for the presence of a recovery period. To investigate relationships between behavioural metrics and hour post-release, several models were built using the nlme (Pinheiro *et al.*, 2007) and mgcv (Wood, 2015) R packages. All statistical analyses treated individual as a random effect. First, each metric was regressed against hour

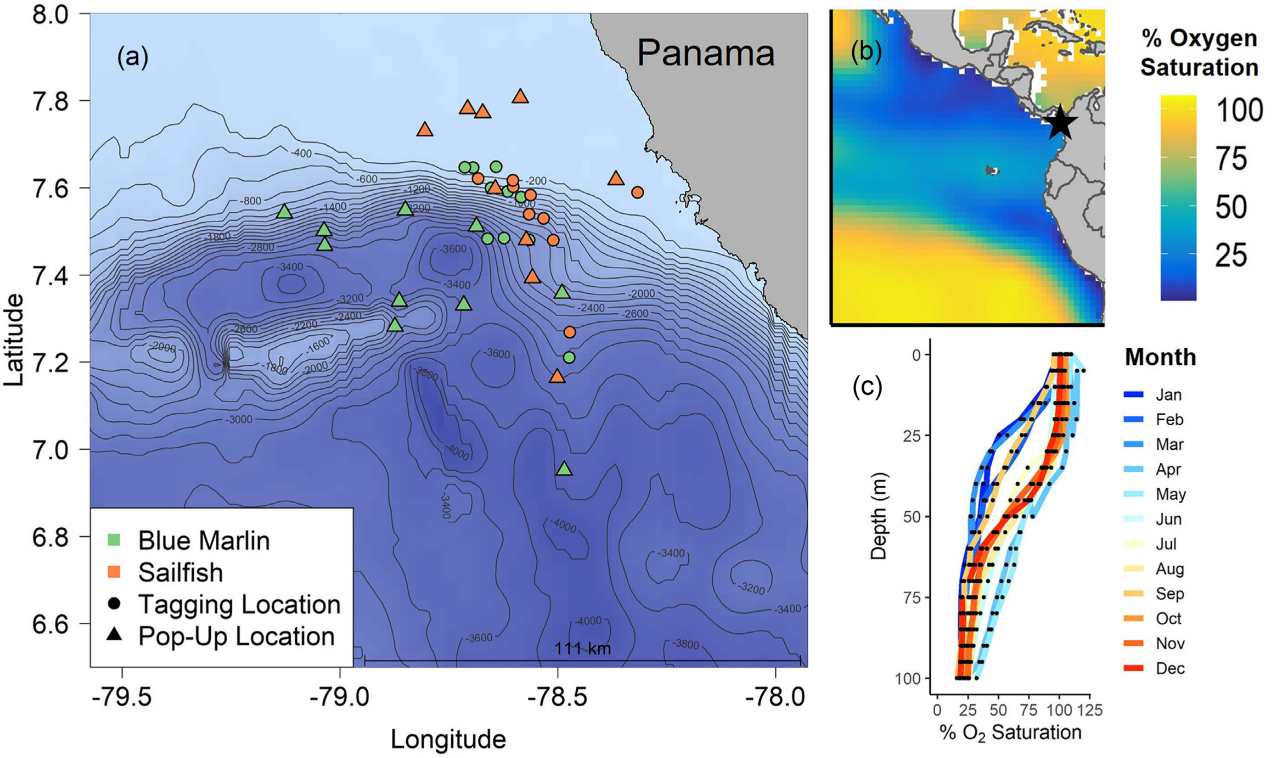

Figure 1. (a) Tagging and tag pop-up locations for blue marlin and sailfish off the coast of southeast Panama, with bathymetric contour intervals of 200 m, (b) the 1° grid cell annual mean % oxygen saturation at 100 m with the study site indicated by a black star, and (c) the monthly mean % oxygen saturation at 5 m depth intervals within the study site (black star). Data for (b) and (c) were obtained from NOAA's National Centers for Environmental Information World Ocean Atlas 2018.

post-release using linear mixed models (LMMs). Each of these models was compared to a null model that did not include hour post-release. Model comparison was performed using Akaike Information Criterion (AIC). Candidate models were deemed significantly better than the null if ΔAIC <10. This threshold was used following Whitney *et al.* (2016), as it is highly conservative to limit type I error during repeated analyses. Many of the metrics displayed nonlinear relationships, thus, were subsequently fitted using generalized additive mixed models (GAMMs) with a smoother around hour post release. GAMMs were compared to LMMs and deemed significantly better than the LMM if ΔAIC <10. Due to the relatively rapid recovery of sailfish across all metrics examined, LMMs did not sufficiently capture the short recovery period. As such, only GAMMs were used to investigate the relationships between each behavioural metric and hour post-release for sailfish. An increased threshold of ΔAIC <20 was used to determine significance against the null model to remain consistent across species, where blue marlin GAMMs had to be 10 less than LMMs which had to be 10 less than the null. Many of the metrics examined appeared to follow an asymptotic relationship with time since release. Therefore, if a metric was deemed to have a significant change over time using the previously described methods, the metric was then fit with an asymptotic regression nonlinear mixed model (NLMM). Models were run for each metric with random term structures that incorporated individual variability into the asymptote, the initial value at time zero (hour 0 post release), and the rate constant that controls the speed at which the metric reached the asymptote. This procedure allowed for flexibility in determining how the individual fish recovered, accounting for variability within the population and different sized fish with varying fight times.

For metrics that displayed a recovery period, we calculated time to recovery as the time at which the metric had changed by 90% of the difference between the initial post-release value (hour 0) and the recovered value (the asymptote). Finally, to test if fight time or fish size were significant predictors of recovery time across all metrics, estimated recovery times from all metrics were compared to fight time and estimated weight in a Generalized Linear Model (GLM; each species analysed separately), where the recovery times were the response variable and fight time, estimated weight, and the interaction between fight time and estimated weight were used as predictor variables.

