



## Post-release behaviour and survival of recreationally-angled arapaima (*Arapaima cf. arapaima*) assessed with accelerometer biologgers

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### ABSTRACT

Recreational fisheries are increasingly important sectors of tourism-based economies. In the last decade, new recreational fisheries have emerged that target species of varying conservation status including vulnerable, endangered, and unassessed species. In Guyana, catch-and-release angling tourism has begun to target arapaima, a genus of giant air-breathing fishes. Given the uncertain conservation status of this species and that no information is available to evaluate the sustainability of this activity, we sought to describe the responses of arapaima to recreational angling. We harnessed tri-axial accelerometer biologgers around the trunk of fish that had been captured and released by recreational anglers, allowing us to monitor post-release survival and behaviour, including surfacing, which is essential for this air-breathing fish to recover from exhaustion. Twenty-seven individuals were instrumented ( $162 \pm 25$  cm), 24 of which were considered survivors (89%) during the  $47 \pm 35$  (SD) min monitoring period. Fish that died were observed to drown soon after release (i.e. within minutes), not surfacing to breathe air. Supervised machine learning classification of behaviours using a random forest algorithm identified surfacing events with 80% accuracy (i.e. out-of-bag error rate = 20%), which we applied to unobserved data periods to estimate breathing frequency after release, along with overall dynamic body acceleration (ODBA) as a proxy for activity. Neither mean breathing frequency nor ODBA were related to body size (total length), handling time (which incorporated facilitated recovery of individuals), nor time of capture (early or late in the dry season spanning water temperatures of 29.3–34.1 °C). The precise angling-related factors that led to arapaima mortality were unclear, but the frequency of mortality aligns with the mortality documented in other recreational fisheries. This mortality source can be incorporated into conservation plans and provide context to the impacts of recreational angling relative to the costs of legal or illegal harvest.

### 1. Introduction

Recreational fisheries are rapidly globalizing as mobile anglers seek out novel fishing experiences around the world (Ditton et al., 2002). Many anglers are motivated by catch-based objectives (i.e. not necessarily motivated by harvest) and will release fish that they capture alive (Arlinghaus et al., 2007). The practice of catch-and-release is supported by evidence that released fish survive (Cooke and Schramm, 2007). An important caveat, however, is that recreational fisheries often rely on the identification, development, and implementation of best-practices for fish capture and handling to avoid excessive stress or injury to fish that can result in mortality (Brownscombe et al., 2017a). Establishment of recreational catch-and-release fisheries guidelines or best practices can contribute to sustainable development for economies

and can galvanize a transition towards tourism-based economies that contribute to resource protection and long-term sustainability (Barnett et al., 2016). Scientific assessment has played an important role in evaluating fishing practices and developing evidence-based recommendations to fisheries sectors that can ensure long-term success and sustainability. Species-specific assessments are necessary because of the vast differences among fish species in their physiological responses to stress (Cooke et al., 2013), mouth morphology (which influences hook damage; Cooke et al., 2013), and general biology, which can result in lethal or sublethal impairments that can differ greatly among species (Cooke et al., 2002; Cooke and Suski, 2005; Raby et al., 2013).

The Neotropical fish fauna endemic to South America is the most biodiverse on Earth (Levêque et al., 2008). Much of the freshwater

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habitat in South America, its ecosystem integrity, biodiversity, and peoples, are threatened by development and industrial encroachment, exacerbated by employment insecurity and declines in sources of traditional natural resources for food and building (Castello et al., 2013; Soares-Filho et al., 2006). Ecotourism can provide employment and income to the indigenous communities and can support conservation of culture and ecosystems with less extractive practices. Recreational fishing ecotourism is popularizing as a sector of ecotourism that can allow communities to use their traditional ecological knowledge to develop successful and sustainable recreational fisheries (Barnett et al., 2016; Bower et al., 2017).

*Arapaima* spp. are giant freshwater fishes native to South American rivers (Castello and Stewart, 2010; Stewart, 2013; Watson et al., 2016). *Arapaima* species have traditionally been an important source of protein to local subsistence fishers of South America (Veríssimo, 1895 in Hrbek et al., 2005) but are now becoming sought-after by recreational anglers, who target *arapaima* during the low-water dry season in floodplain ponds where they appear to prepare nests (further research is needed to confirm the life history of this species). *Arapaima* cf. *arapaima* (Valenciennes in Cuvier and Valenciennes, 1847; also see Watson et al., 2016) was described from the Rupununi basin of southwestern Guyana, but Watson et al. (2016) encountered a pair of sympatric genotypes (based in microsatellite markers) in that drainage. So, although the genus *Arapaima* is protected in Guyana by national legislation, the global conservation status of *arapaima* species is pending because of data deficiencies that preclude an accurate assignment of species (Stewart, 2013). More data from this region are needed to conclusively determine the stock complex in Rewa. Nonetheless, recreational fisheries are established and may be expanding in popularity and participation in Guyana. The biology of *arapaima* as obligate air breathing fishes renders them relatively unique as recreationally targeted species (Stevens and Holeyton, 1978; Brauner et al., 2004), particularly when considered along with its large size, which may make this fish more vulnerable to angling-related stressors and post-release mortality. Anglers target *arapaima* throughout the dry season and may fight fish for long durations, handle them in air for photographs, and release them after variable intervals of handling including facilitated recovery (i.e. breaths taken by the fish before release). Although local fishing guides believe that most *arapaima* survive angling, quantification of the survival and identification of best practices is necessary to assess sustainability of the fishery.

