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Perspective

It's a catfish! Novel approaches are needed to study the effects of rapid decompression on benthic species

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Abstract. Barotrauma as a result of rapid decompression has been recorded as the most common injury among fish captured in the tailrace of hydropower dams in Brazil, with catfishes representing the majority of them. Nevertheless, studies investigating barotrauma on catfish are scarce, with the majority determining dose–response curves and thresholds of pressure changes for nektonic species, such as salmonids. Experiments conducted with *Pimelodus pictus* showed that the current hypo-hyperbaric chambers used to study barotrauma in nektonic species can have limitations when applied to benthic groups. The negative buoyancy showed by the catfish prevented the definition of the acclimation pressure of the fish before exposure to decompression and, therefore, the method had to be adapted to allow the calculation of the ratio of pressure change (RPC). The adaptation involved anaesthetising the fish, which added a potential bias to the experiments. Therefore, new approaches deemed to be needed to complement barotrauma studies with benthic fish. We aimed to discuss the limitations observed for studies with benthic species and present potential methods to overcome them. The diversification of approaches for barotrauma studies with benthic species is critical to provide information for the development of mitigation and new turbine designs that would improve protection of this group.

Additional keywords: draft tubes, fish mortality, hydropower, pressure changes.

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Introduction

Fish kills caused by the passage through turbines have, historically, been described as a major issue related to the operation and development of existing (Čada *et al.* 2006) and future hydropower plants respectively (Brown *et al.* 2014). Fish entrained in a turbine is exposed to various forces (Čada 2001) that can lead to mortality, namely shear stress (Baumgartner *et al.* 2017), blade strike (Deng *et al.* 2011), cavitation (Pracheil *et al.* 2016) and pressure changes (Brown *et al.* 2014). However, the extent to which each force will primarily affect fish moving through turbines vary with fish age and size. For instance, blade strike is intrinsically related to fish size, because larger fish are more susceptible to this type of mechanical injury. In contrast, shear stress affects smaller fish and early life stages more severely. Finally, pressure variation affects fish from larvae to adults, regardless of size, therefore becoming an important component for investigation.

In a recent review of fish entrainment in hydropower across the USA, Pracheil *et al.* (2016) observed that, indeed, the majority of the studies were focussed on understanding the biological effects of pressure changes in turbines. However, all studies have also focussed only on fish mortality resulting from passage through the turbines, disregarding scenarios where mortality events can occur as a result of the entrance of fish into the draft tubes of the turbines during different operational procedures. This mortality scenario is present on various hydropower plants in tropical rivers in Brazil (Godinho and Loures 2017). For instance, Rego *et al.* (2017) described that barotrauma can occur on fish during a turbine operational procedure nominated 'speed no load' where the turbine discharge is

Table 1.	Most common Siluriformes species (catfishes) collected in the tailrace of hydropower plants in Minas Gerais state, Brazil, after mortality
	events related to interaction with turbines

Order	Species	Basin	Reference
Siluriformes	Pimelodus maculatus Lophiosilurus alexandri Wertheimeria maculata Zungaro jahu Pseudoplatystoma corruscans Pinirampus pirinampu	São Francisco River; Paranaíba River São Francisco River; Jequitinhonha River Paranaíba River	(de Andrade <i>et al.</i> 2012; Pérez 2014; Beirão 2015) (Beirão 2015) (Beirão 2015) (Pérez 2014)

reduced, and it rotates with no load, allowing fish to enter the draft tube and approach the turbine rotor (Rego *et al.* 2017).

It is known that fish exposed to rapid decompression in turbines can suffer barotrauma (Brown *et al.* 2012*a*), which is defined as a series of injuries resulting from pressure changes, leading to instant or delayed mortality. Most commonly, researchers have been aiming to develop dose–response relationships or to identify thresholds for pressure changes and the likelihood of barotrauma through simulated decompression in a laboratory (Brown *et al.* 2012*b*; Boys *et al.* 2016*a*) using hypo–hyperbaric chambers (hereafter, barotrauma chambers).

However, the majority of the studies investigating pressure effects on fish has been biased towards juvenile salmonids in the USA (Pracheil et al. 2016) and are still very restricted elsewhere in the world, with a few examples for species from Australia (Boys et al. 2016a, 2016b) and Brazil (Pompeu et al. 2009; Beirão et al. 2015). Brown et al. (2014) highlighted that more research is needed to incorporate a greater diversity of fish and life stages in barotrauma studies, with special attention particularly required for benthic species, such as catfishes. For those authors, benthic-oriented species would be capable of attaining neutral buoyancy at deeper depths (i.e. benthopelagic), owing to its natural association with the substrate, and, therefore, be more susceptible to barotrauma. In contrast, other benthic species are considered to be negatively buoyant and sit on the substrate of aquatic systems. Therefore, those benthic species may not be affected by barotrauma to the same extent as are benthopelagic species because they will not be acclimatised to the depth where they are located (negative buoyancy). Indeed, catfishes (Order Siluriformes) have been, by far, the most common species recorded in the tailrace of hydropower dams after mortality events associated with turbines in tropical rivers (de Andrade et al. 2012; Pérez 2014; Suzuki et al. 2017; Table 1). Nevertheless, barotrauma studies with those species have been scarce, if not limited to the study developed by Beirão et al. (2018). Therefore, the potential limitations to study benthic species using barotrauma chambers have yet to be explored.