Results

Recovery behaviour

Data were recovered from nine blue marlin and nine sailfish ($n = 18$) after deployments ranging from 6.1 to 70.5 h (mean ± *SD*; 36.2 ± 19.2 h). Analyses were limited to the first 36 h of each deployment to keep sample size high through the models, culminating in a total of 293 h of blue marlin and 233 h of sailfish depth, temperature, and inertial measurement data. Despite some animals moving up to 47 km (28 ± 13 km) from their point of capture, 100% of tag packages deployed were successfully recovered. Blue marlin tended to move further from the point of capture (38 ± 7 km) than sailfish (18 ± 9 km), even with similar deployment durations (Figure 1a; Table 1), and all fish remained within the region

Table 1. Tagging summary of the fish used in recovery behaviour and recovery period analysis.

Tagging date (d/m/y)	Estimated weight (kg)	Fight time (min)	Deployment duration (h)	Displacement distance (km)
		Blue marlin		
22/09/2019	160	80	14.8	30
24/09/2019	205	90	34	45
3/10/2019	115	12	35.9	45
3/10/2019	90	8	36.4	47
5/10/2019	90	26	35.9	42
9/10/2019	115	40	32	31
21/10/2019	115	13	32.7	42
25/10/2019	180	73	67	32
30/10/2019	70	61	70.5	29
Blue marlin mean ± *SD*	125 ± 45	44.8 ± 30.1	39.9 ± 16.7	38 ± 7
		Sailfish		
19/09/2019	50	8	16.8	18
23/09/2019	30	10	13.4	20
9/10/2019	25	8	33.5	21
14/10/2019	45	6	36.8	21
15/10/2019	45	10	60.2	7
18/10/2019	45	6	67.2	34
27/10/2019	35	4	38.7	12
31/10/2019	45	14	18.9	20
4/11/2019	35	5	6.1	6
Sailfish mean ± *SD*	40 ± 10	7.9 ± 2.9	32.4 ± 19.8	18 ± 9

defined by hypoxia-based habitat compression throughout the duration of their tracks (Figure 1).

After being released blue marlin typically exhibited a long dive (Figure 2) varying in duration from 14 to 383 min (mean 153 ± 120 min). The length of this initial dive increased with fight time [$\log(y) = 1.02 \times \log(x) + 0.47$, $r^2 = 0.68$, $p = 0.006$; Figure 3]. Among all blue marlin, regardless of dive duration, depth of the initial dive was consistent across individuals (29.5 ± 6 m; Figure 2). While some vertical activity was apparent in sailfish after release, they did not exhibit a similar characteristically long dive immediately after release (Figure 2). There was considerable individual variability in sailfish vertical movements after release, however (Figure 2). Sailfish 1 and 2, for example, display very limited diving behaviour compared to the others and the reasons for this are not clear. After sailfish 9, sailfish 1 and 2 have the shortest tag attachment durations which could be a contributing factor.

The circular mean heading (degrees) was significantly different among individual blue marlin [Watson–Williams test; $F_{(8,1\,059\,388)} = 145\,800$, $p < 0.001$] and sailfish [$F_{(8,820\,181)} = 127\,340$, $p < 0.001$]. The mean overall heading between species though was not significantly different (Watson's two-sample test of homogeneity $T = 0.03$, $p = 0.19$). The overall circular mean ± *SD* heading from the point of capture for all blue marlin combined was 260 ± 70° (clockwise range 172–342°), while the mean heading for all sailfish was 249 ± 98° (clockwise range 19–320°), indicating the mean direction of travel for both species was west southwest from the point of release.

Recovery period

Sailfish #9 was omitted from recovery period analyses because of its short track duration (6 h). Immediately after release, marlin and sailfish typically displayed rapid, high-amplitude tailbeats with elevated speed, and had a deeper average depth compared to the rest of the track. During this initial period after release, they actively swam during descents, periods of level swimming, and ascents. Average depth became shallower, and speed decreased as tailbeats became slower and less forceful with time.

Nonlinear relationships with time since release were found for 14 and 13 of the 40 metrics calculated for blue marlin and sailfish, respectively (Table 2). The categories of data that indicated a recovery period were depth, diving behaviour, TBP, TBA, ODBA, swim speed, tortuosity, and % dissolved oxygen content of the water. Metrics derived from vertical velocity, pitch, and temperature use did not display a change over time.

Depth use and diving activity

During the first hour after release, blue marlin and sailfish on average used deeper depths, which became shallower until 90% of the asymptote was reached at 6.7 and 3.8 h, respectively (Table 2; Figures 4a and d). After this period, predicted depth values were similar between blue marlin (6.9 m) and sailfish (5.8 m) with average decreases of 78 and 65%, respectively (Table 3). Average maximum depth was also greatest for blue marlin in the first hour after release but did not stabilize until 8.2 h after release. For sailfish, average minimum depth decreased from 5.4 to 1.9 m (63%) after 2.5 h (Table 3). Like the average overall depth, average depth of level swimming decreased (became shallower) by 81 and 72% for blue marlin and sailfish, respectively.

While sailfish did not exhibit a characteristically long dive immediately after release like blue marlin, their average dive duration decreased by 87% after 1.1 h post-release when 90% of the asymptote was reached. Blue marlin average dive duration immediately after release was nearly 2.5× that of sailfish and decreased by 98% after 90% of the asymptote was reached at 2.4 h after release (Table 3).

