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American eel state of buoyancy and barotrauma susceptibility associated with hydroturbine passage

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Abstract – American eel are likely to encounter and pass through hydropower turbines, particularly during the downstream spawning migration, where exposure to stressors can potentially lead to injuries and mortality. Previous research has recovered dead eels downstream of hydropower facilities and, for some fish, injuries were easily attributed to blade strike; however, others showed no external signs of injury suggesting that other stressors, such as rapid decompression may be a potential source of mortality. For this research, yellow– and silver-phase American eel were held and allowed to acclimate to 172 kPa (absolute pressure) in hyper/hypobaric hydro-chambers for about 1 d. After acclimation, the state of buoyancy was determined prior to exposure to a rapid decompression simulating pressures encountered during hydroturbine passage. Fish were then examined for signs of barotrauma. Eel did not attain a state of neutral buoyancy but rather maintained negative buoyancy suggesting that eels, and possibly other benthic species, likely maintain a state of negative buoyancy to facilitate occupancy on or near the substrate. Additionally, eel were found to be resilient to rapid decompression, displaying no instantaneous mortality and minimal injuries, suggesting that barotrauma is not likely a major concern for American eel passing downstream through hydroturbines.

Keywords: downstream fish passage / rapid decompression / hydropower / swim bladder / hyperbaric / hypobaric

Résumé – État de flottabilité de l'anguille d'Amérique et sensibilité aux barotraumatismes associés au passage des hydroturbines. L'anguille d'Amérique est susceptible de rencontrer et de traverser des turbines hydroélectriques, en particulier pendant la dévalaison, où l'exposition aux facteurs de stress peut potentiellement entraîner des blessures et la mortalité. Des recherches antérieures ont permis de récupérer des anguilles mortes en aval d'installations hydroélectriques et, pour certains poissons, les blessures étaient facilement attribuables à des coups de lame ; cependant, d'autres n'ont montré aucun signe externe de blessure, ce qui laisse croire que d'autres facteurs de stress, comme la décompression rapide, peuvent être une source potentielle de mortalité. Pour cette recherche, des anguilles d'Amérique en phases jaune et argentée ont été maintenues et acclimatées à 172 kPa (pression absolue) dans des hydrochambres hyper/hypobares pendant environ 1 jour. Après acclimatation, l'état de flottabilité a été déterminé avant l'exposition à une décompression rapide simulant des pressions rencontrées lors du passage de l'hydroturbine. Les poissons ont ensuite été examinés à la recherche de signes de barotraumatisme. L'anguille n'a pas atteint un état de flottabilité neutre, mais a plutôt maintenu une flottabilité négative, ce qui donne à penser que les anguilles, et peut-être d'autres espèces benthiques, maintiennent probablement un état de flottabilité négative pour faciliter l'occupation sur le substrat ou à proximité. De plus, on a constaté que l'anguille résistait bien à la décompression rapide, qu'elle ne présentait aucune mortalité instantanée et qu'elle n'avait subi que des blessures minimes, ce qui laisse supposer que le barotraumatisme n'est probablement pas une préoccupation majeure pour l'anguille d'Amérique qui passe en aval par des hydroturbines.

Mots-clés : passage de poissons en aval / décompression rapide / hydroelectricité / vessie natatoire / hyperbare / hypobare

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1 Introduction

Hydropower has long been a favored choice of energy generation, accounting for $>16\%$ of global electricity production owing to its reliability compared to other renewables and lower greenhouse gas emissions compared to non-renewable forms of energy production (Agency, 2017). Although hydropower is a major producer of renewable and relatively inexpensive energy, its production can come at a cost to the environment, especially the aquatic ecosystem. In addition to impairments to water quality, habitat and ecosystem connectivity (Liermann *et al.*, 2012; Ziv *et al.*, 2012; Fantin-Cruz *et al.*, 2016; Buddendorf *et al.*, 2017), hydropower facilities can cause direct injury and mortality of fishes during dam passage (Coutant and Whitney, 2000; Pracheil *et al.*, 2016). Dam passage mortality is of particular concern for migratory fish species that must pass through hydropower facilities to complete their life cycle (Francfort *et al.*, 1994; Haro *et al.*, 2000b; Jager, 2006).