Considering that a global boom for hydropower development is expected (Zarfl *et al.* 2015) and that the impacts of these dams have promoted severe declines of freshwater fish diversity and fishery around the globe (Dugan *et al.* 2010; Ziv *et al.* 2012), advancing scientific knowledge of different issues, such as fish mortality in turbines, is critical to inform new designs and mitigate those impacts. Furthermore, some of the hotspots for hydropower development are located in areas that are home of a mega-diverse fish fauna (e.g. Amazon, Mekong and Congo Rivers; Winemiller *et al.* 2016), reinforcing the need to diversify the range of species and, therefore, posing great challenges to barotrauma studies. Such global challenge requires international collaboration and the use of standardised approaches to quicken data gathering and reduce redundancy (Brown *et al.* 2014). Nevertheless, it may also require either the adaptation of current methods or development of new approaches.

In this sense, we argue that the current approach using barotrauma chambers to understand the effects of pressure change on benthic species is limited and new procedures are required to complement or, perhaps, modify the status quo of the actual method. We provide further clarification and explore potential limitations of the current approach based on the key variables to understand barotrauma on fish. We use a series of evidence based on the work conducted by Beirão *et al.* (2018) to support our claims. Finally, we suggest new approaches to contribute to the understanding of barotrauma on benthic species (benthic and benthopelagic).

Key variables to understand barotrauma on fish

Brown et al. (2014) provided one of the most comprehensive bodies of literature to understand some of the key variables driving barotrauma in fish as a result of rapid decompression in turbines. Also, Pracheil et al. (2016), in a recent review, summarised the most important factors on the basis of the work conducted by Brown et al. (2012a). Basically, the likelihood of barotrauma in fish is related to (1) the acclimation pressure, (2)the ratio of pressure change (RPC, defined as the ratio between the acclimation pressure (pressure and its correspondent depth to which fish is acclimatised before turbine passage) and the nadir pressure (lowest pressure to which fish is exposed)), (3) the swim-bladder morphology, (4) the rate of pressure change (speed at which pressure changes occur) and (5) life stages. The first three variables are considered the most critical to determine barotrauma studies, and less attention has been given to the rate of pressure change and life stages. Indeed, the limitations observed for the use of barotrauma chambers to study benthic species were primarily related to the first three variables and, therefore, they were selected for further discussion in the present study.

Acclimation pressures and associated depth

Before decompression, it is critical to determine at which depth and, consequently, at which pressure, fish are acclimated. Fish acclimation is established by its buoyancy in the water column, which can exhibit the following three states: (1) positive, (2) neutral and (3) negative buoyancy (see Pflugrath *et al.* (2012) for illustration). Neutrally buoyant fish is judged to be acclimated to its surrounding water once its body is horizontally positioned in the water column, therefore meaning that the density of fish is equal to that of the water at that particular depth and its correspondent pressure. The mechanisms used by fish to regulate its buoyancy varies among groups, with the majority of living teleosts (Teleostei, modern bony fish) using a swim bladder for this function (Fänge 1983).

Fish regulate their density by altering the swim-bladder volume. The volume of the swim bladder is expected to change according to Boyle's law $(P_1V_1 = P_2V_2)$; volume change is inversely proportional to pressure change; Alexander 1959). Therefore, as fish descend to higher depths, the pressure in the surrounding water increases and the swim bladder is compressed (Pflugrath et al. 2012). To compensate for the increase in pressure, fish transfer gas to the swim bladder (Fänge 1983) to attain neutral buoyancy. In contrast, as fish ascend towards the surface, the swim-bladder volume is expected to increase. Hence, the ability of a fish to acclimate to deeper depths is dependent on the functionality (morphology and physiology; see Fänge 1983 for details) and the volume of gas that can be transferred to the swim bladder. A neutral buoyant fish at deeper depths (higher pressures) will have a higher volume of gas in the swim bladder than its conspecific in shallower water (lower pressure; Pflugrath et al. 2012).

This mechanism of gas-volume regulation in the swim bladder is the main factor explaining the importance of determining the acclimation pressure of fish before exposure to decompression (Brown *et al.* 2014). Fish acclimatised to a higher pressure would be more susceptible to barotrauma because they would have a higher volume of gas in the swim bladder. During decompression, according to Boyle's law, the volume in the swim bladder would increase as a function of the ratio of pressure change (RPC). Therefore, for experiments using barotrauma chambers, there is a need to determine the acclimation pressure of the fish to provide for the RPC calculation. In this case, the acclimation pressure is defined as the maximum pressure at which fish can still attain neutral buoyancy.

