

**The swimming performance of Freshwater Drum (*Aplodinotus grunniens*) below Claiborne Lock and Dam and in various temperature and dissolved oxygen treatments**

by

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## Abstract

Alterations to temperature and dissolved oxygen regimes in the tailwaters below dams can cause harmful stress to fish. Although Freshwater Drum *Aplodinotus grunniens* are widespread in rivers across North America, this species has received little attention relative to effects of these potential stressors. Quantifying their detection and simulating their swimming performance in tailwaters can provide insight as to how riverine species are affected by these alterations. In an acoustic telemetry study, I categorized the tailwaters below Claiborne Lock & Dam along the Alabama River in southwestern Alabama into three distinct habitat zones and found a majority (51.6%) of Freshwater Drum detections occurred within the gated spillway habitat zone. One passage event was observed, likely over the crested spillway during inundation. I quantified Freshwater Drum critical swimming speed ( $U_{crit}$ ), tail beat frequency, and tail beat amplitude under all combinations of hypoxic (4 ppm), normoxic (9), and hyperoxic (14) conditions at low (10°C), intermediate (20°C), and warm (30°C) water temperatures in 90-L and 850-L swim flumes. Dissolved oxygen concentration did not affect swimming performance.  $U_{crit}$  and tail beat frequency decreased with fish length but increased with temperature. Tail beat amplitude increased with fish length but did not statistically differ across temperature. Analysis of field data suggest a habitat preference in the downstream tailrace of Claiborne Dam in deep, open water. Hypoxia within the tested range may not be as detrimental to swimming performance as once thought. The influence of temperature on Freshwater Drum swimming performance suggests that the depth at which water is withdrawn at dams can impact the potential for fish to hold position or even pass that structure and may vary seasonally. Management practices can promote the probability of successful passage by reducing fishing pressure during winter months within the tailrace habitat. Appropriate water velocity criteria for

withdrawal and by-pass channel design can be established using information presented in this thesis. Adjustments in flume size and solid-blocking correction should be considered for future experimentation.

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## **Introduction**

Over 7,000 dams at a height of three meters or higher currently exist across United States rivers (NID 2018). These structures retain water, helping to control high water flows, reduce flood damage, and assist with navigation (Juracek 2015; NID 2018). In addition, dams can provide recreational opportunities, generate hydroelectric power, and regulate water levels, providing economic and social benefits to communities that use the advantages they provide (Lessard and Hayes 2003). Dams impact riverine systems in fundamental ways. They slow the flow of water by creating reservoirs which, in turn, influence downstream conditions by altering flow and potentially other physical-chemical parameters. Overall, dams modify connectivity among stream reaches (Juracek 2015). While upstream reservoirs provide habitat for lentic organisms, dams present challenges for riverine organisms such as migratory fishes that rely on unimpeded river flow (Lessard and Hayes 2003; Cooper et al. 2017). These fish swim upstream and downstream during various life stages, migrating between spawning grounds and feeding habitat. When dams block their pathway, fish may struggle to find appropriate habitat (Jager et al. 2001; Lessard and Hayes 2003; Cooper et al. 2017). Reproductive isolation can lead to changes in genetic diversity and raises the risk of population extinction (Jager et al. 2001). Dams impose other challenges that can affect both migrating and non-migrating fishes (Lessard and Hayes 2003). Depending on height, width, and release method, dams can influence water quality, most importantly temperature and dissolved oxygen in the downstream waters (Armour 2001; Lessard and Hayes 2003; Olden and Naiman 2010; Franklin 2014).

Tailwater temperature and dissolved oxygen concentration are directly affected by the depth from which water is released from the reservoir (Lessard and Hayes 2003; Olden and Naiman 2010). Upstream reservoirs can stratify seasonally (Wetzel 2001; Olden and Naiman

2010). Through hypolimnetic versus epilimnetic withdrawal from the reservoir, dams can significantly modify downstream thermal regimes (Stanford and Ward 2001; Olden and Naiman 2010). Hypolimnetic (or coldwater) withdrawal provides desirable thermal habitat for coldwater species, especially in regions where these organisms are challenged by hot summers (Krause et al. 2005; Olden and Naiman 2010). However, coldwater releases can be detrimental to some warmwater species commonly found in the Southeastern United States (Olden and Naiman 2010). In contrast, dams that operate via epilimnetic release may elevate water temperatures relative to natural conditions (Lessard and Hayes 2003; Olden and Naiman 2010). Epilimnetic release is often in the form of a surface or crested spillway, that is, where water naturally flows over the top of the dam.

These changes in temperature can cause detrimental stress to organisms residing in the affected areas. Selye (1973) defines stress as “the nonspecific response of the body to any demand made upon it.” Activity occurring outside of tolerable dissolved oxygen and temperature ranges can lead to physiological stress, given that many species are only tolerant of limited conditions (Krause et al. 2005). Stress is not necessarily detrimental, as an organism’s stress response is considered an adaptive mechanism to maintain homeostasis (Barton 2002). However, if the stressor is long-lasting or of high intensity, physiological and behavioral changes may be initiated which can be detrimental (Barton 2002). As illustrated by Barton (2002), primary and secondary responses to stress are typically physiological, involving neuroendocrine and metabolic responses, respectively. Tertiary responses modify behavioral patterns, affecting whole-organism growth, disease resistance, and, in the case of fish, swimming performance (Olden and Naiman 2010; Aboagye and Allen 2014; Franklin 2014). These responses not only affect the individual but can negatively impact a population if the stressors cause individual

behavioral changes across all members of the population (Barton 2002; Olden and Naiman 2010; Franklin 2014).

Muscle activity during anaerobic respiration can lead to stress and fatigue (Aboagye and Allen 2014). Anaerobic respiration can occur when a fish exceeds aerobic capacity and when low dissolved oxygen concentrations are present, known as hypoxia (Mallya 2007). Hypoxic conditions often exist in the hypolimnion of a stratified body of water commonly found in the reservoir upstream of a dam (Lessard and Hayes 2003). When water is released from the hypolimnion, fish in the tailwaters can simultaneously experience hypoxic conditions, lower temperatures, and increased flow rates (Stanford and Ward 2001; Lessard and Hayes 2003; Olden and Naiman 2010). In response, fish may physiologically increase blood flow and the red blood cell count in their gills to enhance the respiratory area (Randall 1982; Mallya 2007). Behaviorally, fish can attempt to bring more water in contact with the gills by increasing swim speed or opercular movement (Randall 1982; Mallya 2007), although these simultaneously increase metabolic costs as well. Increased water flow over the gills does not always increase oxygen consumption (Randall 1982; Mallya 2007). Fast moving water tends to by-pass the respiratory surfaces of the secondary lamellae, limiting gas exchange (Randall 1982; Mallya 2007). As a result, there may be no significant change in oxygen removal from the volume of water as it encounters the gills during hypoxia (Randall 1982). While fish can respond by swimming faster, some species will swim with open mouths, causing the onset of fatigue to happen more quickly (Randall 1982; Hammer 1995).

Fish may also experience stress in super oxygenated, or hyperoxic, water conditions (Espmark and Baeverfjord 2009). Supersaturation can occur from photosynthesis by microscopic organisms, and with rapid aeration from hydropower dam generation and spillway

waterfalls (Liepelt et al. 1995). In contrast to hypoxic conditions, fish experiencing hyperoxia may reduce ventilation rates (Gilmour and Perry 1994; Shultz et al. 2011). This inhibits the ability to excrete wastes such as carbon dioxide and can lead to internal acidosis and other primary stress responses, causing increased energy consumption (Gilmour 2001).

Dissolved oxygen concentration and temperature are both important environmental factors affecting fish metabolism and behavior (Reynolds and Casterlin 1980; Armour 2001; Franklin 2014). Changes in these two variables can affect survival, growth, and reproduction (Olden and Naiman 2010; Aboagye and Allen 2014). Immediate effects are seen in respiration rates, metabolic activity, and swimming performance (Aboagye and Allen 2014). Indices of swimming performance are commonly defined at three different levels by the organism's endurance. These three levels are maximum sustained (>200 min), prolonged (20 s – 200 min), and burst (<20 s) swimming speed (Beamish 1978; Tierney 2011). Both prolonged and burst swimming use fatigue as an endpoint whereas sustained swimming occurs at a speed that can be maintained for long periods with no time constraints (Blake 2004). The maximum velocity that a fish can maintain for a specific time period is known as the critical swimming speed ( $U_{crit}$ ) (Beamish 1978; Plaut 2001; Blake 2004; Tierney 2011). The effects of various water conditions on fish swimming performance can be quantified by comparing  $U_{crit}$  values (Hammer 1995; Tierney 2011).

Aside from dissolved oxygen concentration, temperature alone may also strongly influence swimming performance. In temperate climates, riverine fishes typically experience a wide range of temperatures throughout the year, and perhaps variation in water temperatures throughout the water column (Fuiman and Batty 1997). Studies suggest temperature influences both the rate of gas exchange during respiration and the speed of muscle contractions in

poikilotherms where body temperature conforms closely to that of the surrounding water (Randall and Brauner 1991; Guderley 2004; Krause et al. 2005). Temperatures outside a fish's preferred range can reduce swimming performance (i.e.,  $U_{crit}$ ) due to changes in oxygen delivery and reduced muscle power (Randall and Brauner 1991). At warmer temperatures, dissolved oxygen decreases and oxygen carrying capacity of the blood is reduced, combining to limit oxygen delivery to the tissues (Randall and Brauner 1991). In colder water, dissolved oxygen is higher, and one might expect swimming performance to improve; however, this is generally not the case (Randall and Brauner 1991). Instead, colder water is believed to reduce muscle power through a complex reduction of red muscle fiber recruitment, particularly seen in fish acclimated to warmer water (Randall and Brauner 1991). The reduction in muscle recruitment results in fish reaching fatigue faster and at a lower swimming velocity (Randall and Brauner 1991). As a result, a decrease in water temperature for a fish accustomed to higher water temperatures may lead to reduced swimming performance.

Here I tested the effects of both temperature and dissolved oxygen on the swimming performance of a widely distributed freshwater fish. I expected both predictors to have significant impacts on swimming such that performance would increase as temperature and dissolved oxygen increase. I anticipated  $U_{crit}$  values to be highest in warm, hyperoxic water and lowest in cold, hypoxic water. I predicted that these results would reflect habitat preference in the field downstream of Claiborne Dam with a higher density of tag detections occurring beneath the crested spillway.

## Methods

### *Study Species*

Previous research has addressed the ecological changes that occur in the tailraces of dams affected by hypolimnetic releases (Stanford and Ward 2001; Lessard and Hayes 2003; Krause et al. 2005). Some studies have examined these effects on fish assemblages and the tolerance of individual species to dissolved oxygen content and varying temperatures (Aboagye and Allen 2014). To date, the focus of research on the effects of temperature and dissolved oxygen have been on coldwater species such as trout and salmon (*Salmonidae*), with relatively less emphasis on warmwater species (Bodensteiner and Lewis 1992; Lessard and Hayes 2003; Olden and Naiman 2010; Aboagye and Allen 2014).

A relatively common lotic species that can tolerate a large temperature range but is one of the least studied species relative to hydraulic withdrawal effects is the Freshwater Drum *Aplodinotus grunniens*. This species occupies the largest latitudinal range of all North American freshwater fish, surviving in both warm and cold water systems, and making it an excellent study species when considering a wide range of tailrace conditions (Bodensteiner and Lewis 1992; Rypel et al. 2006). Freshwater Drum are generally benthivorous, using their large and powerful pharyngeal teeth to feed on benthic macroinvertebrates, bivalves, crustaceans, and detritus (Rypel et al. 2006). The tailwater habitat found below dams supports this diet, allowing Freshwater Drum to live and grow significantly larger here relative to lentic settings (Rypel et al. 2006). However, their use of tailwater habitat makes Freshwater Drum susceptible to rapid changes in water temperature and dissolved oxygen due to hydraulic release (Rypel et al. 2006). In a situation where Freshwater Drum reside below a spillway, warm water and hyperoxic conditions may exist (Rypel et al. 2006; Olden and Naiman 2010). Alternatively, Freshwater

Drum that feed below a dam or hydropower facility with hypolimnetic release may periodically experience colder water and hypoxic conditions (Olden and Naiman 2010). Although Freshwater Drum have not been known to migrate, their life history characteristics parallel other migratory benthivorous species, some of which are endangered and/or difficult to study (e.g., Southeastern Blue Sucker *Cycleptus meridionalis*).

For these reasons, Freshwater Drum is an appropriate study species. Their critical swimming speed in simulated water conditions commonly found in the tailraces below dams can be quantified, and their swimming mechanics (in the form of tail beat frequency and amplitude) can be observed and quantified in the laboratory. Furthermore, Freshwater Drum in the tailraces below dams can be tagged and relocated using acoustic telemetry, allowing documentation of habitat fish are using before possible passage attempts. Results from this work can be used to predict and suggest tailrace conditions more conducive to successful passage attempts.

### ***Field Study***

The Alabama River is formed by the confluence of the Coosa and Tallapoosa rivers (Freeman et al. 2005). Three lock-and-dam structures span the Alabama River between its formation and the river's confluence with the Tombigbee River to form the Mobile River. The upper two structures contain only gated spillways. Claiborne Lock and Dam, the lowermost structure, is the only one that contains both a crested spillway and a gated spillway, both of which draw water from the epilimnion of Claiborne Reservoir. The crested spillway allows the potential for fish passage, particularly during high flow periods. Given this structural design, Claiborne Lock and Dam is appropriate for comparing habitat preference between the crested spillway and gated spillway structures of fish staging for a passage attempt.

