Quantifying fish swimming performance and behavior in two diverse environments: a
multifaceted approach.

by

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Abstract

In the southeastern United States, low-head dams are common and the effects of these structures on migratory fishes are relatively unknown. Studying how migratory fish behave in habitats altered by dams such as the upstream impoundments that are formed and the downstream tailrace areas is important for understanding and predicting the overall biological and ecological impacts of dams on riverine fish populations and ecosystems. Here I quantified a variety of aspects of behavior, movement, physiology, and hematology of three species of fish in two distinct systems-- a small impoundment that is reflective of upstream habitat created by a dam, and in the tailrace of a dam on the Alabama River.

In the small impoundment, I quantified behavior of two species (American paddlefish *Polyodon spathula*, a riverine fish, and largemouth bass *Micropterus salmoides*, a lacustrine fish) in an enclosed small impoundment using a combination of acoustic and radio biotelemetry. An array of acoustic receivers allowed me to quantify 2-dimensional movement throughout the impoundment and the radio receiver allowed me to collect data from electromyogram (EMG) tags quantifying fish muscle activity. I found that paddlefish swam constantly throughout the impoundment, and moved faster at night, while largemouth bass were much less active, and showed no diel behavioral pattern. In contrast to my expectations, activity data from the EMG tags were not correlated with 2-dimensional movement calculated from the acoustic tracking data, even when the two data streams were merged at the finest

time-scale possible. The EMG data I collected may not be representative of average swim speed, but rather of very fine-scale locomotor activities which are undetectable in the acoustic tracking data. Although these results may not be directly applicable to paddlefish in a riverine setting (e.g., due to effects of flow), they do speak to situations where paddlefish are cultured or are used in a reservoir ranching environment, as well as for lentic habitats such as backwaters where riverine fishes may spend a substantial amount of their lives.

The second aspect of my research involved study of the behavior of paddlefish and smallmouth buffalo (*Ictiobus bubalus*) in the tailrace of a low-head dam on the Alabama River using the same telemetry techniques as in the small impoundment, but at a much larger scale as well as with the addition of quantifying physiological states of fish as they staged and potentially passed the dam during periods of spillway inundation using hematology. In total, 88 of 330 tagged fish passed the dam. I was able to triangulate over 46,000 positions in the tailrace from 35 paddlefish, and 22 smallmouth buffalo. Additionally, EMG transmissions were logged from 180 unique fish in the tailrace, including from 22 individuals during the actual time windows when they passed the dam. I found that paddlefish slightly increased their activity (EMG) above their normal average to pass the dam, while smallmouth buffalo were able to pass with less than average activity. Activity in the tailrace was highest for both species at a gage height of approximately 10.7m. Finally, although paddlefish were able to pass the dam, I measured unprecedentedly high concentrations of cortisol in their plasma. Levels of all blood parameters for smallmouth buffalo were relatively consistent to those measured in other migratory catostomids in tailrace settings.

Differences in the passage rates and physiological states of these species could be due to microhabitat preferences in the tailrace, and swimming performance. The results of this riverine portion of my work will provide valuable information for use by the US Army Corps of Engineers and aquatic conservation and/or management organizations in determining and designing species-specific mitigation measures for low-head lock-and-dam structures across a wide array of rivers nationwide.

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Organisms in lotic systems can depend on energy inputs from both upstream and downstream environments, making connectivity very important. Energy generally flows downstream and is used by specialized aquatic communities that are adapted to the longitudinally organized ecological niches of a river ecosystem (Vannote et al. 1980). However, energy can also move upstream, and in fact, many ecosystems depend on resource pulses from downstream environments (Schindler et al. 2013). As such, riverine ecosystem functioning depends upon the overall longitudinal connectivity of main channels, and interruption of this connectivity can cause basin-wide biotic and abiotic changes (Ward 1989).

In over half of the world's rivers, connectivity has been disrupted by dams (Nilsson et al. 2005). Although dams can benefit humans in many ways (e.g., facilitating navigation, providing water supply, recreation, hydroelectric power generation, and flood control), their presence fragments and even eliminates habitat by altering hydrology (changing from lotic to lentic systems) and sedimentation patterns. They also have direct effects on aquatic organisms, particularly those that require migration to spawn. When dams interrupt fish migrations, populations can be reduced due to the prevention of spawning (Bunn and Arthington 2002; Braaten et al. 2015).

To mitigate the effects of dams, a number of solutions have been implemented, including trapping and hauling fish beyond the dam, and installation of structures such as ladders, lifts, vertical-slot passages, and even launching fish over the dam using cannons (Geist et al. 2016). These engineered solutions have served to increase rates of movement of

migratory species past dams (Noonan et al. 2012). However, they do not entirely re-create pre-impoundment conditions, and fish do incur costs when passing dams (Roscoe and Hinch 2010).

Migrating adult fish can incur two kinds of costs when passing dams that include two distinct aspects (Roscoe et al. 2011; Cook et al. 2011). One is the cost of a temporal delay below a dam, which is often the result of failure to find fishway entrances due to a lack of directional cues or attraction flows (Roscoe and Hinch 2010; Izzo et al. 2016). Fish have evolved precise timing of migrations so if they experience a delay, they may not arrive at their spawning sites when conditions allow for egg survival and development (Caudill et al. 2007). The second cost is physiological. Passage can induce physiological stress responses, and increase energetic costs of migration which can ultimately impact survival. Although acute stress responses can be beneficial for predator escape scenarios (c.f., spawning migrations), they can be energetically demanding. If an animal has a finite amount of energy, then stress responses might reallocate energy that would otherwise be used for gonad development, migration, and/or spawning (Wingfield et al. 1998; Ricklefs and Wikelski 2002; Cook et al. 2011). If the energetic costs of migration are too high due to the potentially exhaustive activity required for passage over a dam, then the fish might not spawn that year, choosing instead to use their energy for survival versus reproduction. Given this, artificial fishways have been designed to minimize stress and energetic effort required to pass in an effort to mitigate energetic costs (Peake et al. 1997; Haro et al. 2004).

To understand the impacts of passage on fish, researchers have used techniques ranging from laboratory experiments on swimming performance to large scale telemetry studies on movement and behavior. An advantage of laboratory experiments is that performance, stress,

and respiration can be measured precisely in a controlled environment. However, they do not necessarily replicate conditions faced by animals in the field. Telemetry offers researchers a way to study movement, behavior, and even physiology of animals *in situ*. Numerous such field studies have been conducted relative to fish passage, and with recent advances in tagging technology, researchers can more accurately describe fine-scale behavioral patterns and estimate physiological costs of those behaviors (Cooke et al. 2004).

Electromyogram transmitters measure fish muscle activity, reporting the data via radio or acoustic signals. Early iterations of such transmitters worked by sampling electrical impulses from fish muscle and transmitting pulsed signals. The pulse rate of the transmission was correlated with swimming speed. More recent versions integrate voltage measurements over a set interval and transmit an arbitrary coded signal (from 0 to 50) that corresponds to a relative index of the muscle activity measured over that interval. Researchers have used electromyogram telemetry to estimate activity levels and swimming speeds of migrating fish through both artificial and natural passages (e.g., Hinch et al. 1996, Quintella et al. 2004, 2009, Pon et al. 2009a, Alexandre et al. 2013,), to estimate discrete behaviors (Berejikian et al. 2007), as well as to estimate stress and respiration (e.g. Hinch et al. 1996, Cooke et al. 2004, 2002, Geist et al. 2003, Chandroo et al. 2005, Lembo et al. 2008).

Artificial fishways are not the only way past dams. Other ways to pass exist, and the physiological costs of using those pathways are not well understood. Some dams on navigational corridors have locks to allow for boats to pass, and the operation of these locks can also allow fish to pass (Keefer et al. 2004; Brown et al. 2006). At some dams, special lock operations have been conducted for the sole purpose of enhancing fish passage opportunities

(Moser et al. 2000; Young et al. 2012; Simcox et al. 2015). Another way fish can travel upstream without a fishway is over fixed-crest spillways, although the success of this approach depends on the height of the water coming over the dam (i.e., the "head"). Passage via these "alternative fishways" has been documented for several species (Mettee et al. 2005; Simcox et al. 2015), but little is known about the physiological costs incurred during the process.

To better understand the impacts of passage using alternative fishways at low-head dams, I studied the behavior, activity, and physiology of migratory fish passing a low-head dam using a suite of techniques, including acoustic telemetry, coded electromyogram telemetry, and hematology. Here I combine two separate but complementary studies on the behavior and physiology of two migratory fish species as they relate to staging below and passage over a low-head dam in the Alabama River. The first study had two aims: to establish a coupled biotelemetry observation system and to quantify the behavior and activity of paddlefish *Polyodon spathula* in a large lentic system as compared to a less active species, the largemouth bass *Micropterus salmoides*. The second study also had two aims: use the same combined biotelemetry observation system in the tailrace of a low-head dam for the study of paddlefish and smallmouth buffalo *Ictiobus bubalus* behavior and activity, as well as to describe the physiological state of these fishes during staging and potential passage using hematology.

The effects of dams on paddlefish have been well studied in many systems (Purkett 1961; Pasch et al. 1980; Rosen and Hales 1980; Paukert and Fisher 2001; Zigler et al. 2004; Firehammer and Scarnecchia 2007) but in Alabama, they have been less studied, with passage over low-head dams only recently documented (Mettee et al. 2005, 2006; Simcox et al. 2015). The smallmouth buffalo is also a long-lived migratory species native to large rivers of North

America. Although it is not of the same conservation concern as the paddlefish, it is still imperiled by dams for the same reasons. I chose these two species for their similar life histories, but contrasting habitat uses. While paddlefish maintain position in the middle of the water column to filter feed (Allen and Riveros 2013), smallmouth buffalo are benthophilic and tend to occupy more littoral habitats with slower water (Adams and Parsons 1998). I predicted that these fish would experience different energetic costs from one another as they migrate up to and over the dam, which could be due to differences in swimming performance, microhabitat preferences, run timing, or a combination of factors.

In addition, little is known about seasonal changes in baseline activity levels and metabolic processes of these study species. That migration is energetically demanding is well established, but little is known about the physiological changes undergone by migratory species, let alone as they relate to the challenge of passing a low-head dam (Cooke et al. 2008). This is why I sampled and analyzed blood chemistry of both species throughout the migration season and in different locations, ranging from the tailrace to areas downstream of the dam. I predicted that both species would experience increased baseline levels of biochemicals linked to stress and respiration as they freed up energy stores for migration and spawning. Establishing baseline levels of these blood parameters is key to laying the groundwork for further study on their physiology and swimming performance. The data assembled and analyzed herein provide an insightful look at the impacts of a low-head dam on migratory fishes.

Chapter 2: Characterizing the behavior and activity patterns of paddlefish and largemouth bass in a small impoundment using a coupled biotelemetry system.

Introduction

The American paddlefish *Polyodon spathula* is a potamodromous fish native to the large rivers of central North America that is exploited commercially and recreationally throughout their range. Like other acipenseriforms, it is characterized by a long life-span, slow growth, delayed maturation, and infrequent spawning, which make it intolerant to disturbances and amplifies its risk of extinction (Tripp et al. 2019). Paddlefish populations are in decline because of overfishing, pollution, and the construction of dams (Carlson and Bonislawsky 2011). Dams can destroy spawning habitat, block migrations, isolate populations, and disrupt the flow cues that trigger the start of the paddlefish migration. However, despite these challenges paddlefish still persist in these altered environments.

When a dam is constructed, large reaches of the river are flooded and changed from lotic to lentic habitats. Depending on the hydrography of the river and the type of dam structures built, the relative availability of riverine and backwater habitats can change drastically post-impoundment. Multiple aspects of paddlefish populations have been compared between lotic and lentic environments within the same impounded systems, including their age structure, abundance, growth, condition, and exploitation (Reed et al 1992; Lein and DeVries 1998; Leone et al. 2012), and their movement and habitat use (Hoxmeier and DeVries 1997; Paukert and Fisher 2000). In general, habitat selection is thought to be driven by seasonal changes in productivity, and abiotic factors, but little is known about how paddlefish behave at fine spatiotemporal scales when they occupy these different environments.

In free-flowing rivers, paddlefish are free to move between lentic and lotic environments. However, when pathways between these habitats are blocked by dams, paddlefish may be unable to access preferred habitats. Furthermore, for a ram-ventilating, filter feeding, migratory fish that depends on flow for feeding, navigation, and spawning, reducing or eliminating flow may have consequences for growth and survival.