Our objective was to assess the short-term post-release behaviour and survival of *arapaima* released by recreational anglers in the emerging recreational *arapaima* fishery in Guyana. To accomplish this, we equipped *arapaima* with accelerometer biologgers, which are devices capable of quantifying fine scale activity and behaviour in diverse species (Gleiss et al., 2010; Brown et al., 2013), including fish (Whitney et al., 2016; Broell et al., 2013; Brownscombe et al., 2013, 2014; Wright et al., 2014; Cooke et al., 2016a). For *arapaima*, accelerometers were used to quantify post release activity, as well as the frequency of surfacing behaviour that is essential for obligate air breathers to repay oxygen debt (Stevens and Holeyton, 1978; Brauner et al., 2004). We used survival data from post-release tracking and accelerometer-derived activity and behaviour metrics to characterize the fate of released fish evaluate angling practices determine to what extent capture and handling affect this species. This information is crucial to develop strategies that promote post-release vitality of fish released by anglers and sustainability of the recreational *arapaima* fishery.

## 2. Methods

### 2.1. Study site

Rewa Eco-Lodge, located in Rewa Village, Guyana (3.885888, -58.798410) is a tourism outfitter operated by the Amerindian community of Rewa (3.883096, -58.805726). Rewa village is located at

the confluence of the Rewa and Rupununi Rivers in District 9 of Guyana. The Rupununi region of Guyana is part of the Essequibo watershed, which drains the eastern Guiana Shield (Lundberg et al., 1998). The region experiences an annual wet season enduring May–August, which inundates the savannah and forests (Lowe-McConnell, 1964). Water recedes from September–April, leaving persistent floodplain ponds along the river margin where *arapaima* aggregate during this dry season and may spawn.

Rewa Eco-Lodge has operated along the Rewa River since 2005 and has been granted consideration by the government of Guyana to practice recreational fishing for *arapaima*, which is otherwise a protected species in the country. Rewa Eco-Lodge offers guided fly fishing for *arapaima* during the dry season in the marginal ponds in the forest along the Rewa and Rupununi rivers. We did not find any differences in water surface temperature in late dry season compared to the early dry season. Average surface water temperature when *arapaima* were caught was 31 °C.

### 2.2. Focal species

Briefly, we describe the biology of *arapaima* here to provide important context to readers about this rare and relatively poorly understood species, much of which is based on research conducted on *Arapaima gigas*, native to Amazonian waters, with some notes based on discussions with local Amerindians with traditional knowledge of Guyanese *arapaima* from subsistence fishing in the past.

*Arapaima* migrate between the flooded forests in the wet season and sloughs or latitudinal ponds in the dry season. Nesting is believed to occur during the late dry season or rising water season when partners excavate nests in the substrate to lay eggs (Castello, 2008a). *Arapaima* exhibit parental care and juveniles are observed travelling with parents in the ponds later in the dry season (R.J. Lennox, personal observation). According to Castello (2008b), parental care of *arapaima* in the central Amazon continues beyond the dry season and young-of-the-year remain with parents in the flooded forests, which provide refuge against predators. When the wet season resumes and the forests flood, most juvenile *Arapaima gigas* are likely to exceed 50 cm TL and to have deposited a bi-annulus on the scale, two of which are believed to form per year (Queiroz, 2000; Arantes et al., 2010). Arantes et al. (2010) and Queiroz (2000) estimated age of maturity of *arapaima* in the central Amazon between 3 and 5 years of age around 157 cm TL.

In Guyana, it is not quite certain when exactly breeding commences or ceases during the dry season, but juveniles are more frequently observed later in the dry season in January and February. There are many differences in the density of *arapaima* among ponds in Rewa; Arantes et al. (2013) suggested that pond depth is an important determinant given that higher vulnerability to drought imperils *arapaima*. We observed some ponds desiccating in Guyana and total mortality of the *arapaima* residing in those ponds (R.J. Lennox, personal observation). The degree of site fidelity of *arapaima* to ponds is necessary to study for determining whether such habitats can recover from disturbances including environmental stress as well as impacts of fishing. Presently, it is not well known to what degree individuals exhibit inter-annual site fidelity.

### 2.3. Sampling

*Arapaima* were captured on barbed artificial flies (sizes 6/0–8/0) using 12 wt fly rods early (November 5–25, 2016) and late (April 4–7, 2016; February 2017) in the dry season. The time (s) from hooking to landing the fish (i.e. fight time), total length (cm), and girth (cm) were measured, and each fish was scanned for a PIT tag or marked with one injected into the muscle with a hypodermic needle (Biomark, Boise, Idaho, USA). To measure the post-release activity and identify post-release behaviour, accelerometer logger tags (Gulf Coast Data Concepts X16-mini, Waveland, Mississippi, USA) temporarily waterproofed with



**Fig. 1.** Researchers attaching an accelerometer logging package (yellow) to the trunk of *Arapaima cf. arapaima* captured by recreational angling in Rewa, Guyana. The accelerometer was waterproofed and secured to a plexiglass plate, which was harnessed with elastics and attached to a fishing rod without drag ('free spooling') to allow the fish to swim freely within the pond. Photograph provided by Jared Louviere (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

liquid rubber coating (Performix Brand Plasti-Dip, Blaine, Minnesota, USA; see Brownscombe et al., 2013, 2014) were mounted to custom-made 2 mm thick plexiglass plates with rounded edges, which were harnessed to the mid body of the fish with elastics (Fig. 1). Tags were attached in consistent positions and orientations on the fish to standardize data collection amongst individuals and enable identification of fine scale behaviours. Arapaima has an elongated swimming stroke and the position of the harness was such that it would record longitudinal movements of the body trunk along the x-axis representing tail beats. To retrieve the loggers, the harness was attached to a fishing rod with braided dacron fishing line or a metal float attached to wire leader. At the end of a monitoring interval, the package was manually removed from the fish by pulling the trailing line, removing the elastics, and retrieving the logging package. Visual observations of the fish's surfacing activity were made so that annotations could be used to train algorithms based on the output of the accelerometer logger (e.g. Sakamoto et al., 2009; Brownscombe et al., 2014).