Freshwater Drum ( $n = 63$ ; minimum of 270 mm TL to ensure sexual maturity according to Rypel et al. [2007]) were collected for tagging from the tailwaters below Claiborne using boat electrofishing during February 2019 through June 2020. Acoustic/radio transmission tags (Lotek Wireless Combined Acoustic and Radio Tag model MM-MC-11-45 and Acoustic Only Tag model MM-MC-8-SO) were surgically implanted into individual fish using standard surgical protocol (Summerfelt and Smith 1990) and used to track individual Freshwater Drum movements. Tag weight never exceeded 2% of the fish's wet weight (Summerfelt and Smith 1990). These tags emitted a signal that could be received by an array of 15 Lotek WHS 3250L series receivers located in the dam tailrace (Figure 1). Receivers were arranged in an array so that multiple receivers could simultaneously pick up a signal, allowing for triangulation and two-dimensional time-stamped location within the tailrace. Data were stored on the receivers until they were downloaded, which occurred at regular intervals as water levels allowed. Tagged fish were released where water from the crested spillway and gated spillway converged in the tailwaters (Figure 1; 31.61283N, -87.55163W) to present them with an unbiased choice of habitat use locations.

Surface, mid-water, and benthic water temperature, and dissolved oxygen concentration were recorded both upstream and downstream of the dam during each sampling trip, as well as in the main channel 1 km further down river using a YSI 55 Dissolved Oxygen Instrument. In addition, Onset HOBO data loggers (Onset Computer Corporation HOBO Pendant MX2201 Water Temperature Data Logger) were attached to Lotek receivers upstream and downstream of the dam, recording water temperatures every 20 min 1m above the riverbed (Table 1).



## *Laboratory Study*

### Fish Collection, Transportation, and Holding

Freshwater Drum ( $n = 75$ ; minimum of 270 mm TL to ensure sexual maturity according to Rypel et al. [2007]) were collected from the Alabama River using boat electrofishing. Collected fish were held in the boat's live well until they were transferred to a 1000-L hauling tank and returned to Auburn University's Ireland Center wet lab facility. The hauling tank was filled with on-site river water and aerated using a portable aerator. Fish were transferred from the hauling tank to an outdoor quarantine tank upon arrival at the wet lab facility. The water temperature of the quarantine tank was set within 1°C of the hauling tank's water temperature using a chiller or heater. After two days in the quarantine tank to allow for recovery from transportation stress and to observe for any potential disease, fish were transferred into two flow-through 681-liter tanks (Polytank Part # PT-5228) in the wet lab under a 12:12 light:dark regime (Herbert and Steffensen 2005). Fish were acclimated to treatment temperatures by adjusting the water temperature by no more than 2°C/day via a water chiller/heater (Aqua Logic DS-9/ Pentair ETA10) (Roots and Prosser 1962). Once treatment temperature was achieved, fish were allowed to acclimate for one additional week before swim trials were conducted (Roots and Prosser 1962; Kern and Langerhans 2019). During holding, fish were fed 2% of the total fish mass in earthworms once every morning. Feeding ceased 48 hours before a swim trial (Bhujel et al. 2007; Aboagye and Allen 2014). All holding tanks were filled with dechlorinated city water, received constant water flow, and contained a biofilter to eliminate any waste build-up. Normoxic dissolved oxygen concentrations were maintained between 7 and 9 ppm.

## Experimental Design

Three temperatures (10°C, 20°C, 30°C) were selected to simulate deep reservoir hypolimnetic release (Wismer and Christie 1987), normal temperatures around the time of spawning (Wismer and Christie 1987; Swedberg and Walburg 2011), and epilimnetic release (Reutter and Herdendorf 1976; Armour 1991), respectively. Three dissolved oxygen concentrations (4, 9, 14 ppm) were selected to simulate hypoxic, normoxic, and hyperoxic conditions, respectively (Caldwell and Hinshaw 1994). These conditions were combined to form nine total treatments that spanned the range of conditions potentially occupied by Freshwater Drum. Four to seven unique fish per treatment were tested in a Loligo Systems 90 L swim tunnel (model SW10210), and three unique fish per treatment were tested in a Loligo Systems 850 L swim tunnel (model SW10300). The swim chamber to be used was determined based on the size of the fish. Each trial temperature was determined randomly before fish were acclimated in the wet lab. Dissolved oxygen concentration was determined dependent on fish size to maintain an even size distribution across all treatment combinations.

## Laboratory Swim Trials

City water was dechlorinated in two 2,900 m<sup>3</sup> reservoirs located inside the wet lab. Once the treatment temperature was reached, water was transferred via a large water pump (Eheim 1262, Germany; 3,400 L/h) into the appropriately-sized Loligo Systems swim tunnel. A single fish was netted randomly from the indoor holding tanks and placed in a water bath with approximately 75 mg/L tricaine methane-sulfonate (MS-222) anesthesia with 2x sodium bicarbonate buffer for no more than 3 minutes to reduce handling and transportation stress (Popovic et al. 2012; Mattson and Ripley 1989). The fish's total length (cm), depth (cm), width

(cm), and mass (g) were measured. The fish was placed in the swim tunnel's swim chamber and acclimated at a velocity of 0.5 body lengths per second (BL/s) for 30 minutes to recover from anesthesia before the swim trial began (Hammer 1995, Plaut 2001, Prenosil et al. 2015). The entire area around the swim tunnel was partitioned with black plastic to eliminate external visual cues (Herbert and Steffensen 2005).

Following this initial acclimation period, water exchange with the indoor reservoir halted. Dissolved oxygen in the swim tunnel was lowered/raised to treatment conditions using nitrogen and/or oxygen gas (Airgas NIZ15A, OX125), respectively (Butler et al. 1994). Each fish was allowed another 30 minutes at 0.5 BL/s to acclimate to the treatment dissolved oxygen concentration. After this second acclimation period, a constant acceleration test was conducted beginning at 1.0 BL/s with an increase rate of 0.5 BL/s every 30 minutes to determine the critical swimming speed of each fish (Hammer 1995; Plaut 2001; Tierney 2011; Aboagye and Allen 2014, Prenosil et al. 2015). If a fish did not swim past the initial 30-minute increment, it was removed and counted as a non-performer and replaced by a new fish (Prenosil et al. 2015).

Tail beats were manually counted by reviewing video footage of each trial recorded with Noldus Ethovision cameras and software. For each 30-minute velocity increment, one to three quality swimming periods of at least 10 sec were identified. Quality swimming was determined when the caudal fin movement of a fish was not inhibited by the back screen of the swim chamber and when the fish was not bursting forward; a maintained swimming position in the middle of the swim chamber was ideal. Within each period of quality swimming, the total number of tail beats and the elapsed time were quantified. The mean tail beat frequency for each velocity increment ( $n = 1-3$  measurements/velocity increment) was reported in tail beats per second (Tb/s).

Tail beat amplitude was quantified during the same periods of quality swimming used for quantifying tail beat frequency. Within the period of quality swimming, 1-3 individual tailbeats were randomly selected and measured using Noldus Ethovision software as the tail passed from one side to the other. The mean tail beat amplitude for each velocity increment was reported in centimeters (cm).

Fatigue was determined by impingement on the screen at the rear of the tunnel for 15 seconds (Aboagye and Allen 2014, Prenosil et al. 2015). Upon impingement, the measurement time was paused, and water velocity reduced to 0.5 BL/s for at least 2 minutes, allowing the fish to move off the rear screen and re-attain swimming composure (Aboagye and Allen 2014). Following recovery, velocity resumed at the fatigue velocity and measurement time continued (Aboagye and Allen 2014). The trial ended when impingement occurred three times in one velocity increment. Requiring three impingements provided a higher probability that the swimming endpoint was due to physical exhaustion rather than a behavioral refusal to swim (Aboagye and Allen 2014). After the trial, the fish was euthanized in a 300 ppm MS-222 bath according to Auburn University IACUC protocol #2018-3387. All water in the small swim flume was drained prior to the next trial, the large flume was half drained then refilled.

The ending velocity was recorded and used to calculate the fish's critical swimming speed ( $U_{crit}$ ) (Plaut 2001, Adams et al. 1997) according to Brett (1964):

$$U_{crit} = U_1 + \left( \frac{T_1}{T_2} * U_2 \right)$$

where  $U_1$  is the highest velocity maintained for the entire prescribed time period,  $T_1$  is the amount of time swam at the fatigue velocity,  $T_2$  is the prescribed interval of swimming (30 minutes), and  $U_2$  is the velocity increment (0.5 BL/s). The critical swimming speeds of fish with a cross-sectional area greater than 10% of the cross-sectional area of the swim chamber ( $n = 7$ )

are recommended for correction due to the solid blocking effect according to methods described by Bell and Terhune (1970). However, these corrections were not implemented in this study (see Discussion).

## *Analysis*

### Field Study:

Three habitat zones were distinguished in the tailrace based on hydrology and surrounding terrestrial habitat: below the crested spillway, below the gated spillway, and in the downstream main channel (Figure 2). Detections from tagged Freshwater Drum released in the tailrace below Claiborne Lock and Dam were collected and stored on Lotek WHS 3250L series receivers. Data from these receivers were downloaded and converted into CSV files through Lotek software for each individual fish with location coordinates in UTM's. Using ArcMap programming software (ESRI ArcGIS 10.7.1), these data points were mapped on top of the World Imagery basemap with WGS 1984 UTM Zone 16N as the projected coordinate system (Figure 3). False detections (detections outside the riverbanks) were deleted. A heat map of Freshwater Drum detections was generated with an output cell size of 1 m<sup>2</sup> and a radius of 10 m<sup>2</sup> (Figure 4). The number of detections, percent of detections, total habitat area, percent of habitat, and detection density were all calculated for each habitat zone (Table 2; ESRI ArcGIS 10.3).

Using the observed detections and the percent of each habitat as the probability of detection, a chi-squared test for given probabilities was used to compare detection frequency among habitat zones for all deployed tags and for the 10 most frequently detected tags. All statistical tests were performed in RStudio.

### Laboratory Study:

For the laboratory swim trials, results were analyzed separately for each swim flume (see Discussion). Models included temperature and dissolved oxygen as independent predictors of swimming performance response variables ( $U_{crit}$ /tail beat frequency/tail beat amplitude) with length as a covariate. Linear regression was used to analyze the sole effect of length on swimming performance within each flume size but not between flume sizes. ANCOVA's were used to analyze the effect of temperature and dissolved oxygen on swimming performance with length as a covariate in similar fashion. Tukey's Honest Significant Difference (HSD) Post-hoc test was used for ANCOVA test results to adjust pair-wise p-values to maintain the experiment-wide error rate (Steury and Murray 2005). All statistical tests were performed in RStudio.

## Results

### *Field Acoustic Telemetry Study*

Across all sites, maximum temperature was highest during June and July and minimum temperature was lowest during February (Table 1). Maximum dissolved oxygen concentration was highest during November or December, and minimum concentration was lowest during August or September (Table 1). The greatest temperature difference between minimum and maximum values occurred in the tailrace, with a range from 9.4°C to 35.4°C. The greatest dissolved oxygen difference between minimum and maximum values occurred in the upstream reservoir, with a range from 4.3 ppm to 12.3 ppm.

I had a total of 15,959 detections among 30 tagged individual Freshwater Drum during February 2019 through May 2020 (Table 2). All tagged individuals (n = 33) were collected in the tailrace below Claiborne Lock and Dam and after being tagged they were released in the tailrace at the interface between water from the crested spillway and the gated spillway (the star in Figure 1). Three fish (tag IDs 28608, 28612, and 28630) were not detected by the acoustic array. One tag (tag ID 28600) was detected both upstream and downstream of the Claiborne tailrace array suggesting passage.

Individual tag detection frequencies ranged from 2 to 3,220, with a mean of 532 and a median of 80 detections per individual (Table 2; Figure 5). Within the crested spillway habitat zone, detection frequencies ranged from 0 to 2,892, with a mean of 143 and a median of 5 (Table 2; Figure 6). Within the gated spillway habitat zone, detection frequencies ranged from 0 to 1,681, with a mean of 274 and a median of 15 (Table 2; Figure 6). Within the main channel habitat zone, detection frequencies ranged from 0 to 1,894, with a mean of 115 and a median of 28 (Table 2; Figure 6).

Tagged Freshwater Drum were detected significantly more often than expected based on habitat area in the gated spillway habitat zone versus in the crested spillway or main channel habitat zones (Table 3;  $\chi^2$  test,  $\chi^2 = 8234.4$ ,  $df = 2$ ,  $p < 0.0001$ ). Detection density within a habitat zone (determined by dividing the number of detections by the habitat area) was greatest in the gated spillway habitat zone, followed by the crested spillway, and the main channel (Table 3).

The 10 most frequently detected tags accounted for most (91.6%) of the detections from all deployed tags, as well as the most detections in all three habitat zones (Table 4). Habitat use differed among these individuals (Figure 7). As with all tagged fish, these most often detected fish were detected significantly more often than expected based on habitat area in the gated spillway habitat zone versus in the crested spillway or main channel zones (Table 4;  $\chi^2$  test,  $\chi^2 = 9375.1$ ,  $df = 2$ ,  $p < 0.0001$ ).

### ***Laboratory Swim Trial Study***

#### **Length as a Covariate**

The effects of temperature and dissolved oxygen on fish swimming performance were strongly influenced by body length. To fully capture the influence of length on fish performance and swimming mechanics, it was necessary to challenge fish across a wide range of lengths (27 cm – 53.5 cm), thereby requiring both a small ( $n = 48$ ) and a large ( $n = 27$ ) swim flume to test across this range of fish. Mean fish body length in the small flume was 10.2 cm less than in the large flume (Figure 8; ANOVA,  $F_{1, 73} = 79.60$ ,  $P < 0.001$ ). Results from the small and large swim flumes were analyzed separately due to bias between flume size and fish length.