Ratio of pressure change

Brown *et al.* (2012*b*) calculated the RPC as RPC = PA \div PN, where PA is the acclimation pressure and PN the nadir pressure, defined as the lowest pressure that the fish is exposed to. Using an extensive database for experiments with juvenile Chinook salmon, Brown *et al.* (2012*a*) analysed the effects of rapid decompression and compared pathways for the occurrence of barotrauma-related injuries. Brown *et al.* (2012*a*) concluded that the expansion of pre-existing gas in the body, as governed by Boyle's law, would be the main pathway to barotrauma on fish exposed to rapid decompression during turbine passage. Consequently, the expansion and rupture of the swim bladder would, forcefully, push gases into the surrounding tissues, causing further injuries such as emboli, haemorrhage and exophthalmia (Brown *et al.* 2012*a*).

The RPC has been shown to be critical in determining barotrauma susceptibility of fish, yet it has been extensively



Fig. 1. Schematic of the expected effect of the ratio of pressure change on the volume expansion of the swim bladder and gases within fish neutrally buoyant (acclimated) at different depths (pressures). Fish acclimated in deeper depths (e.g. 30 m) are exposed to higher pressure in the surrounding water (404 kPa) than are its conspecific at shallower depths (10 m; 202 kPa). Following Boyle's law, as fish moves towards the surface, the pressure decreases and, therefore, swim-bladder volume increases. The expansion of the swim bladder of the deeper fish would be higher (4 times) than that of the swim bladder of the shallower fish (2 times), where *X* is the expected volume expansion.

analysed only for Chinook salmon. On the basis of the results of Brown et al. (2012b), a fish acclimatised to a higher pressure (e.g. 175.8 kPa, equivalent to 7.6-m depth) was more susceptible to barotrauma than were those at a lower pressure (e.g. 101.4 kPa, equal to surface pressure) when exposed to the same PN (e.g. 50 kPa), therefore exhibiting different RPCs (3.5 and 2 respectively). The first fish would have a greater mass of gases inside its body, especially in the swim bladder, to compensate for compression and attain neutral buoyancy at a higher pressure (deeper depths). That same fish, on the basis of Boyle's law, would experience an expansion of gases corresponding to three times the initial volume of the swim bladder, and would have a higher probability of incurring injuries if exposed to rapid decompression, with a PN of 50 kPa. This relationship between RPC and gas volume increases within the fish body or expansion of the swim bladder (Fig. 1) have been considered critical in determining the likelihood of barotrauma.

Since then, understanding the relationship between RPC and the severity of barotrauma injuries has become the primary objective of barotrauma studies (Brown et al. 2014; Boys et al. 2016a). Results of experiments with barotrauma chambers have been used to establish dose-response curves (Neitzel et al. 2004; Brown et al. 2012a) or thresholds (Boys et al. 2016a) to inform or suggest the magnitude of pressure changes (acclimation in relation to nadir pressure) that are more likely to cause severe injuries on fish exposed to rapid decompression. However, tested species has to attain neutral buoyancy and acclimatise to a certain pressure within the barotrauma chamber to allow for calculation of RPC after exposure to PN. The capacity of fish to acclimatise to a higher pressure will vary depending on the type of swim bladder, which will determine the quickness that fish can transfer gas to that organ (Brown et al. 2012a), and the behaviour of fish (nektonic v. benthic species; Brown et al. 2014). For instance, Brown et al. (2014) hypothesised that benthopelagic species would be able to attain neutral buoyancy at deeper depths and, therefore, would be more susceptible to barotrauma.

Swim-bladder type

According to Fänge (1983), teleosts can be organised into the following three groups according to the swim-bladder type: (1) physostomes; (2) physoclists; and (3) fish with no swim bladder. The physostomes and physoclists manage gas volume in the swim bladder differently. Physostomes are also known as fish with an opened swim bladder as it connects to the oesophagus via the pneumatic duct. Therefore, it would be expected that physostomes can quickly inflate or deflate the swim bladder by gulping or expelling air through the pneumatic duct, the later a phenomenon known as gas-puck reflex (Franz 1937). Nevertheless, this capacity is influenced by the morphology of the swim bladder, including the number of chambers (Brown et al. 2014). Moreover, for some species, such as deep-water species, gas secretion, known as the deposition of gas from the blood into the swim bladder (Fänge 1983), is also used for swim-bladder inflation. This process takes longer to complete than does the inflation achieved by gulping air.

Swim-bladder inflation and deflation are also slow in physoclist species, compared with physostomes. Physoclists are known as fish with closed swim bladders because they lack a pneumatic duct. Therefore, inflation and deflation are managed by a complex physiological process that uses the circulatory system to input or output gas to the swim bladder via an extensive anastomosed vasculature, namely *rete mirable* (Fänge 1983).