Tailbeat period and amplitude

Immediately after release, both blue marlin and sailfish exhibited rapid tailbeats, which slowed with time after release (Figures 4b and e; Figure 5). Blue marlin and sailfish TBP (the time to complete one full tailbeat) increased (i.e. slowed down) by 26 and 93% when 90% of the asymptote had been reached at 10.2 and 5.7 h, respectively (Table 3), with

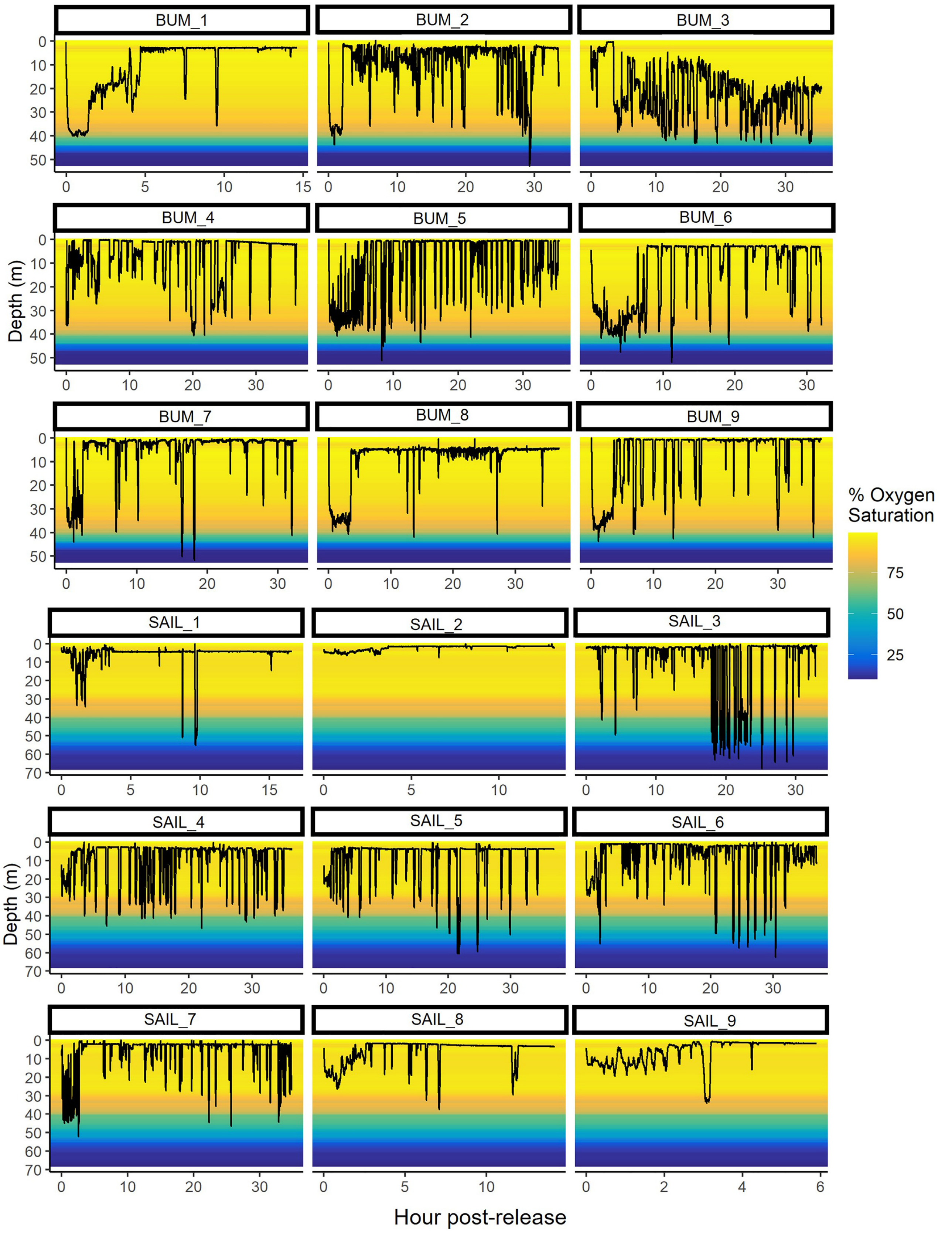

Figure 2. Depth profiles for each fish overlaid on mean % oxygen saturation level at 0.5 m depth intervals obtained from animal borne oxygen sensors. Note *x*-axes differ based on the individual deployment duration, and *y*-axes differ by species.

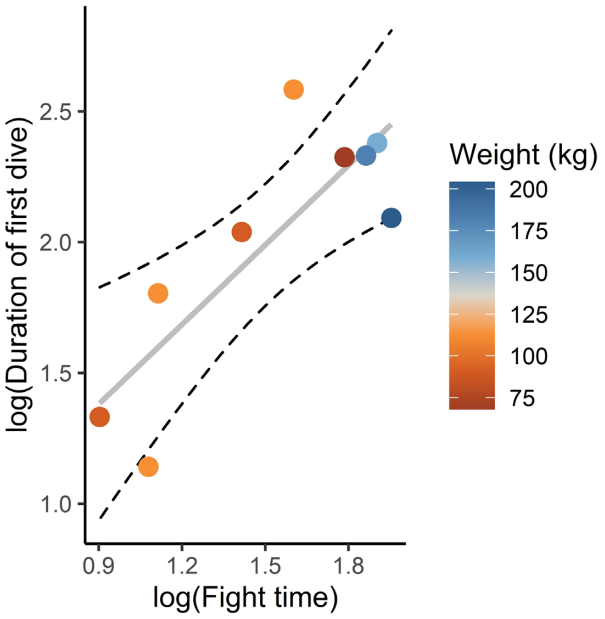

Figure 3. Relationship of initial dive duration with the duration of fight time for blue marlin, colour coded by the estimated weight of the individual. Both variables were log transformed so residuals approximated a normal distribution. Line of best fit $\log(y) = 1.02 \times \log(x) + 0.47$, $r^2 = 0.68$, $p = 0.006$. Dashed lines indicate standard errors.

similar results for TBP of level swimming periods in both species (Table 3). Compared to the overall TBP, the average TBP of ascents reached 90% of the asymptote much faster for blue marlin (4.7 h) than sailfish (8.2 h).

Tailbeat amplitude, a proxy measure of how forceful each tailbeat is, decreased during descents, periods of level swimming, and overall for both blue marlin and sailfish as fish recovered. TBA of level swimming periods displayed the greatest change over time for both species, decreasing by 61 and 80% for blue marlin and sailfish after 90% of the asymptote was reached at 9.7 and 4.4 h, respectively (Table 3; Figures 4c and f).