### Critical Swimming Speed

$U_{crit}$  decreased with fish length in both small and large swim flumes (Figure 9; GLM, small flume:  $F_{1,45} = 61.86$ ,  $P < 0.001$ ; large flume:  $F_{1,25} = 6.73$ ,  $P = 0.016$ ).  $U_{crit}$  increased significantly with temperature in both the small and large swim flumes (Table 5; Figure 10). Fish length significantly affected the influence of temperature on  $U_{crit}$  for fish in the small flume, but not in the large flume (Table 5).  $U_{crit}$  did not differ across dissolved oxygen concentrations in either flume size (Table 5; Figure 11), and fish length did not affect the influence of dissolved oxygen on  $U_{crit}$  (Table 5).

### Tail Beat Frequency

Tail beat frequency decreased significantly with fish length in both small and large swim flumes (Figure 12; GLM, small flume:  $F_{1,45} = 10.27$ ,  $P = 0.002$ ; large flume:  $F_{1,23} = 6.74$ ,  $P = 0.016$ ). Tail beat frequency increased with temperature in both flume sizes, although the relationship was only marginally significant in the large flume (Table 5; Figure 13). Fish length significantly affected the influence of temperature on tail beat frequency for fish in the large flume, but not in the small flume (Table 5). Tail beat frequency did not differ across dissolved oxygen concentrations in either flume size (Table 5; Figure 14), and fish length did not significantly affect the influence of dissolved oxygen on frequency (Table 5).

### Tail Beat Amplitude

Tail beat amplitude increased significantly with fish length in both small and large swim flumes (Figure 15; GLM, small flume:  $F_{1,45} = 197.10$ ,  $P < 0.001$ ; large flume:  $F_{1,23} = 28.79$ ,  $P < 0.001$ ). Tail beat amplitude did not statistically differ across temperature or dissolved oxygen treatments

(Table 5; Figures 16, 17). However, fish length significantly affected the influence of temperature on tail beat amplitude, although the effect was only marginally significant in the large flume (Table 5). Fish length did not significantly affect the influence of dissolved oxygen on frequency (Table 5).

## Discussion

### *Detection Frequency below Claiborne Lock and Dam*

Freshwater Drum, as generalist benthivores, share some life history characteristics with other warmwater fish residing in tailraces (e.g., Smallmouth Buffalo *Ictiobus bubalus*), such as age at maturity, body shape, and food habits. Investigating the effects of dams on this widely-distributed species as a potential surrogate for other species may aid in determining habitat preference and swimming performance of migratory species attempting passage, many of which may be more difficult to study (e.g., Southeastern Blue Sucker *Cycleptus meridionalis*).

Freshwater Drum tended to congregate in the tailwaters of Claiborne Dam directly below the crested and gated spillways more so than in the main channel of the river. Considering just the two spillway habitat zones, detections below the gated spillway were nearly double those below the crested spillway. Additionally, detections in the gated spillway zone were distributed evenly among multiple individuals. In contrast, a single individual in the crested spillway (Tag ID 28600) and main channel (Tag ID 28648) habitat zones contributed to more than half of the detections in each of those zones, suggesting individuals may frequent the gated spillway habitat zone even more often and/or for a longer period of time than the other habitat zones.

In general, detections of Freshwater Drum were more concentrated in deep, open water habitats than along shallow, nearshore habitats, although the distribution of individuals was not restricted to one area. This was similar to observations by Bur (1984) in Lake Erie (a lentic system), who noted that older Freshwater Drum occupied deeper waters while young-of-year were more commonly distributed in shallower waters. In a lotic system, Rypel and Mitchell (2007) also found that smaller and younger Freshwater Drum occupied shallow nearshore habitats, and they suggested that this was due to both predation pressure and to allow feeding on

macroinvertebrates instead of larger diet items (e.g., bivalves, the diet of larger Freshwater Drum) given gape limitations. In another lotic setting, Jacquemin et al. (2014) documented similar variation in diet choice across Freshwater Drum sizes while French and Bur (1996) found that zebra mussels were a staple diet item for older Freshwater Drum. Larger individuals such as those tagged in my study whose body sizes exceed predator gape limitations may occupy deeper water to feed on larger bivalves and reduce competition with smaller individuals.

The results of the field portion of my study demonstrate habitat preferences that were expressed across most individuals. These preferences may have derived from size-dependent foraging opportunities and/or schooling behavior, although additional work is required to identify specific mechanisms. Other species with similar food habits and/or behaviors may share such habitat preferences, including species staging for a passage attempt. For example, Smallmouth Buffalo have been documented as opportunistic bottom feeders that migrate away from their preferred bottom substrate to flooded fields and shallower water to spawn when water levels rise in the spring (Edwards and Twomey 1982; Adams and Parsons 1998). Smallmouth Buffalo could be using the tailrace habitat as a staging area for reproduction and possibly passage.

These data are important for predicting where fish populations might congregate within a tailrace. For species that support a fishery (for who Freshwater Drum may serve as a surrogate), exploitation rates and fishing pressure, particularly on migratory species, can be managed within these habitats to reduce stress and improve the chances for successful reproduction and passage. And successful passage in my study system is possible (likely via the crested spillway), as evidenced by a single tagged individual that made both upstream and downstream cross-dam movements. Translocation efforts that include actively trapping and hauling fish from tailrace to

upstream habitats can operate more efficiently when the location of the highest concentration of individuals is known. My results suggest high catch rates can be expected below the gated spillway in the tailrace below Claiborne Dam, specifically for Freshwater Drum and possibly for other generalist benthivores.

### *Swimming Performance in Simulated Tailrace Conditions*

#### Effect of Temperature and Dissolved Oxygen on Swimming Performance

Temperature and dissolved oxygen are important in determining overall water quality and habitat suitability for fish. Tolerance of temperature and dissolved oxygen ranges can determine species distributions and spawning cycles, and can influence swimming performance by affecting metabolic costs (Aboagye and Allen 2014). For migratory species in an anthropogenically segmented habitat, maximizing swimming performance can increase the probability of passage past human-located structures. In addition, tailwaters downstream of dams can represent important habitat for fish in which to stage before making a dam passage attempt. Optimum temperature and dissolved oxygen levels for passage attempts can be determined by simulating tailwater conditions in a laboratory setting and quantifying fish swimming performance by measuring critical swimming speed ( $U_{crit}$ ) (Tierney 2011). Here I challenged Freshwater Drum to nine total simulations through a combination of three temperatures (10°C, 20°C, 30°C) and three dissolved oxygen concentrations (4 ppm, 9 ppm, 14 ppm).

Freshwater Drum  $U_{crit}$  increased with water temperature. Fish in 10°C and 20°C water treatments were unable to continue swimming for as long as fish in warm water, suggesting cold water may more negatively affect swimming performance despite reduced carrying capacity of

oxygen in blood in warm water (Randall and Brauner 1991). These results were consistent with other studies that have shown temperature affecting fish muscle performance (Johnson and Johnston 1991; Randall and Brauner 1991). Randall and Brauner (1991) proposed that colder water may reduce muscle power, particularly in fish acclimated to warm water. And Johnson and Johnston (1991) found that muscle power output was higher in fish acclimated to warm water than in fish acclimated to cold water; when two treatment temperatures were presented to fish acclimated to warm water, power output was higher in warm water treatment temperatures than in cold water. Interestingly, for fish acclimated to cold water, the opposite was observed; power output was lower in warm water treatment than in cold water for these cold water-acclimated fish. Heap and Goldspink (1986) found similar results when swimming Common Carp *Cyprinus carpio*. Their findings suggest that replicating my study, but with Freshwater Drum acclimated to a cold water system, might yield different results. Freshwater Drum from cold water systems may have higher critical swimming speeds in cold water treatments than in warm water treatments. Clearly given that Freshwater Drum occupy the largest latitudinal range of any freshwater fish in North America, the results of this study should not be assumed for all populations across latitudes.

Tail beat frequency and amplitude are indicators of power output mechanisms. Although amplitude did not differ among treatments, I found that tail beat frequency increased with temperature, suggesting high power output in warm water may derive from caudal muscle fibers. Briefly, fish muscle types include red fibers (aerobic) used at slow swimming speeds and white fibers (glycolytic) active only at higher speeds (Bone, 1978). Higher tail beat frequency indicates a faster recovery time for red muscle fibers following contraction (Graham et al. 1990). Heap and Goldspink (1986) suggested white muscle fibers fatigue faster than red, so the longer a

fish can use red fibers for sustained swimming, the slower it will succumb to fatigue. Rome et al. (1984) determined that white muscle fibers in Common Carp were recruited at a higher swimming velocity in higher temperatures, suggesting increased aerobic power output available from red fibers at higher temperatures. My results are similar to these findings. Higher  $U_{crit}$  values and tail beat frequencies in the warm water treatments suggest fish may be recruiting white muscle fibers later in the trial at higher velocities. This suggests that fish in warm water may swim using red muscle fibers longer than fish in cool water, swimming longer without fatiguing as a result.

Fish attempting passage of a crested spillway structure like the one at Claiborne Lock and Dam may be required to swim at burst speeds in relatively fast flowing water. The inability of fish in cold water treatments to maximize tail beat frequency is concerning, suggesting that fish in cold water may be unable to reach speeds required for successful passage. Claiborne Dam can be seasonally inundated, but these high flow periods typically occur during winter and spring when water temperature is lowest (Freeman et al. 2005). While there is no significant fishing pressure for Freshwater Drum, other comparable species may be impacted by the combined effect of fishing and cold water during migration. In the previous section, I propose management practices that could relieve fishing pressure within tailrace habitats to reduce stress on fish potentially staging for a passage attempt during these times. Based on my lab results, such practices could be taken a step further to reduce fishing pressure during winter months altogether when passage events over the crested spillway are most likely. With fish already underperforming at lower temperatures, fishing pressure could compound metabolic costs and increase the probability of unsuccessful passage attempts and the resulting physical strain from them.

Dissolved oxygen concentration did not affect any measure or mechanism of swimming performance. This suggests that dissolved oxygen levels in the tailrace below dams within a range of 4 ppm – 14 ppm may not be as important a concern as once thought, at least as related to fish swimming performance and abilities. These results are consistent with results of a similarly designed study on Crucian Carp *Carassius carassius* by Penghan et al. (2014), which found  $U_{crit}$  did not differ between 9 ppm and 5 ppm dissolved oxygen, but did significantly decrease at 2.5 ppm. In a study on Mulloway *Argyrosomus japonicus* (a fish in Sciaenidae, as is Freshwater Drum), Fitzgibbon et al. (2007) similarly found that  $U_{crit}$  did not significantly decrease from 6.85 ppm to 5.23 ppm dissolved oxygen but did between these two normoxic levels and 3.64 ppm and 1.86 ppm. Both studies also observed a significant decrease in metabolic rate for fish experiencing hypoxia. Although hypoxic concentrations are below my field observations and swim trial parameters, its effect on  $U_{crit}$  and metabolic rate has relevance. Fish have the ability to maintain consistent metabolic function and swimming performance during mild hypoxia. However, below a critical dissolved oxygen level, fish lose this ability (Fitzgibbon et al. 2007; Wood 2018). In the event of a failed passage attempt, recovery may be further exacerbated by stress resulting from a hypoxic environment. Fortunately, my results and those by Fitzgibbon et al. (2007) suggest that the Sciaenidae family may be better adapted to hypoxia relative to other species. Further investigation using even lower dissolved oxygen concentrations is required to fully understand these effects.

Temperature played a more important role in the swimming performance of Freshwater Drum than did dissolved oxygen.  $U_{crit}$  of fish at 30°C was significantly higher than at either 20°C or 10°C at all dissolved oxygen concentrations. Tail beat frequency followed a similar pattern with the highest values for each dissolved oxygen concentration generally occurring at



30°C. Amplitude did not significantly differ between or within any treatment level, suggesting tail beat frequency and the muscle fibers involved may play an important role in maintaining swimming performance.

### Effect of Flume and Body Size on Swimming Performance

Although determining the effects of temperature and dissolved oxygen on the swimming performance of Freshwater Drum was a primary goal for this work, significant effects of flume size and fish body length were identified. It has long been known that tail beat frequency decreases and amplitude increases as fish grow (Bainbridge 1958). This relationship was observed during this study. It has also been documented that  $U_{crit}$  decreases with fish length, although recent studies involving a wide range of flume sizes suggest otherwise (Heap and Goldspink 1986; Peake 2004; Tudorache et al. 2007; Deslauriers and Kieffer 2011). My experiment was designed such that each treatment combination would receive similarly sized fish within a given flume size. This ensured that fish length as a covariate would have a minimal effect on the relationship between swimming performance and temperature and dissolved oxygen treatment. However, the experimental design purposefully biased fish length within flume sizes with smaller fish swimming in the small flume and large fish in the large flume, causing flume size to be confounded by fish length. Therefore, flume size could not be considered as an independent predictor of swimming performance.