This difference in swim-bladder traits can help determine the likelihood of barotrauma in fish exposed to rapid decompression. Physoclists would be more susceptible to swim-bladder rupture because of their inability to quickly expel gas before exposure to decompression (Čada and Schweizer 2012; Brown et al. 2014). Also, for physostomes species with a two-chamber swim bladder, the likelihood of rupture of the anterior chamber can be higher than for those with a single-chamber swim bladder, because it has been shown that the anterior chamber is likely to be responsible for swim-bladder volume control (Dumbarton et al. 2010). Despite that, the majority of the barotrauma studies have been conducted with physostomes, mainly salmonids with a single-chamber swim bladder (Pracheil et al. 2016), and a few studies with physoclists (Boys et al. 2016a) or fish with no swim bladder such as lampreys (Colotelo et al. 2012). There is still a considerable knowledge gap, and a strong need to both diversify the species tested in barotrauma studies and to understand better how differences in swimbladder morphology and functionality, such as biomechanics, can influence the susceptibility of fish to barotrauma.

Limitations to apply the key variables to benthic species: the case of the Pictus catfish

Acclimation pressure and RPC

Brown *et al.* (2014) already highlighted the need to test the effects of rapid decompression on benthic-oriented species, hypothesising that they would be more susceptible to baro-trauma as a result of rapid decompression. These authors used primarily the acclimation pressure and the RPC to support their

hypothesis, stating that benthonic species would acclimate to higher pressures and, therefore, be more likely to be exposed to a higher RPC. However, the study of Beirão *et al.* (2018) with *Pimelodus pictus*, a benthic species from the Amazon region in Brazil, showed limitations to use both acclimation pressure and RPC as key variables to explain barotrauma in such species. Beirão *et al.* (2018) used the same barotrauma chambers as described by Stephenson *et al.* (2010) and also utilised by Brown *et al.* (2012*a*, 2012*b*) for their experiments with Chinook salmon, showing that the current method (barotrauma chamber) and data analysis (establishment of a dose–response relationship of injuries with the RPC) were potentially compromised for benthic species.

The Pictus catfish did not attain neutral buoyancy throughout all experiments conducted by Beirão *et al.* (2018). Instead, the species maintained negative buoyancy throughout the acclimation stage (Fig. 2*a*), even fish that were exposed to the acclimation pressure for over 72 h (B. Beirão, pers. comm.). Hence, fish had to be anaesthetised before decompression to allow determination of the acclimation pressure and, therefore, further calculation of RPC. A similar scenario has been observed for sturgeon and American eels during barotrauma trials in the Pacific Northwest National Laboratory (PNNL) where fish were negatively buoyant throughout the experiments and this prevented the calculation of RPC. These species were also negatively buoyant during acclimation pressures tested and did not respond to decompression (B. Beirão, pers. comm.).

This condition where fish maintain negative buoyancy has implications for determining the impact of pressure changes on barotrauma occurrence experimentally. Indeed, Brown et al. (2014) suggested that determining whether benthic-oriented species are neutral or negatively buoyant would be imperative because this would have implications to the impact of pressure changes on barotrauma. That is because a neutral buoyant fish at a particular depth has sufficient gas in the swim bladder to equalise the surrounding density, so as to sustain neutral buoyancy. Therefore, it would be possible to establish a direct relationship between pressure changes and the likelihood of barotrauma (dose-response relationship with RPC, assuming that Boyle's law explains the main pathway of injuries). If fish is negatively buoyant, it will have less gas in the swim bladder than what is required to be neutrally buoyant at a particular depth and that would hinder the establishment of a dose-response relationship with RPC because it is not possible to determine the pressure (or equivalent depth) at which fish was acclimatised before decompression.

Because the Pictus catfish did not attain neutral buoyancy during the acclimation stage, Beirão *et al.* (2018) adapted the experimental protocol to determine the pressure at which fish would be neutrally buoyant. Beirão *et al.* (2018) injected anaesthetic tricaine methanesulfonate (MS-222) into the barotrauma chamber to daze the fish before decompression and, thereafter, to determine the pressure of neutral buoyancy (PNB). When fish was judged to be in 3B analgesia stage (Mattson and Riple 1989), the barotrauma chamber was decompressed very slowly until the fish floated mid-column in the water (Fig. 2b). The corresponding pressure where fish floated was considered as the PNB and used for further analysis (Fig. 2c). The use of anaesthetics may relax the pneumatic duct facilitating gas Barotrauma on benthic-oriented species



Fig. 2. (*a*) Negative buoyancy (white arrow) showed by the Pictus catfish *Pimelodus pictus* in the barotrauma chamber during the acclimation stage (black arrow shows fish in the bottom of the chamber). (*b*) *P. pictus* anaesthetised and initiated flotation. (*c*) Schematic of the pressure change to determine the pressure of neutral buoyancy (PNB) of *P. pictus* in the barotrauma chamber (solid line represents acclimation pressure of the chamber and dashed line indicates slow decompression manually conducted to determine PNB, which was defined as the pressure value when fish floated mid-column in the water.

expelling by the fish (Beirão *et al.* 2018). However, Beirão *et al.* (2018) explained that the results obtained from that study might be underestimated because fish were not able to compensate for

decompression and, eventually, expel gas out of the swim bladder.