#### 2.4. Data processing

Accelerometer logger data were converted to units of  $g$  (equal to  $9.8 \text{ m s}^{-2}$ ) by dividing the three axes: pitch (x-axis), roll (y-axis), and yaw (z-axis) by 2048, the standard conversion factor associated with the tag. Static acceleration (i.e. posture) was calculated by passing a 2 s box smoother over each axis with the *rollmean* function in the R package zoo (Zeileis and Grothendieck, 2005) and converted to degrees by multiplying values by  $180 \pi^{-1}$ ; these values were used to calculate pitch (for the x-axis) and roll (for the y-axis). Dynamic acceleration ( $g$ ) was calculated by subtracting static acceleration from raw acceleration values. Overall dynamic body action (ODBA) was calculated by summing the absolute values of dynamic acceleration in each axis (Gleiss et al., 2010). Post-processed accelerometer data were used to calculate mean and standard deviation of the three dynamic axes, pitch, roll, and ODBA. With the *summarize* function in dplyr (Wickham and Francois, 2016), values of these variables were subsequently summarized across a time frame of 20 s, which was determined to be the optimal time frame for identifying behaviours including breathing events given their temporal duration.

#### 2.5. Data analysis

Arapaima condition factor was calculated by dividing length by

girth, and was compared between early and late in the dry season using a *t*-test with the *t.test* function in R (R Core Team, 2017). This tested for a difference in body condition of fish at different periods of the dry season, early or late, during or after putative nest excavation, copulation, and rearing of young. We regressed fight time against total length using simple linear regression implemented with the *lm* function in R. Survival data were collected from observations of tagged individuals. These data were collected across post-release intervals that differed in duration owing to constraints imposed by timing of capture, fish movement into reeds or under logs that dislodged the accelerometer package, or interactions with black caiman (*Melanosuchus niger*) that stripped the package from the fish. For this reason, we experimented with the use of survival analysis, specifically Cox proportional hazards regression, however, the analysis did not converge so we opted for the more conservative logistic regression in an attempt to explain mortality of individuals. Because length and fight time were correlated, we used only length as a predictor variable to avoid problems of collinearity. We also incorporated handling time as a predictor variable, which was correlated with the number of recovery breaths taken by the fish before release (see Results).

Visual observations of resting, swimming, and surfacing behaviour noted while monitoring arapaima after release were matched to the appropriate individual fish and 20 s time bin. Observed events were passed into a random forest algorithm with the function *randomForest* in the randomForest R package (Liaw and Wiener, 2002) using mean and standard deviations of dynamic x, y, and z movement, pitch, roll, and ODBA as independent variables to predict the observed event. The random forest was run with 500 trees and three variables tried at each split. Random forest was useful for these data because of its flexibility and insensitivity to distributional assumptions, interactive effects, or random effects. Variable importance was assessed by mean decrease in Gini coefficient, a measure of how a given variable performs in splitting the data into classes. Classification error is presented as the out-of-bag error available from the *print* function in randomForest. Predictions were generated from the *predict* function to predict breathing events in unobserved data and complete the dataset with event-based data. Average breathing frequency was calculated for each fish using the output of predicted breaths and modeled by linear regression to determine whether catch variables: total length, handling time, and time of season (early or late) influenced the frequency of breathing after release. Handling time was used as a predictor variable because it was correlated with the number of recovery breaths ( $t = 13.13$ ,  $P < 0.01$ ,

$R_{adj}^2 = 0.90$ ). Overall dynamic body action was used as an index of the total activity exhibited by arapaima. We calculated the average of ODBA during the monitoring period using the *tapply* function in R. The R function *lm* was implemented to regress catch variables total length, handling time, and time of season (early or late). For these analyses only survivors of catch-and-release were considered because the values of breathing and ODBA derived for fish that died were confounded by handling. The ODBA analysis was repeated using only up to the first 10 min of data in consideration of possible bias introduced by including individuals that were monitored for longer intervals. We rationalize analyzing both breathing frequency and ODBA as dependent variables because they were not significantly related to each other according to linear regression (R function *lm*;  $t = -1.18$ ,  $P = 0.26$ ). Figures were generated with *ggplot2* (Wickham, 2009).

### 3. Results

#### 3.1. Summary of angling statistics and observations

We tagged 27 individuals measuring  $162 \pm 25$  cm (range: 125–213 cm) TL captured either early ( $N = 13$ ) or late ( $N = 14$ ) in the dry season. There was no difference in the length of fish captured between seasons ( $t_{df = 15,57} = -0.51$ ,  $P = 0.62$ ). Fish were fought on average  $327 \pm 104$  s (range: 155–568 s) and there was a significant relationship between the body size and fight duration of arapaima (linear regression:  $t = 3.78$ ,  $P < 0.01$ ) described by the equation  $t_{\text{FIGHT}} = 2.57 \times L - 85.39$  (Fig. 2).