The effects of temperature and dissolved oxygen on swimming performance were analyzed separately within each flume size, although results rarely differed between flume sizes. Overall, I found that  $U_{crit}$  decreased with fish length, but when comparing fish of similar size between the small versus large,  $U_{crit}$  values were greater in the large flume. Graphically, Figure

9 shows this apparent effect of flume size on  $U_{crit}$ , suggesting swimming performance may increase with flume size. This effect of flume size could result from the solid blocking effect described by Bell and Terhune (1970) which states that fish occupying a larger cross-sectional area of the swim chamber within a swim flume will experience a higher realized velocity, leading larger fish to fatigue faster and have a lower  $U_{crit}$ . A correction for solid blocking exists (based on Bell and Terhune 1970) and is recommended when calculating the  $U_{crit}$  of fish with a cross-sectional area 10% or greater than the cross-sectional area of the swim chamber. As a result, studies involving swim flumes typically use fish that are all only above or all only below this 10% threshold (Bell and Terhune 1970, Graham and Laurs 1982, Adams and Parsons 1998). Very few studies have needed this correction on only a small subset of fish within the experiment.

In my case, only 7 of 75 fish would have required correction (all in the small flume), presenting a unique situation. The cross-sectional areas of these fish were all within 15% of the cross-sectional area of the swim flume (10.1% - 14.2%), meaning a measuring difference of only 1-2 mm in fish width and/or depth could have changed the cross-sectional area of a fish to be within versus beyond the 10% threshold. As a result, I chose to not correct any  $U_{crit}$  values for the solid blocking effect in this experiment. Some form of graduated blocking effect would be more biologically reasonable, such that a small shift in surface area would not result in a dramatic change in  $U_{crit}$  values. Toward this end, I suggest removal of the seemingly arbitrary 10% threshold and correct for the solid-blocking effect for all fish, regardless of the cross-sectional area relationship between fish and flume swim chambers. Clearly more research into the effects of flume size on fish swimming performance is needed.

Although my results demonstrate a decrease in swimming performance with fish length, other studies have found swimming performance increased with length. Peake (2004) found Smallmouth Bass *Micropterus dolomieu*  $U_{crit}$  to be positively related to fish length. However, their experiment was performed in a 50 m raceway, a swim chamber much larger than even the large swim flume used in my work. Within this system, the solid blocking effect would be extremely low, suggesting that the relatively higher solid blocking factor within the flumes I used (even though generally  $< 10\%$ ) could affect the relationship between Freshwater Drum  $U_{crit}$  and fish length. Graphically (Figure 9), my results demonstrate that when given a larger chamber to swim in, fish swimming performance is improved. Previous studies have shown there may be even more factors affecting the positive relationship between flume size and fish  $U_{crit}$ . Tudorache et al. (2007) suggested that larger flumes allow less restricted burst-coast swimming behavior. And Deslauriers and Kieffer (2011) implied that longer flumes provided fish with a greater distance to re-establish swimming control after it is lost.

The effect of flume size and body size on swimming performance has tremendous ecological importance. My study along with previous studies suggest larger fish may have a higher swimming performance in the open water than when confined to small spaces such as gated release openings in dams. When considering Claiborne Lock and Dam, larger fish may have more success passing over the inundated crested spillway instead of attempting passage through the gated release and lock chamber. From a management perspective, this information can be used to establish field-applicable water velocity criteria for water withdrawal to promote successful passage, such as the water velocity and temperature within by pass channels (Peake 2004). In combination with the detection frequency study, such by pass channels should be accessible from the tailrace where individuals may be concentrated.

## Summary

This study of Freshwater Drum documents patterns of habitat use in the tailrace of a dam on the Alabama River (Claiborne Lock and Dam) and experimentally derived measures of swimming performance under conditions of temperature and dissolved oxygen often found in tailraces. Freshwater Drum concentrate in areas of deep, open water within the tailrace, specifically below the gated release. This habitat could be used for staging between passage attempts and/or reproduction. Future observations within the system could include detailed flow modelling, individual movement tracking, and food availability through diet analyses.

Temperature, body size, and flume size appear to influence measures and mechanics of Freshwater Drum swimming performance. While dissolved oxygen had no effect in my study, changes in swimming performance could be observed outside the tested concentration range. The effect of temperature could indicate seasonal bottlenecks for movement which seasonal movement tracking could help illustrate. Carefully designed studies to explore flume size effects could be extremely useful in understanding the applicability of a flume effect to open river conditions. Management practices aimed at promoting successful fish passage, especially for migrating species, could reduce fishing pressure during the winter within the tailrace habitat.

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## Tables

**Table 1.** Temperature and dissolved oxygen in Claiborne Reservoir, the tailrace below Claiborne Dam, and 0.8 km downstream of Claiborne Dam. Measurements were recorded during July 2019 through June 2020. There were no readings for March and April due to extremely high water that made the river inaccessible. Bold numbers indicate overall minimum and maximum values for each measurement type at each location.

	<b>Reservoir</b>		<b>Tailrace</b>		<b>Downstream</b>		
	Temp (°C)	DO (ppm)	Temp (°C)	DO (ppm)	Temp (°C)	DO (ppm)	
<b>January</b>	Min.	15.7		11.9		15.6	
	Mean	18.2		15.3		16.9	
	Max.	21.6		21.2		20.3	
<b>February</b>	Min.	<b>11.9</b>	11.5	<b>9.4</b>	11.8	<b>12.2</b>	11.9
	Mean	20.4	11.6	18.9	11.9	20.4	12
	Max.	24	11.8	28.6	11.9	23.5	<b>12.1</b>
<b>March</b>	NA						
<b>April</b>	NA						
<b>May</b>	Min.	20.9	9.2	20.9	9.5	21	9.5
	Mean	22.2	9.6	22.3	10	22.3	10.5
	Max.	23.5	9.9	23.6	10.5	23.6	10.9
<b>June</b>	Min.	25.9		29.2		26.1	
	Mean	28.5		30		28.3	
	Max.	31.1		<b>35.4</b>		31.1	
<b>July</b>	Min.	29.9		28.4	7.6	28.9	7.7
	Mean	30.7		31	8.1	30.6	8.5
	Max.	<b>32.3</b>		32	9.6	<b>32.2</b>	8.8
<b>August</b>	Min.	28.8	<b>4.3</b>	29	<b>6.5</b>	31.5	7.4
	Mean	30.7	5.2	30.5	7	31.5	7.7
	Max.	31.6	5.6	31.5	7.2	31.5	8
<b>September</b>	Min.	28.4	5.2	27.5	7	30.4	<b>7.2</b>
	Mean	30.4	6.2	30.1	7.2	30.7	7.6
	Max.	31.1	7.5	31.1	7.4	31	8.3
<b>October</b>	Min.	21.7	4.7	22.1	7.3	29.2	7.8
	Mean	25.9	6.3	27.6	7.5	29.2	7.9
	Max.	29.8	8.5	29.1	7.7	29.2	8.1
<b>November</b>	Min.	12.6	8	12.8	9.2	15.5	9.6
	Mean	17.3	8.8	17.1	10.4	17.5	10.9
	Max.	22.2	10.4	22.4	<b>12.4</b>	19.9	<b>12.1</b>
<b>December</b>	Min.	12.1	9.9	10.1	10.5	12.5	11
	Mean	13.3	10.6	11.4	10.7	12.6	11.4
	Max.	13.9	<b>12.3</b>	14.1	10.8	12.7	11.8

**Table 2.** Total detections for each individual tag (DET) and the percent of all detections (% TOT). Within each habitat zone I present the number of habitat zone specific detections (Det), the percent of that tag’s detections within that habitat zone (% In), and the percent of that habitat zone’s detections (% Of).

Tag ID	DET	% TOT	Crested Spillway			Gated Spillway			Main Channel		
			Det	% In	% Of	Det	% In	% Of	Det	% In	% Of
28600	3,220	20.2%	2,892	89.8%	67.6%	323	10.0%	3.9%	5	0.2%	0.1%
28602	232	1.5%	2	0.9%	0.0%	21	9.1%	0.3%	209	90.1%	6.1%
28604	228	1.4%	8	3.5%	0.2%	46	20.2%	0.6%	174	76.3%	5.0%
28606	1,768	11.1%	19	1.1%	0.4%	1,590	89.9%	19.3%	159	9.0%	4.6%
28610	963	6.0%	643	66.8%	15.0%	287	29.8%	3.5%	33	3.4%	1.0%
28614	145	0.9%	1	0.7%	0.0%	11	7.6%	0.1%	133	91.7%	3.9%
28616	214	1.3%	93	43.5%	2.2%	86	40.2%	1.0%	35	16.4%	1.0%
28618	13	0.1%	5	38.5%	0.1%	0	0.0%	0.0%	8	61.5%	0.2%
28620	8	0.1%	0	0.0%	0.0%	8	100.0%	0.1%	0	0.0%	0.0%
28622	32	0.2%	0	0.0%	0.0%	13	40.6%	0.2%	19	59.4%	0.6%
28624	30	0.2%	5	16.7%	0.1%	10	33.3%	0.1%	15	50.0%	0.4%
28626	2	0.0%	1	50.0%	0.0%	1	50.0%	0.0%	0	0.0%	0.0%
28632	3	0.0%	0	0.0%	0.0%	1	33.3%	0.0%	2	66.7%	0.1%
28634	7	0.0%	0	0.0%	0.0%	0	0.0%	0.0%	7	100.0%	0.2%
28636	717	4.5%	50	7.0%	1.2%	659	91.9%	8.0%	8	1.1%	0.2%
28638	29	0.2%	3	10.3%	0.1%	2	6.9%	0.0%	24	82.8%	0.7%
28640	1,880	11.8%	181	9.6%	4.2%	1,681	89.4%	20.4%	18	1.0%	0.5%
28644	37	0.2%	3	8.1%	0.1%	11	29.7%	0.1%	23	62.2%	0.7%
28646	49	0.3%	0	0.0%	0.0%	12	24.5%	0.1%	37	75.5%	1.1%
28648	2,419	15.1%	33	1.4%	0.8%	492	20.3%	6.0%	1,894	78.3%	54.9%
28650	53	0.3%	0	0.0%	0.0%	4	7.5%	0.0%	49	92.5%	1.4%
28652	75	0.5%	13	17.3%	0.3%	30	40.0%	0.4%	32	42.7%	0.9%
28654	85	0.5%	16	18.8%	0.4%	9	10.6%	0.1%	60	70.6%	1.7%
28656	542	3.4%	4	0.7%	0.1%	378	69.7%	4.6%	160	29.5%	4.6%
28658	247	1.5%	145	58.7%	3.4%	64	25.9%	0.8%	38	15.4%	1.1%
28660	1,399	8.8%	62	4.4%	1.4%	1,113	79.6%	13.5%	224	16.0%	6.5%
28662	10	0.1%	0	0.0%	0.0%	3	30.0%	0.0%	7	70.0%	0.2%
28664	1,458	9.1%	100	6.9%	2.3%	1,347	92.4%	16.4%	11	0.8%	0.3%
28666	30	0.2%	0	0.0%	0.0%	9	30.0%	0.1%	21	70.0%	0.6%
28668	64	0.4%	0	0.0%	0.0%	16	25.0%	0.2%	48	75.0%	1.4%
<b>Total</b>	15,959		4,279			8,227			3,453		

**Table 3.** Total number of detections, percent of detections, total habitat area, percent of area contributed by each habitat, and each habitat's overall detection density for locations of tagged Freshwater Drum below Claiborne Lock and Dam within each of three habitat zones.

<b>Habitat</b>	<b># Detections</b>	<b>% Detections</b>	<b>Habitat area (m<sup>2</sup>)</b>	<b>Habitat %</b>	<b>Density (detections/m<sup>2</sup>)</b>
Crested Spillway	4,279	26.8%	58,484.30	23.1%	0.07
Gated Spillway	8,227	51.6%	60,160.20	23.8%	0.14
Main Channel	3,453	21.6%	134,542.10	53.1%	0.03
<b>Total</b>	15,959		253,186.60		0.06

**Table 4.** Overall and habitat-specific detection frequencies and percent of detections for the 10 most frequently detected tags. Columns and abbreviations are as defined in Table 2.

Tag ID	DET	%TOT	Crested Spillway		Gated Spillway		Main Channel	
			Det	% Of	Det	% Of	Det	% Of
28600	3,220	20.2%	2,892	67.6%	323	3.9%	5	0.1%
28606	1,768	11.1%	19	0.4%	1,590	19.3%	159	4.6%
28610	963	6.0%	643	15.0%	287	3.5%	33	1.0%
28636	717	4.5%	50	1.2%	659	8.0%	8	0.2%
28640	1,880	11.8%	181	4.2%	1,681	20.4%	18	0.5%
28648	2,419	15.1%	33	0.8%	492	6.0%	1,894	54.9%
28656	542	3.4%	4	0.1%	378	4.6%	160	4.6%
28658	247	1.5%	145	3.4%	64	0.8%	38	1.1%
28660	1,399	8.8%	62	1.4%	1,113	13.5%	224	6.5%
28664	1,458	9.1%	100	2.3%	1,347	16.4%	11	0.3%
<b>Total</b>	<b>14,613</b>	<b>91.6%</b>	<b>4,129</b>	<b>96.5%</b>	<b>7,934</b>	<b>96.4%</b>	<b>2,550</b>	<b>73.8%</b>

**Table 5.** ANOVA table for the effect of temperature and dissolved oxygen on  $U_{crit}$ , tail beat frequency, and tail beat amplitude (response variables) in both swim flume sizes.