Exposure to rapid decompression is one of several stressors that fish passing hydropower facilities may experience, particularly when passing through turbines (Čada, 2001). The degree to which a fish is exposed, to rapid decompression, can vary dramatically (Duncan, 2011, 2013; Duncan and Carlson, 2011; Fu *et al.*, 2016; Hou *et al.*, 2018), but when severe, barotrauma (physical damage to body tissues caused by changes is pressures) can occur, which can potentially be fatal. Initially, the focus of hydraulic structure induced barotrauma has focused on salmonid species passing through large hydroelectric turbines (Brown *et al.*, 2012a; b; Pflugrath *et al.*, 2012); however, to further improve fish passage, additional species and structures are continuously being examined (Colotelo *et al.*, 2012; Brown *et al.*, 2013; Boys *et al.*, 2016; Fu *et al.*, 2016; Pflugrath *et al.*, 2018; Boys *et al.*, 2018; Beirão *et al.*, 2018; Silva *et al.*, 2018). As additional species are examined, it is clear that the methodology of assessing barotrauma, that is suitable for one group of species may not be suitable for other species, particularly the state of buoyancy prior to decompression.

The state of buoyancy prior to decompression has been determined to be a crucial variable for predicting barotrauma susceptibly for fish that are exposed to rapid decompression (Stephenson *et al.*, 2010). Determining the state of buoyancy for fish is quite simple, if the fish is oriented head up or resting on the bottom it is negatively buoyant, head down or floating on the surface it is positively buoyant, and if the fish is horizontal in the water column then it is neutrally buoyant (Harvey, 1963; Stephenson *et al.*, 2010; Pflugrath *et al.*, 2012). A state of neutral buoyancy minimizes swimming efforts needed to remain at a specific level within the water column (Harvey, 1963; Sundnes and Bratland, 1972). If a fish is not neutrally buoyant, it will have to swim against either the buoyant force (positive buoyancy) or gravity (negative buoyancy), which results in the head-down or head-up orientation.

Examining barotrauma in neutrally buoyant fish is advantages, because when neutrally buoyant, the volume of the swim bladder is directly corelated to the mass of the fish and the ambient pressure (Pflugrath *et al.*, 2012). The swim bladder is the foremost driving force of barotrauma in fish and knowing the initial state of the swim bladder prior to decompression allows for an accurate estimate of the degree to which the decompression will affect the fish (Brown *et al.*, 2012b; Colotelo *et al.*, 2012). This is because the gas within the swim bladder follows Boyle's Law, and has an inversely proportional relationship with the pressure. That is, if the pressure is reduced by half, the gas within the swim bladder will double in size (assuming temperature remains constant and no physiological constraints). Therefore, the ratio of the initial pressure (acclimation pressure, P_A) to the lowest pressure that a fish is exposed to (nadir pressure, P_N) is a direct representation of the factor at which the swim bladder expands during decompression. This ratio is known as the ratio of pressure change (RPC) (Stephenson *et al.*, 2010; Brown *et al.*, 2012a; b). For example, a fish that is acclimated to a depth of 10 m ($P_A = \sim 200$ kPa) and decompressed to 50 kPa (P_N) will be exposed to a RPC of 4 ($200/50 = 4$) and the gas within the swim bladder will quadruple in size. This method has allowed researchers to develop clear relationships between mortality or injury and RPC, allowing for the prediction of the likelihood that a fish will die or be injured when exposed to a specific decompression (Brown *et al.*, 2012a; Pflugrath *et al.*, 2018). However, for benthic fish, it is not likely advantageous to attain neutral buoyancy, as maintaining a state of negative buoyancy would allow a fish to rest on the substrate (Beirão *et al.*, 2018). Therefore, the current method of using RPC to predict barotrauma may not be suitable for benthic species (Silva *et al.*, 2018).

American eel (*Anguilla rostrata*) are known for their iconic spawning migrations from rivers to the Sargasso Sea and is likely to encounter hydropower plants during these migrations, which may cause injury or mortality via turbine entrainment. Prior to these migrations, yellow-phase eel live in rivers and reservoirs where they can also potentially be entrained. American eel was listed as “Endangered” by Ontario's (Canada) Endangered Species Act in 2008, “Threatened” by the Committee on the Status of Endangered Wildlife in Canada (Tremblay, 2012), and is under current reviews for inclusion in multiple other conservation lists. In North America, the species has become a particular concern for resource and hydropower managers. During their downstream migration, American eel may encounter hydroelectric dams and turbine passage has been identified as one of the potential factors contributing to population declines over the past several decades (Haro *et al.*, 2000b).