Arapaima were tracked from 11 to 155 min (mean  $47 \pm 35$  min). After release, there were two general patterns in movement that were visually observed (but not quantified); some fish settled motionless on the bottom of the pond before eventually surfacing to breathe and then swimming away from the release site, whereas others immediately swam away from the area. The arapaima mostly swam slowly and surfaced at regular intervals to breathe. Although we did not record the precise path that each individual followed after release, we noted, anecdotally, that they did not necessarily return to the site of capture. Rather, they often swam continually within the pond. There was one pond surrounded by emergent vegetation in which arapaima consistently swam away from the release site into the vegetation, which dislodged the logging package and prematurely terminated our observation period in several instances. Similar evidence of refuge-seeking behaviour was not observed in other ponds from our observations. Three individuals that died after release were all observed to be motionless after release. Two of the three took breaths at the surface before returning to the bottom and never resurfacing whereas the third never surfaced.

All three mortalities were recorded later in the season during late

dry season fishing, so survival of late dry season caught fish was 79% compared to 100% survival of fish caught during the November fishing period. However, the sample size was small and did not detect a statistically significant difference in survival between the two seasons ( $P = 0.97$ ).

#### 3.2. Accelerometer analysis

Random forest predictions identified post-release breathing occurring on average every  $376 \pm 172$  s, ranging from as frequently as every 177 s to every 890 s (see Fig. 3 for example of post-release breathing from the accelerometer). Although average breathing frequency was more rapid early in the season (November) than later (February–April), season was not a significant predictor of breathing frequency ( $t = 1.95$ ,  $P = 0.07$ ), nor was handling time ( $t = -1.12$ ,  $P = 0.28$ ) or length ( $t = 0.45$ ,  $P = 0.66$ ). Average ODBA of arapaima that survived catch-and-release ranged from 0.02 to 0.07 with a mean of  $0.03 \pm 0.02$ . ODBA after release was not influenced by the fish body size ( $t = -1.07$ ,  $P = 0.30$ ), handling time ( $t = -0.43$ ,  $P = 0.63$ ) or the season in which the individual was captured ( $t = 1.61$ ,  $P = 0.13$ ). The result was functionally identical when considering average ODBA within 10 min of release (all  $|t| < 1.77$ , all  $P > 0.10$ ).

### 4. Discussion

We worked alongside Amerindian fly fishing guides at Rewa Eco-Lodge to characterize the fate of arapaima captured in an emerging recreational fishery in the Rewa and Rupununi Rivers of the Guyanese rainforest. This is a unique effort to develop science-based best practices for recreational fishing for a rare and poorly understood species that is poorly studied and not assessed independently by IUCN (i.e. because it has historically been classified as *A. gigas*; Stewart, 2013). Our findings provide an important perspective into the survival of arapaima captured by anglers, suggesting that individuals that are released survive and recover patterns of activity that we hypothesized to represent recovery from stress and exhaustion, with frequent surfacing to breathe. We also present evidence that some arapaima die following encounters with anglers. Our collaboration with Rewa Eco-Lodge provided a necessary perspective into arapaima biology via stakeholder and traditional ecological knowledge and emphasized the cultural value of arapaima to the village and region. Working with local guides was also insightful to understand the rationale for fishing and handling practices developed based on traditional knowledge and observations made by the lodge staff and villagers. Our partnership to evaluate short-term fate of the fish released by anglers supplements the knowledge about arapaima and individual responses to recreational angling and will hopefully support improvements in the sustainability and management of

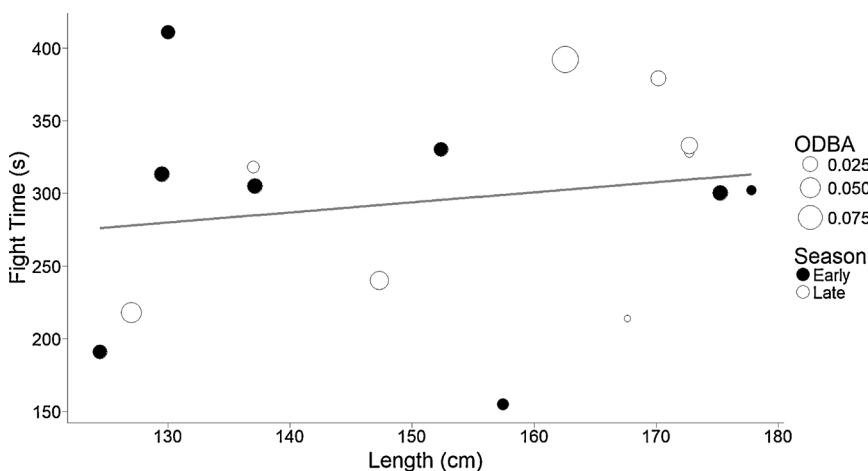
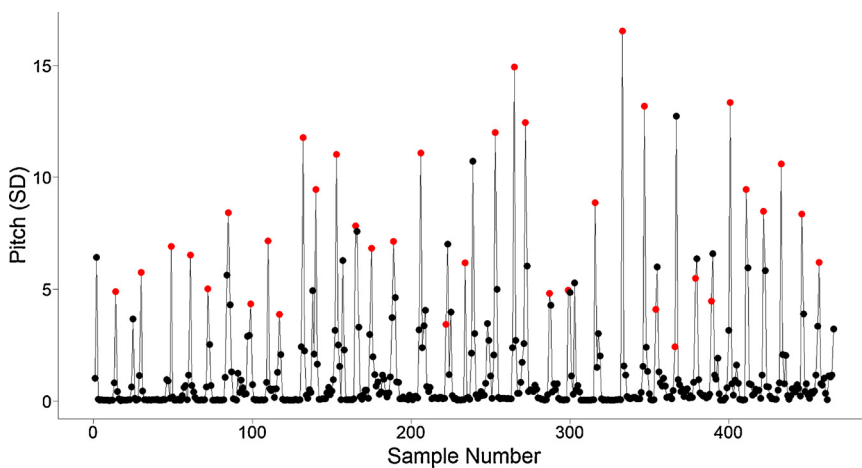


Fig. 2. Fight time was significantly related to length of *Arapaima* cf. *arapaima* in Rewa. The grey line represents the regression line and the size of the points indicates the overall dynamic body action (ODBA) of the individual based on accelerometer data (see Methods). Three individuals that died following catch-and-release are excluded from the figure. Early season (black) corresponds to fishing in November and late season (white) is the February–April.