I had a unique opportunity to study the behavior and activity of adult paddlefish that had been stocked in a research pond more than 20 years ago. This system is comparable to lentic systems in the wild, and also representative of some aquacultural venues used to raise paddlefish for caviar production ("reservoir ranching": Mims et al 1999, Mims 2001; Onders et al 2001). The objective of this study was to quantify behavior and activity patterns of paddlefish in a large lentic system, and compare them to those of a lentic specialist, the largemouth bass *Micropterus salmoides.* I used a coupled biotelemetry system (an acoustic 2D receiver array, and a radio antenna) to quantify their movement and muscle activity over a period of one year.

By double-tagging fish with acoustic transmitters and electromyogram radio transmitters, I was able to simultaneously track the study animals in two-dimensional space while monitoring their muscle activity. This allowed me to measure their activity both in terms of physical displacement and swimming speed, as well as in terms of electrical output from the muscle. While several studies have correlated EMG output with swimming speed in the lab, only one other study has tried to correlate activity data from EMG tags with swimming speed as measured with positional telemetry (Demers et al 1996).

I predicted that paddlefish would exhibit both seasonal and diel patterns in movement, and that those patterns would also be reflected in the muscle activity data. Furthermore, I

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hypothesized that paddlefish would move more and be more active than largemouth bass, with differences varying in magnitude with season and diel period.

Study Site

The site for this study is an 8 ha impoundment at the EW Shell Fisheries Research Center in Auburn, Alabama. It reaches a maximum depth of 4.5 m, with an average depth of ~2 m. The stocking history of the impoundment has been haphazard, but it has supported a small population of paddlefish for more than 20 years, and a reproducing population of largemouth bass since its construction in the 1940s.

Methods

In total, six largemouth bass and six paddlefish were tagged with a combined acoustic and radio transmitter (LOTEK Wireless CART tag models MM-MC-11-45 and MM-MC-16-50). Of those fish, five paddlefish and four largemouth bass were also implanted with a coded electromyogram transmitter (LOTEK Wireless CEMG tag models R11-35 and R16-50). To capture paddlefish and largemouth bass, I used a large-mesh gillnet and a boat electrofisher respectively. Tag size was chosen based on fish size, and if fish were double-tagged the combined tag-weight never exceeded 2% of the individual's body-weight. I surgically implanted the tags through one incision in the left ventral side of the belly, approximately 5 cm anterior to the pelvic girdle in paddlefish, and 5 cm posterior to the pelvic girdle in bass. Fish were anesthetized in a live well with dilute MS222 solution and live well water was pumped over the gills for the duration of the surgery. Surgeries did not last longer than 5 min, and all the bass

were allowed to recover in a live-well containing fresh pond water before release. Paddlefish were revived in the pond by manually moving water through their gills until they swam off voluntarily. The two gold-tipped CEMG electrodes were inserted into the muscle at approximately 70% of the eye-to-fork length along the lateral line with 10 mm spacing between electrodes. The large and small CART tags I used transmit a signal once every 20 seconds, the mini CART tags every 8 seconds and the CEMG tags every 3 sec.

The first fish tagged were two paddlefish in March 2017. Next were two largemouth bass implanted with CART tags in July 2017. Then, in September 2017 two largemouth bass and two paddlefish were double-tagged with CART and EMG tags. Finally, in May 2018 two additional largemouth bass and two additional paddlefish were double-tagged, and one of the fish that had been tagged in March 2017 was also implanted with an EMG transmitter. See Table 1 for tag models used, and Tables 2 and 3 for tagging history and detection summaries for each individual.

At the beginning of the study, I recorded individual fish positions with an array of 3 submersible acoustic receivers (LOTEK Wireless WHS 3250L). In August 2017, I added three more receivers to increase the coverage, and improve triangulation precision. I recorded EMG tag transmissions (henceforth called EMG scores) using a stationary 4 element YAGI antenna positioned on the pond dam and connected to a radio receiver (LOTEK Wireless SRX800) by a 30m coaxial cable. Positions were triangulated using UMAP software from LOTEK Wireless, filtered down to a dilution of precision of 2, and spatially clipped to the pond boundary using program R. Positions with duplicate timestamps were deleted. Also, positions were filtered based on the ping interval of each transmitter; if the number of seconds elapsed between two

consecutive positions was not a multiple of the ping interval for that transmitter type, then the later of the two positions was deleted.

Mortality was determined by examining positional data, and identifying fish whose movement became suddenly restricted to a very small area and remained in that area for the duration of the study. Because tags did not stop transmitting after mortality, the exact time of death of a fish was determined using piece-wise regression on the cumulative distance traveled, and all positions after the break point of the regression were deleted from the dataset. If fish were double-tagged, EMG scores were also deleted after the breakpoint.

Activity rates were quantified using the data streams from both transmitter types (CART and CEMG). I quantified movement-based activity with two indices: minimum displacement per hour (MDPH) and minimum average swimming speed per hour (MASS) (Rogers and White 2007). MDPH was calculated as the sum of the Euclidean distances (in m) between consecutive relocations for each hour of the study, which was then log transformed. Distances were only used in the analysis if the time elapsed between relocations did not exceed one hour. Minimum average swimming speed (MASS) was calculated as the displacement between relocations divided by the time elapsed between those relocations. I compared MDPH and MASS between diel periods for both species using paired t-tests. Due to mortalities and differences in tag battery life, there was only a 1-month window when all of the tags were active and transmitting, so seasonal comparisons could not be performed. EMG scores were averaged for each hour, and each individual over the entire study period. Diel comparisons were then made for both species using paired t-tests, by averaging the EMG scores for night and day hours for each individual.

I also used linear regression to test for correlation between EMG scores (standardized to the Z distribution– thus scaling the between-observation variation to the total variance for each individual, and eliminating the between-individual differences in both raw and scaled EMG scores), and movement (displacement and speed). Because EMG score and movement were not measured at the same time intervals, the data from the two transmitter types could not be merged at the finest time scale. That is, EMG scores were measured every 3 sec (at minimum), while the location of the fish could only be known every 20 sec (at minimum). Therefore, I used two separate merging techniques and show the results for both.

The first approach was to average the EMG scores over time intervals specified by two consecutive acoustic transmitter positions. For example, if a double-tagged fish was detected in one place at time= t0 and in another at t0 + 20 sec, then all its EMG scores that were recorded during that time interval were averaged. Thus, the average EMG score for that interval could be directly correlated with the minimum displacement and average speed over that interval. The second approach was to use a standard time interval – one hour – and correlate the average EMG activity in each hour of the study with the minimum displacement during that hour of the study. For example, from 7:00:00 AM to 8:00:00 AM on December 14th, 2019 Paddlefish X may have moved a total of 200 m with an average scaled EMG score of 0.14.

Results

All but one fish survived tagging, and there was also one delayed mortality. One fish (Largemouth Bass 28684) was not detected by the acoustic array beyond 4 days post-release. Because data were only available for a short time after its release, data from this fish were

excluded from all analyses. Delayed mortality occurred in one paddlefish. Using a piece-wise

regression approach, I estimated that Paddlefish 28690 died approximately 1 month after it was

tagged (on October 27th 2017 at 19:51:24) (Figure 1). All detections from this fish's

transmitters logged after that timestamp were excluded from analysis.

In general, paddlefish had higher detection frequencies than largemouth bass, likely

because their movements carried them throughout the pond, increasing the likelihood of their

detection by the receivers. Largemouth bass relocations tended to be more locally intense with

very small areas of higher density, while paddlefish tended to have much larger areas of higher

density. Furthermore, paddlefish were located more often in the middle of the pond than

largemouth bass, which were more commonly located in littoral habitat (Figures 2,3).

Movement

Using the filtered data, I found that paddlefish moved at an average rate of 223.9 m*hr^{-1}

(106.1 - 472.8; lower - upper 95% CI) over the course of the study. This did not differ from that

of largemouth bass, which moved at an average rate of 171.7 (69.1 - 426.2; lower - upper 95%

CI) m*hr^{-1} (Figure 4). In total, Paddlefish swam distances ranging from 381 km in 43 days to

4,967 km in 436 days (Table 2). Largemouth bass swam total distances ranging from 74 km in 19

days to 1,351 km in 313 days (Table 2).

Minimum displacement per hour (MDPH) of paddlefish differed between night versus

day hours (P = 0.0027). The average log(day-night) difference was -0.39 (-0.61 – .017; lower –

upper 95% CI) for paddlefish. Back transformed to the natural scale, paddlefish moved

approximately 129.57 m more during night than day (Figure 5). In contrast, largemouth bass

mean MDPH did not differ between day and night (Figure 5). As with displacement, paddlefish

minimum average swimming speed (MASS) differed significantly between day and night (log (day MASS – night MASS) = -0.048 [-0.075 – -0.021; lower and upper 95% CI] P = 0.0026), but the difference was not significant for largemouth bass (P=0.68). Back transformed to the natural scale, paddlefish swam approximately 6cm*s-1 faster at night than during the day.

Given that there was no difference between night versus day movement in largemouth bass, I also tested for a difference in movement between crepuscular hours (1 hour before and after sunrise and sunset) and non-crepuscular hours. The t-test showed no statistically significant difference in MDPH (P = 0.52).

EMG Activity

After excluding EMG transmissions after the death of Paddlefish 28690, I found that EMG activity varied greatly both among and within individuals across time. Average scaled EMG scores ranged from 0.12 to 0.99 while the coefficients of variation ranged from 4% to 62% (Table 4). Largemouth Bass 28692 had an average scaled EMG score of 0.99, which is probably due to faulty tag electrode implantation, so it was excluded from the analysis (the data from the acoustic transmitter were retained).

EMG activity did not differ between night versus day for either species (Figure 6). Also, Largemouth Bass EMG activity did not differ between crepuscular and non-crepuscular hours (Figure 6). Although paddlefish EMG activity was not higher at night versus day – despite the fact that they moved significantly more and swam significantly faster – I tested for a direct correlation between EMG activity and swimming speed. In order to test for a relationship between EMG activity and swimming speed, I standardized the raw EMG scores to a Z

distribution for each transmitter. Z score ranges for each individual ranged from 2.94 SD to 20.42 SD (Table 5).

Using approach 1 to merge the data, EMG Z scores were positively related to log mean displacement and log speed for paddlefish, but negatively related for largemouth bass (Figure 7). Using approach 2, EMG Z scores were negatively related to log mean displacement and log speed for both species (Figure 8). However, r^2 values were less than 1% for each of the regressions performed, indicating a poor fit, and that statistical significance was likely an artifact of the very high sample size, and is likely not biologically significant. Despite these apparent relationships between EMG score and swimming speed, most of the high EMG Z scores (> 2 standard deviations) were recorded at low swimming speeds (< 1 m/s) (Figure 9).

Discussion

All paddlefish moved constantly over the entire study period, although they moved slower during the day versus at night. Diel patterns in paddlefish movement have been recorded in one other study in Navigation Pool 8 on the Upper Mississippi River in Wisconsin, although that study was limited to locations of fish every 3 hr over a selected number of days across seasons (Zigler et al. 1999). Paddlefish behavior has not been measured at the fine spatiotemporal scale as was used in this study as well as being conducted in a more controlled environment such as a small impoundment. Although no measurement of zooplankton productivity or temperature were taken, I expect that increased activity at night was likely due to decreased water temperature combined with increased food availability. The vertical

migration of zooplankton prey into the upper water column (Hutchinson 1967) combined with cooler temperature could lead to more efficient foraging at night for paddlefish.

The paddlefish is a highly vagile species, and individuals have been documented traveling hundreds of kilometers a year across various habitat types (e.g. backwaters, reservoirs, rivers, etc.). Paddlefish movement in backwater habitats is relatively understudied, particularly at fine scales, so my goal was to document their behavior and compare it to previous findings in riverine systems. According to my results, some paddlefish covered total distances of more than 3,000 km in less than a year. A recent study by Tripp et al. (2019) showed that the maximum distance traveled by any of 77 tagged paddlefish in the Mississippi River Basin over a ten-year period was only 807 km. In a riverine habitat, paddlefish can maintain position in flow and passively trap food and absorb oxygen from the water moving through their mouths and over their gills. However, in a pond without flow, the paddlefish must move to actively ram-ventilate and filter water for food (Burggren and Bemis 1992), which could explain why they moved so much and so often in this study. Although paddlefish may not be capable of the same amount of movement in a riverine environment for a number of reasons (i.e., passage barriers, flow, etc.), additional comparisons of movement in lotic vs. lentic systems are needed to determine if the true distance that these animals are capable of swimming is being underestimated.