Because of the importance of determining the RPC to understand the likelihood of barotrauma for fish, Brown et al. (2014) indicated the necessity to determine the acclimation depth of fish approaching hydro-structures. These authors suggested the use of the barotrauma chamber to identify the maximum pressure, and its equivalent depth, to which fish would acclimatise and use that in conjunction with other variables to predict susceptibility of fish to barotrauma. However, as demonstrated for the Pictus catfish, the methods proposed by Brown et al. (2014) may not work well for benthic or benthopelagic species. Hence, Brown et al. (2014) proposed field approaches, such as monitoring, observing or capturing fish at different depths in reservoirs, to potentially determine the pressure to which benthic fish would be acclimatised. The use of underwater remote videos as a prospective method to provide for that type of information will be discussed further in the present paper.

The ability to expel gas from the swim bladder in expansion would be expected in the Pictus catfish because it is a physostome species. However, the morphology of the swim bladder of catfishes has been deemed to exhibit the highest morphological diversity among otophysan fishes (Birindelli *et al.* 2009), with variations occurring within the same family (Birindelli *et al.* 2009; Birindelli and Shibatta 2011). These variations are related to the size of the chambers, and shape and presence of diverticula. Interestingly, the swim bladder of catfishes is considerably different from the morphologies discussed in barotrauma studies conducted with other species exhibiting single or double chambers (Brown *et al.* 2014). This morphological aspect is another factor that requires the adoption of new or complementary approaches to the barotrauma chamber to study barotrauma in catfishes.

Swim-bladder morphology

The Pictus catfish (P. pictus) belongs to the family Pimelodidae and, as in all Siluriformes (Birindelli et al. 2009), its swim bladder has three chambers (Jones and Marshall 1953; Fig. 3) divided by a T-shaped septum, with a similar morphology as described for species of the Pseudopimelodidae (Birindelli and Shibatta 2011) and Doradidae (Birindelli et al. 2009) families. The presence of three chambers in the swim bladder of the species from the Pimelodidae family has been suggested in some of the few studies available. An evolutionary hypothesis suggests that the swim bladder in benthic-oriented freshwater species has a reduced volume, mainly through the encapsulation of the anterior chamber in bone or membrane or its separation into right and left valves (Jones and Marshall 1953). This reduction in volume and encapsulation would increase the body density and, consequently, the sinking factor, which appears to correlate well with the habit of living associated with the substrate (Jones and Marshall 1953).

Moreover, Jones and Marshall (1953) indicated that the pneumatic duct of some Siluriformes species might also have diminished or completely disappeared. Birindelli *et al.* (2009) noted that the pneumatic duct in this group is located ventrally in the swim bladder, at the intersection of the transverse and longitudinal parts of the T-shaped septum (see Birindelli *et al.*



Fig. 3. Three-chambered swim bladder of the Pictus catfish, *Pimelodus pictus*. The dotted lines show the presence of a T-shaped septum separating the anterior from the posterior chamber and dividing the posterior chamber in two. The pneumatic duct is present in the intersection of the transverse and longitudinal parts of the T-shaped septum (*).

2009 for images). The location of the pneumatic duct can influence the ability of the species to rapidly exchange gas in the swim bladder, and this topic has to be further explored for Siluriformes.

All these singularities of the swim-bladder morphology may explain the negatively buoyant behaviour exhibited by the Pictus catfish in the barotrauma chamber, which posed challenges for determining the acclimation pressure for this species. They also hindered interpretations of the results of rapiddecompression experiments developed by Beirão (2015). Indeed, because barotrauma studies have commenced diversifying species tested, the difficulties in interpreting the results, especially owing to the buoyancy behaviour or swim-bladder morphology, are emerging more often, reinforcing the need to explore other approaches to understand these topics better. For instance, Brown et al. (2013) indicated that the lack of information on the developmental biology of the swim bladder in sturgeon hampered interpretation of some observations in their study with larval and juvenile white sturgeon. Furthermore, Boys et al. (2016a) suggested that physoclist species can be more (Bidyanus bidyanus) or less (Maccullochella peelii) susceptible to swim-bladder rupture, when compared with Oncorhynchus tshawytscha, implying that other morphological traits of the swim bladder, such as elasticity and thickness of the wall,

could play an important role in determining rupture susceptibility.

Modifications in the swim-bladder morphology can alter its functionality and, therefore, help understand the effects of rapid decompression on fish. Dumbarton et al. (2010), studying physiological responses of the double-chambered swim bladder of Zebrafish (Danio rerio), showed that the anterior chamber exhibits an essential function in controlling swim-bladder volume and, therefore, buoyancy. This function had been, otherwise, deemed to be related to the posterior chamber (Fänge 1983). These authors also showed that the posterior chamber is likely to be more rigid than the anterior chamber, owing to a thicker muscle layer present in the former. This variation in the morphology and physiology of the swim-bladder chambers would be of paramount importance to understand barotrauma in fish with this type of swim bladder and, clearly, sustains the need to explore these topics more deeply as a greater diversity of fish species are tested. In this sense, experiments to determine the tensile strength of the swim-bladder tissue can significantly contribute to this understanding, especially for benthonic species, for which the current methods have shown limitations.