**Fig. 3.** Standard deviation in pitch of the accelerometer representing breathing events of arapaima. Classification of breathing events was performed by visual identification, which was used to train a random forest algorithm to identify other breathing events. The algorithm performed with 80% accuracy (out-of-bag error). Sample number is the timepoint after release in 20 s bins.

the fishery.

Our observation of short-term survival of arapaima, 89%, is consistent with other fish survival rates in recreational fisheries of 90% (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). Based on our findings, we suggest that it would be beneficial to continue post-release monitoring of arapaima using the minimally invasive floats to expand knowledge of post-release survival. Continued short-term monitoring would refine estimates of post-release mortality (i.e. strengthen sample size) and facilitate development of best practices while also allowing the local villagers to harvest individuals that die rather than to leave them to decompose in the ponds, contributing to food security in the village (Cooke et al., 2018). From our modelling, it was evident that greater sample size is needed to identify significant predictors of post-release survival, including extending the comparison between early- and late-season captured fish. Indeed, we found that all mortalities occurred late in the dry season, yet high standard errors of regression estimates owing to small sample sizes rendered our models unreliable for assigning significance to the main effects on mortality. However, late season vulnerability to angling could in fact be higher and this merits further investigation. Other fishes often fast during spawning and decrease in condition, such as nesting centrarchids (Gillooly and Baylis, 1999; Cooke et al., 2006) and migratory salmon (Jonsson et al., 1997). Watson et al. (2013) found fish remains in the stomachs of arapaima in dry season ponds, but samples were taken only in the early part of the dry season (October–December) prior to when we begin observing juveniles in Rewa and before the late-season fishing occurs. Loss of energetic reserves during reproductive periods may increase vulnerability to stress and exhaustion imposed by angling. Data from other species do not corroborate this hypothesis, for example Pacific salmon (*Oncorhynchus gorbuscha*, *O. keta*; Raby et al., 2013) and Atlantic salmon (*Salmo salar*; Brobbel et al., 1996) survival has been shown to be higher later in the migration when energetic reserves are depleted; however, this may be conflated by colder water temperatures later in the season (but see Wilkie et al., 1997). Further study could therefore focus on understanding how environmental factors contribute to risk of mortality of arapaima, although water temperatures are relatively stable (Lowe-McConnell, 1964). Telemetry would be an effective tool to expand observations to long-term survival and extend monitoring and increase the precision of mortality estimates for the species (Pollock et al., 2004).

Recreational fisheries capture is an acute stressor of fishes. When hooked, an individual elicits an escape response by recruiting anaerobic muscular pathways, which metabolize phosphocreatine, ATP, and glycogen and produce lactic acid (catabolized to lactate and a free metabolic proton) as a by-product (see Kieffer, 2000). We did not observe arapaima fighting for prolonged intervals but fights were intense and included powerful jumps from the water. For gill-breathing fishes, post-

release recovery is often characterized by slow movement while the gills are ventilated, metabolic byproducts are cleared from the blood and muscle, and energetic substrates are restored (Milligan, 1996; Milligan et al., 2000). In gill-breathing fish, pre-release recovery methods (i.e. facilitated recovery, assisted ventilation) often involve holding fish in water current, or manoeuvring the fish through the water in figure-8 motion; however there is little evidence supporting use of these techniques (Robinson et al., 2015; Brownscombe et al., 2017a, b). For fish that struggle to swim away from the angler, it is therefore recommended to hold the fish in a retention device ideally, or alternatively by hand until it swims away on its own volition (Brownscombe et al., 2017a). However, there is little knowledge of release tactics for obligatory air-breathing fish, which must actively surface to breathe and recover from exhaustion (Brauner et al., 2004; Stevens and Holeton, 1978). In this arapaima fishery, fishing guides always hold fish at the surface, enabling fish to access air for 3–4 breaths (typically) prior to release. Presumably, if fish are highly impaired and unable to access the surface to breathe, assisting arapaima to access air manually is a potentially important release strategy. Although we were not able to assess its efficacy through experimental tests, the generally high survival of arapaima in this fishery suggests this release method is reasonably effective. However, one individual perceived by a guide to be in poor condition received 23 breaths prior to release but still died, suggesting that even with recovery some level of post-release mortality should be anticipated.

Previous research suggests arapaima surface to breathe every 5–15 min during natural activity (Castello, 2004). In future studies, it would be valuable to characterize post-release surfacing intervals across longer periods to identify the period of recovery to normal breathing frequency, which could be a relevant measure of recovery rates assuming that it approximates ventilation rates (e.g. Raby et al., 2015; Whitney et al., 2016; Prystay et al., 2017). There was no pattern in the number of breaths among the three individuals that died or in handling time when comparing mortalities to survivors. One of the individuals received 23 recovery breaths and was held at the water surface for over an hour before being released. After release, it was motionless except for one breath before dying and being recovered from the bottom of the pond. Although we did not compare water depths at which fish were released, further consideration should be given to releasing fish into shallow water where they can move to the surface easily. Specialized recovery slings could also be tested to hold fish near the surface to assist their recovery while minimizing handling.