Without calibrating study fish in a respirometer, little can be said about the absolute energetic costs of the behaviors that I observed in this system (Alexandre et al 2013). However, in a smaller impoundment, or in an impoundment with less pelagic habitat (with more structure or obstructions to movement) the constant movement that paddlefish require to feed and

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ventilate could be restricted, which would have consequences for growth. If foraging ability is restricted, paddlefish may not be able to take in enough energy to grow, let alone forage and ram-ventilate. Future work should identify the degree to which ventilation and/or foraging requirements actually drive how much paddlefish move, and quantify the relative energetic costs of swimming at various speeds. If a relationship exists between impoundment design (size, depth, etc) and movement, and these movements have predictable consequences for growth (based on both intake and expenditures), then impoundments could be designed that optimize paddlefish production, particularly for reservoir ranching situations or in natural backwater habitats along lotic systems. As such, this behavior may be replicable in lentic habitats in the wild, where paddlefish might suffer from changes in habitat availability that restrict their movement.

Largemouth bass moved less than paddlefish, and showed no diel or crepuscular patterns in behavior. However, their average scaled EMG scores were higher than those of paddlefish. Previous studies have described both diurnal and diel patterns in bass activity, as well as seasonal shifts in those patterns (Warden and Lorio 1975; Mesing and Wicker 1986; Cooke et al. 2002). Seasonal comparisons were not feasible for fish in my study because individuals were tagged during different seasons and were not all detected in all seasons. Average swimming speeds of largemouth bass documented in this study were lower than have been previously documented (Hanson et al. 2007).

I expected to find a correlation between EMG activity and swimming speed, but no strong correlation was evident for either species. However, a small positive trend was statistically significant for paddlefish, which could mean that paddlefish are able to swim

relatively quickly with relatively low energetic outputs. Neither the observed nor predicted EMG Z scores that corresponded with long movements were much higher than for lower speeds, meaning that paddlefish could travel at higher speeds without greatly increasing their energetic output.

Although small correlations between EMG score and swimming speed were detected, most of the high EMG Z scores (> 2 standard deviations) were recorded at low swimming speeds (< 1 m/s) (Figure 9). This could be due to the fact that the EMG transmitters may be measuring the output of burst swimming activity at fine temporal scales (every 3 seconds), but these behaviors were not detectable by the acoustic tags, which measure location every 20 seconds. This problem was likely exacerbated by the second data-merging approach which aggregated EMG and movement over an hourly time scale. Other experiments have also failed to find a correlation between activity and swimming speed, and also cite the difference in spatiotemporal scales as the crux of the problem. Demers et al. (1999) located EMG–tagged largemouth bass and smallmouth bass *Micropterus dolomieu* at 30-min intervals and found no correlation between their average swimming speeds and muscle activity. Lucas et al. (1991) used heart rate telemetry to study the activity metabolism of northern pike *Esox lucius* and found that activity metabolism as measured from the heart rate tags was much higher than estimates based on mean swimming speed. Furthermore, they found that most of the activity metabolism was the result of localized bursts of activity, not large-scale movements. As such, measurements of movement will need to be made at a fine scale in order to draw inferences as to the activity metabolism of fishes.

Future work in biotelemetry should prioritize measuring energetic output and movement at the finest spatiotemporal scale possible. This would allow for the estimation of the metabolic costs of activities that occur at very fine spatial scales, which could account for a significant portion of a fish's energy budget, especially for less mobile species like the largemouth bass. According to my findings, 20-sec tracking intervals may still not be fine enough to accurately describe the energetic output of largemouth bass or paddlefish.

Reservoir ranchers and paddlefish aquaculturists that culture paddlefish in impoundments should remove structure and submerged obstacles from their habitat so as to maximize the swimming space available. Furthermore, managers of riverine backwater habitats who wish to enhance paddlefish populations may remove obstacles for the same reason. Connectivity between large areas within backwaters may be important for paddlefish to swim freely, and meet foraging and ventilation requirements for survival and growth.

Table 1. Transmitter models used in this study, with specifications on expected battery life, and total weight.

Transmitter	Battery Life (Days)	Transmitter Total Weight (g)
CART MM-MC-11-45	479	16
CART MM-MC-16-50	1409	37
CEMG2-R11-35	143	15
CEMG2-R16-50	490	33

Table 2. Detection summaries for combined acoustic and radio transmitters after filtering the data. Dates of first and last detections are given, as well as the duration of the tag's life, the number of detections (N), the detection frequency (F) in detections per day, and the total distance the fish traveled over the course of the study period (total dist). *This is the estimated death date of paddlefish 28690. **This fish was excluded from analyses due to tagging mortality.

Species	IDs	first	last	duration	N	F (#/day)	total dist (km)
Paddlefish	ID28506	9/19/17	6/15/18	269	302356	1125	3258
	ID28600	4/4/17	6/15/18	436	369568	847	3750
	ID28602	4/4/17	6/15/18	436	427554	980	4967
	ID28690	9/19/17	10/27/17*	39	34608	898	397
	ID28996	5/2/18	6/15/18	44	21571	493	381
	ID29000	5/2/18	6/15/18	44	25098	573	439
Largemouth	ID28692	9/18/17	6/8/18	263	25086	95	215
	ID28694	7/20/17	5/30/18	314	44166	141	149
	ID28696	7/20/17	5/30/18	313	160536	512	1351
	ID29070	5/2/18	6/1/18	30	25605	853	144
	ID29072	5/2/18	5/21/18	19	21637	1127	74
	ID28684**	9/19/17	9/22/17	3	1058	401	NA

Table 3. Detection summaries for all coded electromyogram transmitters deployed in the study. Dates of first and last detections are given, as well as the duration of the tag life, the number of detections logged (N), and the detection frequency (D) in detections per day.

	EMGID	First Detection	Last Detection	Duration (days)	N	F (#/day)
Paddlefish	12	10/5/17	10/15/17	10	65579	6557.9
	31	10/5/17	12/21/18	442	1928722	4363.6
	59	5/2/18	12/21/18	233	433490	1860.5
	60	5/2/18	12/20/18	232	279718	1205.7
	62	5/2/18	12/21/18	233	632487	2714.5
Largemouth	11	10/5/17	12/20/18	441	1505758	3414.4
	29	10/5/17	12/20/18	441	17374	39.4
	61	5/2/18	12/21/18	232	657479	2834.0
	63	5/2/18	12/20/18	232	400230	1725.1

Table 4. Scaled EMG data summarized by the average scaled EMG score for each individual, as well as the coefficient of variation. This fish was rejected from the analysis.

ID	species	Scaled EMG mean	CV
ID28684*	largemouth bass	0.60	56.73
ID28692	largemouth bass	0.99	4.61
ID29070	largemouth bass	0.12	62.74
ID29072	largemouth bass	0.43	27.12
ID28506	paddlefish	0.21	22.81
ID28600	paddlefish	0.41	26.48
ID28690	paddlefish	0.27	39.11
ID28996	paddlefish	0.35	31.16
ID29000	paddlefish	0.28	32.94

Table 5. EMG Z score summary. Each individual's average raw EMG score was converted to 0, and all other EMG scores were given a Z score corresponding to the number of standard deviations away from the mean (±). The range (in standard deviations) is given for each individual. Ranges varied considerably across individuals.

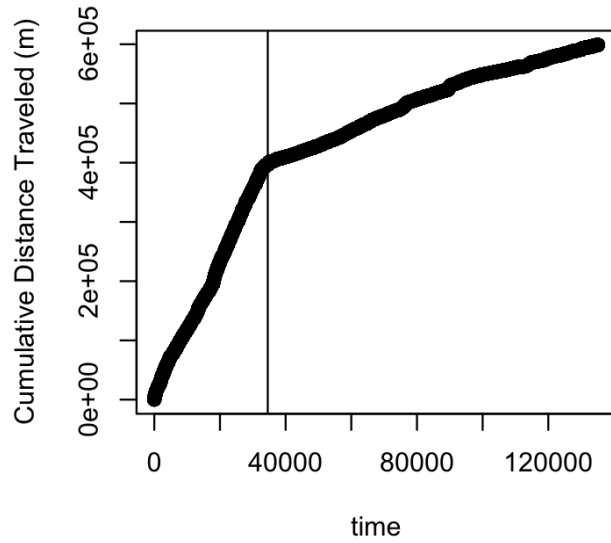| ID	species	min	max	range
ID28506	paddlefish	-4.38	16.03	20.42
ID28600	paddlefish	-3.78	5.40	9.17
ID28690	paddlefish	-2.56	6.95	9.51
ID28996	paddlefish	-3.21	5.97	9.18
ID29000	paddlefish	-3.04	7.64	10.68
ID28684	largemouth bass	-1.76	1.18	2.94
ID29070	largemouth bass	-1.59	11.26	12.85
ID29072	largemouth bass	-3.69	4.89	8.58

