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The effects of simulated hydropower turbine rapid decompression on two Neotropical fish species

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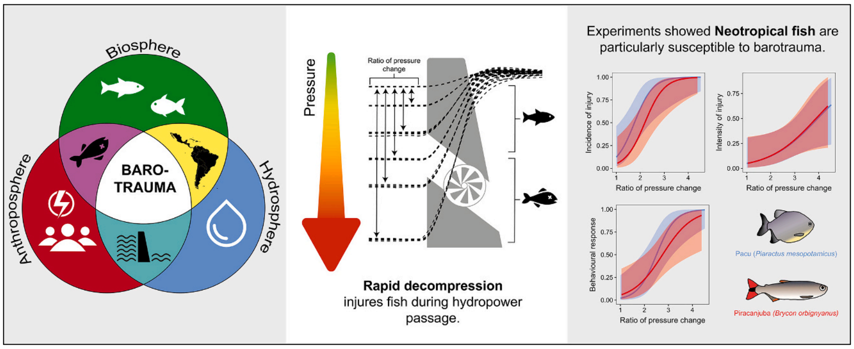
HIGHLIGHTS

- Barotrauma in two Neotropical fish exposed to rapid decompression was assessed.
- Both species had dual chambered swim bladders, an understudied morphology.
- Post decompression behaviour and intensity of barotrauma injury were quantified.
- Results suggest that Neotropical species are highly susceptible to barotrauma.

GRAPHICAL ABSTRACT



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ABSTRACT

Barotrauma is a major cause of injury and mortality of fish as they pass through hydropower turbines. Current understanding of hydropower related barotrauma is biased towards northern temperate and southern subtropical species with single chambered swim bladders, specifically North American and Australian species, respectively. Today, unprecedented hydropower development is taking place in Neotropical regions where many species have complex multi-chambered swim bladder architecture. This study investigated barotrauma in two dual-chambered physostomous Neotropical fish (pacu, *Piaractus mesopotamicus*, and piracanjuba, *Brycon orbignyanus*) exposed to rapid (< 1 s) decompression at different Ratios of Pressure Change (RPC), using a hypo-hyperbaric chamber. The incidence and intensity (percentage surface area of organ affected) of injury and physiological and behavioural response (hereafter just response) of each species immediately after decompression was assessed. Twenty-two injury types (e.g. gill haemorrhage and exophthalmia) and eight response categories (e.g. rising to the surface and loss of orientation) were identified and the influence of: 1) species, 2) RPC, and 3) swim bladder rupture on each was quantified. There was considerable interspecific difference with emboli type injuries occurring more frequently in piracanjuba, but injury intensity tending to be higher in pacu. Both

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swim bladder chambers tended to rupture in piracanjuba but only the anterior chamber in pacu. RPC was positively correlated with response, incidence and intensity of several injury types for both species with some injuries occurring at very low RPC (e.g. 50 % probability of swim bladder rupture at 2.2 and 1.75 for piracanjuba and pacu, respectively). Multiple responses (e.g. loss of orientation) and injuries (e.g. eye haemorrhage) were correlated with swim bladder rupture suggesting gas venting into the body cavity likely causes secondary injury. When directly comparing our results with those available in the published literature, both pacu and piracanjuba appear to be more susceptible to barotrauma than previously studied subtropical and temperate species.

1. Introduction

The highest diversity of freshwater vertebrates occurs in the Neotropics (Balian et al., 2008). The Amazon River basin alone hosts >2400 documented native fish species (Jézéquel et al., 2020), representing ca. 15 % of the global total (Oberdorff et al., 2019). For this reason, this region is considered a biodiversity hotspot (Ríos-Touma and Ramirez, 2019). However, Neotropical rivers are threatened by multiple anthropogenic stressors (Ríos-Touma and Ramirez, 2019; Sales et al., 2018) and suffer rapid rates of degradation due to unsustainable resource exploitation (Albert et al., 2021), such as for hydroelectricity generation (Pelicice et al., 2017). The impacts of hydropower dams on aquatic organisms have been comprehensively described (e.g. Kemp, 2015), and include the disruption of hydrogeomorphological continuity (Ward and Stanford, 1995; Nestler et al., 2012) and fragmentation and degradation of habitats (Fuller et al., 2015). For fish, dams (Limburg and Waldman, 2009) and the large reservoirs they create (Pelicice et al., 2015) can impede and block their movements and reduce the probability of survival for those that enter turbines (Čada et al., 1997; Coutant and Whitney, 2000). Mean mortality associated with hydroelectric turbine passage is high (ca. 25 %: Radinger et al., 2022) and is governed by multiple mechanisms, including blade strike, cavitation, shear, and barotrauma (Čada, 2001). In Neotropical countries, such as Brazil, severe fish mortality events recorded in tons of fish killed are common (Silva et al., 2021), occurring due to turbine passage under normal operation (Godinho and Loures, 2017) and during dewatering and stop/start maintenance procedures (Andrade et al., 2012). Such mortality limits the potential to advance sustainable exploitation and increases the risk of environmental conflict, e.g. between the operators of dams and those reliant on local fisheries (Gutberlet et al., 2007).

Hydropower related barotrauma usually occurs when downstream moving fish experience rapid (often <1 s) decompression during turbine passage (Brown et al., 2014). The magnitude of the pressure change experienced is governed by the relative difference in pressure between that to which the fish is acclimated on entering the turbine intake (acclimation pressure) and the lowest (nadir) experienced thereafter during passage through the unit (Brown et al., 2014), typically in the vicinity of the turbine blades (e.g. Richmond et al., 2014). The quotient of the acclimation and nadir pressure defines the Ratio of Pressure Change (RPC) and is considered a critical determinant of barotrauma (Brown et al., 2014). Injury occurs due to rapid expansion of undissolved gases contained within the body, predominantly in the swim bladder, which in extreme cases can rupture (Brown et al., 2012a). This can lead to secondary trauma as escaping gases damage surrounding tissues and other organs (Brown et al., 2012a). Common barotrauma injuries include exophthalmia, eversion of the stomach and intestine, internal haemorrhaging, and emboli (gas bubbles) in the gills and fins (Brown et al., 2009).

Knowledge of the mechanisms and potential impacts of turbine related barotrauma have been advanced over several years, predominantly through the pioneering research conducted in the Pacific Northwest of the United States (e.g. Brown et al., 2009, 2012a; Stephenson et al., 2010). Available literature is biased towards species from northern temperate (e.g. *Oncorhynchus* spp.: Brown et al., 2009; *Acipenser transmontanus*: Brown et al., 2013; *Lampetra planeri* and *Entosphenus tridentatus*: Colotelo et al., 2012; *Anguilla rostrata:* Pflugrath et al., 2019) and southern subtropical (e.g. *Maccullochella peelii* and *Bidyanus bidyanus*: Boys et al., 2016; *Percalates novemaculeata* and *Hypseleotris* spp.: Pflugrath et al., 2018) regions. Furthermore, previous research has almost always focussed on species with relatively simple single chambered swim bladders (exceptions: *Pimelodus pictus* [three chambers]: Beirão et al., 2018; *Carassius carassius* [two chambers]: Meng et al., 2018, 2019). There remains limited consideration of the effects of barotrauma on fish within a Neotropical context (exception: Beirão et al., 2018), where the four most common families of fish that comprise almost half (49 %) of the recorded species (Jézéquel et al., 2020) typically have two chambered (Characidae: Netto-Ferreira et al., 2013; Cichlidae: Schulz-Mirbach et al., 2012) or bilobed (Loricariidae & Callichthyidae: Lechner and Ladich, 2008) swim bladders. Although limited, current evidence suggests that fish with multi-chambered swim bladders are highly susceptible to barotrauma, with injuries occurring at low RPC (Beirão et al., 2018). As the impact of rapid decompression cannot be generalised, even among fish from the same family (e.g. Boys et al., 2016), there is an urgent requirement to assess barotrauma in Neotropical species to better understand the potential impacts of hydropower development in this region.

Barotrauma injury is typically quantified using relatively simplistic binary metrics, such as presence or absence during necropsy (e.g. Boys et al., 2016; Pflugrath et al., 2018), and the results used to predict the relationship between mortality and RPC (McKinstry et al., 2007). Injury 'intensity' can be a strong predictor of survival in fish (e.g. percentage scale loss: Kostecki et al., 1987) and other animals (e.g. proportion of epidermis burnt: Berndstson et al., 2013; parasite burden: Nam et al., 2018) and can provide increased statistical power compared to a dichotomous assessment alone (Altman and Royston, 2006). However, injury intensity is rarely quantified in assessments of barotrauma or turbine passage (exceptions: Mueller et al., 2017, 2020). Likewise, fish behaviour post decompression (e.g. floating at the surface) is correlated with mortality during catch and release fishing (e.g. smallmouth bass, *Micropterus dolomieu*: Gravel and Cooke, 2008; red snapper, *Lutjanus campechanus*: Campbell et al., 2010), but rarely considered when assessing the impact of rapid decompression during turbine passage (exceptions: Meng et al., 2018, 2019). Adopting methodologies that account for intensity of injury and fish behaviour will likely improve understanding of long-term impacts (e.g. survival) of barotrauma.