Relatively few field studies have been conducted to quantify the occurrence of turbine passage and associated mortality of American eel during their downstream passage through hydroelectric dams. However, past studies indicate that a large proportion of silver-phase American eel may pass through turbines with high, but variable, mortality. (Haro *et al.*, 2000a; Carr and Whoriskey, 2008; Brown *et al.*, 2009; Eyler *et al.*, 2016). Similar to field studies on American eel, evaluations of European eel (*Anguilla anguilla*) have reported a large proportion of eel passing through turbines with high, but variable, mortality. (Jansen *et al.*, 2007; Calles *et al.*, 2010).

Few field studies have documented the mechanism of dam passage mortality for silver-phase eels. However, evidence of blade strike mortality is easily observed and has been reported on several occasions. For example, wild short-finned eel (*Anguilla australis*) were captured in a fyke net downstream of a hydroelectric dam on the Patea River in New Zealand

(Watene and Boubée, 2005). Of the eight dead eel recovered, three were cut in half, indicating they passed through the turbines, and one other showed signs of external injury; however, the other four dead eel showed no signs of external damage. It is possible that these fish died from internal injuries caused by rapid decompression during turbine passage.

Silver-phase eel are more likely to be entrained into turbines than yellow-phase eel, because of migratory behavior. However, yellow-phase eel may still encounter turbines. A portion of yellow-phase American eel populations have been observed to complete extensive upstream and downstream movements, and were classified as vagrant (Béguer-Pon *et al.*, 2015). Additionally, transformation from yellow– to silver-phase can occur either during or before the downstream spawning migration (Vladykov, 1971; Wenner and Musick, 1974; Winn *et al.*, 1975; Hammond *et al.*, 2003). Since both phases may encounter hydroturbines and American eel undergo significant physiological changes during the transition from yellow– to silver-phase, both phases were included as part of the present research to determine if these physiological changes can effect barotrauma susceptibility. For the present study, we evaluated buoyancy response of American eel when held at simulated depth and assessed barotrauma susceptibility in both yellow– and silver-phase American eel by exposure to simulated turbine passage pressures.

2 Methods

2.1 Fish acquisition

Both yellow– and silver-phase American eel were purchased from South Shore Trading Co. Ltd (Port Elgin, NB, Canada), a distributor and exporter of freshwater eel which purchase eels from fisherman in the New Brunswick (Canada) and Maine (USA) region. Eel were shipped from South Shore Trading Co. to Pacific Northwest National Laboratory's (PNNL) Aquatics Research Lab (ARL). Yellow-phase eel were acquired in the spring of 2016 and silver-phase eel in the fall of 2017.

The median length of yellow-phase eel was 306 mm (range 230–423 mm) with a median mass of 44.4 g (range 16.9–116.1 g) and the silver-phase eel had a median length of 426 mm (range: 216–686 mm) and median mass of 162 g (range: 14–507 g). A total of 105 yellow-phase and 108 silver-phase eel were used for buoyancy assessment and rapid decompression experiments from June 3, 2016 through August 2, 2016, and from November 17, 2017 through January 7, 2018, respectively.

Fish were held in ~1000 L circular tanks at the PNNL ARL and provided with circulating aerated water from the Columbia River (yellow-phase eel: range 17.1–21.7 °C; silver phase eel: range 5.1–12.6 °C). Water quality, including total dissolved gas (TDG), dissolved oxygen (DO), and temperature, was maintained at consistent levels throughout the duration of the study periods. Generally, TDG levels were $\leq 100\%$ and DO levels were $\geq 90\%$. During the holding period, yellow-phase eel were fed with earthworms (*Lumbricus terrestris*) and eventually took to pellet feed (BioVita Fry, Bio-Oregon, Longview, WA) to satiation. Food was restricted 48 hours prior to testing. Silver-phase eel were withheld feed during holding.