Arapaima live in relatively low densities in the ponds and an individual that is lost cannot be replaced until subsequent years because the ponds are disconnected from each other and from the main channel of the river such that immigration is not possible. This raises questions of arapaima demography, such as: what are the rates of maturation and

reproduction of arapaima, what is the carrying capacity of a pond, and what is the site fidelity and therefore the immigration rate across years to replace a deceased individual among years? This is especially important given that there are many ponds within Rewa that are unfished because of depth, clarity, or vegetation that renders fly angling ineffective and it would be relevant to learn whether those ponds could represent source populations for other ponds in the region. Although the transfer rate among ponds is not known, Watson et al. (2016) suggested arapaima within the Essequibo represent a single population and could be considered a management unit. In some smaller ponds, there may be very few individuals and mortality of one individual may be catastrophic for that pond's population unless site fidelity is low and new individuals would likely disperse to that pond in subsequent years. As a precaution, preference should be given to angle in ponds with high arapaima density and research into the basic biology of the species should proceed to answer these important questions that will assist with conservation of the species and precautionary management of the fishery. In most fisheries, low-density populations are protected by the numerical response of anglers, avoiding low-density areas in favour of areas with higher probability of success (Johnson and Carpenter, 1994). However, without competition with other guides/anglers for arapaima, there is less incentive to apply intense pressure to the best fishing locations. A consequence of this is that lower-density areas may be fished during the pond rotation, potentially imperilling stocks in those ponds. Fishing activities should attempt to avoid ponds with low densities of arapaima to mitigate potential negative impacts on the population.

## 5. Conclusions

Developing best practices for emerging fisheries is paramount to ensure that fisheries are operating under auspices of sustainability, particularly for species that may be imperiled (Cooke et al., 2016b). For species such as arapaima, recreational fisheries are only a component of a conservation agenda that must also include protection of habitat and connectivity as well as protection from illegal trade. Recreational fisheries occurring within title lands of the Guyanese Amerindians assist in maintaining protection for the species' habitat by providing economic incentives for conservation while also maintaining watch over the lands and waters to avoid intrusion and poaching (Fernandes, 2006). Protection afforded to arapaima to maintain the recreational fishery spills over to other species that use the ponds during the dry season such that the benefits extend to other local species (i.e. umbrella species; Simberloff, 1998). Recreational fishing will continue to expand in Guyana and other South American nations as fishing is recognized as a lucrative, low impact sector of tourism. The importance of empowering indigenous stakeholders is increasingly recognized as essential to achieve conservation and sustainability objectives (Schwartzman and Zimmerman, 2005). However, recreational fisheries must proceed sustainably for the benefits to persist. Without knowledge of the population biology of arapaima, it is difficult to contextualize the 11% catch-and-release mortality observed here (Coggins et al., 2007). Arapaima are poorly understood and data are urgently needed to support their conservation, particularly information about the movement, reproduction, and demography. High rates of natural mortality can result in very slow recovery from exploitation; it is therefore essential to maintain accurate data about the population including further efforts to refine estimates of post-release survival as well as basic life history information about the species. Catch-and-release for arapaima has the potential to be sustainable given that many individuals survive catch-and-release, but more data are needed on longer time scales to fully evaluate impacts.

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## References

- Arantes, C.C., Castello, L., Stewart, D.J., Cetra, M., Queiroz, H.L., 2010. Population density, growth and reproduction of arapaima in an Amazonian river-floodplain. *Ecol. Freshw. Fish* 19, 455–465.
- Arantes, C.C., Castello, L., Cetra, M., Schilling, A., 2013. Environmental influences on the distribution of arapaima in Amazon floodplains. *Environ. Biol. Fish* 96, 1257–1267.
- Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Rev. Fish. Sci.* 15 (1–2), 75–167.
- Brown, D.D., Kays, R., Wikelski, M., Wilson, R., 2013. Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelem.* 1 (1), 20.
- Barnett, A., Abrantes, K.G., Baker, R., Diedrich, A.S., Farr, M., Kuilboer, A., Mahony, T., McLeod, I., Moscardo, G., Prideaux, M., Stoecki, N., van Luyn, A., Stoeckl, N., 2016. Sportfisheries, conservation and sustainable livelihoods: a multidisciplinary guide to developing best practice. *Fish. Fish.* 17, 696–713.
- Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Rev. Fish. Biol. Fish.* 15, 129–154.
- Bower, S.D., Danylchuk, A.J., Raghavan, R., Clark Danylchuk, S., Pinder, A.C., Alter, A.M., Cooke, S.J., 2017. Involving recreational fisheries stakeholders in development of research and conservation priorities for mahseer (*Tor* spp.) of India through collaborative workshops. *Fish. Res.* 186, 665–681.
- Brauner, C.J., Matey, V., Wilson, J.M., Bernier, N.J., Val, A.L., 2004. Transition in organ function during the evolution of air-breathing; insights from *Arapaima gigas*, an obligate air-breathing teleost from the Amazon. *J. Exp. Biol.* 207, 1433–1438.
- Brobbel, M.A., Wilkie, M.P., Davidson, K., Kieffer, J.D., Bielak, A.T., Tufts, B.L., 1996. Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. *Can. J. Fish. Aquat. Sci.* 53, 2036–2043.
- Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J.F., Auclair, J.P., Taggart, C.T., 2013. Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *J. Exp. Biol.* 216, 1255–1264.
- Brownscombe, J.W., Thiem, J.D., Hatry, C., Cull, F., Haak, C.R., Danylchuk, A.J., Cooke, S.J., 2013. Recovery bags reduce post-release impairments in locomotory activity and behavior of bonefish (*Albula* spp.) following exposure to angling-related stressors. *J. Exp. Mar. Biol. Ecol.* 440, 207–215.
- Brownscombe, J.W., Gutowsky, L.F., Danylchuk, A.J., Cooke, S.J., 2014. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Mar. Ecol. Prog. Ser.* 505, 241–251.
- Brownscombe, J.W., Danylchuk, A.J., Chapman, J.M., Gutowsky, L.F., Cooke, S.J., 2017a. Best practices for catch-and-release recreational fisheries—angling tools and tactics. *Fish. Res.* 186, 693–705.
- Brownscombe, J.W., Parmar, T.P., Almeida, J., Giesbrecht, E., Batson, J., Chen, X., Wesch, S., Ward, T.D., O'Connor, C.M., Cooke, S.J., 2017b. The efficacy of assisted ventilation techniques for facilitating the recovery of fish that are exhausted from simulated angling stress. *Fish. Res.* 186, 619–624.
- Castello, L., 2004. A method to count pirarucu *Arapaima gigas*: fishers, assessment, and management. *North Am. J. Fish. Manage.* 24 (2), 379–389.
- Castello, L., 2008a. Nesting habitat of *Arapaima gigas* (Schinz) in Amazonian floodplains. *J. Fish Biol.* 72 (6), 1520–1528.
- Castello, L., 2008b. Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecol. Freshw. Fish* 17, 38–46.
- Castello, L., Stewart, D.J., 2010. Assessing CITES non-detriment findings procedures for arapaima in Brazil. *J. Appl. Ichthyol.* 26 (1), 49–56.
- Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Renó, V.F., Arantes, C.C., 2013. The vulnerability of Amazon freshwater ecosystems. *Conserv. Lett.* 6 (4), 217–229.
- Coggins, L.G., Catalano, M.J., Allen, M.S., Pine, W.E., Walters, C.J., 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish. Fish.* 8, 196–210.
- Cooke, S.J., Schramm, H.L., 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fish. Manage. Ecol.* 14, 73–79.
- Cooke, S.J., Schreer, J.F., Dunmall, K.M., Philipp, D.P., 2002. Strategies for quantifying sub-lethal effects of marine catch-and-release angling insights from novel freshwater applications. *Am. Fish. Soc. Symp.* 30, 121–134.