To enhance the sustainability of future hydropower development and operation there is a need to better understand the impacts of barotrauma on Neotropical fish. In this study, the relationship between rapid decompression and incidence and intensity of physical injury and physiological and behavioural response (hereafter just response) was quantified for two dual-chambered Neotropical fish species (family: Characidae) in a controlled laboratory setting. The influence of: 1) species, 2) RPC, and 3) swim bladder rupture on barotrauma injury and response were quantified. It was predicted that: 1) despite being members of same family, there would be interspecific differences in barotrauma injury and response between the two subject species, 2) both species would exhibit injuries at lower RPC compared to the frequently studied single chambered northern temperate and southern subtropical species, and 3) incidence of swim bladder rupture would be correlated with other secondary injuries and responses.

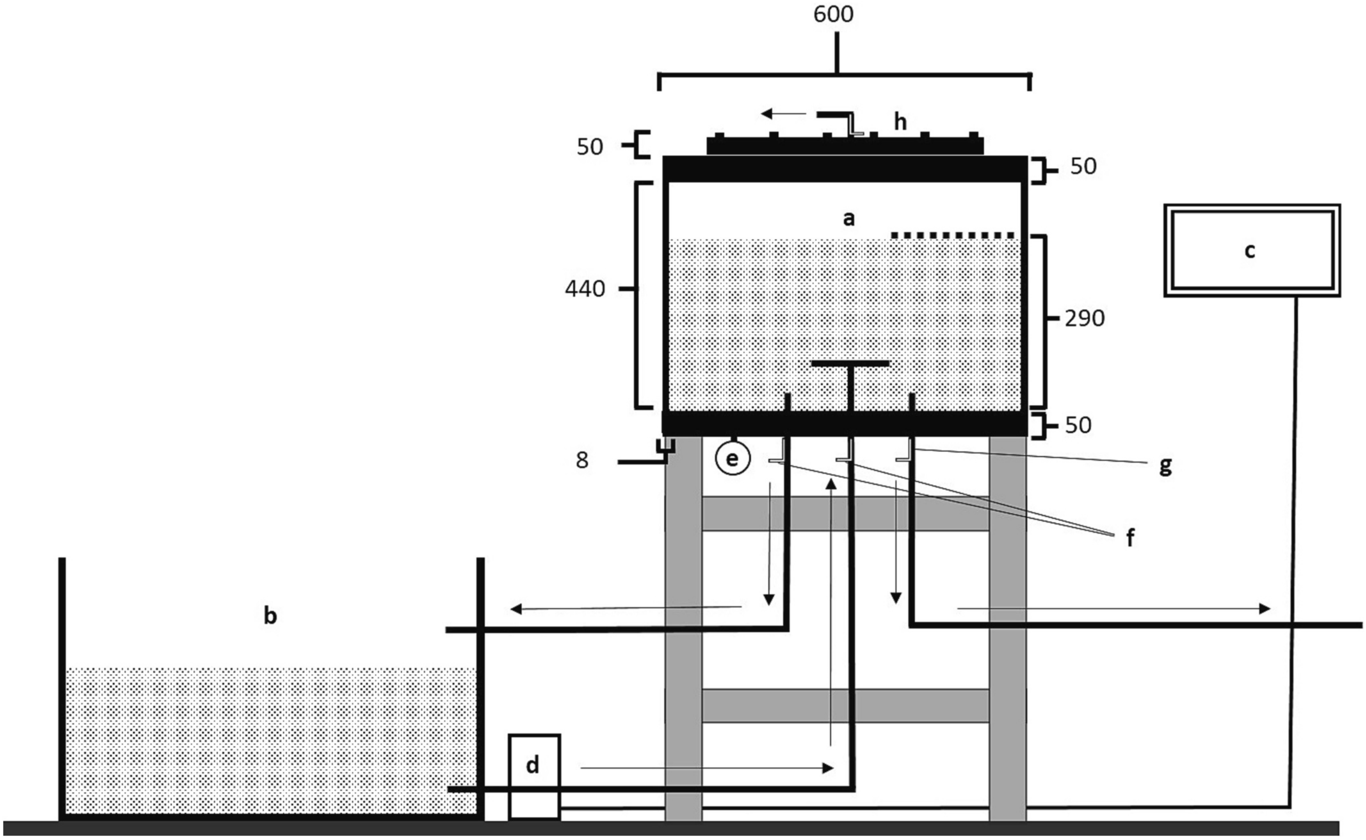

Fig. 1. Schematic of the hypo-hyperbaric chamber used to compress and rapidly decompress fish. a) Experimental chamber - aluminium top and base with a cylindrical Plexiglas middle to allow viewing; b) external sump; c) variable speed drive used to manipulate flow rate; d) water pump supplying the chamber with water from the sump; e) pressure sensor; f) inlet and outlet valve; g) decompression valve; and h) air vent valve. The dashed line represents the water level in the chamber prior to compression. Measurements shown in millimetres.

2. Methods

2.1. Subject fish

Pacu, *Piaractus mesopotamicus* (Holmberg, 1887), and piracanjuba, *Brycon orbignyanus* (Valenciennes, 1850), two Neotropical representatives of the Characidae, were selected as the model species. Both are physostomous, have a dual chambered swim bladder, and are of high economic (Iervolino et al., 2010), ecological (Galetti et al., 2008; Correa et al., 2015), and conservation (Tonella et al., 2019) value. Multiple batches of pacu and piracanjuba were sourced from a local hatchery at the Estação Ambiental de Itutinga (CEMIG, MG) and transported in polythene bags containing oxygenated hatchery water to the Federal University of São João del-Rei, Minas Gerais, Brazil. On arrival, fish were inspected for disease before being transferred to three holding tanks (990 × 660 × 510 mm) containing ca. 280 L of filtered (90 L wet/dry filter) and aerated (ALEAS, AP-3500) water. Ammonia, nitrite, pH and temperature were monitored (Labcon® liquid tests) twice daily and frequent water changes were undertaken to maintain quality. Fish were fed daily with commercial fish food but not for 8 h prior to experimentation.

2.2. Laboratory apparatus

Decompression was simulated in a hypo-hyperbaric chamber at the Federal University of São João del-Rei, Minas Gerais, Brazil. The chamber consisted of a Plexiglass (thickness: 6 mm) cylinder (height: 440 mm, diameter: 600 mm) with an aluminium top and base (thickness: 50 mm) and removable lid (thickness: 50 mm) (Fig. 1). Pressure and flow rate within and through the chamber, respectively, were manipulated using a multistage centrifugal water pump (ME-AL 2250 Schneider®) controlled by a variable speed drive (WEG®) and adjustable inlet and outlet valves. Pressure was monitored using a sensor (Zurich PSI.420) located at the bottom of the chamber and recorded using LabVIEW software (National Instruments Corp). A vinyl curtain was used to isolate the fish from external visual cues (e.g. the observer), except for a small section that remained unscreened to facilitate live recording of fish behaviour using a wireless video camera (GoPro Hero5 Black, 100fps, 1080p).

2.3. Experimental protocol

Separate trials with pacu (mean ± S.D. standard length: 154 ± 11 mm) and piracanjuba (150 ± 16 mm) were undertaken from 13 March to 3 April and 8 April to 3 May 2019, respectively. Groups of fish (piracanjuba $n = 5$; pacu $n = 3$) were exposed to one of seven treatments (Table 1) and no fish were used in more than a single trial. The experimental procedure for treatment 1 (control), mimicked that used in all other treatments with the exception that the internal pressure of the chamber was not artificially increased (mean acclimation pressure: 102 kPa) (Table 1). The control treatment allowed for injuries that might be naturally occurring (i.e. prior to experimentation), or were caused by non-barotrauma related experimental variables (i.e. transportation or husbandry) to be accounted for within the analysis. At the start of each trial, test fish were introduced to the chamber and the pressure increased at a rate of 75 kPa min^{-1} until the desired acclimation pressure was reached (Table 1). Available evidence suggests that rapid (<1 s) compression is not harmful to fish (e.g. Doyle et al., 2020, 2022) but it was decided to be cautious and increase pressure slowly and at a fixed rate for all trials to ensure that compression rate did not confound

Table 1

Treatment parameters used to assess the influence of rapid decompression on pacu (Pa) and piracanjuba (Pi), including mean acclimation (P_a: kPa) and nadir (P_n: kPa) pressures, Ratio of Pressure Change (RPC: dimensionless), decompression time (Dt: s), rate of pressure change (kPa s^{-1}), rate of RPC (RPC s^{-1}), and number of replicates.