Overall dynamic body acceleration (ODBA)

Only sailfish showed a significant decrease in ODBA as fish recovered. The overall average ODBA and the average level phase ODBA showed nearly identical decreases of 43 and 42% after release, yet 90% of the asymptote was reached two hours earlier for overall average ODBA than for the average level phase ODBA (Table 3).

Swimming speed and tortuosity

The overall average swimming speed and average level phase swimming speed decreased by 41 and 39% for blue marlin after 90% of the asymptote was reached at 11.4 and 11.6 h. Sailfish swimming speed did not significantly change over time (Table 3).

While the metric of path tortuosity ($\bar{R}$) only showed a change over time for blue marlin, this metric had the longest overall time to reach 90% of the asymptote (14.1 h) of any metric for this species. The value of 0.99 immediately after release indicates blue marlin heading is highly directional and unimodal, whereas after 90% of the asymptote had been reached, their heading is less directional (0.63), indicative of a more tortuous path (Table 3).

Dissolved oxygen

Blue marlin used water with higher average % oxygen saturation after 90% of the asymptote was reached 7.4 h after release, with an increase of 9% from 86 to 94% O_2 saturation (Table 3).

Recovery periods

By incorporating individual as a random effect in the NLMMs, the overall recovery period for each fish could be calculated, resulting in an individual mean recovery period of 9.8 ± 6.7 h for blue marlin and 5.1 ± 3.2 h for sailfish. The recovery periods across all metrics were variable by species, with a range of 1.2–31.3 h for blue marlin and 0.3–16.8 h after release for sailfish. When all significant metrics were incorporated and averaged for each species, the mean recovery period for this study population of blue marlin was 9.0 ± 3.2 h, and 4.9 ± 2.8 h for sailfish. For blue marlin, dive duration produced the shortest estimated times to recovery (2.4 h), while tortuosity and swimming speed displayed the longest times to recovery (14 and 11.6 h, respectively). Like blue marlin, sailfish dive duration produced the shortest estimated times to recovery (1.1 h), while TBP of ascents and overall average TBP displayed the longest time to recovery (11.9 and 8.2 h, respectively).

Fight time and fish size

As previously discussed, dive duration of the initial dive after release significantly increased with increasing fight time for blue marlin (Figure 3). After averaging the recovery periods from all metrics, however, neither the length of the fight nor the estimated weight of the fish (or the interaction between them) were significant predictors of time to recovery for blue marlin (GLM; fight time, $p = 0.14$; estimated fish weight, $p = 0.29$; fight time × weight, $p = 0.17$), or sailfish (fight time, $p = 0.20$; estimate fish weight, $p = 0.21$; fight time × weight, $p = 0.18$).

Discussion

Our study shows that multi-sensor biologging tags may be used to determine fine-scale habitat use, swimming behaviour, and recovery periods from fishery interaction for large, wide-ranging pelagic predators. Understanding this type of information is important in assessing how these highly sought-after sportfish may be impacted by recreational fishing activity via sublethal behavioural modifications. This type of information additionally has the potential to allow fisheries managers to determine if and how different handling and fishing practices may reduce animal stress and recovery time.

Recovery behaviour

Immediately upon release, blue marlin often exhibit a stereotypic recovery behaviour, where they descend to the upper layers of the thermocline and remain there for an extended period of time, previously described as roughly 4–6 h (Holland *et al.*, 1990; Block *et al.*, 1992a, b). During this time, it has also been observed that blue marlin swim at elevated speeds (via speed of a tracking vessel or through direct measurement; Holland *et al.*, 1990; Block *et al.*, 1992b, respectively). This initial dive may be an attempt to seek cooler waters in response to elevated muscle temperature. For example, Block *et al.* (1992a) found that after only a 15-min fight on rod and reel, epaxial

Table 2. Swimming behaviour metrics calculated from acceleration data-loggers for each hour after release and evaluated for indication of a recovery period in blue marlin and sailfish.

		Blue marlin		Sailfish
Variable	**Description**	**Linear ΔAIC**	**Additive ΔAIC**	**Additive ΔAIC**
Depth-avg	Average depth (m)	**-36.8**	**-108.5**	**-25**
Depth-min	Average minimum depth (m)	3.7	-19.9	**-26.9**
Depth-max	Average maximum depth (m)	**-13.7**	**-12.3**	-11.2
Depth-avg ascent	Average depth during all ascents (m)	-9.5	-32.1	-5.3
Depth-avg descent	Average depth during all descents (m)	-1.8	-10.5	-0.7
Depth-avg level	Average depth during all level swimming (m)	**-42.6**	**-122.5**	**-36.8**
Diving ratio	Amount of time spent moving vertically (s)	8.2	-9.4	-8.8
Dive duration-avg	Average length of dives (s)	**-25.4**	**-49.9**	**-21.1**
Dive depth-avg	Average depth of individual dives (m)	1.9	1.3	-5.4
VV-avg	Average absolute value of ascending or descending swimming (m s^{-1})	11.1	-10.5	-9.3
VV-min	Minimum VV (the fastest ascent) (m s^{-1})	8.1	-7.7	-14.2
VV-max	Maximum VV (m s^{-1})	10.8	-3.1	-5.8
VV-avg ascent	Average VV during ascents (m s^{-1})	10.7	-13.3	-7.2
VV-avg descent	Average VV during descents (m s^{-1})	10.7	-9.3	-6.6
TBP-avg	Average tailbeat period (s)	**-65.1**	**-149.1**	**-114.4**
TBP-avg ascent	Average tailbeat period during ascents (s)	**-13.1**	**-26.8**	**-73.5**
TBP-avg descent	Average tailbeat period during descents (s)	12.1	-5	**-23.4**
TBP-avg level	Average tailbeat period during level swimming (s)	**-66.4**	**-165.9**	**-119.1**
TBA-avg	Average tailbeat amplitude ($^{\circ}$s^{-1})	**-34.4**	**-126.7**	**-123.2**
TBA-avg ascent	Average tailbeat amplitude during ascents ($^{\circ}$s^{-1})	10.8	-16.8	-16.2
TBA-avg descent	Average tailbeat amplitude during descents ($^{\circ}$s^{-1})	**-14.9**	**-36.1**	**-26.4**
TBA-avg level	Average tailbeat amplitude during level swimming ($^{\circ}$s^{-1})	**-39.3**	**-141.2**	**-146.8**
ODBA-avg	Average ODBA (g)	19.3	-34.9	**-44.8**
ODBA-max	Maximum ODBA (g)	11.2	-3.4	-1.2
ODBA-avg ascent	Average ODBA of ascents (g)	16.9	-7.3	-19.7
ODBA-avg descent	Average ODBA of descents (g)	15.8	-7.9	-6.4
ODBA-avg level	Average OBDA of level swimming (g)	19.2	-35.1	**-49**
Swim speed-avg	Average swim speed (m s^{-1})	**-10.9**	**-39.9**	-19.8
Swim speed-avg ascent	Average swim speed during ascents (m s^{-1})	10.1	-7.3	-0.3
Swim speed-avg descent	Average swim speed during descents (m s^{-1})	9.9	-1.9	-12.2
Swim speed-avg level	Average swim speed of level swimming (m s^{-1})	**-11.8**	**-39.5**	-18
Tortuosity-avg	Average hourly tortuosity of 15 min intervals (R)	**-27.5**	**-68.8**	-2.5
Tortuosity-avg level	Average hourly tortuosity of 15 min intervals of level swimming (R)	6.6	-39.6	-3.1
Pitch-avg ascent	Average pitch during ascents (°)	5.9	4.8	-11.9
Pitch-avg descent	Average pitch during descents (°)	5.2	5.4	8.7
Pitch-avg level	Average pitch during level swimming (°)	4.6	-1.2	-7.6
Oxygen-avg	Average dissolved oxygen concentration encountered (%O$_2$ saturation)	**-14.9**	**-54.5**	-17.9
Oxygen-min	Minimum dissolved oxygen concentration encountered (%O$_2$ saturation)	-1.8	0	-11
Temperature-avg	Average temperature encountered (°C)	3.7	-8.9	-3.8
Temperature-min	Minimum temperature encountered (°C)	10	2.3	-19.7