Figure 1. Cumulative distance traveled over time for Paddlefish 28690. The vertical black line delineates the break point in the piecewise regression, and the date that this fish was assumed to have died. All points to the right of the line were removed from analysis.
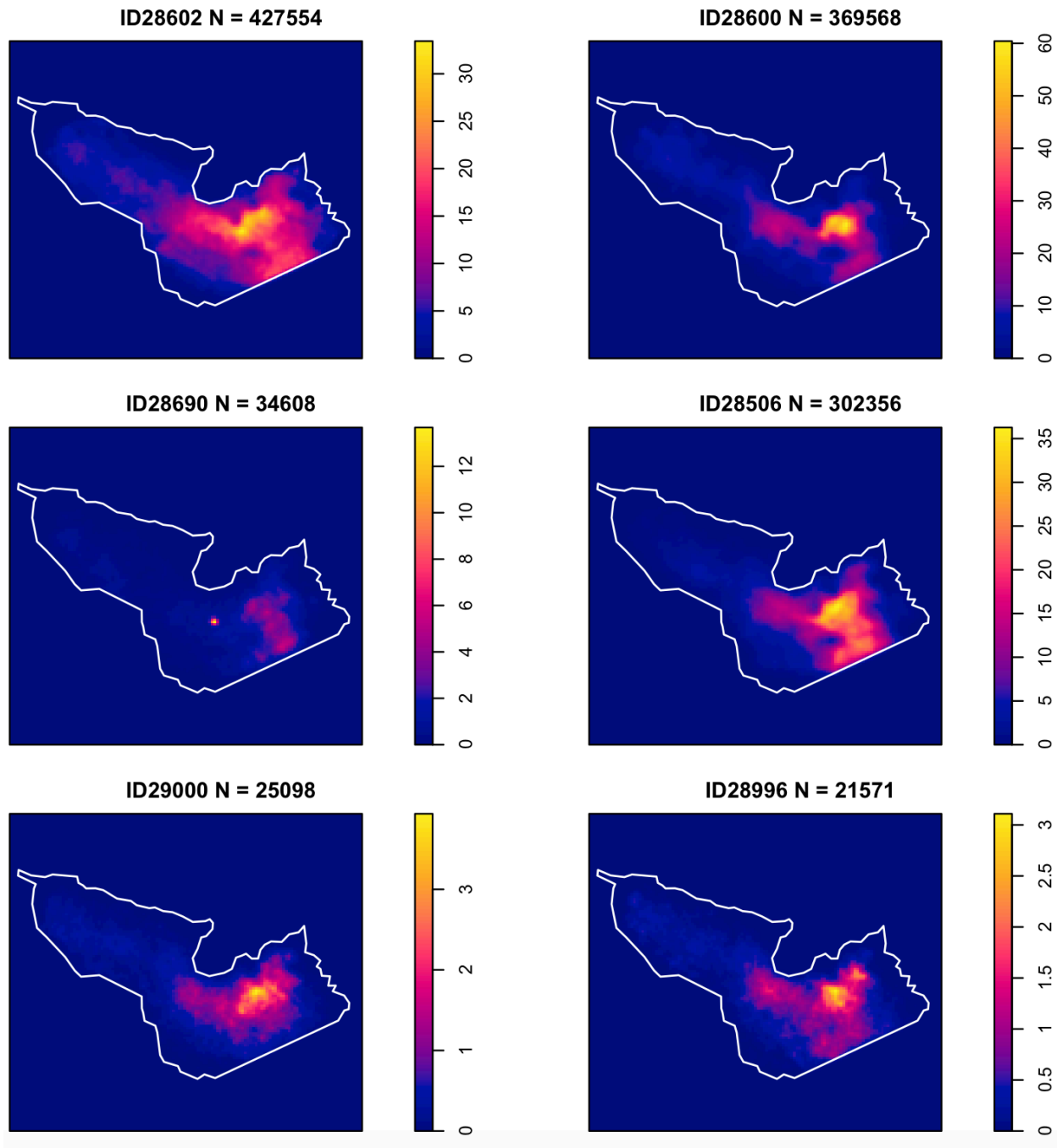
Figure 2. Kernel density plots for the recorded positions of each paddlefish over the entire study period. Bandwidth for density estimation was selected using Diggle cross validation. The white line denotes the pond boundary. Note that the color scale differs across plots, with warmer colors denoting increased density.
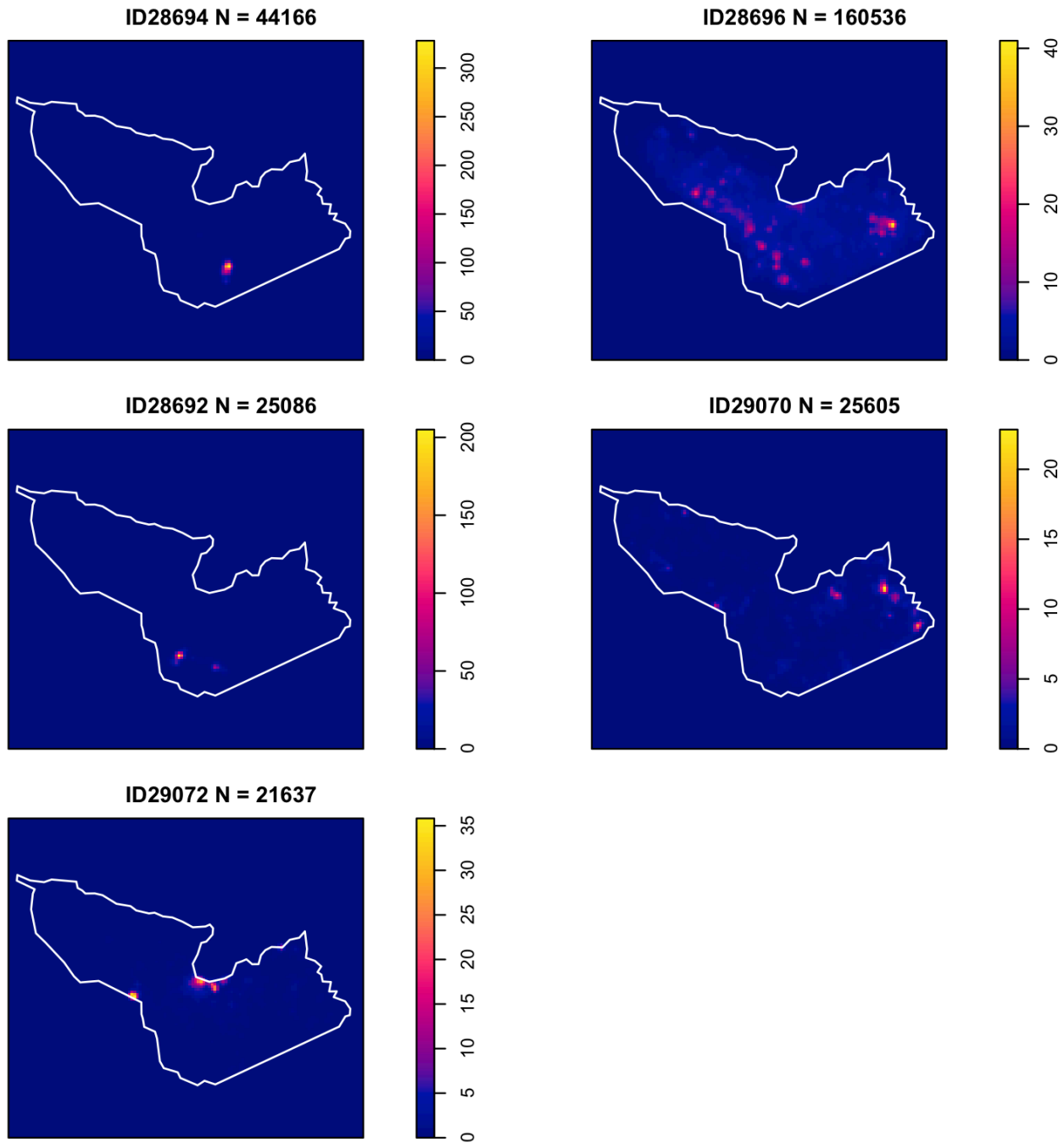
Figure 3. Kernel density plots for the recorded positions of each largemouth bass over the entire study period. Number of detections for each individual are given in the panel titles. The white line denotes the pond boundary. Note the color scale differs across plots, with warmer colors denoting increasing density.
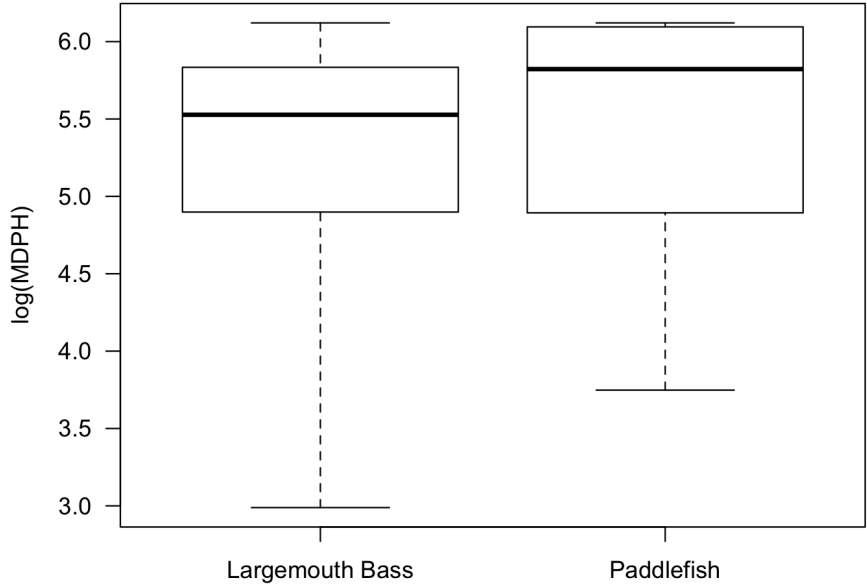
MDPH