Treatment	Mean RPC (Range)	Mean acclimation pressure (P_a - kPa) (Range)	Mean nadir pressure (P_n - kPa) (Range)	Mean decompression time (Dt - s) (Range)	Mean rate of pressure change (kPa s^{-1}) (Range)	Mean rate of RPC (RPC s^{-1}) (Range)	Replicates	
							Pa	Pi
1 (control)	1.1 (1.0–1.2)	102 (99.6–106)	96.6 (89.8–99.9)	0.41 (0.09–0.74)	8 (0.79–18.0)	0.09 (0.01–0.20)	4	4
2	1.3 (1.2–1.3)	117 (116–117)	92.7 (87.8–96.1)	0.73 (0.61–0.84)	32 (27.5–36.9)	0.34 (0.27–0.41)	4	4
3	1.7 (1.7–1.8)	152 (151–152)	88.1 (85.3–90.6)	0.79 (0.65–1.03)	78 (59.5–87.9)	0.85 (0.66–0.95)	4	4
4	2.4 (2.3–2.5)	203 (201–207)	85.0 (81.1–87.4)	0.83 (0.73–1.07)	136 (102–148)	1.49 (1.11–1.61)	4	4
5	2.8 (2.8–3.0)	251 (250–252)	86.1 (84.6–89.0)	0.80 (0.73–0.89)	195 (178–214)	2.07 (1.91–2.29)	4	4
6	3.4 (3.0–3.4)	301(299–303)	90.0 (87.6–101)	0.89 (0.82–0.99)	226 (202–247)	2.25 (1.98–2.50)	4	4
7	4.4 (4.2–4.5)	401 (399–403)	91.7 (88.6–94.4)	0.97 (0.87–1.13)	306 (258–341)	2.86 (2.41–3.16)	4	4

results. Once at acclimation pressure, fish were allowed to acclimate for three hours with a mean (± S.D.) flow rate of water through the chamber of 6.96 (± 0.52) L $\min^{-1}$. All fish were neutrally buoyant, as indicated by an ability to passively maintain vertical position within the water column at the end of the acclimation period. Decompression was implemented by fully opening an outlet valve (diameter: 50 mm) located at the bottom of the chamber (Fig. 1), rapidly (typically <1 s) returning it to ambient pressure (ca. 100 kPa) (Table 1; Fig. 2). Nadir pressures (range: 85–101 kPa), which occurred immediately after decompression, were typically slightly less than ambient, and were caused by the inertia of the water exiting the outlet tube resulting in a slight suction effect (Table 1; Fig. 2). This effect was the reason for RPC values of slightly above unity (range: 1.0–1.2) for the control treatment (Table 1). Fish were removed from the chamber within two minutes of decompression and euthanised by administrating a lethal dose of Eugenol solution after which death was confirmed by severing the spinal cord with a scalpel taking care not to damage the swim bladder. The fish were measured (standard length), weighed (g) and photographed (lateral view, both sides). The RPC was calculated for each trial as P_a/P_n, where P_a and P_n are the acclimation and nadir pressures, respectively (Table 1). External confounding variables (e.g. temperature) were controlled for by predetermining treatment order by random selection without replacement, and this order was repeated until all replicates had been undertaken (Table 1). Mean water temperature (±S.D.) during trials for pacu and piracanjuba was 25.8 (±1.1)°C and 24.3 (±0.9)°C, respectively.

2.4. Assessment of barotrauma

Incidence (presence/absence) of barotrauma injury was identified during necropsy in which multiple external and internal tissues and organs were inspected for either emboli or haemorrhage using microscopy (compound: Zeiss Stemi DV4; Zeiss Stemi 2000-C; Olympus SZ51). To advance on previous work that divided the intensity of injuries into four discrete categories (Mueller et al., 2017), intensity was assessed on a continuous scale by estimating the percentage of the surface area of each organ in which either emboli or haemorrhage was evident (e.g. Fig. S1). Incidence and intensity of injury were recorded externally for the epidermis, operculum, lateral line, fins and eyes, and internally for the gills, pharyngo-clitheral (PC) membrane, viscera (liver, intestine, stomach, interstitial tissues and pyloric caeca), heart and stomach cavity walls. In addition, expulsion of internal organs into the buccal cavity, exophthalmia, and rupture of the swim bladder chambers were recorded.

Fish response to injury was quantified using video footage recorded during a 20 s observation period immediately after decompression. The footage (100 fps) was analysed in slow motion (≤ 20 fps), which enabled determination of the presence/absence of specific responses (Table 2) for individual fish during the observation period, after which the mobility of each was categorised as either unimpaired or impaired (Table 2).

2.5. Data analysis

As the number of treatment replicates for each species was identical, interspecific differences in barotrauma injury and response were assessed independent of RPC by combining all data across treatments for each species. Chi squared (X^2) and Mann-Whitney U tests were respectively used to identify interspecific differences in: 1) the proportion of individuals that exhibited specific injuries and responses, and 2) the intensity of injury and frequency of emboli or haemorrhage type injuries exhibited by each fish. Due to the number (n) of comparisons undertaken when assessing interspecific differences, a Bonferroni correction (α/n) was applied to the significance threshold (α = 0.05) to reduce the risk of a type I error.

The influence of RPC and the probability of swim bladder rupture on incidence and intensity of injury (including secondary injury in the case

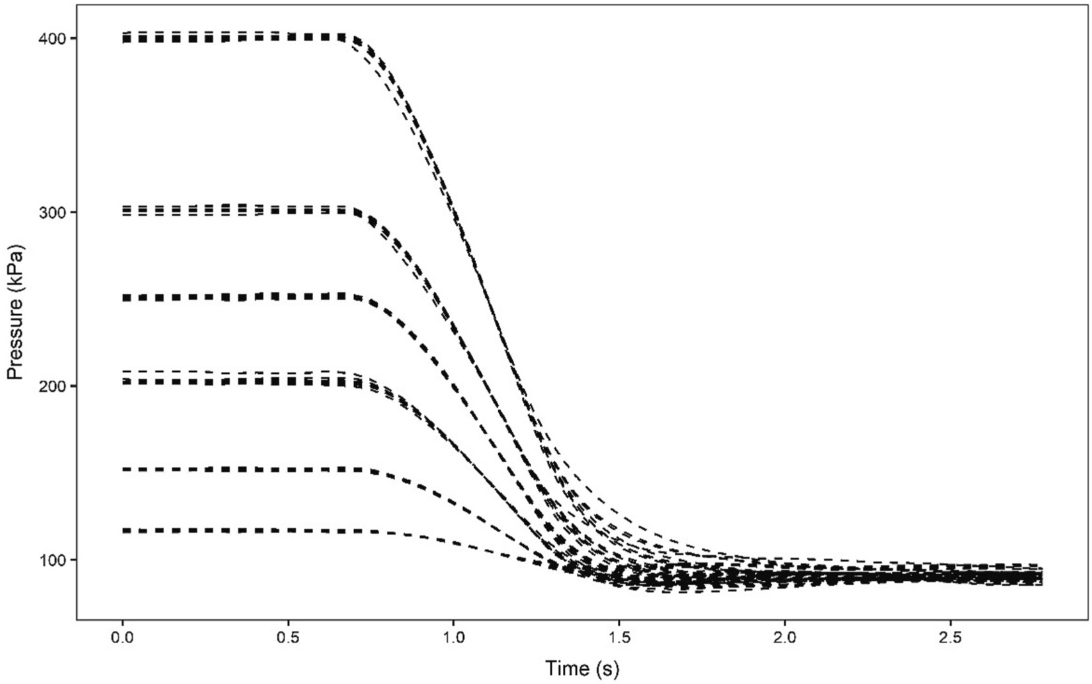

Fig. 2. Profiles for pressure (kPa) over time (s) for all trials (except controls: 1.1 Ratio of Pressure Change [RPC] treatment) used to assess the impact of rapid decompression on pacu and piracanjuba.

Table 2
Fish response categories recorded during (D) and at the end (E) of a 20 s observation period immediately after rapid decompression.