Response	Effect	Small Flume				Large Flume			
		DFn	DFd	F	P	DFn	DFd	F	P
Ucrit	Temperature	2	42	25.08	< 0.001	2	21	11.25	< 0.001
	Length	1	42	101.23	< 0.001	1	21	5.45	0.030
	Temperature:Length	2	42	6.01	0.005	2	21	2.38	0.117
	Dissolved Oxygen	2	42	0.40	0.676	2	21	0.13	0.880
	Length	1	42	59.8	< 0.001	1	21	6.46	0.019
	Dissolved Oxygen:Length	2	42	0.59	0.560	2	21	1.44	0.259
Tail Beat	Temperature	2	41	22.18	< 0.001	2	19	2.91	0.079
Frequency	Length	1	41	8.14	0.007	1	19	12.88	0.002
	Temperature:Length	2	41	0.32	0.728	2	19	6.08	0.009
	Dissolved Oxygen	2	41	0.25	0.781	2	19	1.42	0.267
	Length	1	41	9.12	0.004	1	19	6.72	0.018
	Dissolved Oxygen:Length	2	41	0.18	0.837	2	19	0.06	0.943
Tail Beat	Temperature	2	41	0.17	0.848	2	19	1.38	0.276
Amplitude	Length	1	41	199.93	< 0.001	1	19	37.18	< 0.001
	Temperature:Length	2	41	3.85	0.029	2	19	2.93	0.078
	Dissolved Oxygen	2	41	0.09	0.916	2	19	0.22	0.808
	Length	1	41	198.8	< 0.001	1	19	28.95	< 0.001
	Dissolved Oxygen:Length	2	41	2.32	0.112	2	19	2.24	0.134

## Figures

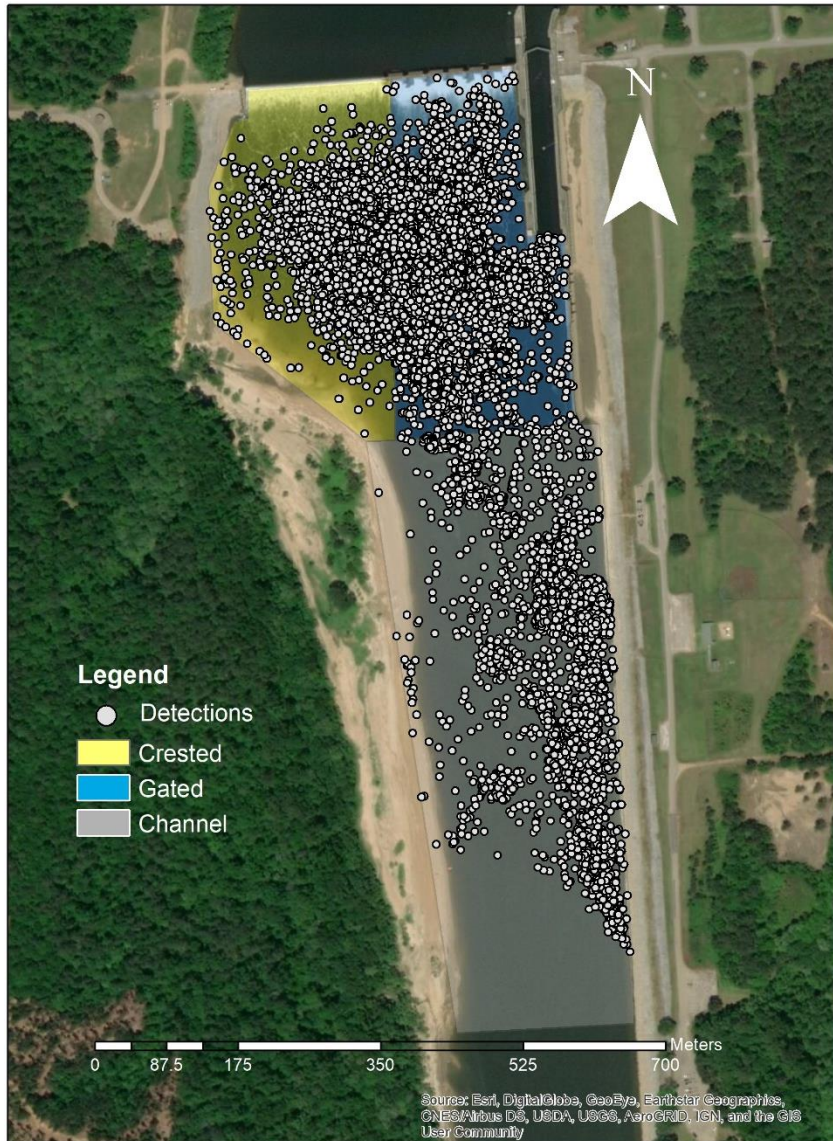


**Figure 1.** The array of 15 Lotek WHS 3250L series receivers located in the tailrace below Claiborne Lock and Dam. Each yellow circle represents the location of a single receiver. The star positioned between the crested spillway (left) and gated spillway (right) marks the release point of tagged fish.

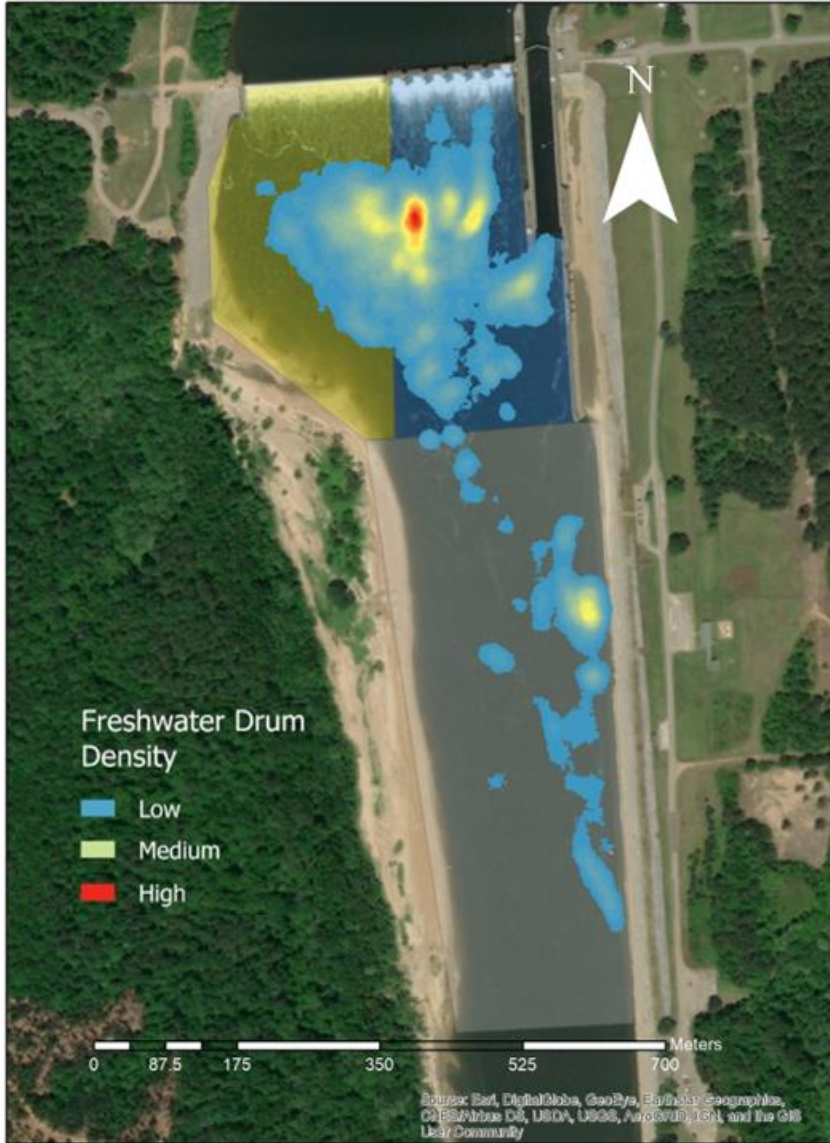


**Figure 2.** Habitat zones of Claiborne Lock & Dam tailrace. The crested and gated spillways are split down the middle of the whole tailrace. The main channel begins on the eastern shore at the edge of the long lock wall along rip rap and on the western shore where the sandy bank starts. It extends to the end of the rip rap and where the sandy bank becomes riverbank.

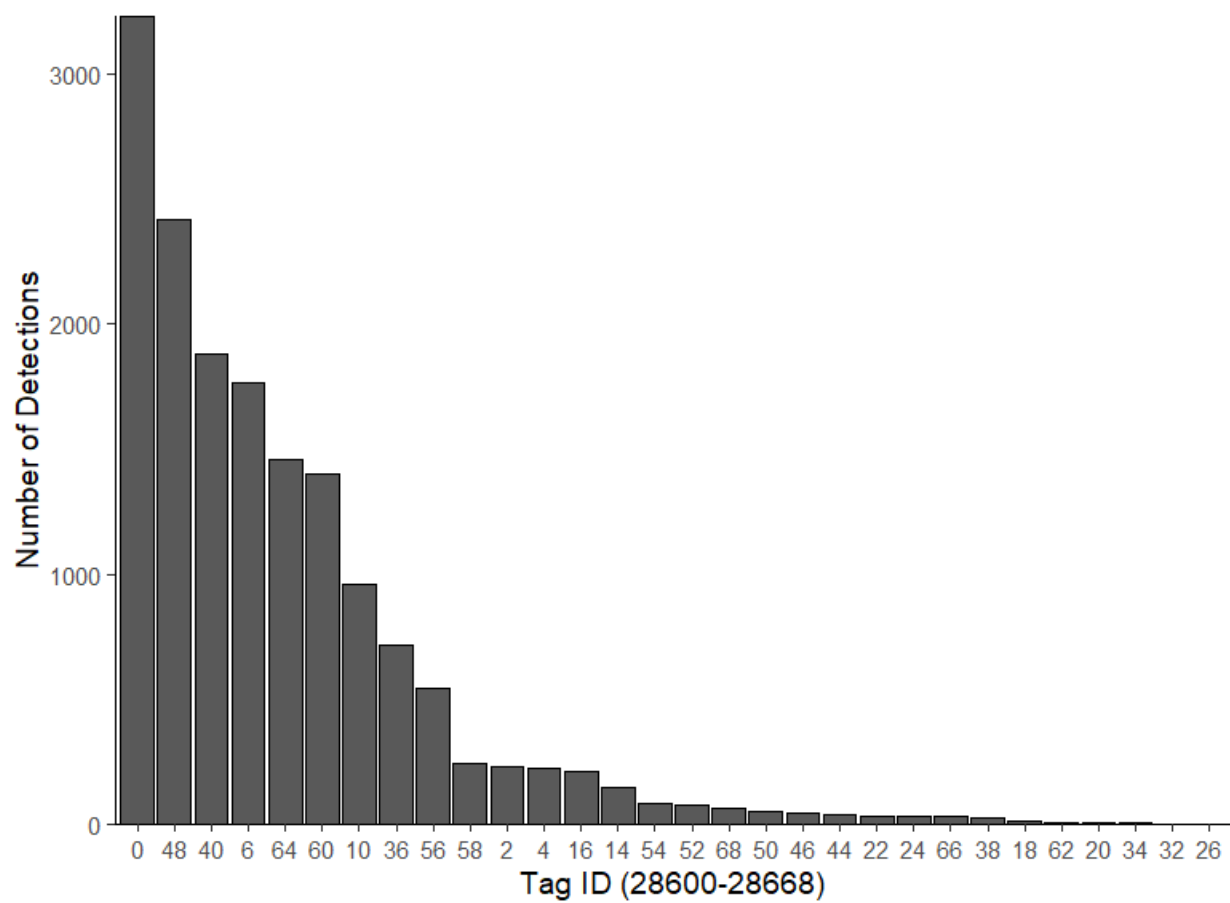




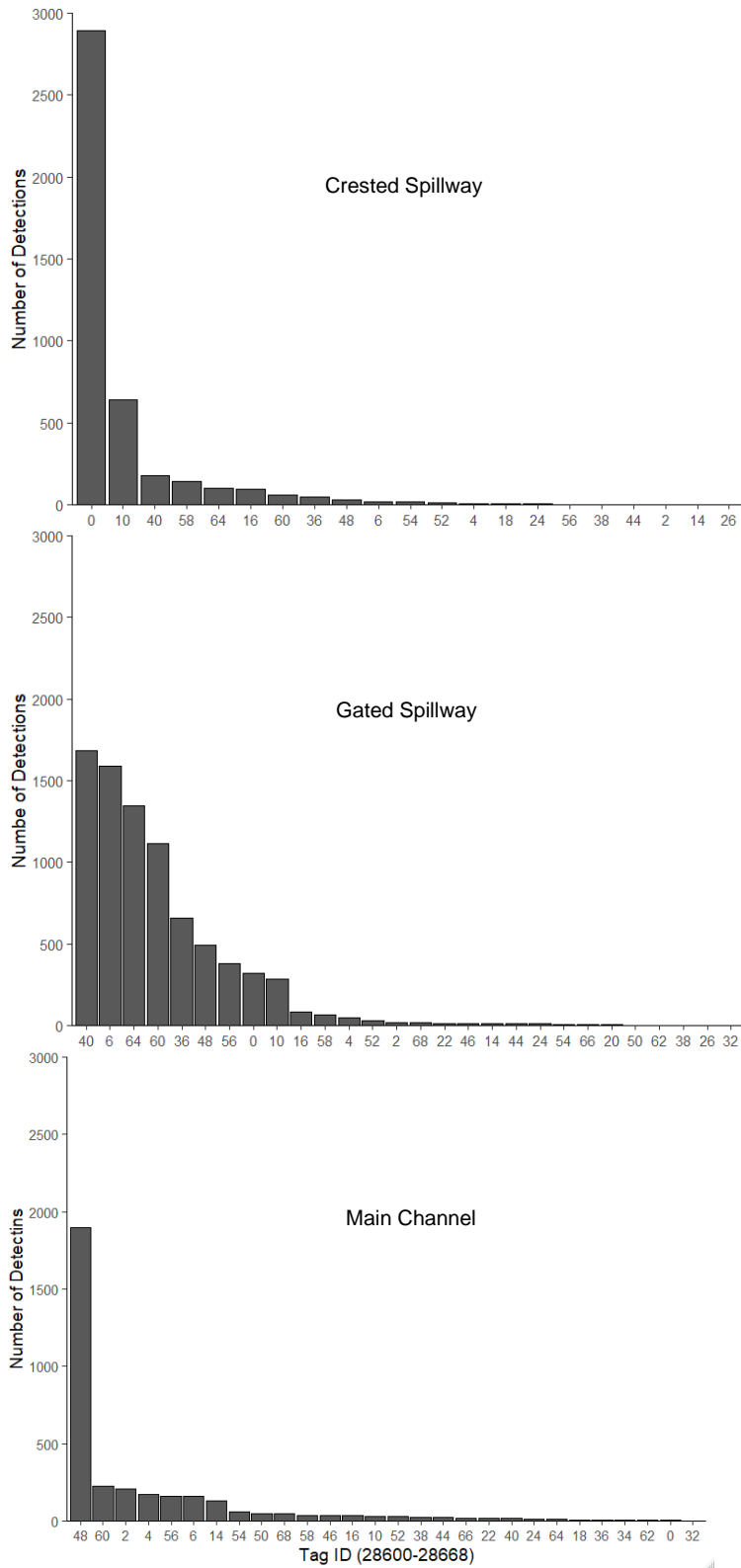
**Figure 3.** Triangulated locations of all Freshwater Drum (n=30) tag detections (within 1 m<sup>2</sup> radius).