Figure 4. Box-and-whisker plot (box = median ± 25% quartiles, whisker = data extremes) showing the variation in average minimum displacement per hour for tagged individuals of both species.
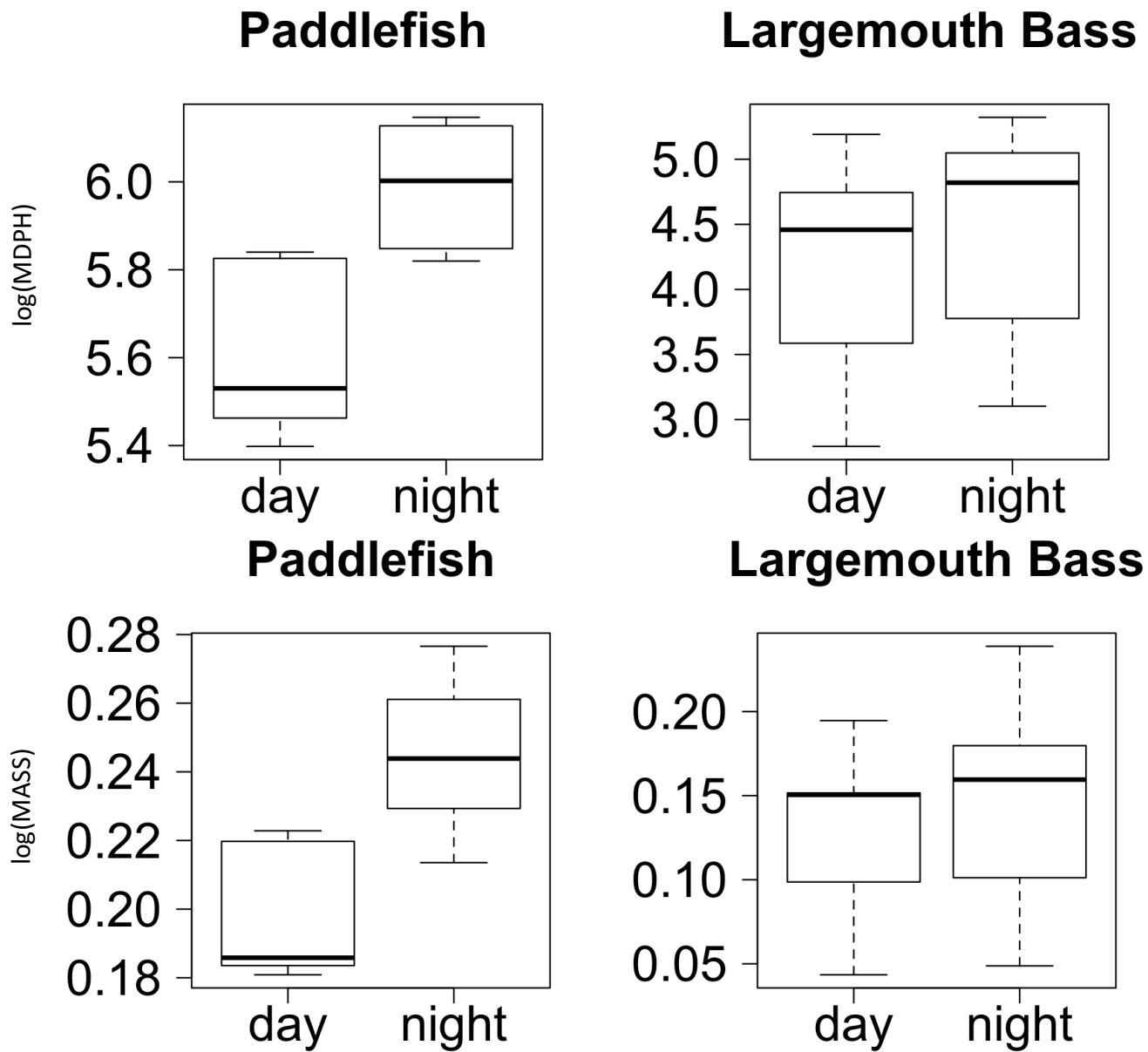
Figure 5. Box and whisker plots showing the difference in log MDPH (above) and log Minimum Average Swimming Speed (MASS) (below) between night and daytime hours for both species. Replicates are the average for each individual. Boxes and whiskers represent the same metrics as in Figure 4.
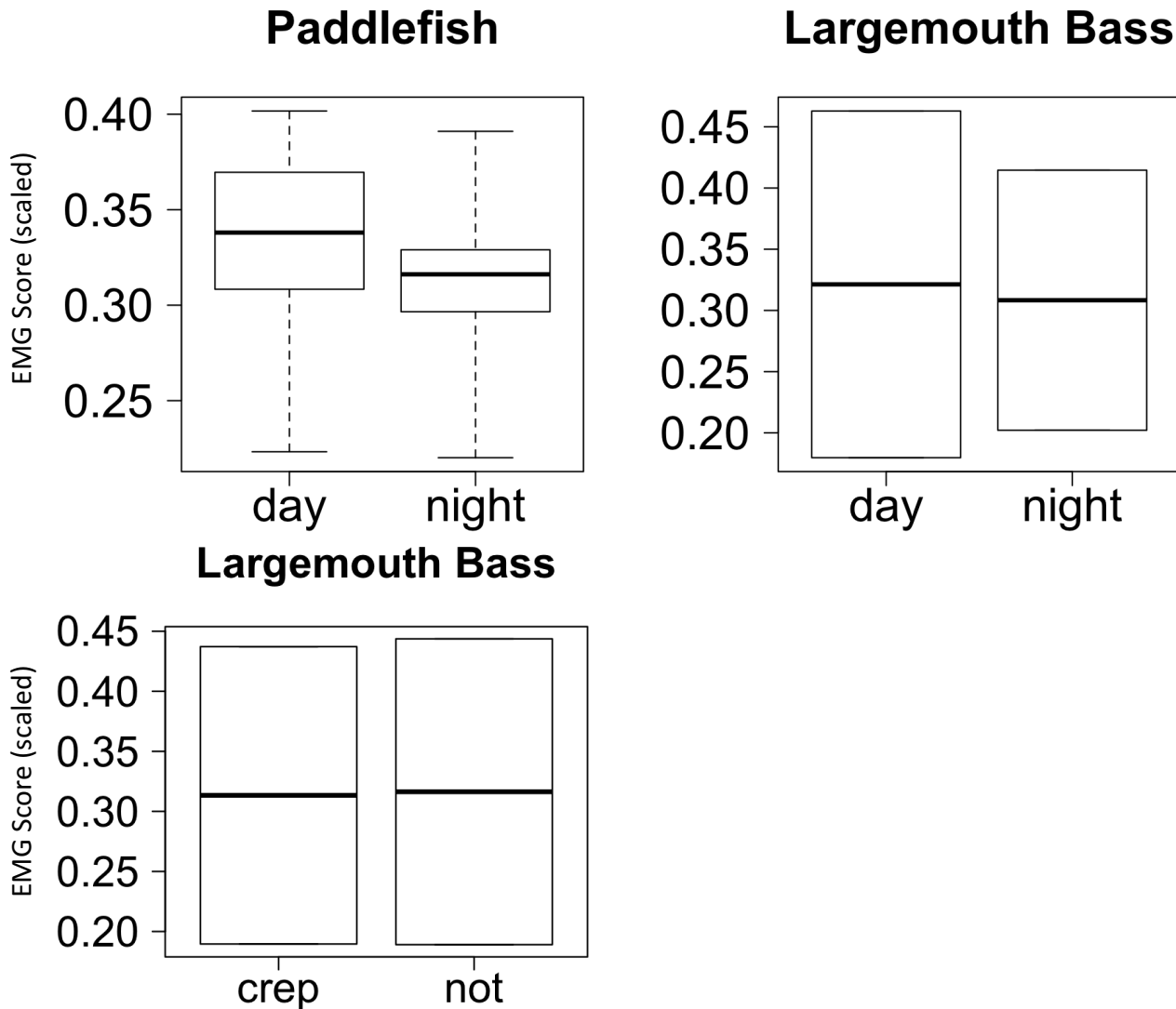
Figure 6. Box and whisker plots showing the lack of differences in EMG scores between night and day hours (above) and crepuscular/non-crepuscular hours (below for largemouth bass only). Boxes and whiskers represent the same metrics as in Figure 4, except that only 3 largemouth bass were used in the analysis, so the boxes encapsulate both the 25% quartiles and the extremes of the data.
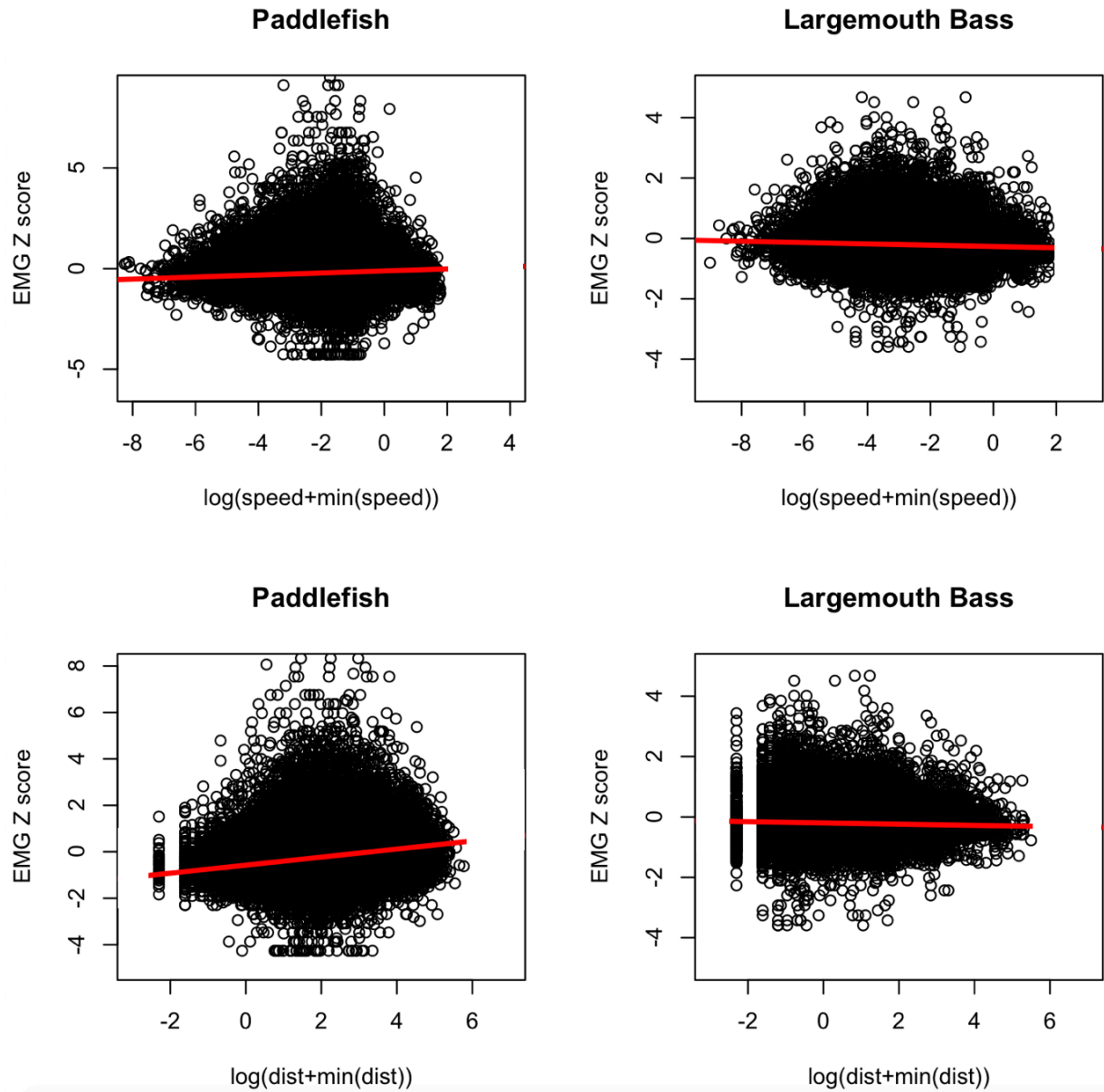
Figure 7. Using the merged data from Approach 1, the upper two panels show the relationship between EMG Z score and average swimming speed measured over the same time intervals. The lower panels show EMG Z score against displacement. Both independent variables were log transformed with the minimum measurement added to avoid log transforming zero values. The red lines are the slopes of the correlations.
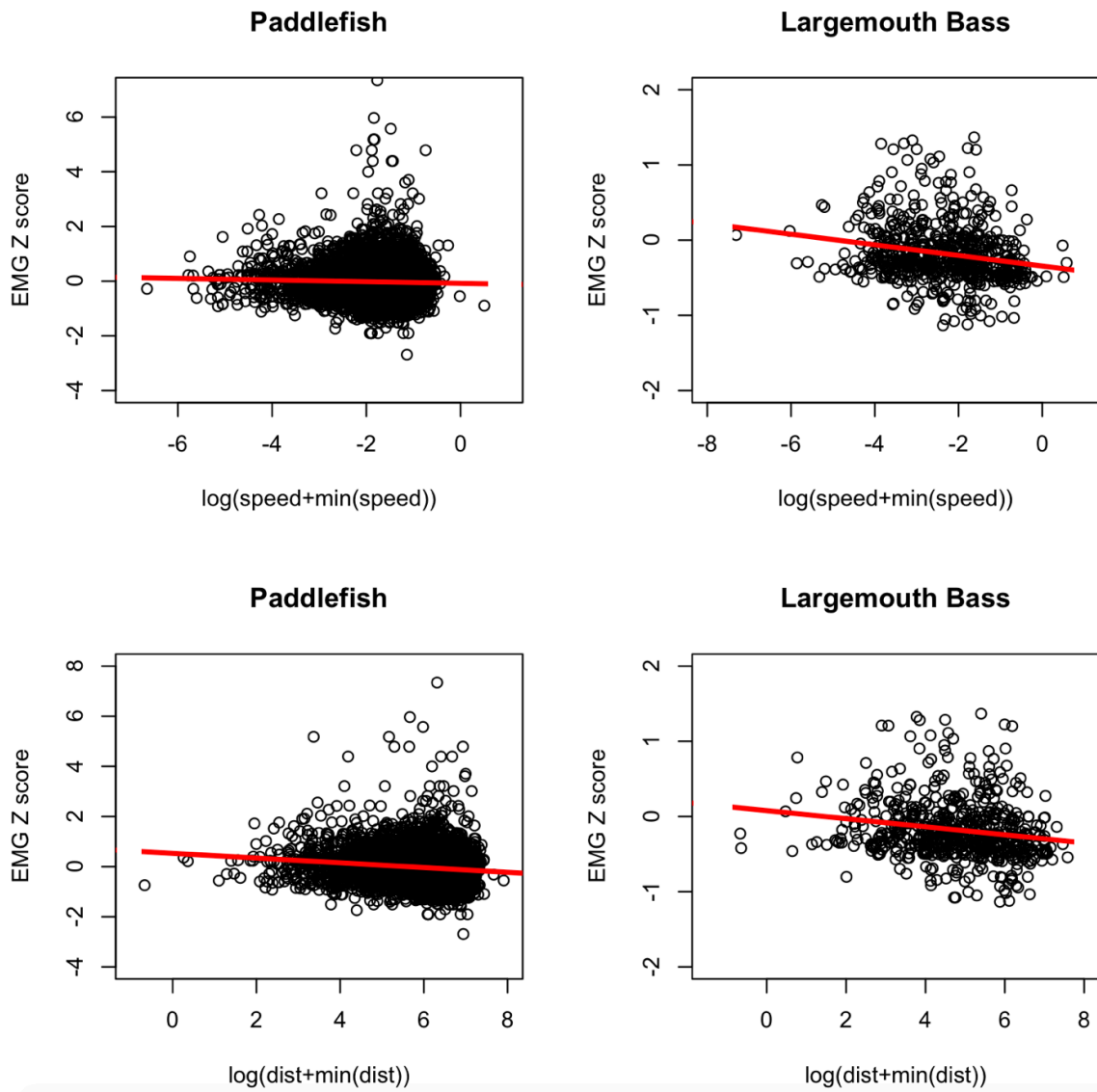
Figure 8 The same figure as Figure 7, but using Approach 2 with the hourly aggregated approach, instead of the fine-scale approach to merge the EMG and movement data.
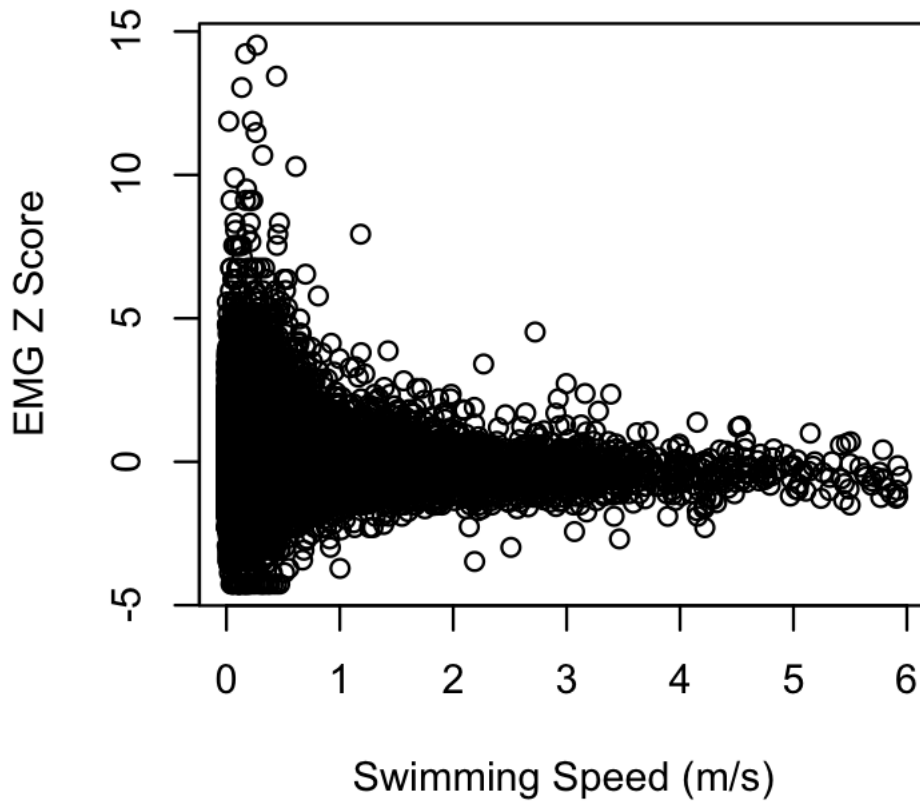
Figure 9. EMG Z score plotted against swimming speed. Most of the Z scores over 2 standard deviations corresponded to time periods in which animals were swimming at relatively low speeds. This could be because the fishes' movements were underestimated for those periods, or because they had strong muscle contractions without moving quickly.