Response	Definition	Assessment period
Loss of orientation	Loss of stability resulting in a roll of >45 degrees.	D
Rise to the surface	Non-volitional elevation in the water column and contact with top of chamber after rapid decompression.	D
Expulsion of bubbles from anus	A minimum of one bubble (independent of size) expelled from the anus or mouth/operculum.	D
Expulsion of bubbles from mouth/operculum		D
Discharge from anus	Expulsion of solid or liquid from anus or mouth/operculum.	D
Discharge from mouth/operculum		D
Stomach repositioning	Exhibition of behaviour indicative of organs displaced towards the mouth: - Mouth held open for a prolonged period and/or operculum held in extended position. - Rapid extension and retraction of jaw and operculum and/or head shaking. - Lowering of hyal bones.	D
Impaired mobility	One or more of the following: - Erratic movements, - Irregular swimming kinematics (e.g. irregular use of fins), - Partial or complete loss of equilibrium and orientation (e.g. floating at the surface)	E

of swim bladder rupture) and resultant response was assessed using general linear models (GLMs) with a binomial error structure and a "logit" link function. The probability of occurrence of each injury type and response was calculated for every trial as the number of fish exhibiting each as a proportion of the total. To achieve a pseudo binomial distribution for the intensity of injury percentages (I), mean values ($\bar{I}$) for each trial were normalised ($\bar{I}_{norm}$) so that the maximum value recorded for all trials ($\bar{I}_{max}$) equalled one: $\bar{I}_{norm} = (I/\bar{I}_{max})/100$. Mass (g), number of days in the holding tank, and water temperature (°C) were included as predictor variables in the models. It was not possible to incorporate either rate of pressure change (kPa s^{-1}) or rate of RPC (RPC s^{-1}) (Table 1) as predictor variables as they were highly correlated with RPC. Initial models contained all predictor variables and manual backwards selection using Akaike's Information Criteria (AIC) and variable significance was undertaken to simplify models. Variables were removed in order of significance (least significant removed first) until only significant variables remained or AIC stopped decreasing. These simplified models were used to identify variables that were significant predictors of: 1) incidence and 2) intensity of injury, and 3) resultant response. For each GLM, the assumptions of homoscedasticity and normality of residuals were assessed through visual inspection of diagnostic plots (Residuals vs Fitted and Normal Q-Q respectively), with no violations found. None of the predictor variables were highly correlated (all Variance Inflation Factor scores <3.89).

Data analysis was conducted using Matlab R2017 (The MathWorks, Inc.) and RStudio version 3.5.1 (R Core Team 2018).

3. Results

3.1. Influence of species

There were no instantaneous (<2 min) mortality incidents after rapid decompression. Twenty and twenty-two injury types were identified for pacu and piracanjuba, respectively (Fig. 3). For eleven of these, interspecific variation in frequency of occurrence was observed (Fig. 3). Six injuries were more frequently observed in piracanjuba, while 5 were

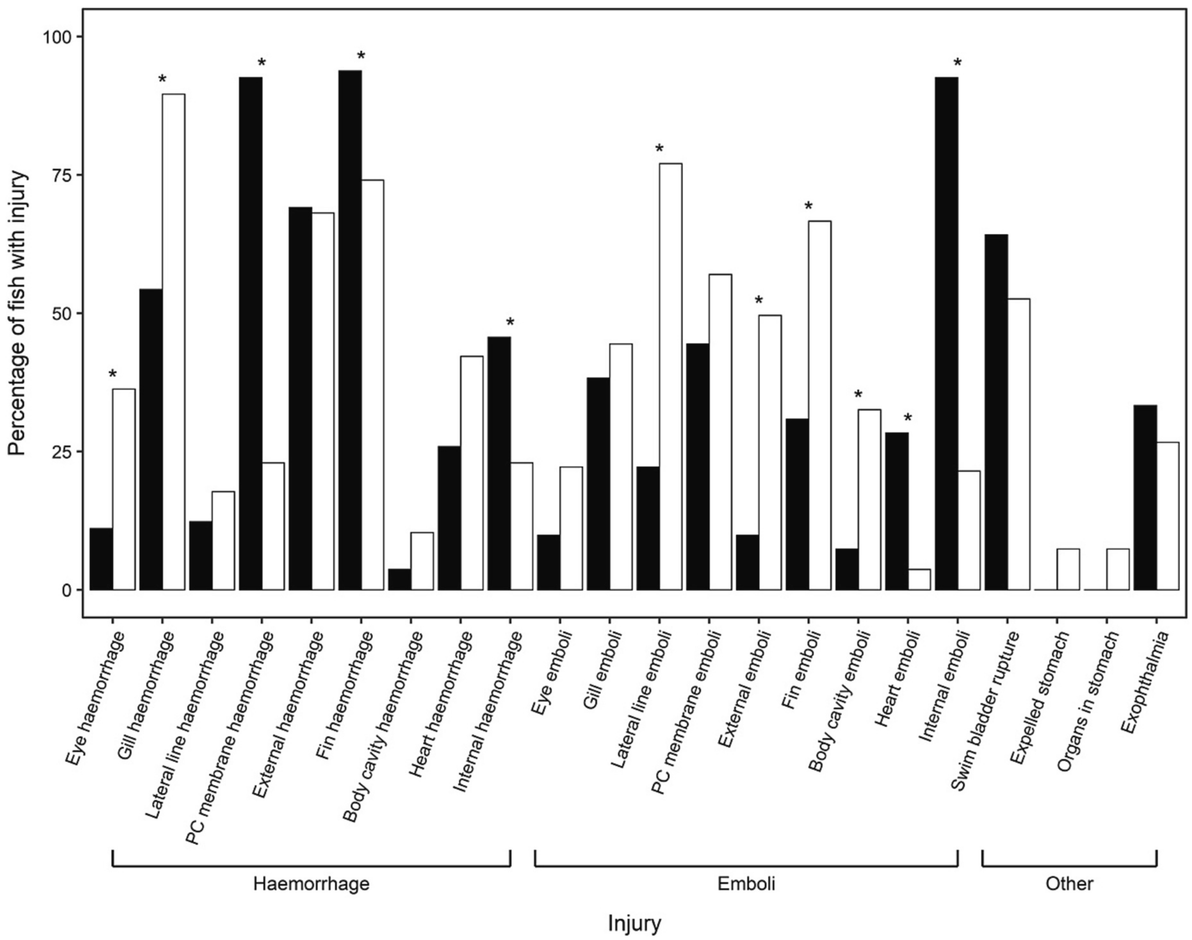

Fig. 3. Percentage of pacu (black bars) and piracanjuba (white bars) that exhibited different categories of barotrauma injury during trials to assess the influence of rapid decompression under experimental conditions. Data combined for all Ratio of Pressure Change (RPC) treatments. Asterisks above bars indicate a significant interspecific difference.