New approaches to contribute to barotrauma studies in benthonic species

Considering that the main limitations observed for barotrauma studies with benthic-oriented species are related to the buoyancy behaviour, which is influenced by the swim bladder morphology, we present potential approaches that can be used to either complement or substitute tests with a barotrauma chamber. These approaches have been tested to gather information related to the swim-bladder resistance (tensile strength), and the identification of maximum depths at which fish can maintain neutral buoyancy or be present before encountering hydro-structures. Therefore, we will describe the potential use of tensile-strength experiments to determine the maximum pressure sustained by a particular swim bladder and baited remote underwater videos (BRUV) to determine the maximum depth at which different fish species can be located.

Tensile experiments

The development of tensile tests has been important to determine the physical and mechanical properties of materials (Ogden *et al.* 2004). Biomechanics has emerged as a way for the development, extension and application of mechanics to better understand the physiology of biological tissues (Humphrey 2003), although its application has been strongly restricted to aid human health and treatment. Just a few studies have tried to understand the mechanical behaviour of animal tissues with no direct application to human health, such as the study of the tracheal tubes of the American cockroach (Webster *et al.* 2011).

Despite the limited number of studies on animal biological tissues, Beirão *et al.* (2015) showed the potential use of such approach to understand barotrauma in fish, especially in benthonic species for which limitations exist in the use of the conventional approach using barotrauma chambers. The tensile strength of the swim bladder can be determined using a universal tensile-testing machine (Carvalho *et al.* 2017). The testing machine can be purchased directly from different manufacturers Barotrauma on benthic-oriented species



Fig. 4. (*a*) Custom-made tensile machine composed of a mobile platform (centre of the figure), a digital ruler (white star) and a force sensor (black circle). (*b*) A swim bladder test specimen at an initial stage of stretching (white arrow) and (*c*) an example of test specimens' rupture in the centre (white arrow).

(e.g. Bose) or can be custom-made (Webster *et al.* 2011), depending on the user's needs. The development of a custom-made tensile-testing machine for experiments with swim bladder requires an interdisciplinary approach. For instance, Carvalho *et al.* (2017) developed tensile experiments with swim-bladder tissue, using a low-cost (~US\$3000) custom-made testing machine (Fig. 4).

To run tensile experiments with fish swim bladder, Carvalho et al. (2017) followed the International Standard Test Method for Tensile Properties of Plastics, developed by the American Society for Testing and Materials (ASTM International 2002). The shape of the testing specimens was defined on the basis of the ASTM International (2002), varying from a 'dog bone' to rectangularly shaped specimens. The loading rate for the experiments was also determined by the international standards (ASTM International 2002). For instance, Carvalho et al. (2017) used a loading rate of $50 \,\mathrm{mm}\,\mathrm{min}^{-1}$ to run tensile experiments with the swim bladder of curimbatá (Prochilodus lineatus). Data are considered suitable to be used if the test specimens rupture in the centre (Fig. 4). In general, the international standards (ASTM International 2002) would be recommended as a guideline for the development of tensile experiments with fish swim bladder because no specific set of methods has yet been developed specifically for this type of biological material. Table 2 presents a summary of the application, resources needed and limitations for the use of this approach.

The data obtained from the tensile experiments can be further explored to predict the likelihood of swim-bladder rupture as a result of pressure change, by using mathematical models. Beirão (2015) explored this approach and tested mathematical models that would determine the maximum pressure sustained by the swim-bladder tissue before rupture.

The model tested by Beirão (2015) was based on the model of Ogden (1984) and was chosen because of its application to biological materials (Ribeiro *et al.* 2012). Ogden (1984) suggested the following model, to which the tensile-strength data could be applied to:

$$F = W_0 \cdot L_0 \cdot \sum_{p=1}^{N} \mu_p (\beta^{\alpha_p - 1} - \beta^{-2\alpha_p - 1})$$

where *F* is the force obtained from the tensile experiments, *W* and *L* are the initial widths of the tested specimen and β is the ratio of the final length divided by the initial length. Given that these variables are obtained from the tensile experiments, this model can be used to infer the parameters μ_p and α_p , which are related to the characteristics of the tested specimen. Then, using this expression for the force and considering that the swim bladder is homogeneous material and has a spherical geometry, it is possible to deduce the following expression for the maximum pressure that the tested specimen would sustain before rupture:

$$P = 2 rac{E_0}{r_0} \cdot \sum_{p=1}^{N} \mu_p \left(eta^{lpha_p - 3} - eta^{-2lpha_p - 3}
ight)$$