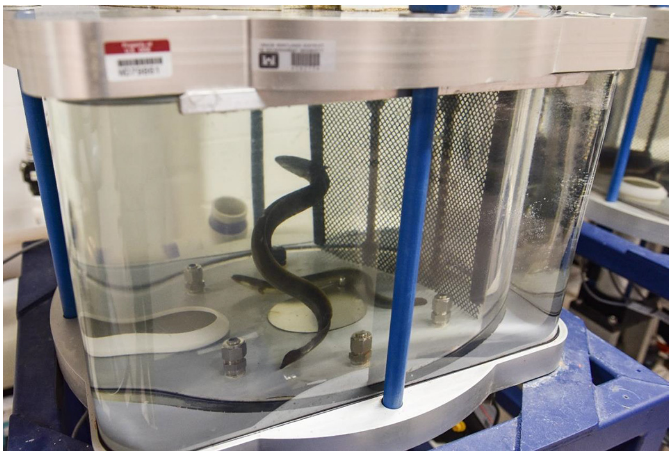

Fig. 1. Two American eel acclimating inside a hyper/hypobaric hydro-chamber.

2.2 Buoyancy assessment

Yellow-phase eel were netted from the general population and anesthetized by placing them in an aerated container with a concentration of tricaine methanesulfonate (MS-222, ~80 g/L). Anesthetized fish were measured for total length and mass. Fish were allowed to recover in aerated fresh water until they regained equilibrium. To minimize handling with silver-phase eel, fish were netted from the general population and directly loaded into hyper/hypobaric hydro-chambers; measuring was conducted prior to necropsy. The computer controlled hyper/hypobaric hydro-chambers follow preprogramed pressure profiles to simulate the pressure fish experience when passing through hydroturbines (described by Stephenson *et al.*, 2010). Two fish were loaded into a single chamber and pressurized to 172 kPa (Fig. 1). The pressure of 172 kPa was used because it is equivalent to approximately 7 m depth, which is the common depth of occupancy for silver-phase American eel reported in the literature (Haro *et al.*, 2000a; McGrath *et al.*, 2002; Geer, 2003).

Fish were allowed to acclimate to 172 kPa for approximately 1 d before they were assessed for buoyancy. To determine the buoyancy, fish were visually examined using the following criteria: fish observed to be free swimming with a horizontal orientation and minimal swimming effort to maintain elevation in the water column were considered neutrally buoyant; fish exhibiting elevated swimming effort and a head-up or head-down orientation were considered negatively and positively buoyant respectively (Harvey, 1963; Stephenson *et al.*, 2010; Pflugrath *et al.*, 2012). Secondly, fish were slowly decompressed to determine the pressure of neutral buoyancy. Decompressing the fish reduces pressure on the swim bladder allowing it to expand which increases the buoyancy of the fish. The point at which the anterior portion of the fish (where the swim bladder is located) floated off the bottom of the chamber was determined to be the pressure at which the fish was neutrally buoyant. Pressures were not reduced below atmospheric pressure as to avoid causing the fish to expel gas from the swim bladder. Once this point was reached for both fish, the chamber was repressurized to 172 kPa.

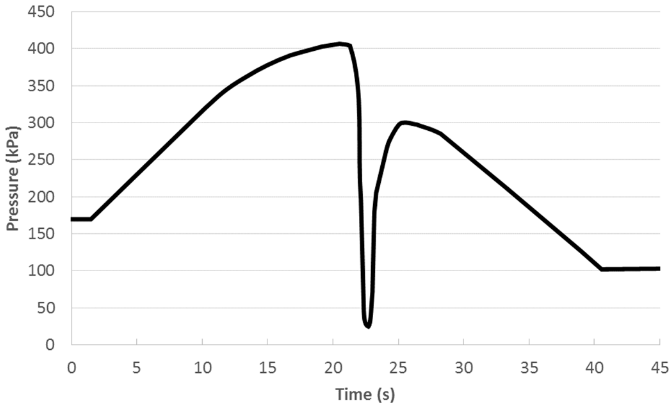

Fig. 2. Example of a pressure exposure simulating passage through a hydroturbine.