- Cooke, S.J., Donaldson, M.R., O'Connor, C.M., Raby, G.D., Arlinghaus, R., Danylchuk, A.J., Hanson, K.C., Hinch, S.G., Clark, T.D., Patterson, D.A., 2013. The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. *Fish. Manage. Ecol.* 20 (2–3), 268–287.
- Cooke, S.J., Philipp, D.P., Wahl, D.H., Weatherhead, P.J., 2006. Energetics of parental care in six syntopic centrarchid fishes. *Oecologia* 148 (2), 235–249.
- Cooke, S.J., Brownscombe, J.W., Raby, G.D., Broell, F., Hinch, S.G., Clark, T.D., Semmens, J.M., 2016a. Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comp. Biochem. Physiol. Part A: Molecular Integr. Physiol.* 202, 23–37.
- Cooke, S.J., Hogan, Z.S., Butcher, P.A., Stokesbury, M.J., Raghavan, R., Gallagher, A.J., Hammerschlag, N., Danylchuk, A.J., 2016b. Angling for endangered fish: conservation problem or conservation action? *Fish Fish.* 17 (1), 249–265.
- Cooke, S.J., Twardek, W.M., Lennox, R.J., Zoldero, A.J., Bower, S.D., Gutowsky, L.F., Danylchuk, A.J., Arlinghaus, R., 2018. The nexus of fun and nutrition: recreational fishing is also about food. *Fish Fish.* 19 (2), 201–224.
- Cuvier, G., Valenciennes, A. 1847. *Histoire naturelle des poissons. Tome dix-neuvième. Suite du livre dix-neuvième. Brochets ou Lucioides. Livre vingtième. De quelques familles de Malacoptérygiens, intermédiaires entre les Brochets et les Clupes.* Bertrand, Paris. v.19:i-xix + 1–544 + 6 pp., pls. 554–590 [not 520–556].
- Ditton, R.B., Holland, S.M., Anderson, D.K., 2002. Recreational fishing as tourism. *Fisheries* 27, 17–24.
- Fernandes, D., 2006. 'More Eyes Watching' Community-Based Management of the Arapaima (*Arapaima gigas*) in Central Guyana. Presented at the Eleventh Conference of the International Association for the Study of Common Property. Available from. Digital Library of the Commons, Bloomington, Indiana (Accessed May 2009). <http://dlc.dlib.indiana.edu/archive/00001894/>.
- Gillooly, J.F., Baylis, J.R., 1999. Reproductive success and the energetic cost of parental care in male smallmouth bass. *J. Fish Biol.* 54, 573–584.
- Gleiss, A.C., Dale, J.J., Holland, K.N., Wilson, R.P., 2010. Accelerating estimates of activity-specific metabolic rate in fishes: testing the applicability of acceleration dataloggers. *J. Exp. Mar. Biol. Ecol.* 385, 85–91.
- Hrbek, T., Farias, I.P., Crossa, M., Sampaio, I., Porto, J.I., Meyer, A., 2005. Population genetic analysis of *Arapaima gigas*, one of the largest freshwater fishes of the Amazon basin: implications for its conservation. *Anim. Conserv.* 8, 297–308.
- Johnson, B.M., Carpenter, S.R., 1994. Functional and numerical responses: a framework for fish-angler interactions? *Ecol. Appl.* 4, 808–821.
- Jonsson, N., Jonsson, B., Hansen, L.P., 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* 425–436.
- Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. *Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol.* 126 (2), 161–179.
- Levêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J., Tedesco, P.A., 2008. Global diversity of fish (Pisces) in freshwater. *Hydrobiologia* 595, 545–567.
- Liaw, A.W., Wiener, M., 2002. Classification and regression by random forest. *R News* 2, 18–22.
- Lowe-McConnell, R., 1964. The fishes of the rupununi savanna district of British Guiana, South America part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *J. Linnaean Soc. Zool.* 45, 103–144.
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L., Wesselingh, F., 1998. The stage for neotropical fish diversification: a history of South American rivers. In: Malabarba, M.C.S.L., Reis, R.E., Vari, R.P., Lucena, Z.M., Lucena, C.A.S. (Eds.), *Phylogeny and Classification of Neotropical Fishes*. Edipucrs, Porto Alegre, Brazil, pp. 13–48.
- Milligan, C.L., 1996. Metabolic recovery from exhaustive exercise in rainbow trout. *Comp. Biochem. Physiol. Part A: Physiol.* 113, 51–60.
- Milligan, C.L., Hooke, G.B., Johnson, C., 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. *J. Exp. Biol.* 203, 921–926.