Model fit (ΔAIC) is shown for linear and additive models with hour post release relative to the null model. Metrics with significant change over time in both the linear and additive models for blue marlin and additive models for sailfish are marked in bold (refer to the "Methods" section for description of significance and the omission of sailfish linear models).

musculature of a blue marlin was 2.1°C greater than ambient water immediately after release, but that muscle temperature equilibrated to ambient temperature 5 h after release. In addition, increased time at depth after release has been related to increases of [Ca^{2+}] in the blood of white marlin after capture and tagging (Schlenker *et al.*, 2016). Furthermore, increased fight time in istiophorid billfish is associated with concentrations of other blood plasma ions and metabolites related to stress (i.e. sodium, chloride, glucose, cortisol, and lactate) (Dobson *et al.*, 1986; Davie, 1990; Schlenker *et al.*, 2016). Because istiophorids are obligate ram ventilators, elevated swimming speed after release is thought to aid in repayment of the severe anaerobic debt incurred during the fight, without being high enough to incur new debt (Holland *et al.*, 1990), and would serve to meet the higher oxygen demand required to metabolize accumulated lactate (Block *et al.*, 1992a). Alternatively, elevated swim speed may simply be a flight response to an unknown stressful event. Indeed, both elevated swim speed and use of deeper water were also generally observed here for blue marlin following release; however, the average depth at which these dives occurred was much shallower (30–40 m) compared to previous studies in Hawaii (70–100 m) (Holland *et al.*, 1990; Block *et al.*, 1992a). This difference is likely due to the shallow thermocline of the ETP, in addition to the concomitant oxycline limiting these fish to shallower water (Prince and Goodyear, 2006; Figures 1 and 2). Importantly, we were also able to determine that the length of the initial dive increased with fight time. While the sailfish studied here did not exhibit a pronounced long duration dive after release, they did use deeper average depths compared to the