Chapter 3: Quantifying the activity and hematology of paddlefish and smallmouth buffalo in a fish passage scenario.

Introduction

Dams have caused declines in fish populations by altering and destroying important habitat, isolating populations, and blocking migrations (Bunn and Arthington 2002; Braaten et al. 2015). In order to mitigate effects of isolating populations or blocking spawning migrations, fish by-pass structures have been designed and installed (e.g., ladders, slotted spillways) that allow fish to swim past these barriers. The ability of migratory fish to pass dams via these structures has been well studied, and numerous studies have indicated a strong positive relationship between fish swimming performance and passage success at these mitigation structures (Jones et al. 1974; Peake et al. 1997; Haro et al. 2004; Brown et al. 2006; Pon et al. 2009b; Noonan et al. 2011). However, most of this previous work has been conducted at dams that cannot be inundated, and relatively little research has been conducted on fish passage at low-head dams, which allow fish to pass under certain flow conditions without additional mitigation structures.

After heavy rains, low-head dams can become inundated, and in addition to swimming through the opened spillway gates, fish can sometimes swim over the top of the spillway, depending on the relative upstream and downstream water levels. The tailrace areas below a dam can represent hydraulically hostile environments for fish, with high water velocities and turbulence that may make it difficult to hold position or navigate upstream. Little is known about the relative effort required to successfully pass low-head dams, the physiological effects

of moving through tailraces, or the relative abilities of different fish species to navigate this environment.

Most studies on the energetic output required for fish passage have been used to inform the design of artificial fishways for large dams (e.g., Peake et al. 1997; Pon et al. 2009b; Cocherell et al. 2011; Alexandre et al. 2013; Burnett et al. 2014). However, such research has generally not been applied to low-head dams, perhaps because the exact pathways that fish might use to move through/over them are not as well understood, so simulating passage conditions in the lab remains challenging. Therefore, instead of simulating conditions, studies of fish passage at low-head dams have used field techniques such as telemetry to study the animals *in situ* (Linnik et al. 1998; Beasley and Hightower 2000; Zigler et al. 2004; Butler and Wahl 2010). While techniques such as radio telemetry, acoustic telemetry, and ultrasonic telemetry have all been used to track fish movements around and past low-head dam structures, other powerful biotelemetry techniques exist that remain relatively unused.

A popular biotelemetry tool that has been used to estimate energetic costs of fish passage at large hydroelectric dams is electromyogram (EMG) telemetry. Electrodes measure the bioelectric voltage of axial muscle tissue contractions, and the tag then broadcasts those data via radio frequency. When these "muscle activity" values are calibrated with metabolic rate or swimming speed, the energetic costs of activity can be estimated for tagged fish in the field (Okland et al. 1997; Geist et al. 2003; Almeida et al. 2007). When uncalibrated, these values can be used as a scaled index of relative activity (Alexandre et al. 2013). Several studies have used EMG tags to quantify the energetic costs of passage through fishways or other velocity barriers. Hinch and Bratty (2002) found that sockeye salmon *Oncorhynchus nerka* that

successfully passed a reach of the Fraser River in British Columbia that is notorious for impeding

migration had slower swim speeds and shorter residence times than those that did not pass

successfully. Pon et al. (2009b) found that EMG telemetered sockeye salmon that successfully

passed a fishway exhibited a variety of behaviors (e.g., burst-coast swimming, and steady

swimming) and quantified the energetic cost of these behaviors using an equation described in

Healey et al. (2003). Alexandre et al. (2013) used EMG telemetry to determine when burst

swimming was required for Iberian barbel *Luciobarbus bocagei* to pass a pool-type fishway. And

Quintella et al. (2004) quantified the number of swimming bursts required for sea lamprey

Petromyzon marinus to pass specific barriers in the River Mondego in Portugal. The techniques

used in these studies could also be extended to studies on passage involving low-head dams.

 Acoustic telemetry is a common tool used to quantify fish movement and behavior, and

its use is increasing due to its diverse applicability to fisheries questions (Crossin et al. 2017).

Positional acoustic telemetry (redundantly locating fish and triangulating their positions in two

dimensions, c.f., documenting presence/absence at a single site) is a powerful application of the

technology, but it has rarely been used to estimate fine-scale behavioral patterns or activity

levels of fish as they approach and possibly pass dams. This is probably due to the extreme

challenges posed by installing and maintaining an array of receivers in the hydraulic

environment that exists in the tailrace of a dam. In this chapter, I describe the second and

largest ever implementation of such an array (see also Suzuki et al. 2016), and how I used the

data to locate fish and estimate their activity rates before and during passage.

 In the Alabama River, the lowermost dam is a relatively large low-head dam at which

fish passage has been documented for several species (Mettee et al. 2006; Simcox et al. 2015).

Here I studied the behavior and activity of both American paddlefish *Polyodon spathula*, and smallmouth buffalo *Ictiobus bubalus* as they approached and passed this low-head dam using a combination of redundant acoustic and electromyogram telemetry. I related measures of fish movement and muscle activity to the hydraulic factors that may contribute or be related to passage success at the dam, and I also performed hematological assays on these species to quantify correlates of stress and respiration (i.e., fish physiological states).

Study Site:

Claiborne Lock and Dam is the lowermost impoundment in the Alabama River Basin, and thus the first barrier encountered by migrating fish. It was constructed in the 1970s for flood control, navigation, and recreation, but is relatively less trafficked compared to low-head dams in the Mississippi River. With 6 gated spillways and a 100 m wide crested spillway, water flows through the tailrace constantly, with river levels depending on releases from impoundments upstream. During the rainy season, December through April, the dam can become inundated, with water reaching almost 7.6 m over the head of the dam. Lock use is sporadic, and infrequent, with most traffic being recreational boaters and some commercial barges. A flow attractant has been used in the past to try to encourage upstream passage of fish through the lock chamber.

Methods:

Fish tagging began in January 2017 and continued through February 2019. In total, 330 combined acoustic and radio transmitters (CART) were deployed over the course of the study,

165 of which were implanted in adult paddlefish, and 165 in adult smallmouth buffalo (SBF). Of those CART-tagged fish, 89 paddlefish and 92 SBF were also implanted with coded electromyogram transmitters (CEMG). Both species were captured with large-mesh (150-200 mm stretch) multi-filament gillnets during October through April, allowing a 4-week gap for a commercial fishing season in February in two consecutive years. After capture, fish were sedated with MS-222 or CO_2 (for paddlefish captured within 21 days of the start of the commercial fishing given that MS-222 would make them unsafe for consumption (Trushenski et al. 2013).

After sedation, surgical tools that had been sterilized in 2% chlorohexidine gluconate solution and rinsed with distilled water were used to make a 2-3 cm incision in the left ventral side of the fish, approximately 6 cm anterior to the pelvic fin base, through which I inserted a CEMG tag and/or a CART tag. Total tag burden never exceeded the recommended 2% of the fish's wet weight. Once inserted, the tag antenna was passed through a separate hole made with a 14-gauge needle 1 cm anterior to the incision. CEMG transmitter electrodes were inserted approximately 1 cm apart in the lateral muscle of the fish at approximately 70% of the individual's standard length with a 14-gauge needle and plunger. Incisions were closed with simple interrupted PDS II sutures and glued with veterinary-grade liquid surgical adhesive (3M Vetbond). Finally, tagged fish were implanted with a uniquely numbered external anchor tag on the right ventral side for external identification in case of recapture. Immediately following surgery, fish were held in a recovery tank until equilibrium was regained, after which fish were released with a recorded GPS point and timestamp. most were in the tailrace of Claiborne Lock and Dam.

An array of 17 submersible acoustic receivers (LOTEK Wireless Model WHS 3250L) was installed in the tailrace in December 2018, using reinforced concrete parking bumper moorings, galvanized steel cable, and acoustic releases with buoys. Receivers were placed close enough to redundantly detect tags for triangulation by the UMAP software from LOTEK Wireless. Data from the receivers were downloaded and moorings maintained as regularly as possible when conditions were safe, but due to extremely wet seasons retrieving the receivers was not always possible before their batteries died. Also, 2 receivers were lost in extremely high waters. Therefore, several detection gaps occurred over the course of the study.

In addition to the acoustic receivers, an array of 5 stationary Yagi antennas and 2 radio receivers (LOTEK Wireless SRX800) were installed on the catwalk of the dam. Each antenna was positioned to cover an adjacent pie-shaped area, covering in total a 300 m radius 360 degrees around the dam. Transmissions from both the CEMG and CART tags were detected by the antennae and recorded by independent receivers for the duration of the study. EMG tag transmissions were then scaled using two methods. They were (1) converted to the percent of each individual's maximum EMG score, and (2) standardized to the mean for each individual (i.e., converted to Z scores for each individual). Scaled EMG scores and EMG-Z scores were both used in the analyses of spatial and temporal activity patterns.

Post-processing of the acoustic positional data was minimal. Because of the turbulent environment, and the noise created by flowing water, a higher threshold of dilution of precision (DOP) was used to filter the data. DOP is a ratio of the receivers' measurement precision to the error in the geometry of the array. Triangulated positions with a high DOP are relatively imprecise. Values of DOP close to 1 are considered excellent, while values closer to 10 are only

moderate. Positions in this study were filtered down to a DOP of 8, which is higher than would

be typically used in a noiseless system, but still moderately precise given the "noisy' system,

and clipped to the boundary of the river's edge at maximum flood stage.

Hematology

During October 2017 through March 2019, blood samples were collected from field-

caught fish from three habitat types: inside the Claiborne lock, in the tailrace, and > 1 km

downstream of the dam, to assess levels of stress indicators and respiratory byproducts. Fish

were captured using the same multifilament gillnets and handling time was measured from the

time the net entered the water until the time blood was sampled from the fish (Hoxmeier and

DeVries 1997). Handling time never exceeded 40 min, and averaged 16 ± 0.7 min. Once a

captured fish was on board the boat, 4 mL of whole blood was drawn from the caudal

vasculature with a 17-gauge needle and syringe (Barton et al. 1998), and collected into each of

two tubes treated with: 1) heparin to stop clotting, and 2) sodium fluoride to stop

gluconeogenesis (Duman et al. 2019). Hematocrit was measured as a percentage of packed cell

volume (Barton et al. 1998) using a Hematastat centrifuge. Pairs of whole blood samples were

centrifuged for 5 min, after which plasma was separated and stored in pairs of 2 mL cryotubes

on dry ice in a polystyrene cooler (Duman et al. 2019). While the blood was being preserved,

labelled and processed, the fish was measured, weighed, and promptly released, minimizing air

exposure post-sampling.

After returning to the lab, plasma samples were stored at -80° C until they could be

analyzed for a suite of biochemicals. Cortisol concentration was determined by an enxyme-

linked immunoassay according to the analytical kit manufacturer's instructions (DRG,

Springfield, NJ). Serum samples were 10μL and the lowest standard included in the standard curve was 5 ng/mL. The average R^2 of the standard curves in the four runs was .96 and a common sample analyzed in each of the runs had a coefficient of variation of 2.5%. Plasma glucose was determined on 10μL samples using the glucose oxidase endpoint assay according to the instructions provided by the analytical kit manufacturer (Pointe Scientific, Canton, MI). Recovery of standard additions of glucose to fish plasma averaged 99.9% by this method. Plasma lactate was also determined on 10μL samples using the lactate oxidase endpoint assay according to the instructions from Pointe Scientific. Lactate standard was recovered at 101% on average when added to fish plasma. Finally, osmolality was measured with the Vapro® 5600 vapor pressure osmometer (Wescor®, Logan, UT).