Method proposed	Application for studies of barotrauma on fish	Resources needed	Limitation	References
Tensile experiments	 Provide data on swim-blad- der biomechanics that can feed into mathematical 	 Universal tensile testing machine 	 Lack of a standard method to develop the experiments 	(ASTM International 2002; Beirão 2015; Beirão <i>et al.</i> 2015; Currie <i>et al.</i> 2016; Carvalho <i>et al.</i> 2017)
	models (see <i>Tensile experi- ments</i> section) to inform the maximum pressure that the swim bladder can withstand	 Custom-made tensile test machine (L. G. M. Silva, unpubl. data; Fig. 3) 	 The size of the fish can constrain the obtainment of test specimens (swim bladder). The larger the fish, the easier to obtain test specimens The application can be limited to fish species in which the swim bladder can be removed intact 	
Baited remote underwater videos (BRUV)	 Allow the obtainment of data on the behaviour and buoyancy of fish species in the wild 	 Waterproof cameras and accessories (i.e. housing, underwater flashlights, camera mounting) suitable 	 Limited application for turbid waters 	A. L. F. de Castro (unpubl. data)
	 Contribute to the determi- nation of maximum depths in which fish will maintain neutral buoyancy 	for the type of habitat to be studied.	 Baits can be species- specific 	
	 Contribute to the under- standing of the vertical dis- tribution of fish in the water column. 		 Need to use different bait types for studies of multi- ple species. 	

Table 2.	Summary of the application, resources needed and limitation associated with the application of two proposed new approaches (tensile
	experiments and baited remote underwater videos) to contribute to barotrauma studies on benthic species

where *E* is the thickness of the tissue, *r* is the radius of the swim bladder, μ_p and α_p are material parameters obtained from the tensile test, and β^{α_p} is the material deformation, given by the ratio of the final length divided by the initial length.

The value obtained with the model would allow analysis of the maximum volume that the swim bladder would achieve before rupture. Therefore, considering that Boyle's law has been used to describe the pressure–volume relationship for the swim bladder, knowing the maximum pressure before tear, the volume of the swim bladder can be calculated and, therefore, the respective RPC that would cause rupture can be inferred.

Baited remote underwater video

One of the main needs related to barotrauma studies is the determination of acclimation depths of fish before exposure to hydro-structures. The maximum acclimation depth where a species is neutrally buoyant would be indicative of the maximum pressure that a fish can acclimate to and, therefore, provide for the calculation of the RPC and its correspondent gas expansion in the swim bladder (Brown *et al.* 2014). Various methods have been used to estimate the depth of fish in freshwater systems, mainly telemetry (acoustic and radio) and hydroacoustics. Nevertheless, each method presents different caveats that may limit the use of data for barotrauma studies. For instance, telemetry tags add mass to the weight of the fish and, therefore, alter fish buoyancy (Brown *et al.* 2009). Hydroacoustics is a great technique to locate the fish depth precisely, but it does not allow species identification (Pflugrath *et al.* 2012;

Prado and Pompeu 2014). In this sense, underwater videos have emerged as a powerful tool to overcome such limitations, providing for fish inventories, investigation of behaviour and passage through artificial structures (Cousins *et al.* 2017).

Baited remote underwater video (BRUV) consists of a nondestructive method that uses a video camera with a bait positioned in front of the camera to attract fish to the camera's field of view. The technique has been rapidly adopted to study composition, richness, habitat association and behaviour of marine fishes (Schmid *et al.* 2017). BRUVs have rarely been used to study fish in freshwater ecosystems, with a few studies in Australia (Ebner and Morgan 2013; Cousins *et al.* 2017) and one in a tropical river in Brazil (Schmid *et al.* 2017).

Baited remote underwater videos have been used in a wide range of benthic habitats and at various depths, with a few studies in tropical freshwater rivers designed to determine the depth-related composition of the fish fauna (Cousins *et al.* 2017). Advancements in camera technology have allowed the use of this method to study fish at depths up to 60 m, using inexpensive action cameras with high-quality images (resolution up to 4 k). We have conducted a few trials using BRUVs in a deep lake in Brazil, to demonstrate the high potential of this method in determining depth and buoyancy of fish. In this trial, crushed sardine was used as bait and fish was recorded at depths varying from 1 to 25 m. Fish buoyancy was reasonably simple to determine during the analysis of the footage, on the basis of the behaviour (continuous use of the fins to maintain position) and body orientation (head towards the surface (negatively



Fig. 5. Still images obtained with baited remote underwater videos (BRUV) at depths over 5 m in Dom Helvécio Lake, Doce River Basin, Brazil, showing (*a*) a school of neutrally buoyant Tucunaré (*Cichla* sp.) moving in front of the camera and (*b*) a trahira (*Hoplias* sp.) chasing the bait in negative buoyancy. Fish buoyancy can be determined on the basis of the body's position in the water column; neutrally buoyant: body horizontal; negatively buoyant: oriented head up.

buoyant), towards the bottom (positively buoyant) or horizontally oriented (neutrally buoyant; Fig. 5)).