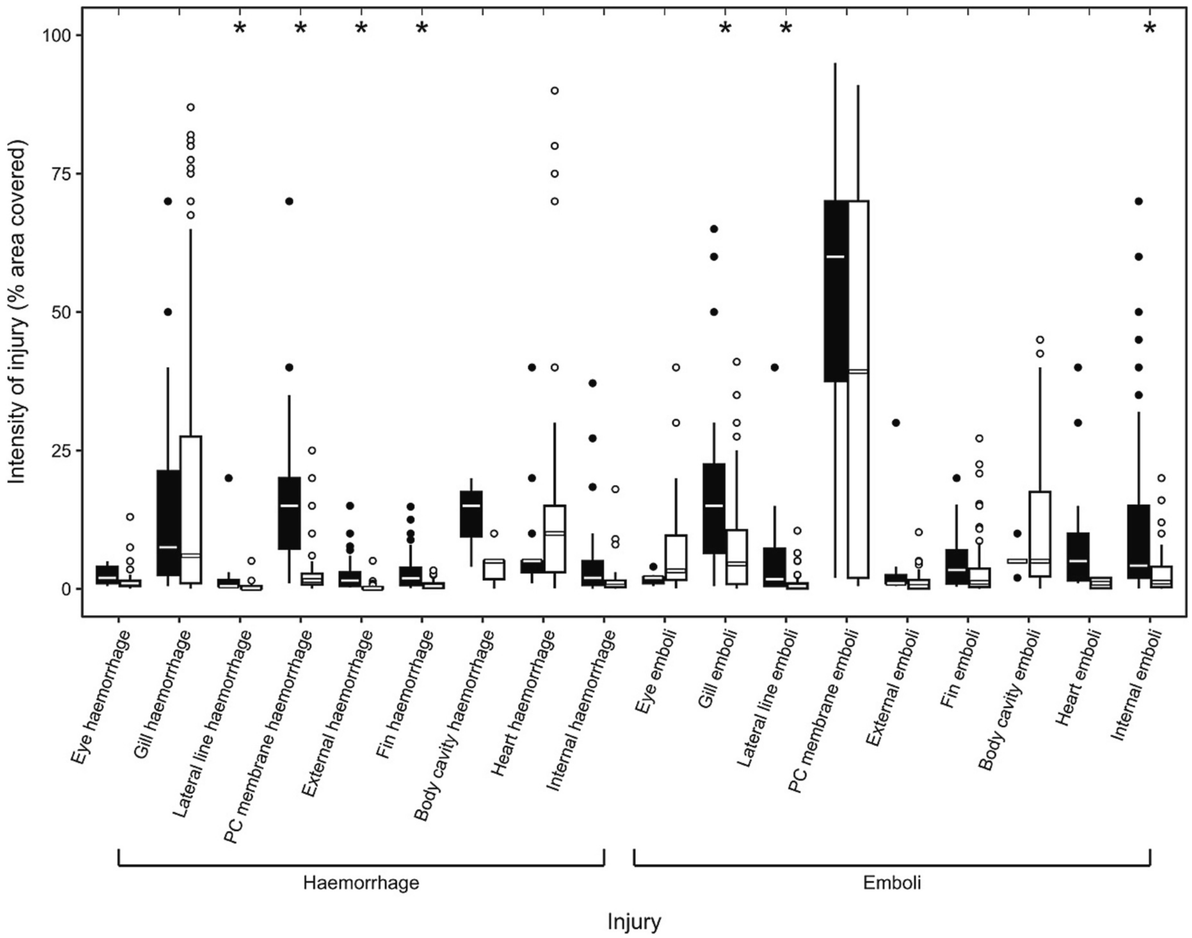

Fig. 4. Injury intensity (percentage area covered) for pacu (black bars) and piracanjuba (white bars) that experienced barotrauma during trials to assess the influence of rapid decompression under experimental conditions. Data combined for all Ratio of Pressure Change (RPC) treatments. Asterisks above bars indicate a significant interspecific difference.

more common in pacu (Fig. 3). The total number of emboli injuries per individual was lower for pacu (median: 2; range: 0–8) compared to piracanjuba (median: 4; range 0–9) (Mann Whitney U = 4353.5, z = −3.279, $p < 0.001$), while there was no interspecific difference in the total number of haemorrhage injuries (median: 4; range: 0–8; Mann Whitney U = 5458.0, z = −0.916, $p = 0.361$).

Although there was no interspecific difference in prevalence of swim bladder rupture (pacu: 65.5 %, piracanjuba: 55.5 %) (Fig. 3), the location of rupture varied with species. For pacu, all ruptures occurred in the anterior swim bladder chamber. For piracanjuba, both chambers were ruptured in 65 % of cases, while 31 % and 4 % of cases were isolated to the posterior and anterior chambers, respectively.

The highest injury intensity recorded for both species was for emboli in the PC membrane, which covered a median surface area of 60 % and 39 % for pacu and piracanjuba, respectively (Fig. 4). For all other injury types, injury intensity tended to be low (median < 20 %), although there was large variability in the data (Fig. 4). There was an interspecific difference in intensity for seven injury types (denoted by asterisks in Fig. 4), with each being greater for pacu than piracanjuba (Fig. 4).

Each of the responses defined was expressed by at least one individual of both species (Fig. 5). Bubbles expelled from the operculum/mouth were the most common response exhibited in both pacu and piracanjuba (Fig. 5). A high proportion of both species also expelled bubbles from the anus, lost orientation, and rose to the surface (Fig. 5). More piracanjuba (47 %) than pacu (5 %) exhibited stomach repositioning ($X^2 = 41.60$, $p < 0.001$) (Fig. 5). At the end of the observation period, the mobility of >20 % of both species was impaired (pacu: 27.4 %, piracanjuba: 20.7 %) (Fig. 5).

3.2. *Influence of RPC*

For both pacu and piracanjuba, the incidence of five injury types was positively related to RPC: exophthalmia ($p < 0.05$), gill emboli ($p < 0.05$), PC membrane emboli ($p < 0.05$), fin emboli ($p < 0.05$) and swim bladder rupture ($p < 0.01$) (Fig. 6). For piracanjuba, RPC was also positively related to the incidence of external emboli ($p < 0.05$) and was included as a predictor in the simplified model for lateral line emboli ($p = 0.07$) and internal emboli ($p = 0.06$), although these relationships were not significant (Fig. 6).

For pacu, the intensity of PC membrane emboli ($p < 0.05$) was positively related to RPC and was retained in the model for fin emboli intensity ($p = 0.08$) (Fig. 7). For piracanjuba, the intensity of gill haemorrhage ($p < 0.05$), gill emboli ($p < 0.05$), PC membrane emboli ($p < 0.05$), external emboli ($p < 0.05$) and fin emboli ($p < 0.05$) were positively related to RPC (Fig. 7). For piracanjuba, the number of tank days was also retained in the model as a predictor of the gill haemorrhage intensity (negative relationship), although it was not significant ($p = 0.07$) (Fig. S2).

Expulsion of bubbles from the anus ($p < 0.05$), loss of orientation ($p < 0.05$), rise to the surface ($p < 0.05$), and impaired mobility ($p < 0.05$) were positively related to RPC for both species (Fig. 8). Expulsion of bubbles from the mouth/operculum ($p < 0.05$) and stomach repositioning ($p < 0.05$) were also positively associated with RPC for pacu and piracanjuba, respectively (Fig. 8).

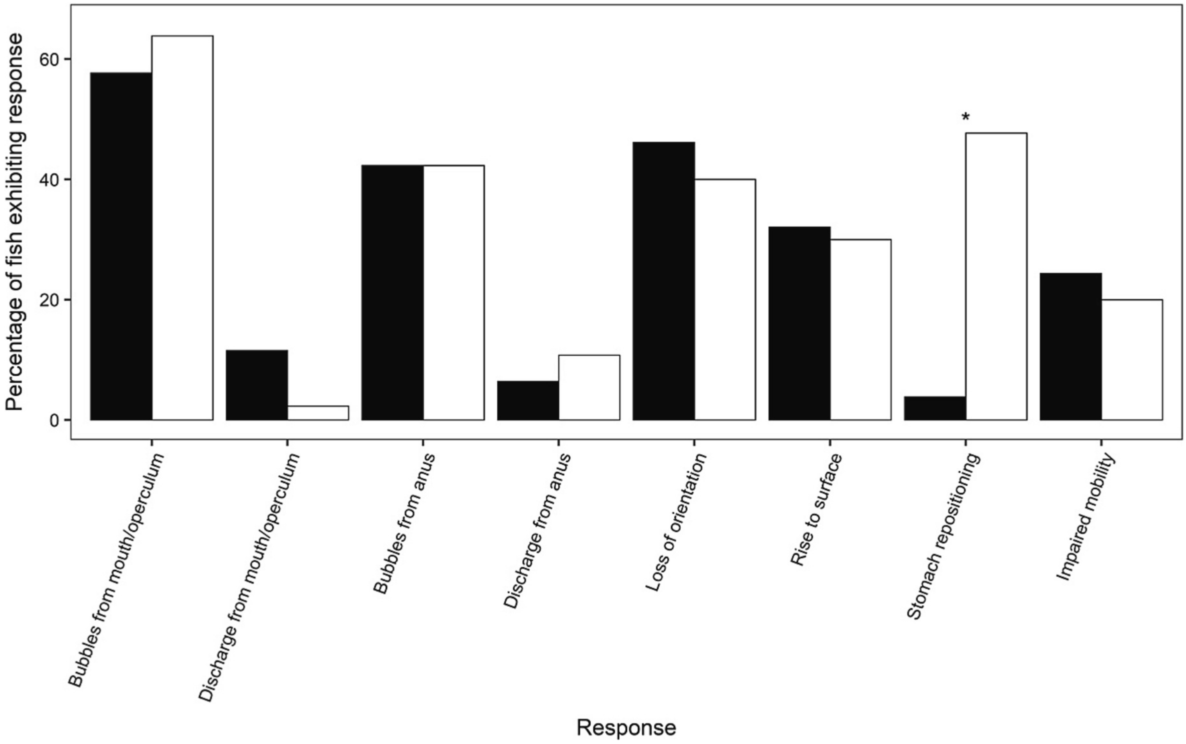

Fig. 5. Percentage of pacu (black bars) and piracanjuba (white bars) exhibiting different responses during the post decompression observation period (20 s). Data was combined for all Ratio of Pressure Change (RPC) treatments. Asterisks above bars indicate an interspecific difference.

3.3. *Influence of swim bladder rupture*

The incidence (Fig. 9a) and intensity (Fig. 9b) of four and two injury types, respectively, and occurrence of three types of response (Fig. 9c) were positively related with the probability of swim bladder rupture. Swim bladder rupture was a strong predictor of incidence of eye haemorrhage (piracanjuba: $p < 0.05$) and lateral line emboli (piracanjuba: $p < 0.05$) (Fig. 9a), and was retained in the model for incidence of exophthalmia (pacu: $p = 0.069$) and internal haemorrhage (piracanjuba: $p = 0.075$) (Fig. 9a) and the intensity of gill haemorrhage (pacu: $p = 0.114$) and emboli (pacu: $p = 0.144$) (Fig. 9b). Swim bladder rupture was also a strong predictor of expulsion of gas bubbles from the operculum/mouth (pacu: $p < 0.01$), loss of orientation (piracanjuba: $p < 0.05$) and stomach repositioning (piracanjuba: $p < 0.01$) (Fig. 9c).