Data Analysis

Locations on an x-y coordinate axis were used to calculate minimum displacement per hour (MDPH) for each individual over the course of the study. Tracks were excluded when more than 1 hr elapsed between positions. Minimum average swim speed (MASS) could not be accurately estimated as it was in the small impoundment (see Chapter 2 methods) because of the confounding effect of water velocity; the Euclidean distance a fish traveled divided by the time it took to travel would not be representative of the actual effort of traveling that distance because the fish's over-ground speed does not factor in the velocity of the water flowing over their body. Scaled EMG scores and MDPH were compared between night and daytime hours for both species using paired t-tests. Then, EMG scores were standardized to the Z distribution (see method in Chapter 2) and compared to gage height over the whole study period. I also compared EMG-Z scores between passage and pre-passage time periods – passage periods

were defined as the interval between the last time a fish was detected downstream of the dam, and the first time it was detected upstream by any receiver. A new merging technique was used to determine whether there were spatial patterns in EMG activity in the tailrace. EMG-Z scores for each individual were assigned to the positions that were recorded nearest in time, and mapped to show areas of increased swimming effort or burst swimming. Finally, I used ANOVA and Tukey pairwise comparisons to compare the levels of measured blood parameters between species and three habitats that were sampled.

Results:

Detection Summary

During May 2017 through January 2019, 88 tagged fish were detected upstream of Claiborne Lock and Dam, after being detected in the tailrace, indicating successful passage. The average gage height during the passage periods for paddlefish was 37.57 ft, which was 1.53 ft higher (0.51–2.55; lower–upper 95% CI) than the average for passing smallmouth buffalo (P=0.0038).

In total, I was able to triangulate 46,856 positions with the acoustic array detections during January through August 2018. A total of 35 paddlefish and 22 smallmouth buffalo were tracked in the array, with some fish being located only one time, up to as many as 10,000 times. No fish were tracked in June because the receiver batteries died sometime in late May. Receivers were retrieved and batteries replaced on July 1st, when river levels were safe enough to work (Table 6).

Of the 57 fish that were tracked in the tailrace, 17 passed the dam in 2018 (11 paddlefish and 6 smallmouth buffalo). Of those fish, most were detected by a receiver upstream of the dam in April or May of 2018. Some of those fish were detected in the tailrace just hours prior to showing up on the upstream receiver, while others took longer to make their way upstream (Table 7).

Movement

Log MDPH did not differ between species, or between fish that passed the dam and those that did not. On average, paddlefish moved at a rate of 252.12 (218.11– 291.49; lower – upper 95% CI) m*hr^{-1}. smallmouth buffalo moved at a rate of 242.26 (181.82– 322.79; lower – upper 95% CI) m*hr^{-1}. Interestingly, estimates of log MDPH for paddlefish were nearly identical to estimates from the pond study in Chapter 2 (223.9 m*h^{-1}). Because these estimates reflect displacement over ground per hour, they do not reflect the net swimming speed of the individual, given that we are unable to measure water velocity in the tailrace. Furthermore, the direction of flow is spatially variable within the tailrace so whether water flow opposed fish movement at any given point is impossible to tell without very detailed hydrodynamic modeling.

In order to compare MDPH to gage height, I took the minimum displacement of each fish during an hour of the study and plotted those values against the gage height during the corresponding hour. I found that at higher gage heights, fish covered less distance (Figure 10). Because there was no significant difference between paddlefish and buffalo activity rates, both species are aggregated in Figure 10 to see the relationship between MDPH and gage height.

EMG Activity

Although the acoustic array was only able to triangulate positions for 57 unique tag IDs in 2018, the radio array on the dam logged EMG transmissions from 180 unique tags, 89 paddlefish and 91 SBF. The average scaled EMG score for SBF was 11.7 percentage points (11.66 – 11.78; lower – upper 95% CI) higher than for paddlefish (P < 0.001). Of the EMG-tagged fish detected by the radio array in the tailrace, 54 paddlefish and 34 SBF were also detected upstream of the dam by acoustic receivers at some point between December 2017 to December 2018. Using the scaled (not standardized) EMG scores, I found that the activity rate of paddlefish that passed the dam was 7.96 percentage points lower (7.85–8.07; lower – upper 95% CI) than fish that were never detected upstream (P < 2.2e-16). Smallmouth buffalo showed the opposite relationship, where fish that passed the dam had an average scaled EMG score that was 12.10 percentage points higher (11.98 – 12.22; lower – upper 95% CI) than that of fish that were never detected upstream. Downstream activity rates reflect the averages in the tailrace during staging, not during passage.

Using the Z-score standardized EMG scores, I examined the EMG data in terms of above and below average activity to see whether activity was higher during passage than staging. Of the tagged fish that passed, only 22 (12 paddlefish and 10 smallmouth buffalo) logged EMG transmissions during their passage windows. The mean Z score for paddlefish EMG activity during passage was 0.017 SD above average, while the mean for smallmouth buffalo was -0.16 SD below average (Figure 11).

Spatial Analysis

Although EMG signals cannot be triangulated, all fish with EMG transmitters were also tagged with CART transmitters. Some of these double-tagged fish were detected by the

acoustic array, and positions were triangulated while the EMG transmissions were measured simultaneously by the radio array on the dam. Given this, I was able to associate some EMG scores with spatial locations. Triangulated positions for each fish were assigned an EMG score that was detected by the radio array at the closest timestamp. In total, 17,241 positions and EMG-Z scores were mapped. To visualize the spatial distribution of the EMG-Z scores, I rasterized the data, averaging the EMG-Z scores in each of the 5,000 grid cells into which I divided the study area. Relative EMG activity was spatially variable. There were no large areas for either species where EMG activity was particularly high or low. Most cells in the raster had EMG-Z scores that were within 0.5 SD of average. The "hottest" areas for paddlefish were in the western part of the crested spillway pool where the direction of flow is actually upstream, and across the width of the river downstream of the lock wall (Figure 12).

Hematology

Plasma was sampled from 81 paddlefish and 29 smallmouth buffalo at three locations downstream of Claiborne Lock and Dam. Due to unsafe river conditions, and differences in the seasonal distribution of fish in the river, fish could not be sampled at all locations across all seasons. I sampled 25 paddlefish and 29 smallmouth buffalo in the tailrace <1km downstream of the dam (Table 8). All were taken within the range of detection by the array. Also, I sampled 28 paddlefish inside the navigational lock, and 28 paddlefish >1km downstream of the dam in backwater pools behind jetties and dykes. Paddlefish were sampled during November 2017 through April 2018, while smallmouth buffalo were sampled during February 2019 through March 2019 (Table 9).

For paddlefish, levels of glucose and lactate were significantly lower in sampling areas downstream of the dam than inside the lock or in the tailrace (P < 0.001, DF= 2) (Figure 13). Cortisol and osmolality were significantly lower downstream than in the tailrace (P = 0.027, P < 0.001 respectively, DF= 2). There were no differences in Hematocrit levels among sampling areas (Figure 13). Average concentrations of plasma lactate and glucose did not differ between paddlefish and smallmouth buffalo. However, average osmolality and hematocrit were significantly lower than in smallmouth buffalo. Cortisol was below detectable levels (###ng/mL) in smallmouth buffalo plasma samples (Table 10).

There was a significant increase of 0.076 units (± 0.043 | 95% CI) of lactate with each additional minute of handling time in paddlefish (P= 0.000834). There was also a marginally significant effect of handling time on cortisol concentrations, where cortisol increased 4.18 units (±4.18 | 95%CI) per minute of handling time (P= 0.053). In smallmouth buffalo, handling time only affected plasma glucose. Glucose concentrations rose 0.98 units (± 0.61 | 95% CI) with each additional minute of handling time (P= 0.00383) (Figure 14).

Discussion:

Movement

Interestingly, despite being in a completely different environment, paddlefish moved in the tailrace at almost the exact same rate as they did in the small impoundment from Chapter 2. Previously documented estimates of paddlefish movement at the hourly time scale are also similar to the ones recorded in this study. Zigler et al. (1999) estimated that paddlefish 0.6 to 1.2 m eye-fork-length swam between 150 and about 450 eye-fork-lengths per hour in

Navigation Pool 8 of the Upper Mississippi River depending on the season and time of day. These estimates are likely conservative because they had difficulty locating the study fish more than once per hour. In contrast, we were able to locate some fish thousands of times in an hour. However, our fish were not detected in the tailrace year-round, because we were passively tracking the fish with acoustic receivers that were only functional/retrievable during narrow time windows during winter and spring 2018.

In previous studies of fish passage, fish migrations have been delayed considerably by their inability to find passageways, although these passageways are often narrow gates to fish ladders, lifts, or slotted spillways (Burnett et al. 2013, Izzo et al. 2016). Furthermore, Caudill et al. (2007) found an inverse relationship between the time it took salmonids to migrate past Columbia River dams and the likelihood of successfully reaching spawning grounds. Fish staging in downstream areas preparing for passage tend to move throughout the tailrace environment searching for passageways, which is why attraction flows have increased passage success at numerous fish passage structures (Bunt et al 1999, 2012). However, if the movements that I observed in the tailrace of Claiborne Lock and Dam are due to searching behavior, then it was certainly not important for passage of our target species. We found that fish movement was highest at a gage height of about 10.7 m, which could be the optimal height for passage. However, neither paddlefish nor smallmouth buffalo that passed the dam moved more in the tailrace than those that did not. So, if movement in the tailrace is not an important predictor for passage at Claiborne Lock and Dam, then what is?

EMG Activity

The relationship between EMG activity levels and passage success is complicated in the literature. Hinch and Bratty (2000) reported that "hyperactivity" was inversely correlated with passage success, where fish that swam too fast for too long became exhausted and died downstream of an area of difficult passage. Pon et al. (2009) showed that EMG activity did not differ between fish that passed or did not pass a slotted fishway in the Seton River, British Columbia. Brown et al. (2006) found that 82% of EMG tagged Chinook salmon successfully passed the Bonneville Dam fishways, and that swim speeds (as measured by EMG telemetry) were higher in the tailrace than in the fishways, but did not show an effect of average swim speed on individual passage success. In contrast, Gowans et al. (2003) showed that three EMG tagged Atlantic salmon had elevated EMG signals during fishway passage versus while staging in the tailrace. In our study, paddlefish that passed the dam had lower EMG activity levels in the tailrace than fish that did not pass, and those individuals increased their activity above average levels during actual passage. In contrast, smallmouth buffalo that passed the dam had higher activity levels during staging, but somehow decreased their activity during passage. These differences in swimming behaviors may be explained by species specific differences in swimming performance.

Although no published studies of paddlefish swimming performance exist, smallmouth buffalo have been shown to have increased swimming performance in winter and spring months, as well as higher swimming efficiency (Adams and Parson 1998). Either smallmouth buffalo are using a different passageway than paddlefish, or their swimming performance and efficiency are so high that they are able to pass the dam without exerting themselves. Future

work should prioritize quantifying passage behavior of these two species with another type of

activity transmitter that does not require calibration.

Because the species used in this study are large fishes, and I had to use adults of mature

size to ensure they would attempt to pass the dam, I was unable to calibrate each individual

fish's EMG transmitter with their swimming speed as is recommended by many studies (Okland

et al. 1997, Thorstad et al. 2000, Brown et al. 2006, Almeida et al. 2007, Lembo et al. 2008,

Quintella et al. 2009). Therefore, I am unable to make claims about the absolute energetic costs

of the behaviors I observed in this study. However, the Z-score standardization technique I used

allowed me to quantify each individual fish's activity scores in terms of their average individual

activity. The studies noted above that used calibrated tags have shown strong positive

correlations between EMG activity and swimming speed, and that very high EMG scores are

often indicative of energetically costly behaviors like burst swimming. Therefore, I am fairly

confident that these standardized scores are representative of relative swimming effort.

Spatial Analysis

This study marks the first time that instantaneous activity rates of fishes have been

mapped at such a fine spatial scale. EMG tags transmit their data via radio frequency so they

are not easy to precisely locate (c.f. acoustic transmitters). Comparisons in EMG activity

between fish using different habitats or structures of a dam have been made before (e.g.,

Brown et al. 2006), but no study has ever been able to map relative swimming effort in two

dimensions. Because I double-tagged the EMG tagged fish, I was able to associate each fish's

EMG scores with two-dimensional positions and create a mosaic of relative swimming effort.

Although the EMG data gathered are certainly not perfect representations of energy use, I

believe that such a technique can be applied in the future to identify areas of high energy use, and areas where mitigation structures might provide refuge or potentially enhance passage success of migrating fishes. These could represent areas with particularly challenging hydraulic conditions, where fish are exerting themselves at higher than average swimming speeds.