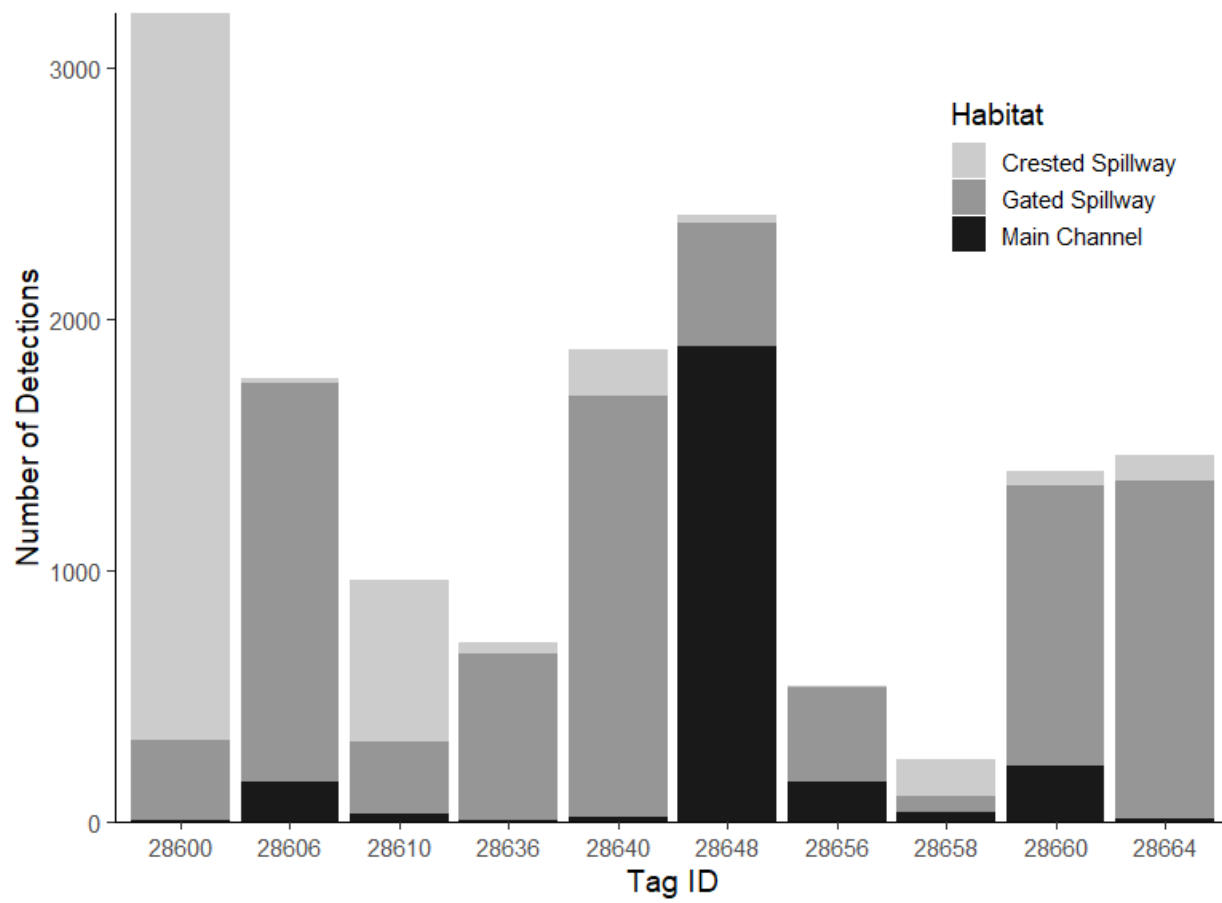
**Figure 4.** A heat map of detection densities with blue shading as the lowest density and red as the highest.



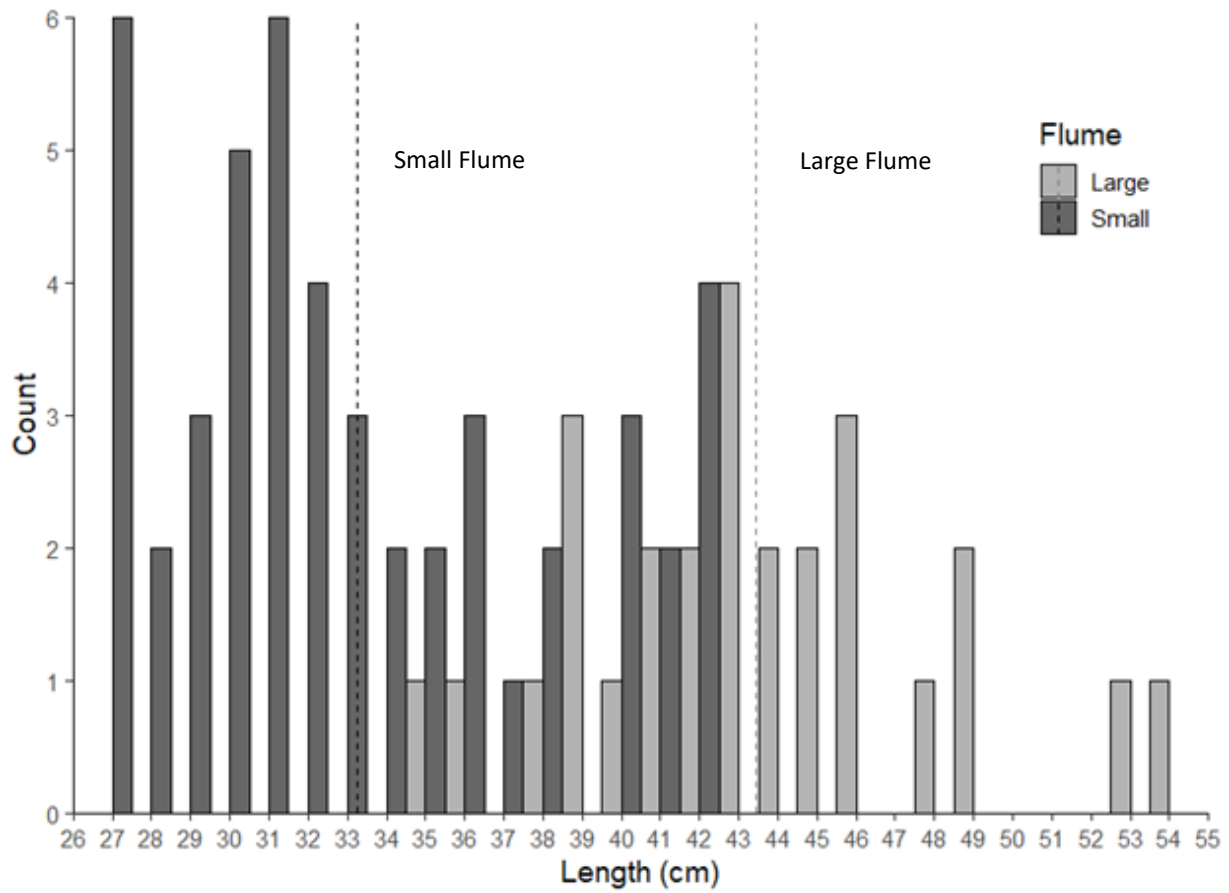
**Figure 5.** Frequency distribution of individual fish tag detections (in descending order of detection). Tag IDs 28608, 28612, 28630 were undetected by the acoustic array are therefore not included.



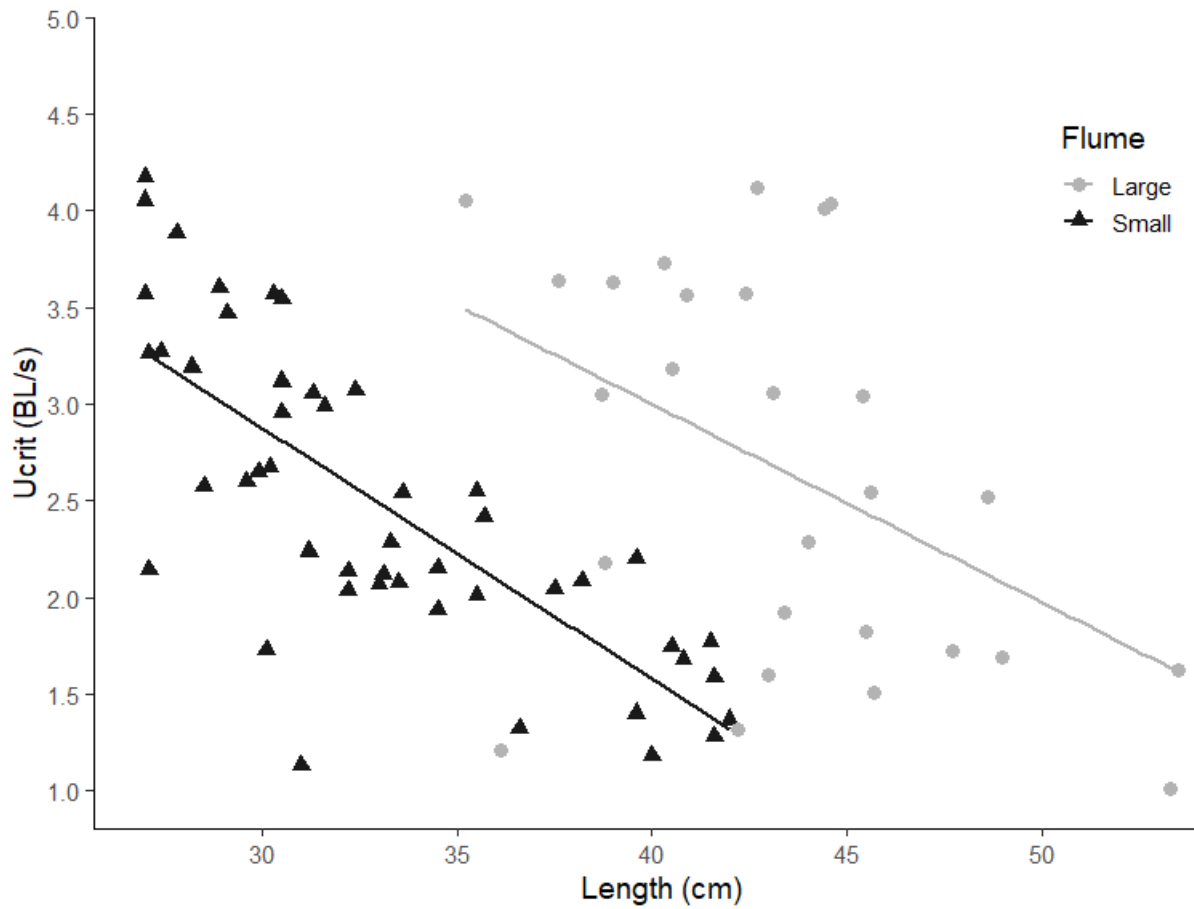
**Figure 6.** Frequency distribution of individual fish tag detections within each of the three habitat zones (in descending order of detection).