2.3 Rapid decompression

After buoyancy was assessed and pressure was restored to 172 kPa, fish were exposed to simulated turbine passage pressures (Fig. 2). Pressure profiles were developed from data obtained from a Kaplan turbine by deploying Sensor Fish, an autonomous senor package that records physical conditions that fish are likely to experience when passing through a hydro structure such as a turbine (Brown *et al.*, 2012a; Deng *et al.*, 2014). The nadir pressure was varied so that fish were examined across a range of RPC, which is not intended to represent a distribution from a specific turbine, but a range that encompasses pressures that might be observed through most turbines. As was observed with Sensor Fish, pressure within the chambers was gradually increased to about 400 kPa over 20 s simulating entry into the penstock. A rapid decompression (< 1 s) to subatmospheric pressures simulated pressures during passage through the turbine runner, and a pressure increase to about 300 kPa (~2 s) before gradually returning to atmospheric pressure, simulated passage through the draft tube and exit into the tailrace. During decompression, fish were observed and recorded via video cameras (8 Camera Pro Series, CCTV Security Pros, Cherry Hill, New Jersey USA), to determine if eel expelled gas from their swim bladders during decompression. A portion of fish was designated as controls, which were treated the same as exposure fish, including observations and necropsy, but were not exposed to the rapid decompression scenario.

2.4 Barotrauma assessment

Fish were removed from the chamber and assessed as alive or dead by presences or lack of ventilating. Fish determined to be dead or showing elevated signs of distress (non-responsive, prolonged disorientation, and swimming erratically) were immediately euthanized and necropsied. Alive fish were moved to holding tanks for up to 48 h. Fish were monitored and if showing signs of distress, were immediately euthanized and necropsied. Following the 48 h post-treatment holding period, all remaining fish were euthanized and necropsied. Necropsies included both an external and internal examination of the eel, looking for barotraumas such as emboli and hemorrhaging throughout the structures and organs of the fish (Stephenson *et al.*, 2010; Brown *et al.*, 2012a; Pflugrath *et al.*, 2018).

Table 1. Pressures at which American eel were found to be neutrally buoyant after 1 d of acclimation to 172 kPa. Pressures were not measured below atmospheric pressures (atm), therefore the median for silver-phase eel is presented as less than or equal to atmospheric pressure.

	Yellow-phase	Silver-phase
n	100	107
$n \leq$ atm	24	67
Max (kPa)	169.6	159.0
Median (kPa)	124.5	$\leq$ 101.3

2.5 Analysis

The neutral buoyancy pressures for both the yellow– and silver-phase American eel were analyzed using a normality test (Shapiro-Wilk; $\alpha = 0.05$; SigmaPlot). The test was found to be non-normal; therefore a rank sum test (Mann-Whitney; $\alpha = 0.05$; SigmaPlot) was used to determine if there were differences between the phases.

The relationship between RPC and injury or mortality was modeled using logistic regression for both yellow– and silver-phase American eel. The natural log of RPC served as the predictor variable and the occurrence of injury or mortality served as the response variable.

3 Results

3.1 Buoyancy

Buoyancy was successfully determined for 100 yellow-phase and 107 silver-phase American eel, all of which were negatively buoyant at 172 kPa (Tab. 1). A majority (67 of 107; 62.6%) of the silver-phase eel were observed to be neutrally buoyant at pressures equal to or less than atmospheric pressure (Fig. 3). Yellow-phase eel was found to be neutrally buoyant at pressures significantly (Mann-Whitney, $p = < 0.001$) greater than silver-phase eel.

3.2 Barotrauma

A total of 101 and 90 yellow- and silver-phase American eel, respectively, were successfully exposed to rapid decompression. Very few injuries and no instantaneous mortalities were observed for both phases of American eel (Tab. 2). Exposures were similar for yellow– and silver-phase eel, with yellow-phase eel on average being exposed to a slightly greater decompression (Tab. 2). Neither the occurrence of injury (Logistic regression, yellow phase $p = 0.964$, silver phase $p = 0.659$) nor mortality (Logistic regression yellow phase no mortality, silver phase $p = 0.963$) was found to be significantly correlated to RPC for either phases. Parasites were commonly found in both phases and were predominately found within the swim bladder (Tab. 2). No injuries or mortality was observed in the control fish for either phase.