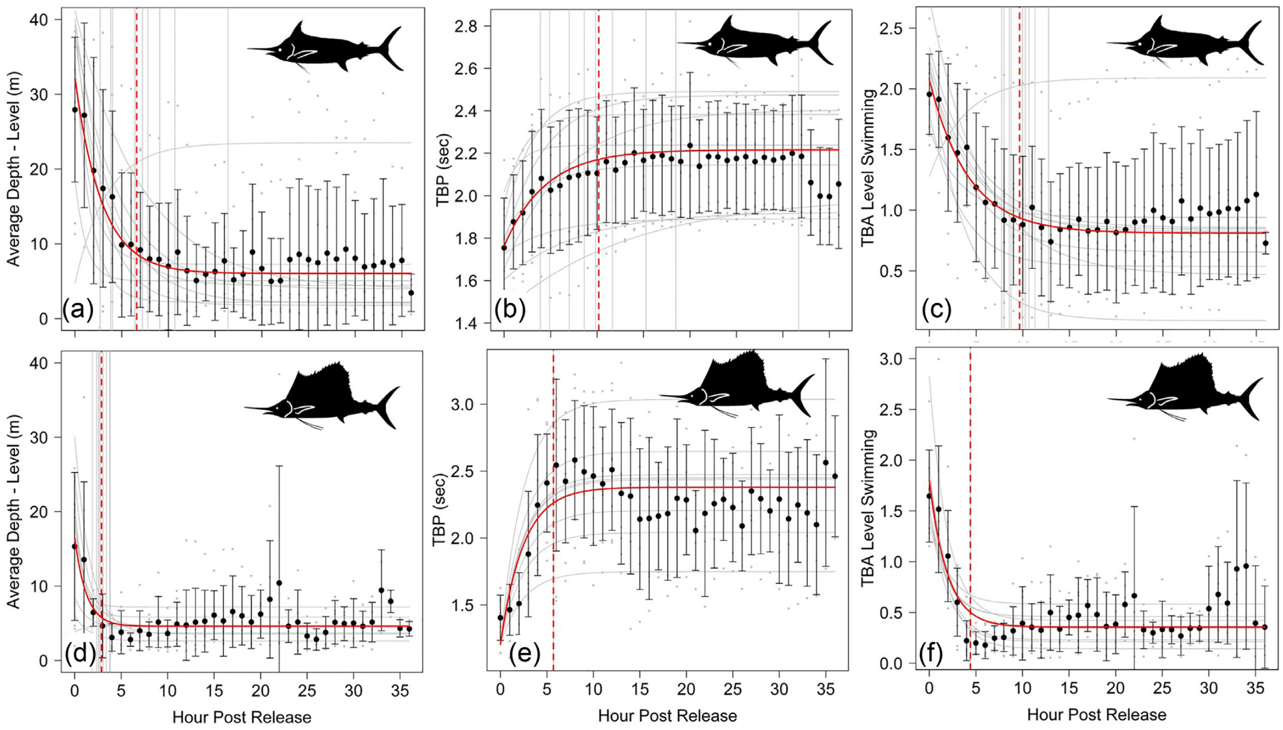

Figure 4. Example recovery periods of blue marlin (a–c) and sailfish (d–f) after being caught and released by recreational fishing gear in southeast Panama. Shown are the hourly means of (a, d) average depth during level swimming, (b, e) overall tailbeat period, and (c, f) tailbeat amplitude during level swimming. Grey lines and dots represent individual hourly means and regressions, with black dots and *SD* bars representing means across individuals. The solid red line is the combined regression, with the vertical red dashed line denoting the point at which this metric reached its 90% threshold and the fish was considered to be recovered for that metric.

Table 3. Metrics that indicated a significant change over time indicative of a recovery period.

	Blue marlin				Sailfish			
Metric	Hour 0 value	90% Asymptote value	% Change	Hour recovered	Hour 0 value	90% Asymptote value	% Change	Hour recovered
Depth-avg	31.4	7	-78	6.7	16.6	5.8	-65	3.8
Depth-max	38.5	21	-45	8.2				
Depth-min					5.4	2	-64	2.6
Depth-avg level	32	6	-81	6.6	16.5	4.6	-72	2.9
Dive duration-avg	150.5	3	-98	2.4	57.1	7.4	-87	1.1
TBP-avg	1.8	2.2	26	10.2	1.2	2.3	93	5.7
TBP-avg ascent	1.5	1.8	21	4.7	1.3	1.6	24	8.2
TBP-avg descent					1.5	1.8	24	11.9
TBP -avg level	1.8	2.2	27	11.9	1.2	2.4	103	5.8
TBA-avg	2.1	0.9	-58	9.8	1.8	0.4	-76	4.5
TBA-avg descent	1.2	1.1	-33	11	1.7	1.1	-39	2.9
TBA-avg level	2.1	0.8	-61	9.7	1.8	0.4	-80	4.4
ODBA-avg					0.04	0.03	-43	4
ODBA-avg level					0.04	0.03	-42	6
Speed-avg	0.8	0.5	-41	11.4				
Speed-avg level	0.8	0.5	-39	11.6				
Oxygen-avg	86	94	9	7.4				
Tortuosity-avg	0.9	0.6	-36	14.1				
				9.0 ± 3.2				4.9 ± 2.8

Percent change represents the % increase (positive) or % decrease (negative) of the value at hour 0 compared to the recovered value. Values come from the line of best fit from the nonlinear mixed models. blank cells indicate the metric was only significant for the other species. See Table 2 for a description of each metric.

rest of their track after release and did exhibit elevated speeds immediately after release.

Fortuitously, the tag of blue marlin 4 was angled down toward the gills allowing the video camera to record the left gill operculum of the fish. Immediately after release, the gill operculum was constantly flared open for roughly 3 h, after which the fish began actively pumping the operculum at a rate of roughly 1 pump s^{-1} during routine swimming, regardless of depth (see Supplementary Video 1). Sharksuckers (*Echeneis naucrates*) transition from buccal pumping to ram ventilation depending on the travelling speed of their host, and it was found that oxygen consumption increased between 3.7 and