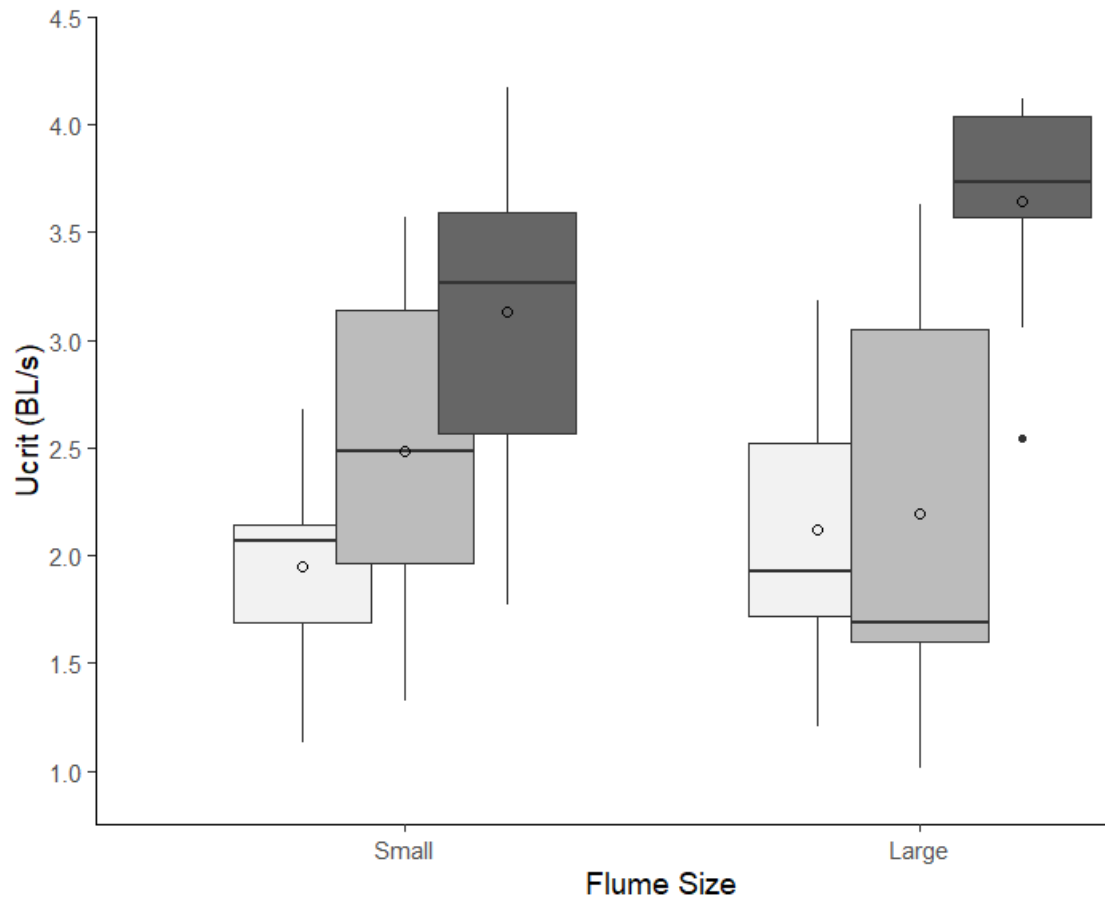
**Figure 7.** Habitat-specific detections for the 10 most frequently detected tags.



**Figure 8.** Fish body lengths for small (dark) and large (light) flume sizes. Vertical dotted lines indicate the mean body length for each flume.

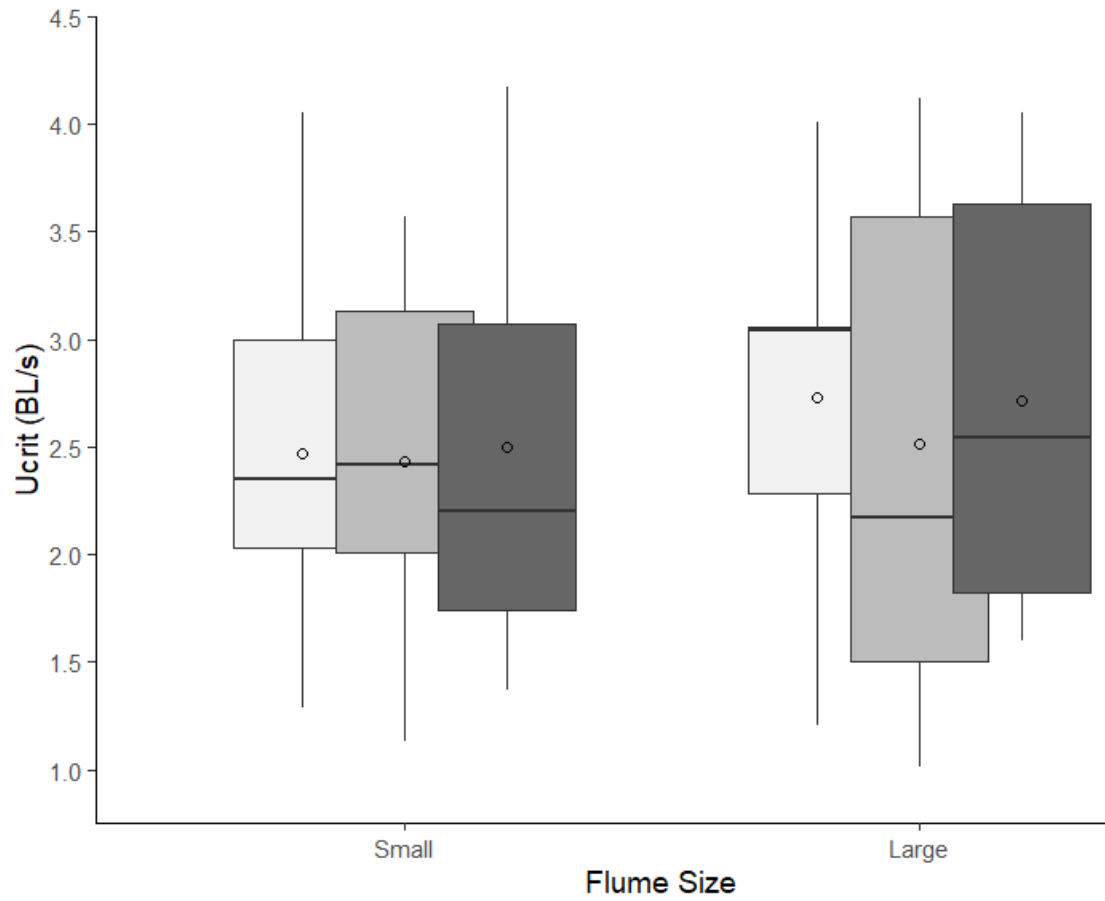


**Figure 9.**  $U_{crit}$  values (BL/s) as a function of fish length (cm) and flume size. Values from the small flume are black triangles and values from the large flume are gray dots.

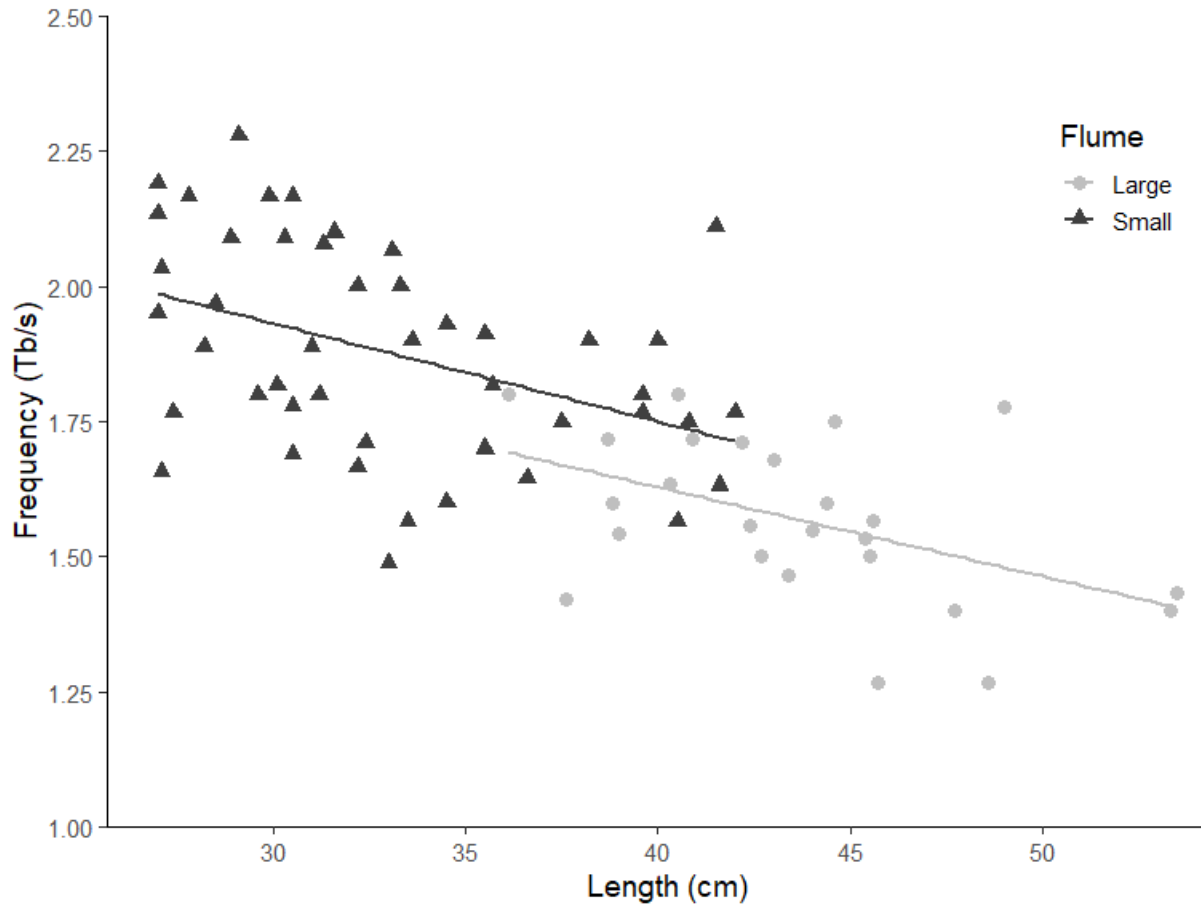


**Figure 10.**  $U_{crit}$  values (BL/s) for each temperature treatment (10°C = white, 20°C = gray, 30°C = dark gray) in both flume sizes. The median  $U_{crit}$  value for each temperature is marked within each box by a straight line, and the open circles represent the means. The box represents the 25<sup>th</sup> and 75<sup>th</sup> percentile and the whiskers represent the range of the data.