4 Discussion

When held at elevated pressures, eel did not attain a state of neutral buoyancy. This differs greatly from Chinook salmon

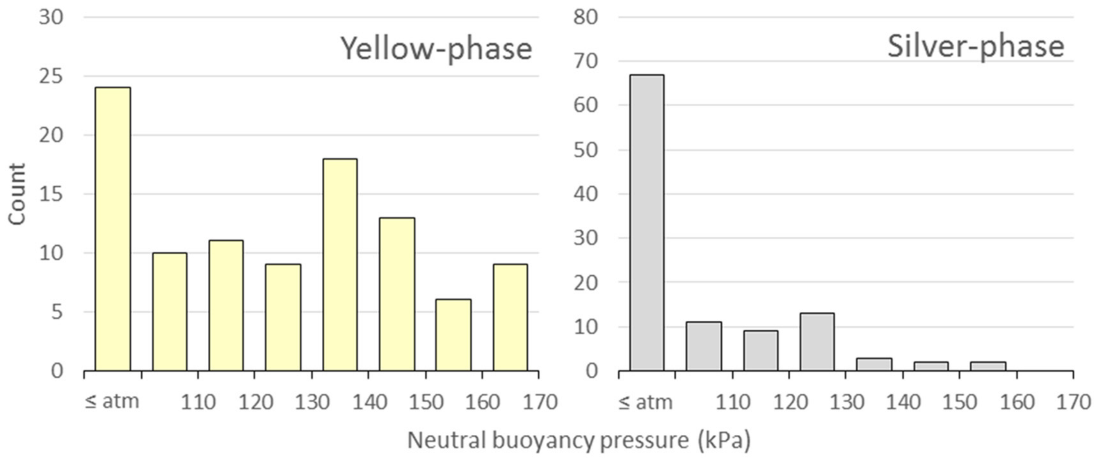

Fig. 3. Distribution of pressures that yellow– and silver-phase American eel were found to be acclimated to after 1 d of acclimation to 172 kPa. The first column in each chart represents the number of eel that were acclimated to pressures less than or equal to atmospheric pressures (101.3 kPa).

(*Oncorhynchus tshawytscha*), of which 79% became neutrally buoyant when acclimated to 175 kPa for 1 d (*unpublished data from* (Stephenson *et al.*, 2010)). This supports the hypothesis that American eel may prefer a state of negative buoyancy to reduce energy expenditures while inhabiting the bottom of the water column.

Both phases of American eel were observed to have very low susceptibility to barotrauma. The silver-phase eel was exposed to a median RPC of 9.3 (10.2 for yellow-phase), which would be expected to inflict mortality rates of approximately 95% in Chinook salmon (Brown *et al.*, 2012a). Yet, no instantaneous mortality was observed in either phase of American eel and only about ten percent of either phase was observed with injuries attributed to barotrauma. These low injury rates and no instantaneous mortality, at relatively high RPC, suggest that barotrauma at hydropower facilities is not likely a major concern for yellow– and silver-phase American eel.

Yellow-phase eel were found to be neutrally buoyant at greater pressures when compared to silver-phase eel. Therefore, yellow-phase eel would have a greater amount of gas within the swim bladder on average and would therefore likely be more susceptible to barotrauma than silver-phase eel. Swim bladder ruptures were observed in yellow-phase eel and not in silver-phase eel, supporting this hypothesis. However, other injuries did not follow the same trend, as a similar but slightly greater portion of silver-phase eel sustained injuries. This is contrary to previous research, which has found that swim bladder rupture is highly correlated to injury and mortality (Brown *et al.*, 2012a), and may suggest that physiological changes that occur during transformation from yellow– to silver-phase eel, may alter barotrauma susceptibility.