The type of bait can influence the fish assemblage observed by the BRUVs and, therefore, running pilot tests with different bait types to determine the best type for a target species would be recommended before commencing a new study. Schmid *et al.* (2017) suggested the use of crushed sardine as a bait to optimise BRUV sampling because that bait recorded the highest richness, relative abundance and many specific rheophilic species in the Xingu River. Table 2 also addresses the potential application, resources needed and limitations of the use of BRUVs for studies that would contribute to understanding barotrauma in fish.

Therefore, BRUVs can be used to sample for fish in a stratified manner in the water column, so as to identify fish at different depths and determine their buoyancy. This method would meet one of the recommendations provided by Brown *et al.* (2014) related to the identification of migration depths of different fish. Even though the efficiency of the BRUVs can be affected by water turbidity, which can be a significant issue in tropical rivers, there is still a large number of rivers, lakes and reservoirs where the transparency would allow the acquisition of

high-quality footages, and, consequently, the evaluation of fish buoyancy. For instance, the work by Schmid *et al.* (2017) was conducted in the Xingu River, a tributary of the Amazon. To reduce potential issues owing to turbidity in the studied area, the authors developed the study in the dry season, when water transparency was higher. Species-specific data acquired on habitats auspicious for the use of BRUVs (i.e. high water transparency) can be easily extrapolated for similar species from catchments where the low visibility would limit the use of remote video. Given the potential and relatively low cost of the method compared to other technologies, such as telemetry, we encourage the development of trials to establish its effectiveness throughout a range of conditions.

Conclusions

The evidence observed in the experiments with the Pictus catfish have clearly demonstrated limitations that may occur in barotrauma studies with benthic species. The negative-buoyancy behaviour shown during the experiments prevents the definition of the acclimation pressure and, therefore, further calculation of the RPC. The RPC has been defined as the primary factor to predict the likelihood of barotrauma on fish. With limitations to calculate RPC, the development of dose–response relationships to determine barotrauma for benthic-oriented species may be hindered, requiring new approaches to complement the studies.

The limitations discussed in the present work may be directly related to the morphological traits of the swim bladder of Siluriformes. Evolutionary patterns show modifications on the swim bladder of Siluriformes fishes, such as reduction in volume and encapsulation of the anterior chamber in bone, that are likely to increase the sinking factor, which may explain the benthic behaviour. Also, Siluriformes have swim bladders with three chambers, and there is a knowledge gap concerning the understanding of the physiological processes to control the gas volume within this organ. Indeed, the development of studies aimed to understand the physiology of such swim-bladder types can provide data that can contribute to barotrauma studies.

Furthermore, the development of tensile experiments with the swim-bladder tissue has shown great potential in providing information related to the biomechanics of this organ. Biomechanic data can feed mathematical models that would allow calculations to define the maximum pressure supported by the swim bladder and, therefore, contribute to the definition of pressure-change thresholds more likely to provoke swimbladder rupture and further barotrauma. Given the potential application of the mathematical models described in the present study, we recommend the development of tensile experiments with the swim bladder of a variety of species, not only Siluriformes. International cooperation can be established for future efforts to obtain tensile-strength data that can feed a database that would allow for calculations of pressure thresholds for multiple swim-bladder types.

The need for studies to determine the acclimation depth for different species can be aided with the use of underwater cameras such as BRUVs. It is expected that benthic-oriented species would be able to acclimatise (attain neutral buoyancy) to deeper depths and, therefore, be more susceptible to barotrauma. However, there is also a considerable knowledge gap related to both the understanding of the maximum depths occupied by benthic-oriented species in freshwater ecosystems and the determination of buoyancy achieved at different depths. The BRUVs can be used to sample for fish in a stratified manner across a range of depths (up to 60 m, using low-cost, highresolution action cameras such as GoPro and Sony 4k) to detect and identify fish, as well as to determine buoyancy.

Finally, catfishes are within the major groups of the megadiverse tropical river basins and, in Brazil, represent the majority of the species identified in mortality events in turbines. Considering that the tropical region is expected to face an unprecedented development of hydropower plants, there is a pressing need to quickly gather information that would contribute to better inform mitigation plans and sustainable designs of such water infrastructure. Probably, the thresholds for pressure changes identified for nektonic species, such as salmonids, do not apply to demersal groups, both benthic and benthopelagic species. Therefore, mitigation measures or definition of new designs for turbines based on those thresholds may not contribute to the protection of catfishes and this constraint should be acknowledged in future studies. At those megadiverse tropical freshwater ecosystems, catfishes are generally within the groups of significant importance to both recreational and artisanal fisheries, containing gigantic species, such as the Piraíba (Brachyplatystoma filamentosum) in the Amazon, the Mekong giant catfish (Pangasianodon gigas) and the Kokuni catfish (Chrysichthys cranchii) in the Congo basin. Indeed, hydropower dams pose a significant threat to these species, highlighting the urgent need to broaden the approaches for barotrauma studies to provide better information for the development of mitigation and new turbine designs that would improve protection of such iconic species of Siluriformes.

Conflicts of interest

Luiz G. M. Silva is an Associate Editor for *Marine and Freshwater Research*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept entirely separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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