4. Discussion

This study quantified the incidence and intensity of injury and the subsequent behavioural and physiological response of two Neotropical fish species that experienced experimentally controlled rapid decompression. There were considerable interspecific differences in the frequencies of barotrauma injuries and responses exhibited. Emboli type injuries and stomach repositioning were more common for piracanjuba, while intensity tended to be greater for pacu. Ratio of Pressure Change (RPC) was positively correlated with incidence and intensity of several injury types and responses for both piracanjuba and pacu, with some injuries frequently occurring at very low RPC (e.g. 50 % probability of fin emboli and swim bladder rupture at a RPC of ≤1.8 for piracanjuba and pacu, respectively). Multiple responses (e.g. loss of orientation) and injuries (e.g. eye haemorrhage) were correlated with swim bladder rupture, suggesting gas venting into the body cavity is an important cause of secondary injury.

In support of our first prediction, interspecific differences in incidence and intensity of barotrauma injury between pacu and piracanjuba were recorded, suggesting variation in their physiological response to rapid decompression. Piracanjuba tended to exhibit a greater number of emboli type injuries, while intensity of injury tended to be greater for pacu, suggesting that when injury did occur it was more severe for this species. Interspecific differences in response to barotrauma was also observed. For example, although expulsion of the stomach into the buccal cavity was rare (<5 %) in either species, stomach repositioning was more frequently exhibited by piracanjuba (47 %). This suggests that piracanjuba are able to swallow their stomach if it is expelled, as has been observed in other species, although typically only after recompression (e.g. yelloweye rockfish, *Sebastes ruberrimusm*: Rankin et al., 2017).

The number of injuries and responses for which RPC was a predictor and the strength of those relationships also varied with species. RPC was a predictor of the incidence and intensity of injury more frequently for piracanjuba than pacu, and for certain injuries (e.g. fin embolism) there was a much higher probability of occurrence at a lower RPC for piracanjuba (e.g. 50 % probability at 1.7 vs. 3.4 for pacu). Such interspecific variation in response to RPC has been observed in other studies (e.g. Pflugrath et al., 2018) and for species that are closely related (e.g. Perciformes: Murray cod, *Maccullochella peelii*, and silver perch, *Bidyanus bidyanus*: Boys et al., 2016), highlighting the difficulty in generalising results and the need to expand understanding of the impact of rapid decompression for a wider range of species (Brown et al., 2014; Silva et al., 2018).

RPC is frequently observed to be one of the principal predictors of barotrauma in fish (Brown et al., 2012a, 2012b, 2014; Silva et al., 2018). In agreement with these observations, the incidence (e.g. gill emboli, swim bladder rupture and exophthalmia) and intensity (e.g. fin and PC membrane emboli) of injury and resultant responses (e.g. expulsion of bubbles from the anus and rising to the surface) were positively correlated with RPC for both pacu and piracanjuba in this study. Furthermore, barotrauma injuries were observed at a very low RPC. For example, the GLMs predicted a 50 % probability of swim bladder rupture at an RPC of 1.7 and 2.2 for pacu and piracanjuba, respectively. These results are comparable to those obtained for the only other

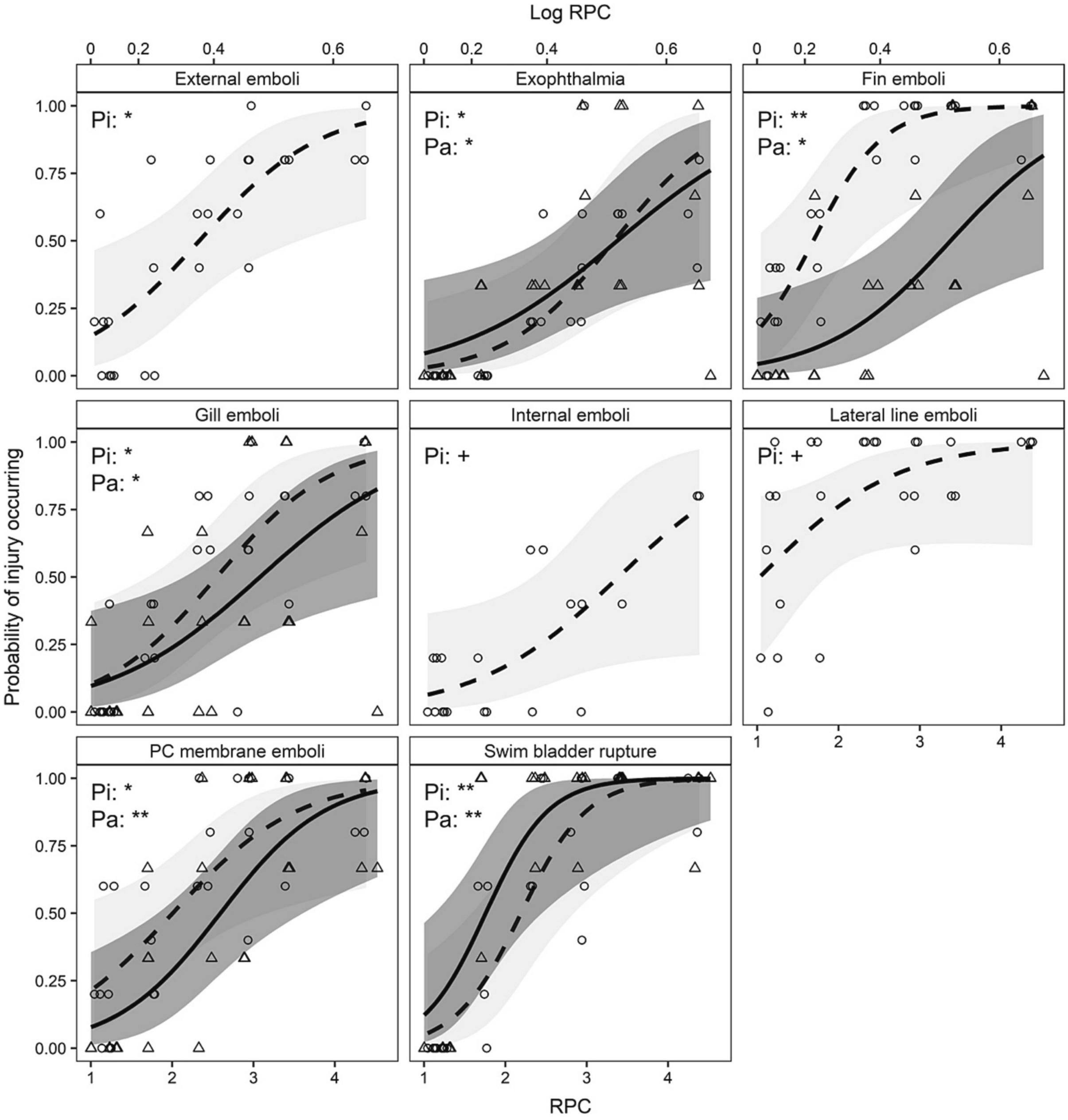

Fig. 6. Injuries for pacu (triangles, solid black line with dark grey confidence interval [CI]) and piracanjuba (circles, dashed black line with light grey CI) for which the Ratio of Pressure Change (RPC) was a significant predictor of their occurrence (* $p < 0.05$; ** $p < 0.01$) or they were retained in the model but the relationship was not significant (+).