Throughout the American eel life-cycle, the swim bladder undergoes various changes. The development of the eel swim bladder is linked directly to the life cycle of this catadromous fish and develops for specific purposes as the eel matures. Larval eel spends one to three years migrating from the Sargasso Sea to inland freshwater systems, and, during this time, eel develop a physostomous swim bladder, which is primarily filled and expelled via the pneumatic duct, a direct connection to the esophagus of the fish (Fänge, 1966; Pelster, 2013). Once they enter freshwater, eel transform into sexually immature yellow-phase eel (Pelster, 2013). A yellow-phase eel's metamorphosis into a silver-phase eel starts once the fish becomes sexually mature and begins its return journey to the Sargasso Sea (Pelster, 2013). It is during this time that the eel's swim bladder starts functioning similar to a physoclistous fish (Pelster, 2013), which relies on a rete (vascular bundle) to add or remove gas from the swim bladder (Fänge, 1966). The transformation of the eel swim bladder is essential during their spawning migration from freshwater to the Sargasso Sea wherein they undertake diel vertical migrations between depths of 200 and 1000 m (Aarestrup *et al.*, 2009). There is currently a lack of literature to suggest when, during this transition from yellow-phase to silver-phase, the swim bladder changes, particularly if this occurs in freshwater, or once they enter saltwater.

During the present study, a majority of silver-phase eel (64 of 90) was observed expelling gas from the swim bladder during decompression, whereas, slightly less than half (45 of 101) of the yellow-phase eel exhibited this reflex. This suggests that the pneumatic duct is still functional in silver-phase American eel. To attain depths of 1000 m (> 10 000 kPa) during the migration to the Sargasso Sea, it is not practical for an eel to fill the swim bladder by gulping air at the water surface. In order to attain a state of neutral buoyancy at a depth of 1000 m, the eel would be required to gulp a volume of air equal to 100 times the volume needed for neutral buoyancy at atmospheric pressure. Not only is this impossible, but the eel would then have to fight a significant buoyant force in order to dive to deeper depths. Therefore, to introduce gas into the swim bladder, the eel must rely heavily, if not exclusively, on the rete. However, if the pneumatic duct still remains functional, the eel may be capable of expelling gas from the swim bladder rapidly, rather than relying on the rete which can take considerably longer (Fänge, 1983). This would aid eel in the extensive diel vertical migrations that have been observed (Aarestrup *et al.*, 2009). Eel have a considerably more developed rete on the swim bladder than most other physostomous fish and can regulate gas within the swim

Table 2. Number, exposure, and occurrence of mortality and injuries in yellow– and silver-phase American eel exposed to rapid decompression simulating hydroturbine passage. Percentages represent the portion of exposed fish that were recorded with the designated injury or observation.

	Yellow-phase	Silver-phase
Exposure		
Nadir (kPa) median (range)	2.4 (1.2–8.1)	2.7 (1.6–8.4)
RPC median (range)	10.2 (3.1–21.4)	9.3 (3.0–16.1)
n	105	108
Control	4	18
Exposed	101	90
Instantaneous mortality	0	0
Injured	11 (10.9%)	12 (13.3%)
Swim bladder rupture	6 (5.9%)	0
Emboli		
Heart	0	1 (1.1%)
Hemorrhaging		
Intestinal	1 (1.0%)	0
Liver	0	4 (4.4%)
Heart	0	1 (1.1%)
Swim bladder	3 (3.0%)	1 (1.1%)
Pectoral fin	3 (3.0%)	1 (1.1%)
Anal fin	0	3 (3.3%)
Dorsal fin	0	1 (1.1%)
Hematoma		
Liver	1 (1.0%)	1 (1.1%)
Ruptured gall bladder	0	5 (5.6%)
Intestinal volvulus	1 (1.0%)	0
Burst capillaries along kidney wall	1 (1.0%)	0
Parasites	52 (49.5%)*	98 (90.7%)*
Expelled gas during decompression	45 (45.0%)	64 (71.1%)

* Percentages include controls.

bladder by gas exchange at similar rates to physoclistous fish (Fänge, 1983). Because the swim bladder expansion that occurs during rapid decompression is one of the driving forces of barotrauma, the ability to quickly remove gas from the swim bladder has been proposed as an ability that may prevent barotrauma (Brown *et al.*, 2012a; b). Swim bladder rupture was not an issue for silver-phase eel, likely due to their ability to expel gas from the swim bladder and the state of negative buoyancy prior to decompression.