- Muoneke, M.L., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. *Rev. Fish. Sci.* 2 (2), 123–156.
- Pollock, K.H., Jiang, H., Hightower, J.E., 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Trans. Am. Fish. Soc.* 133 (3), 639–648.
- Prystay, T.S., Eliason, E.J., Lawrence, M.J., Dick, M., Brownscombe, J.W., Patterson, D.A., Crossin, G.T., Hinch, S.G., Cooke, S.J., 2017. The influence of water temperature on sockeye salmon heart rate recovery following simulated fisheries interactions. *Conserv. Physiol.* 5, cox050.
- Queiroz, H.L.D., 2000. Natural history and conservation of pirarucu, *Arapaima gigas*, at the Amazonian Várzea: red giants in muddy waters. Doctoral dissertation. University of St Andrews.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. URL: R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Raby, G.D., Cooke, S.J., Cook, K.V., McConnachie, S.H., Donaldson, M.R., Hinch, S.G., Whitney, C.K., Drenner, S.M., Patterson, D.A., Clark, T.D., Farrell, A.P., 2013. Resilience of pink salmon and chum salmon to simulated fisheries capture stress incurred upon arrival at spawning grounds. *Trans. Am. Fish. Soc.* 142 (2), 524–539.
- Raby, G.D., Clark, T.D., Farrell, A.P., Patterson, D.A., Bett, N.N., Wilson, S.M., Willmore, W.G., Suski, C.D., Hinch, S.G., Cooke, S.J., 2015. Facing the river gauntlet: understanding the effects of fisheries capture and water temperature on the physiology of coho salmon. *PLoS One* 10 (4), e0124023.
- Robinson, K.A., Hinch, S.G., Raby, G.D., Donaldson, M.R., Robichaud, D., Patterson, D.A., 2015. Influence of postcapture ventilation assistance on migration success of adult sockeye salmon following capture and release. *Trans. Am. Fish. Soc.* 144 (4), 693–704.
- Sakamoto, K.Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S., 2009. Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS One* 4 (4), e5379.
- Schwartzman, S., Zimmerman, B., 2005. Conservation alliances with indigenous peoples of the Amazon. *Conserv. Biol.* 19 (3), 721–727.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol. Conserv.* 83 (3), 247–257.
- Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A., Voll, E., McDonald, A., Lefebvre, P., Schlesinger, P., 2006. Modelling conservation in the Amazon basin. *Nature* 440 (7083), 520–523.
- Stevens, E.D., Holeton, G.F., 1978. The partitioning of oxygen uptake from air and from water by the large obligate air-breathing teleost pirarucu (*Arapaima gigas*). *Can. J. Zool.* 56 (4), 974–976.
- Stewart, D.J., 2013. Re-description of *Arapaima agassizii* (Valenciennes), a rare fish from Brazil (Osteoglossomorpha: Osteoglossidae). *Copeia* 2013 (1), 38–51.
- Veríssimo, J., 1995. *A pesca na Amazônia*. Livraria Clássica Francisco Alves, Rio de Janeiro 206 p.
- Watson, L.C., Stewart, D.J., Teece, M.A., 2013. Trophic ecology of Arapaima in Guyana: giant omnivores in Neotropical floodplains. *Neotrop. Ichthyol.* 11 (2), 341–349.
- Watson, L.C., Stewart, D.J., Kretzer, A.M., 2016. Genetic diversity and population structure of the threatened giant Arapaima in southwestern Guyana: implications for their conservation. *Copeia* 104 (4), 864–872.
- Whitney, N.M., White, C.F., Gleiss, A.C., Schwieterman, G.D., Anderson, P., Hueter, R.E., Skomal, G.B., 2016. A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers. *Fish. Res.* 183, 210–221.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wickham, H., Francois, R., 2016. *dplyr: A Grammar of Data Manipulation*. R Package Version 0.5.0. <https://CRAN.R-project.org/package=dplyr>.
- Wilkie, M.P., Brobbel, M.A., Davidson, K.G., Forsyth, L., Tufts, B.L., 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 54 (3), 503–511.
- Wright, S., Metcalfe, J.D., Hetherington, S., Wilson, R., 2014. Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. *Mar. Ecol. Prog. Ser.* 496, 19–32.
- Zeileis, A., Grothendieck, G., 2005. Zoo: S3 infrastructure for regular and irregular time series. *J. Stat. Softw.* 14 (6), 1–27. <http://dx.doi.org/10.18637/jss.v014.i06>.