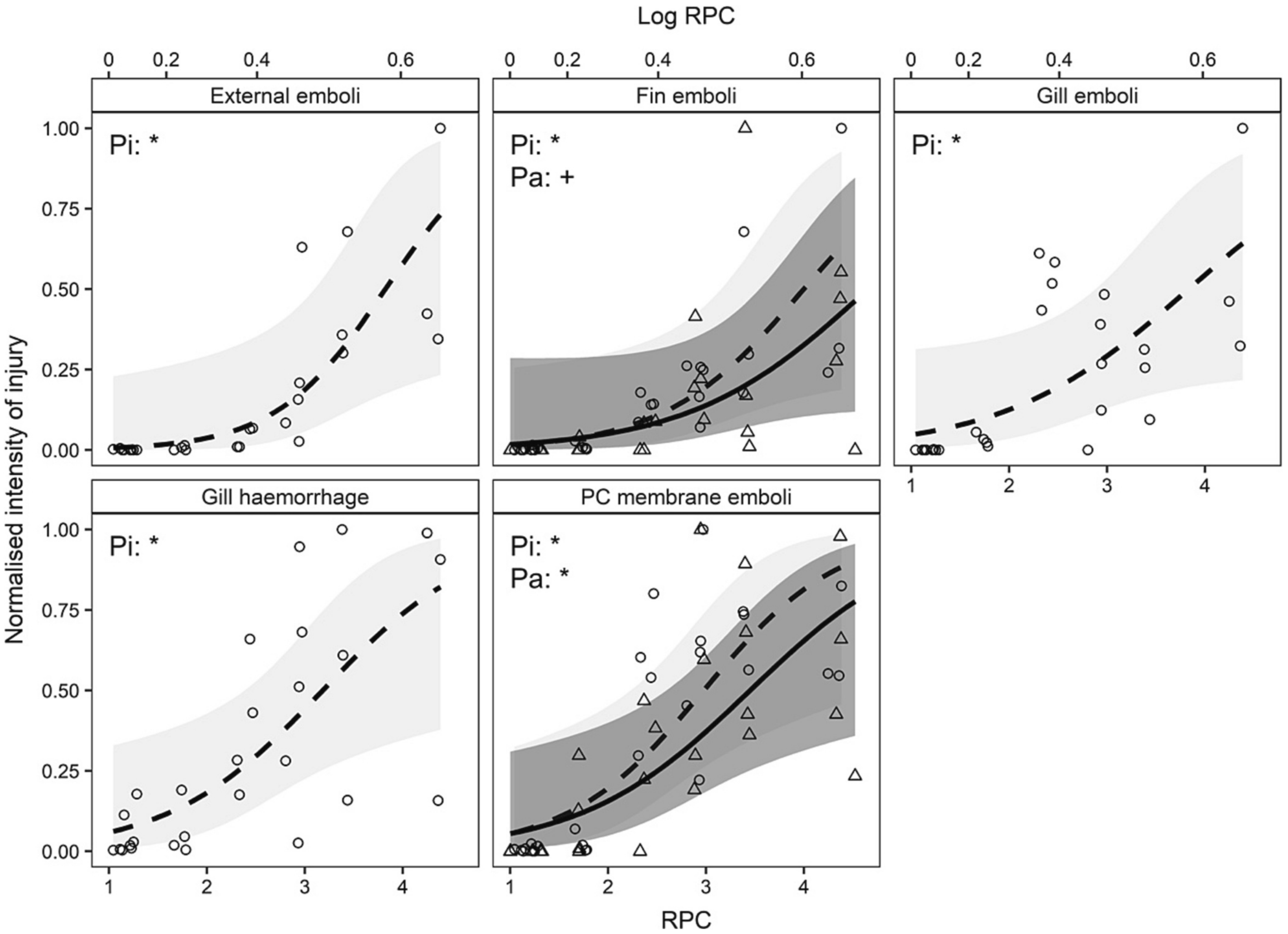

Fig. 7. Injuries for pacu (triangles, solid black line with dark grey confidence interval [CI]) and piracanjuba (circles, dashed black line with light grey CI) for which Ratio of Pressure Change (RPC) was a significant predictor of their intensity (* $p < 0.05$) or for which it was retained in the model but the relationship was not significant (+).

Neotropical species assessed to date, the pictus catfish, for which a sharp increase in the probability of swim bladder rupture occurs at an RPC of ca. 1.2 (Beirão et al., 2018), with 100 % probability of rupture at 1.5. In comparison, injuries were infrequently observed in temperate physostomous juvenile Chinook salmon exposed to an RPC of 2.12 or less (Brown et al., 2012b) and four Australian species had a ≥50 % probability of remaining injury free below an RPC of between 2.45 (silver perch) and 3.75 (Murray cod) (Pflugrath et al., 2018). In support of our second prediction, evidence suggests that Neotropical fish with multi-chambered swim bladders are more susceptible to barotrauma than single chambered subtropical and temperate species, although further work is required to identify the mechanisms driving this difference.

Swim bladder rupture was frequently observed in both pacu and piracanjuba, and in agreement with our third prediction, it was correlated with the multiple other injury types and responses, including emboli. This was also observed in the pictus catfish in which emboli were present predominantly among those with a ruptured swim bladder (Beirão et al., 2018). Interestingly, although both pacu and piracanjuba possess a similar dual-chambered swim bladder, individual piracanjuba exhibited emboli more frequently and in different locations compared to pacu. For example, piracanjuba more frequently exhibited external, fin, lateral line, and body cavity emboli, while pacu suffered more frequently from heart emboli. The more frequent occurrence of emboli in piracanjuba, as well as the potential expulsion of internal organs, evidenced by stomach repositioning behaviour, may have related to greater venting of gas for this species in which both chambers tended to rupture, as opposed to only the anterior chamber in pacu. Rupture location might relate to morphological variations in the swim bladder tissue between chambers (e.g. Dumbarton et al., 2010 for zebrafish, *Danio rerio*), and may provide a means to predict the impact of barotrauma on fish (Silva et al., 2018). In the case of pacu, the expulsion of bubbles from the mouth/operculum immediately following decompression was positively correlated with RPC. It is possible that pacu were able to vent more gas through their oesophagus during decompression, therefore reducing damage to the swim bladder, and hence the frequency of emboli type injuries. Although it is currently unclear why species with multi-chambered swim bladders are more susceptible to barotrauma, it is likely that interspecific differences in bladder morphology influence the probability and location of rupture, which in turn influences individual injury and response.

The decompression profiles used here differed from those used in other experimental studies in that the acclimation pressures were high (up to ca. 400 kPa) and the nadir values (range: 85–101 kPa) were only slightly lower than atmospheric pressure. Previous studies have typically created high RPC by exposing fish to much lower nadir pressures (e.g. 8–19 kPa: Brown et al., 2009; 6–145 kPa: Brown et al., 2012a, 2012b; 10–79 kPa: Boys et al., 2016; 4–79 kPa: Pflugrath et al., 2018) using a combination of either surface or slightly higher acclimation pressures (e.g. 101–221 kPa: Brown et al., 2009; 101–176 kPa: Brown et al., 2012a, 2012b; 101–200 kPa: Boys et al., 2016; 101–201 kPa: Pflugrath et al., 2018). Most severe barotrauma injuries are thought to be linked to swim bladder rupture and secondary injury, with the