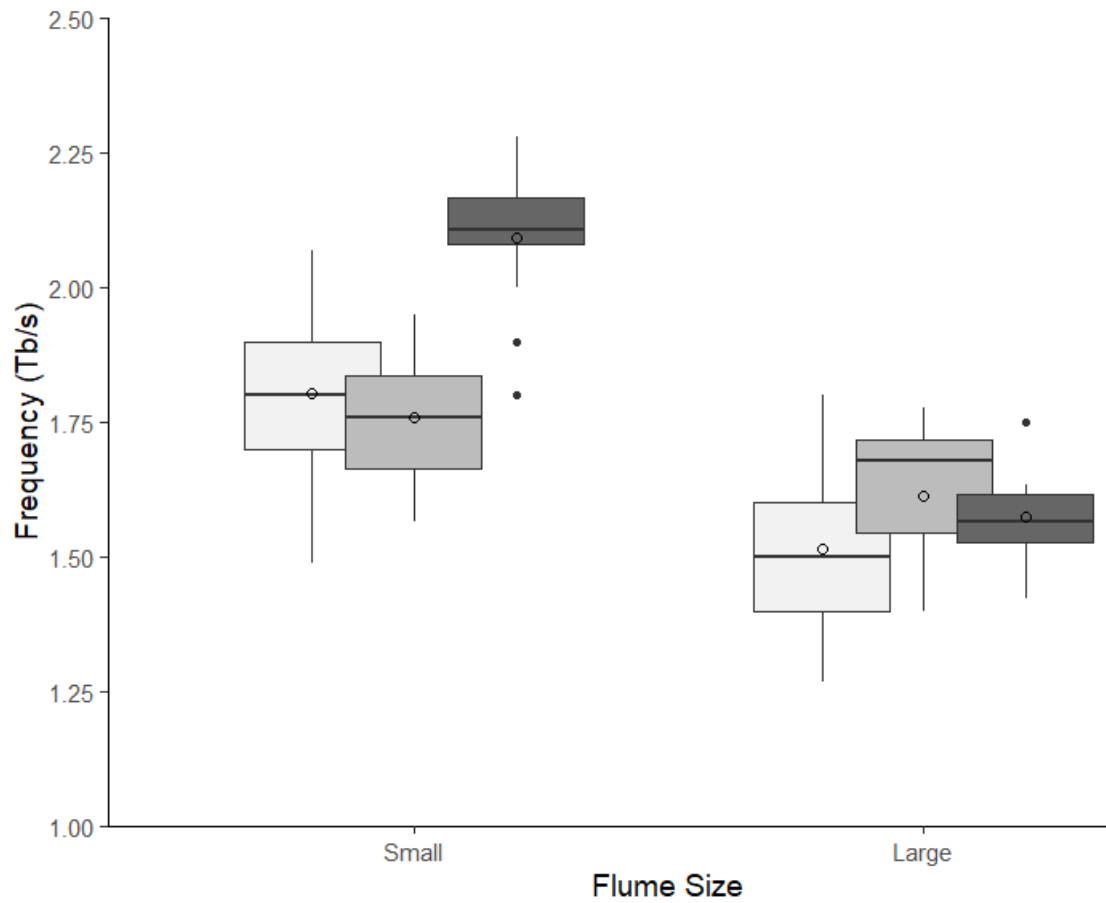




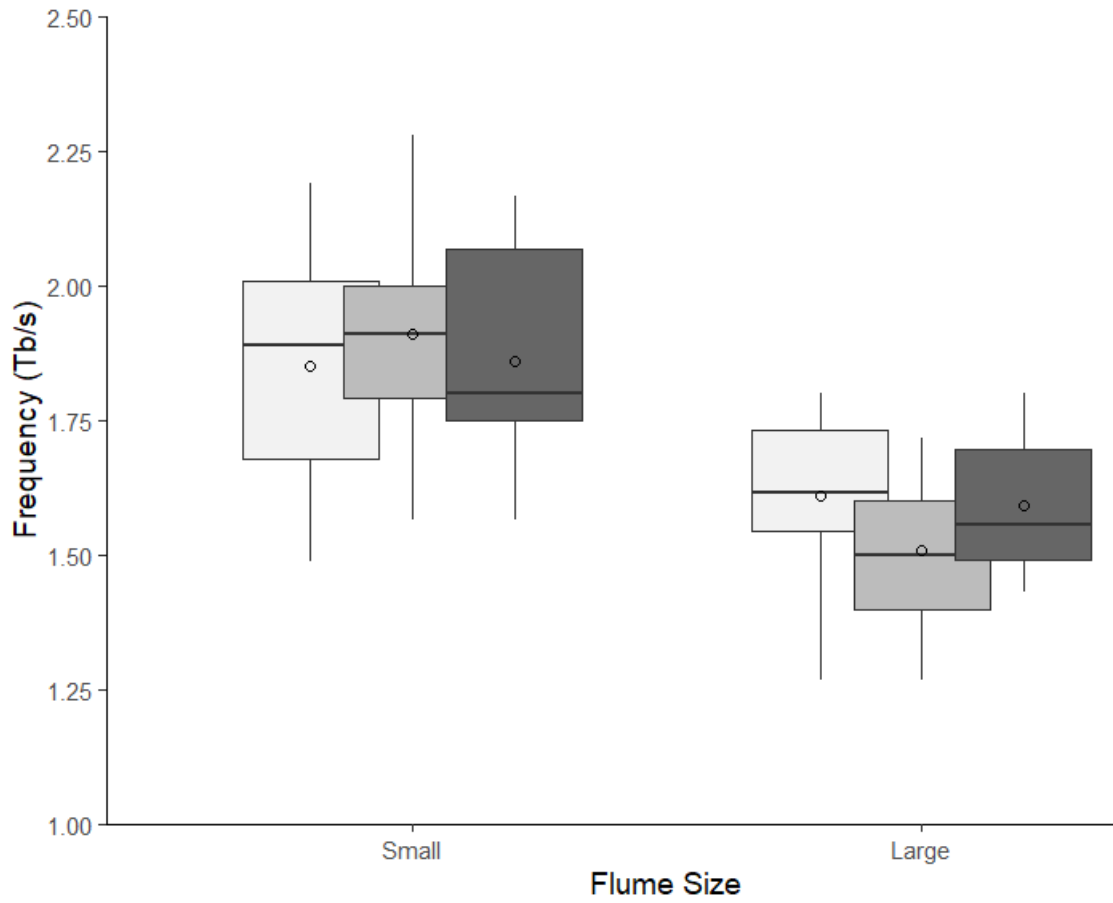
**Figure 11.**  $U_{crit}$  values (BL/s) for each dissolved oxygen concentration (4 ppm = white, 9 ppm = gray, 14 ppm = dark gray) in both flume sizes. Symbols and data are as defined in Figure 10.



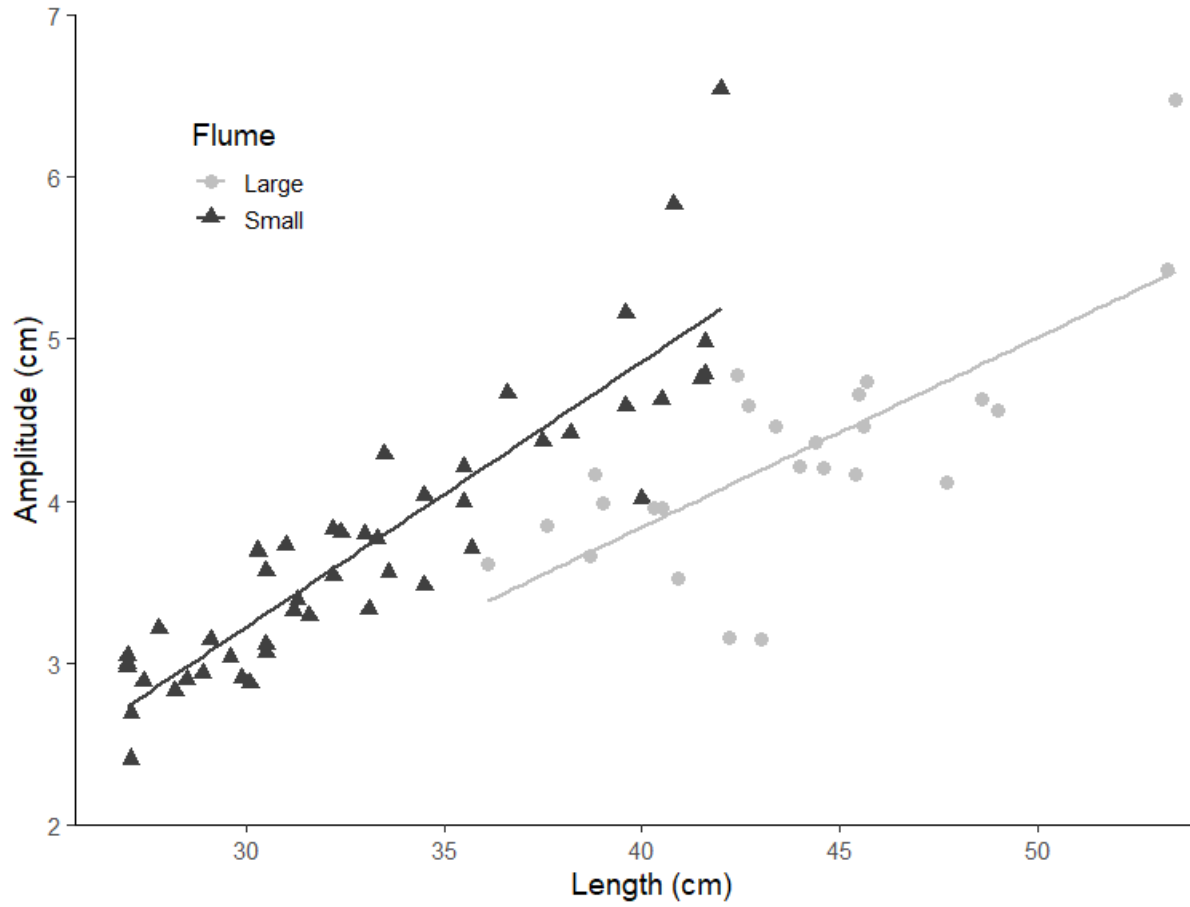
**Figure 12.** Scatter plot of tail beat frequency values (Tb/s) at 1 BL/s velocity as a function of fish length (cm) and flume size. Symbols are as defined in Figure 9.



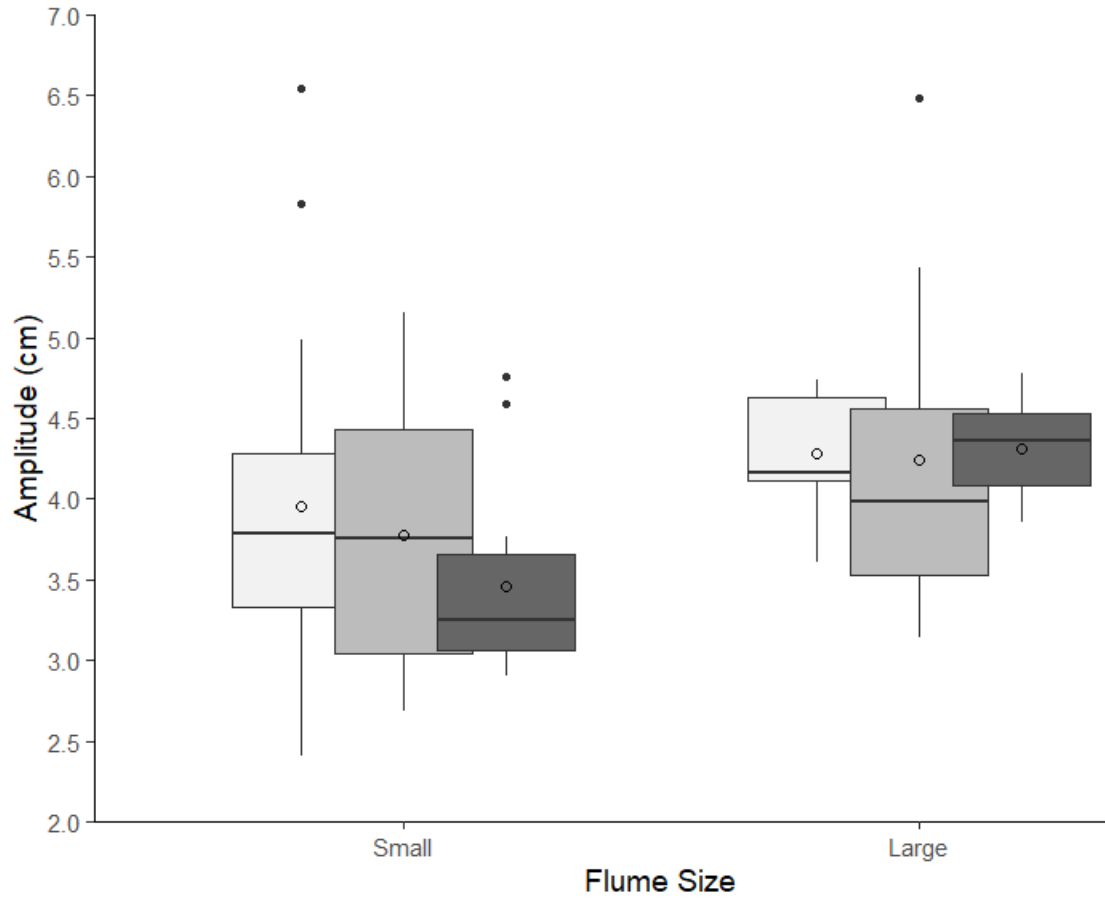
**Figure 13.** Tail beat frequency values (Tb/s) for each temperature treatment. Symbols and data are as defined in Figure 10.



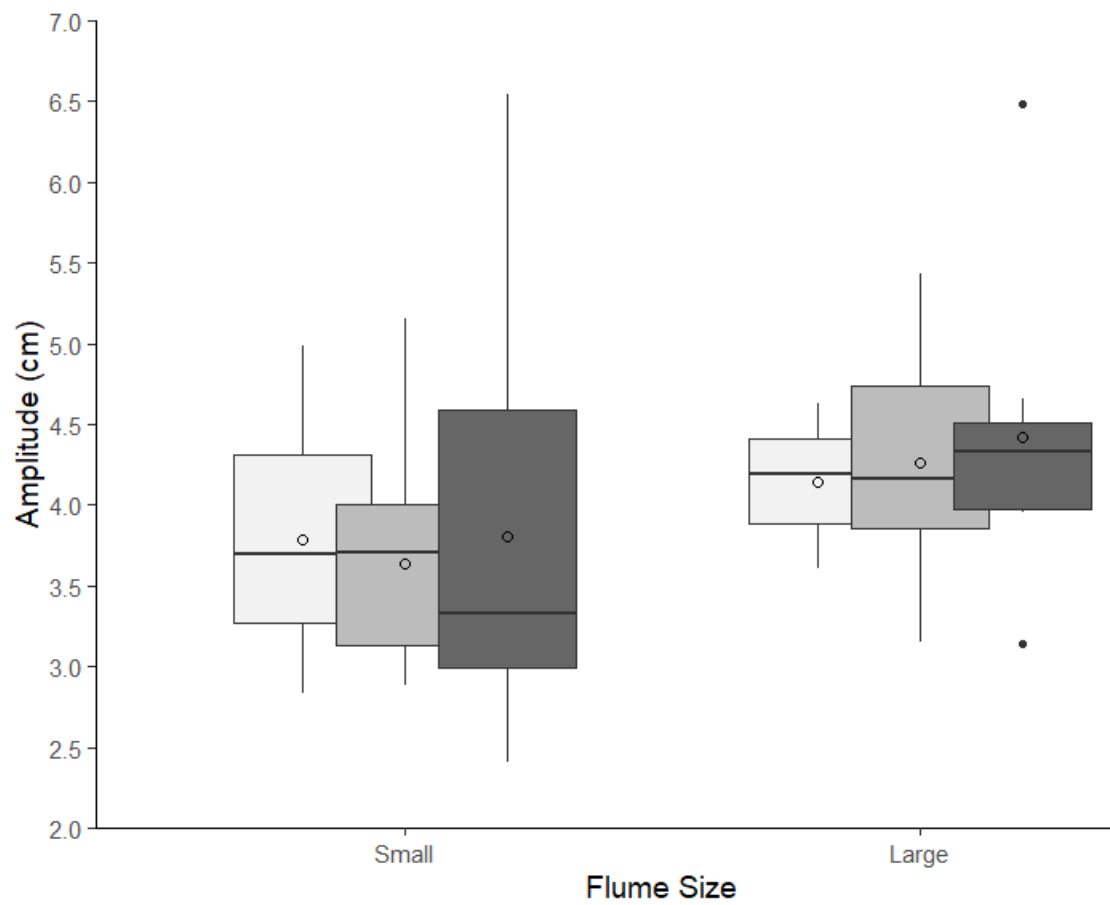
**Figure 14.** Tail beat frequency values (Tb/s) for each dissolved oxygen treatment. Symbols and data are as defined in Figure 11.



**Figure 15.** Tail beat amplitude values (cm) at 1 BL/s velocity as a function of fish length (cm) and flume size. Symbols are as defined in Figure 9.



**Figure 16.** Tail beat amplitude values (cm) for each temperature treatment. Symbols and data are as defined in Figure 10.



**Figure 17.** Tail beat amplitude values (cm) for each dissolved oxygen treatment. Symbols and data are as defined in Figure 11.