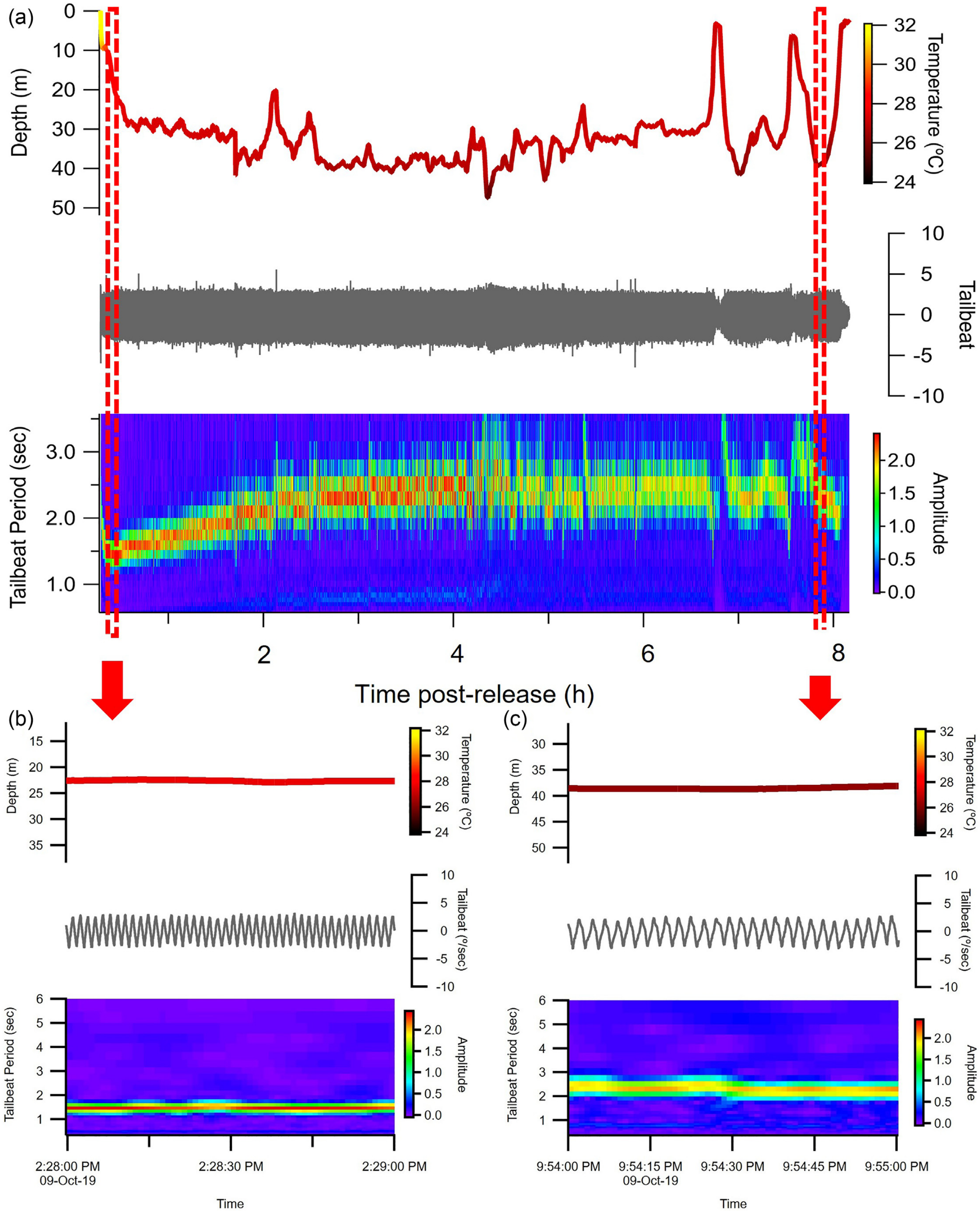

Figure 5. Recovery dive of a blue marlin. Depth, sway angular velocity (tailbeats; °rotation s^{-1}), and the output of the wavelet transformation of tailbeats during the initial dive of blue marlin #6 after release. (a) The fish rapidly descends after being released to a mean depth of 33.5 ± 5.2 m and remains near this depth in a constant temperature during this initial dive period of nearly eight hours, with constant tailbeat activity. The wavelet transformation reflects a gradual increase in tailbeat period of the fish (i.e. tailbeats become slower) to an asymptote while the average amplitude of tailbeats decreases. (b) Immediately upon release, tailbeats are rapid (dominant period of ∼1.4 s) with low variability in period and amplitude, whereas (c) near the end of this initial dive period (nearly 8 h after release), tailbeat period is slower with more variability (dominant period of ∼2.1–2.5 s). Note scale of *x* axis in (a) is ∼8 h, versus 1 min in (b) and (c).

5.7%, when shifting from ram gill ventilation to active branchial pumping (Steffensen and Lomholt, 1983). While blue marlin are known to be obligate ram ventilators, it is possible that they may increase oxygen uptake, or flush accumulated metabolites and CO_2 from the gills more readily via opercular pumping at low swimming speeds.

Since the thermocline and oxycline often occur at similar depths in the ETP, it is difficult to discern the relative influence of the two variables on billfish depth use after release. But given that they do co-occur, these fish are still able to dive to cooler waters to thermoregulate, while also remaining in sufficiently oxygenated water to ram ventilate. Climate change, however, is predicted to lead to oceanographic changes in this region, such as warming and acidification of surface waters, increased stratification, and upwelling of hypoxic waters into the surface layer (Fiedler and Lavín, 2017). Further, hypoxia-based habitat compression is predicted to become widespread as global climate change intensifies and oxygen minimum zones are expected to become shallower (Laffoley and Baxter, 2019; Leung *et al.*, 2019). In the ETP and other regions where the oxygen minimum zone is already shallow, this will cause the oxygen minimum zone to shoal above the thermocline, potentially prolonging or inhibiting recovery of marlin as they seek cooler water temperatures at depth.

Another feature common among fine-scale post-release movement studies of istiophorid billfishes is the tendency of the fish to move away from the coast after release. This directional movement has been observed in active acoustic tracking studies of blue marlin (Holland *et al.*, 1990; Block *et al.*, 1992a), striped marlin (Brill *et al.*, 1993), and sailfish (Jolley Jr and Irby Jr, 1979). Although we found substantial individual variability in mean direction of travel for the duration of the track in both blue marlin and sailfish, the overall mean resultant length for each species indicated a west-southwest mean direction of travel, opposite that of the Panamanian coast nearest the tagging locations. This offshore movement has been suggested as a response to tagging, but may also reflect use of local currents to aid in recovery (Brill *et al.*, 1993; Pepperell and Davis, 1999). Prevailing currents in the region during the study were predominantly north-northwest nearshore, becoming more easterly further offshore (R. Logan pers. obs.; Fiedler and Lavín, 2017). Given that the mean direction of travel for blue marlin and sailfish was west-southwest, it is possible they were swimming into the current to aid in oxygen debt recovery, or aid in predator detection via olfaction while in a more vulnerable swimming state. Interestingly, due to the high-resolution magnetometer heading data obtained, we were able to detect a significant increase in path tortuosity after blue marlin had recovered, suggesting they were less inclined to stay swimming into the current.

Recovery period

In addition to gathering information on depth, heading, and temperature use to determine a post-release recovery period, we found that swimming kinematics (particularly tailbeat period and tailbeat amplitude) follow a predictable response among individuals indicating a recovery period. Combining all significant metrics reveals a recovery period of ∼9 h for blue marlin, and ∼5 h for sailfish. These measurements are similar to that of Holland *et al.* (1990) and Block *et al.* (1992a, b) for blue marlin, where depth, heading, and speed information were used to estimate a recovery period of roughly 4–6 h. In addition, Jolley Jr and Irby Jr (1979) suggest that sailfish acoustically tracked along southeast Florida appeared to recover within 1–3 h following release as indicated by inshore movement and an increase in activity (i.e. changes in vessel tracking speed and heading). Additionally, using acceleration data loggers similar to those described here, Atlantic bluefin tuna (*Thunnus thynnus*) displayed increased speed and tailbeat activity for ∼6 h after release from recreational angling (Gleiss *et al.*, 2019).