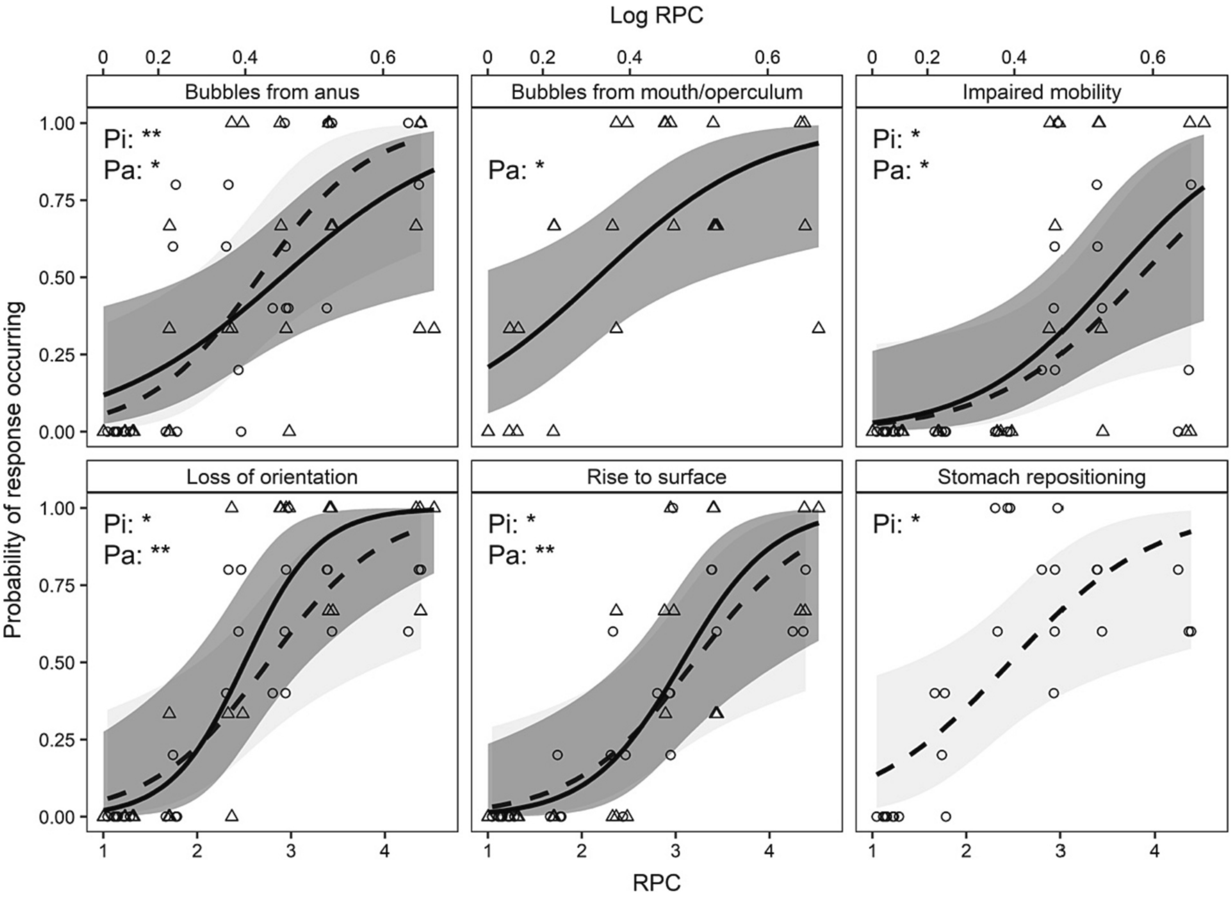

Fig. 8. Responses displayed by pacu (triangles, solid black line with dark grey confidence interval [CI]) and piracanjuba (circles, dashed black line with light grey CI) after rapid decompression for which the Ratio of Pressure Change (RPC) was as a significant predictor (* $p < 0.05$; ** $p < 0.01$).

prevalence of rupture directly linked to the RPC (Brown et al., 2014). The RPC is the ratio of the acclimation and nadir pressures and is independent of the 'absolute' or 'absolute difference in' values. Hence, results of barotrauma studies can generally be considered comparable, regardless of acclimation pressure, if RPC is used as the predictor variable (caveat: if the test fish are allowed adequate acclimation time, see Silva et al., 2018 for discussion). However, for the studies that created high RPC by using surface acclimation pressures and very low nadir pressures (e.g. Brown et al., 2009, 2012a, 2012b; Boys et al., 2016; Pflugrath et al., 2018), fish were recompressed back to acclimation pressure prior to necropsy. This transition back to acclimation pressure may recompress (i.e. Boyle's Law) and potentially redissolve (i.e. Henry's Law) any emboli that have formed causing them not to be registered during necropsy. Hence, caution should be used when comparing the prevalence of certain injury types (i.e. emboli) between studies that use different acclimation pressures. The pressure profiles that fish are exposed to during hydropower turbine passage are highly variable, being site-specific (Fu et al., 2016) and dependent on fish proximity to the blades during passage (Richmond et al., 2014). Further work is required to standardise methodologies for evaluating hydropower turbine passage barotrauma. The research field will also benefit from the development of equipment that can precisely reproduce a range of site-specific conditions.

Rapid unsustainable hydropower development in Neotropical regions threatens fluvial biodiversity and degrades associated ecosystem services. The results of this research improve understanding of the potential impacts of hydropower operation on Neotropical fish so that steps can be taken to advance the development of more sustainable hydropower infrastructure in this region. This is especially important considering the several large high head impoundments that have been built in the Neotropics (System for Electricity Generation of Aneel, 2023) at which there is a high risk of fish experiencing large pressure changes (i.e. high RPC). This study also highlighted the interspecific differences in fish barotrauma, likely linked to differences in swim bladder morphology affecting rupture location and the prevalence and type of secondary injury. Further work is needed to establish why Neotropical fish with complex multi-chambered swim bladder architecture are more susceptible to barotrauma than single chambered northern temperate or southern subtropical species. It is recommended that future studies: 1) increase the number of Neotropical species assessed, 2) quantify the long-term fitness cost of different barotrauma injury and responses, and 3) identify how the probability of rupture and prevalence of secondary injury is influenced by swim bladder architecture. This work is important to help identify RPC thresholds that minimise barotrauma risks to acceptable levels for a range of species, allowing for the sustainable development of hydropower technology in the Neotropics and elsewhere.

CRediT authorship contribution statement

J.R. Kerr: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **A.L.F. Castro:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Resources, Project administration. **N.O. Melo:** Methodology, Investigation, Writing – original draft. **J.A. Daniels:** Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **A. Holgate:** Investigation, Writing – original draft, Writing – review & editing. **L.A. Dolman:** Investigation, Visualization, Writing – original draft, Writing – review & editing. **L.G. M. Silva:** Conceptualization, Methodology, Writing – original draft,

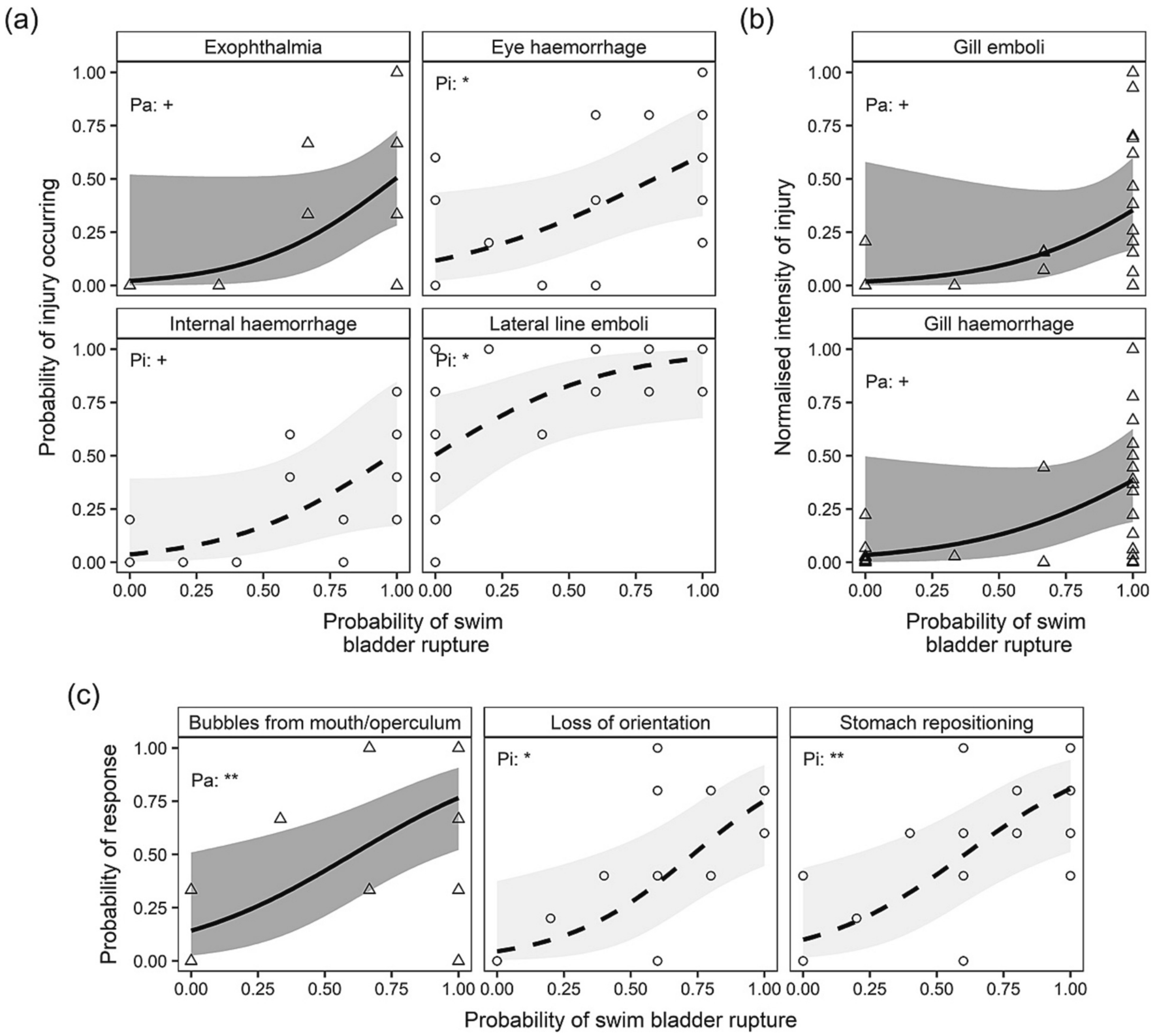

Fig. 9. Injury incidence (a) and intensity (b) and resultant responses (c) for pacu (triangles, solid black line with dark grey confidence interval [CI]) and piracanjuba (circles, dashed black line with light grey CI) for which swim bladder rupture was a significant predictor (* $p < 0.05$; ** $p < 0.01$) or retained in the model ($^{+}$).

Writing – review & editing, Project administration, Funding acquisition. **P.S. Kemp:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data supporting this study are openly available from the University of Southampton repository at https://doi.org/10.5258/SOTON/D2698.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.166770.

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