Testing further acclimation pressures may reveal buoyancy capabilities of eel. During necropsy, eel did not appear to have under inflated swim bladders. This may suggest that at maximum capacity, the volume of the swim bladder may not provide sufficient buoyancy for the fish to even attain neutral buoyancy. Testing the maximum capacity of the swim bladder (Pflugrath *et al.*, 2012) may reveal that eel are actually incapable of attaining neutral buoyancy. Additionally, during other rapid decompression studies, Chinook salmon was acclimated to three different pressures, and as the pressures increased, less and less fish attained neutral buoyancy after 1 d of acclimation (unpublished data from (Stephenson *et al.*, 2010; Brown *et al.*, 2012a)). This was noteworthy because fish were provided a gas pocket to enable gulping gas into the swim bladder and this gas pocket was pressurized. Access to a pressurized air pocket should enable these fish to artificially fill the swim bladder with more gas than would be possible in nature and allow them to attain neutral buoyancy at any pressure within the chambers. However, at the greater acclimation pressure, which happened to be near the maximum pressure at which Chinook salmon would be capable of attaining neutral buoyancy in nature (Pflugrath *et al.*, 2012), a significant portion of fish did not attain neutral buoyancy. If eel were held at a pressure closer to surface pressure, they may have attained neutral buoyancy. For the present study, acclimation pressures were selected based on the likelihood that eels inhabit the bottom of the water column and will enter turbine intakes from depth (Haro *et al.*, 2000a; McGrath *et al.*, 2002; Geer, 2003). However, there is potential, especially in cases where low-head hydropower is installed, that eels may enter turbines from shallower depths and it may be beneficial to examine additional acclimation depths.

The health of the swim bladder is likely critical for migrating eel. During the extensive spawning migrations to the Sargasso Sea (Aarestrup *et al.*, 2009), eel require a highly functioning swim bladder and any impairment of swim bladder function significantly threatens the success of the spawning migration (Pelster, 2015). Though no instantaneous mortality was observed in the yellow-phase American eel, nine fish were observed to have injuries to the swim bladder. Additionally, parasitic nematodes (*Anguillicoloides crassus*) were observed in many of the swim bladders of both phases of examined fish. These nematodes cause physiological damage to the swim bladder of infected eels and impair swim bladder function (Székely *et al.*, 2009; Pelster, 2015). European eel has been observed to have a reduced rate of gas secretion when infected, which could affect buoyancy (Würtz *et al.*, 1996). In the present study, infected yellow-phase eel had a much lower frequency of expelling gas from their swim bladder during exposure to rapid decompression (about 55%) compared to non-infected eel (about 88%). In this study, it is unclear whether the presence of these parasites in the swim bladder prevented them from expelling gas through the pneumatic duct or whether infected eel had less gas in their swim bladders prior to decompression due to the presence of the nematodes. However, previous research has shown that adult eel with more than 10 adult parasites in their swim bladder have been observed to contain 60% less gas in their swim bladders compared to uninfected eel (Würtz *et al.*, 1996). Either way, the presence of parasites in the swim bladder, which was observed in 70% of eel in this study and is suggested to be a common issue for many species of eels (Székely *et al.*, 2009), is likely to influence the response to rapid decompression events that occur during turbine passage.

The present study and others have demonstrated that the state of the swim bladder, and therefore buoyancy of the fish, is a critical variable for predicting barotrauma. However, no field studies have been able to determine the state of buoyancy of fish in situ. Three-dimensional (3D) acoustic telemetry has been used to determine the depths of active migrating fish, but this has been limited to juvenile Chinook salmon (Li *et al.*, 2018). 3D acoustic telemetry provides significant insight as to what depth fish may be acclimated to prior to entrainment through turbines;

however, it doesn't determine the state of buoyancy. Further research is needed to develop methods to determine the state of buoyancy prior to turbine passage, especially in species such as eels and other benthic fish (Silva *et al.*, 2018).

5 Conclusion

The present study suggests that yellow– and silver-phase American eel are not likely to attain neutral buoyancy, but rather maintain a state of negative buoyancy, possibly to aid in remaining at the bottom of the water column. Additionally, this state of negative buoyancy, and the ability to expel gas from the swim bladder, may provide a safe guard to barotrauma as these fish were found to have a high tolerance to rapid decompression. An *in situ* examination of the state of buoyancy is advisable to confirm that these results are not biased by any artificial variables that are inherent while conducting laboratory studies.

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