Due to the need to affix acceleration data loggers with two points of attachment on bony fish to obtain accurate tailbeat signatures, most effort to date using acceleration data loggers in marine fish has been focused on elasmobranchs, whose rigid dorsal fin makes tag attachment more straightforward. Estimated recovery periods of elasmobranchs using these methods range from 4 to ∼11 h (Whitney *et al.*, 2016; Andrzejaczek *et al.*, 2019). Similar to Whitney *et al.* (2016), metrics derived from tailbeat activity here (tailbeat period and amplitude) often displayed a more consistent period of recovery among individuals than those derived from depth. In contrast to blacktip sharks (Whitney *et al.*, 2016), recovery periods derived from tailbeat activity in blue marlin and sailfish were longer than those derived from depth, indicating that depth information alone does not fully encompass swimming behaviour, and may not be sufficient to accurately describe a recovery period for pelagic fish where seafloor depth is deeper than maximum diving depth.

While our methodology and results increase the knowledge base of sublethal stress impacting post-release behaviour in istiophorid billfishes, caution is warranted in interpreting these data. Due to the nature of the high-resolution data being collected and needing to physically recover the tag package, the amount of time a tag can be attached to an individual is limited, particularly for highly migratory pelagic species such as blue marlin and sailfish. As such, it is possible that the short duration deployments reported here may not have extended beyond the true recovery periods, and what we determined to be recovered behaviour may not be representative of normal behaviour. Using a majority of Argos transmitted summary depth-temperature profiles (PDT), Hoolihan *et al.* (2011) found that blue marlin and sailfish displayed post-release behaviour modification for an average of 8.2 ± 8.5 and 3.5 ± 5.8 d after release, respectively. Interestingly, larger blue marlin (≥90 kg; like 89% of the blue marlin tagged in this study) were significantly less likely to show signs of behaviour change after release than smaller blue marlin (Hoolihan *et al.*, 2011).The large variability (indicated by the large *SD*) in the duration of behaviour modification in the Hoolihan *et al.* (2011) estimates is indicative of the comparatively low resolution of transmitted summary data from PSAT tags used in their study compared to the sub-second resolution presented here. In addition, Hoolihan *et al.* (2011) stipulate in their findings that species-specific behaviours and environmental conditions could not be taken into account. Comparisons of vertical movements from short term acoustic telemetry and acceleration studies (this study; Jolley Jr and Irby Jr, 1979; Holland *et al.*, 1990; Block *et al.*, 1992a; Gleiss *et al.*, 2019), and longer duration implanted archival and PSATs (Schaefer *et al.*, 2011; Chiang *et al.*, 2015; Lam *et al.*, 2015; Carlisle *et al.*, 2017; Vaudo *et al.*, 2018) suggest that, when investigated, recovery following release for tunas and billfishes is on the scale of hours rather than days, and that changes in vertical habitat use can largely be explained by differences in oceanographic conditions and prey distributions.

Likewise, physiological parameters suggest billfish are capable of rapid recovery. Tunas and billfish white muscle exhibit some of the highest, if not the highest, lactate levels and accompanying lactate dehydrogenase (LDH) activity of any vertebrate (Dickson, 1995; Bernal *et al.*, 2010), thus facilitating rapid metabolism of accumulated lactate to pre-exercise levels, much faster than other fish (Arthur *et al.*, 1992). This is largely a result of these fish large gill surface area (Wegner *et al.*, 2010) and cardio-respiratory system being able to deliver oxygen and metabolic substrates at high rates compared to other species (Bernal *et al.*, 2010). We therefore believe the findings presented here are an accurate representation of the species-specific recovery period for blue marlin and sailfish in the ETP.

Conclusions

Here, we provide the first high-resolution insights into the recovery behaviour of istiophorid billfish after release from a recreational fishery via accelerometry. We demonstrate the utility of and the ability to use (and recover) acceleration data loggers in these large pelagic fish without a rigid dorsal fin conducive to tag attachment, as well as highly migratory species capable of long-distance movements. We show that post-release behaviour and recovery periods are individual and species-specific, even under identical environmental conditions and handling practices, indicating that fine-scale swimming and diving kinematics can provide insight to the underlying physiological impacts of recreational fisheries capture. While it was not specifically measured here, we propose that acceleration data loggers would be a useful method to determine the impact of various oceanographic conditions, handling practices and gear types on the recovery of these highly sought-after recreational species. For example, because sailfish are smaller and more easily handled, they are often lifted out of the water for anglers to take a picture, exposing them to substantial time out of water, increasing stress and potentially post release mortality (Schlenker *et al.*, 2016). In addition, fly fishing and lightweight gear has become a common angling practice for these species, considerably increasing fight time and therefore potential stress and recovery time. Gaining an understanding of impacts such as these would aid in sustainable catch and release fishing practices and fisheries management for these large, highly mobile predators in the face of global climate change.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Conflict of interest statement

We have no conflicts of interest to disclose.

Author contributions statement

RKL, JJV, and MSS contributed to the design and conception of the study. RKL led the methodology, data collection, data analysis, and drafting the original version of the manuscript. All authors contributed to revising the manuscript and approved the final draft.

Funding

This was supported by the Guy Harvey Ocean Foundation [grant number GHOF 2019], the Guardians of the Eastern Tropical Pacific Seascape donor group, Nova Southeastern University, and the Gallo-Dubois Scholarship, Fish Florida Scholarship, and Batchelor Foundation Scholarship to RL. In-kind logistical support in the field was provided by Tropic Star Lodge.

Acknowledgments

We thank T. Plum, R. Andrews and the Compass Rose crew, and the staff, captains, and mates of Tropic Star Lodge for their support during fieldwork, and J. Stieglitz for help with the flow tank speed sensor calibration.

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Handling Editor: Simon Weltersbach