Hematology

This study is the first time plasma has been sampled and analyzed from smallmouth buffalo and the second time from paddlefish in the Mobile River Basin. Davis and Parker (1986) collected adult paddlefish in the tailraces of Millers Ferry and Jones Bluff dams on the Alabama River and sampled blood immediately after capture via electrofishing, and again after 2-3 hours of transport in a hauling tank. They documented an increase in cortisol from 11 ± 1.9 ng/mL to 72 ± 12.5 ng/mL. Such an increase was also observed by Barton et al. (1998), who exposed juvenile hatchery-raised paddlefish (of Missouri River origin) to 6hrs of "severe confinement with handling" in a lab. They found that cortisol increased from 6.2 ± 1.6 ng/mL to 74 ± 6.3ng/mL. In my work, I measured cortisol levels up to 384 ng/mL which is an order of magnitude higher than the concentrations found previously in extremely stressed paddlefish. Furthermore, the average (178 ± 13.8 ng/mL) of the fish I sampled was two orders of magnitude greater than the unstressed concentrations previously documented. In contrast, the glucose, lactate, and hematocrit levels measured in this study were all within the ranges reported in Barton et al. 1998.

The abnormally high cortisol levels observed in the paddlefish sampled in this study could be due to a number of factors. Handling stress can be ruled out because even the intercept of the cortisol vs. handling time regression was over 100 ng/mL. One explanation is

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that the fish with elevated cortisol levels were captured during their spawning migration, and

that cortisol was elevated to upregulate gluconeogenesis to fuel the increased metabolic

requirements of migration (Carruth et al. 2000, Barton 2002, Birnie-Gauvin et al. 2019). In

addition, paddlefish with elevated cortisol levels may have been swimming at exhaustive

speeds before they were captured. Zelnik and Goldspink (1981) showed that cortisol levels

increased during periods of exercise in laboratory swimming experiments on rainbow trout

Oncorhynchus mykiss. Future work should prioritize measuring the swimming performance and

physiological correlates of passage success in adult paddlefish, perhaps in a controlled

laboratory setting.

There are no published ranges of the measured blood parameters for smallmouth

buffalo, but other studies have measured plasma glucose of migratory catostomids including

the white sucker *Catostomus commersonii* (Mackay and Beatty 1968) and several species of

redhorse *Moxostoma* spp. (Hatry et al. 2013). The levels of plasma glucose, and lactate that I

measured are all within the normal ranges reported in those studies.

An important limitation of my study was the utility of the EMG data without calibrating

the tags. Although the raw data from the transmitters are not meaningless, they lack the

information that is attainable with calibration, which could include swimming speed, and even

metabolic rate. Another limitation of the study was that plasma was not sampled from tagged

fish, so levels of the blood parameters measured could not be used to predict passage success

at the dam. Finally, I was not able to triangulate positions for a large proportion of the fish that

I tagged. Although environmental conditions are unpredictable, the array design might be

improved to increase the likelihood of detection during high flows.

Future work should expand these techniques and relate the behaviors that I observed to the fitness and vital rates of fish populations by tracking fish to their spawning grounds. Survival rate for those individuals that pass dams versus those that do not could be estimated using modeling techniques such as those described in Hightower and Harris (2017). Understanding how dams impact fish on an individual level is important for designing efficient fish passage structures and managing flows, but until we understand how many fish are passing low-head dams, how many of those fish are reproducing, and how the populations may be affected by increased passage, we may not know whether it is worth adding expensive mitigation measures to current structures. Furthermore, this work should be expanded to more species, including invasive species, to determine the generality of fish passage characteristics across a range of species of varying size, behavior, and life-history at low-head lock-and-dam structures.

Table 6. Acoustic array detection summary for the months of January to August 2018. No tags were detected in June due to batteries having died. The columns on the right show the minimum and maximum gage heights at which fish were detected. They do not reflect the hydrograph for the entire month. No tags were detected when water level exceeded 41 feet or was less than 33 feet.

			Gage Height		
Month	**Total Detections**	**Unique Tags**	**min**	**mean**	**max**
January	14976	14	33.95	35.04	36.10
February	4	1	34.76	34.76	34.76
March	98	16	34.84	34.91	35.29
April	13053	40	34.37	36.65	40.63
May	5704	11	33.72	34.99	35.91
June	NA	NA	NA	NA	NA
July	11637	5	33.49	34.95	35.90
August	1384	4	33.45	35.01	35.88

Table 7. Important detection dates for the fish I was able to track in the tailrace: the last date each fish was tracked in the array before it passed the dam, and the day it was first detected above the dam. Tagging dates for each fish are also listed. **ID 28752 was not detected by the array before it was detected upstream. It was detected in the array after it had already been detected upstream. "Paddlefish" and "Smallmouth Buffalo" are abbreviated in the first column as "PDF" and "SBF" respectively.

Species	tagID	Tagging Date	Last Time in Array	First Time Upstream	Duration (days)
PDF	ID28580	2017-12-13	2018-04-23 10:43:56	2018-04-23 12:32:36	0.1
PDF	ID28584	2017-12-13	2018-01-16 22:06:29	2018-04-12 21:28:19	86.0
PDF	ID28586	2017-12-14	2018-04-18 11:28:14	2018-04-18 20:07:39	0.4
PDF	ID28662	2018-01-03	2018-02-01 20:18:39	2018-04-02 19:38:32	60.0
PDF	ID28752	2018-01-19	NA**	2018-04-06 01:42:43	NA
SBF	ID28770	2018-01-21	2018-01-21 04:32:27	2018-04-25 14:35:22	94.4
SBF	ID28772	2018-01-21	2018-04-15 23:08:08	2018-04-16 10:42:34	0.5
SBF	ID28942	2018-01-21	2018-01-21 11:26:42	2018-05-09 12:04:09	108.0
PDF	ID28776	2018-01-27	2018-05-06 19:06:50	2018-05-15 04:47:36	8.4
PDF	ID28796	2018-03-08	2018-04-17 09:55:40	2018-04-17 20:32:26	0.4
PDF	ID28806	2018-03-08	2018-05-17 03:37:04	2018-06-03 19:52:44	17.7
SBF	ID28876	2018-03-12	2018-04-16 00:43:51	2018-04-16 12:15:37	0.5
SBF	ID28896	2018-03-13	2018-04-09 01:48:27	2018-04-16 16:03:47	7.6
PDF	ID28904	2018-03-13	2018-04-17 14:21:31	2018-04-17 23:29:17	0.4
PDF	ID28908	2018-03-13	2018-04-18 02:53:43	2018-04-18 10:02:29	0.3
SBF	ID28916	2018-03-13	2018-04-16 05:02:45	2018-04-16 17:09:11	0.5
PDF	ID28918	2018-03-13	2018-04-18 19:45:53	2018-04-19 02:21:58	0.3

Table 8. Numbers of paddlefish and smallmouth buffalo captured at each sample location for hematology.

	Paddlefish	Smallmouth Buffalo
tailrace	25	29
lock	28	0
downstream	28	0

Table 9. Numbers of paddlefish and smallmouth buffalo sampled in each month in each year for hematology.

Year	2017	2018			2019	
Month	Nov	Jan	Mar	Apr	Feb	Mar
Paddlefish	9	25	22	25		
Smallmouth Buffalo					18	11

Table 10. Means and standard errors of plasma concentrations of each measured blood parameter for both species, as well as the P value of the T tests comparing them. The cortisol assay for smallmouth buffalo failed. **The true difference in the means is statistically significantly different from 0.

	Paddlefish		Smallmouth Buffalo		
	Mean	SE	Mean	SE	t test p value
Lactate	1.83	0.15	2.56	0.42	0.11
Glucose	31.12	1.30	33.30	3.04	0.51
Osmolality	246.81	1.95	287.79	4.45	2.40E-10**
Hematocrit	0.21	0.01	0.25	0.01	1.47E-05**
Cortisol	177.97	13.78	NA	NA	NA
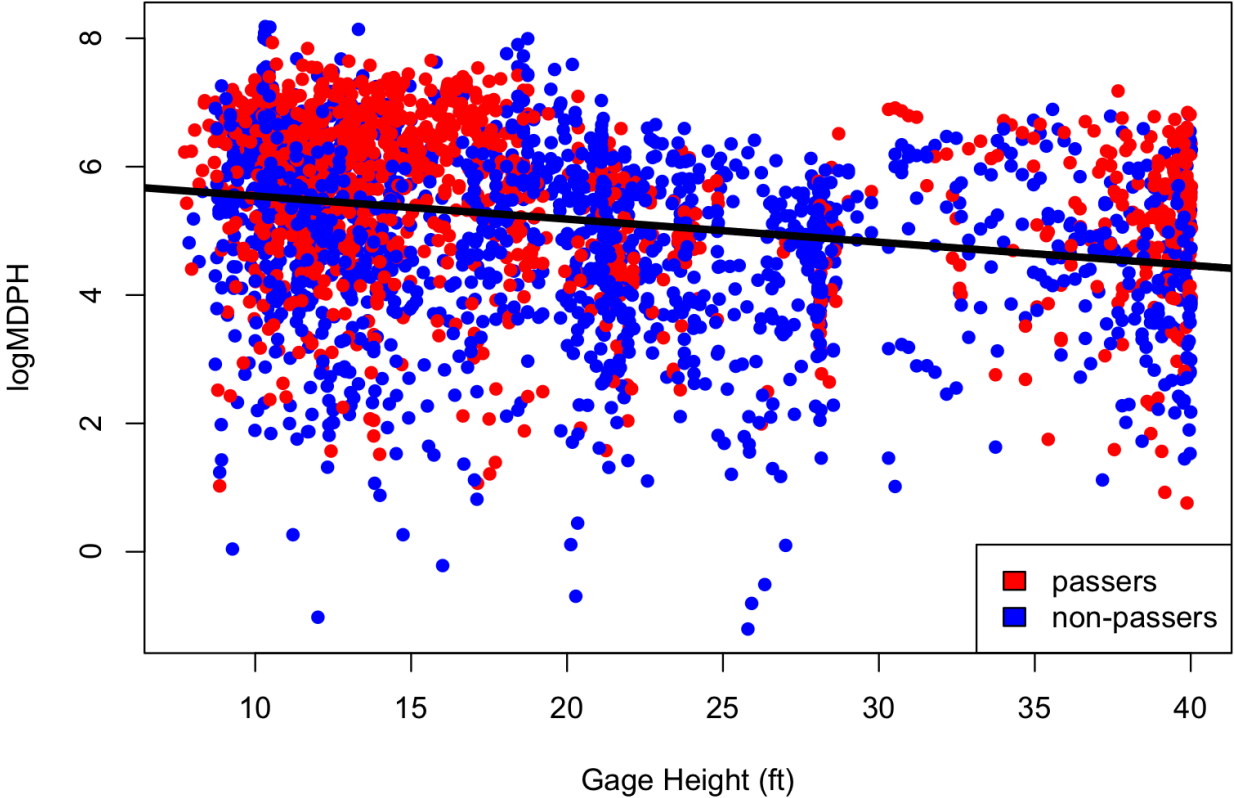
Figure 10. Each point represents the minimum displacement of a fish in a certain hour of the study. Each "fish-hour" is plotted against the gage height during that hour. There is a slight negative relationship between activity and gage height, where fish do not move as much at high gage heights.
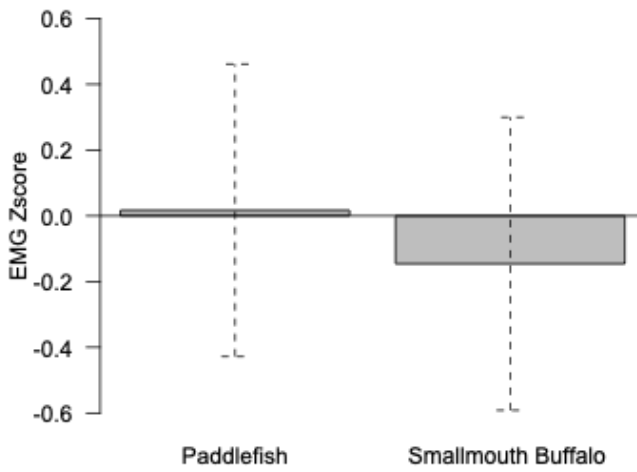
Figure 11. Average Z scores for the 12 paddlefish and 10 smallmouth buffalo that logged EMG transmissions as they passed the dam. Error bars represent the 95% confidence interval around the mean.
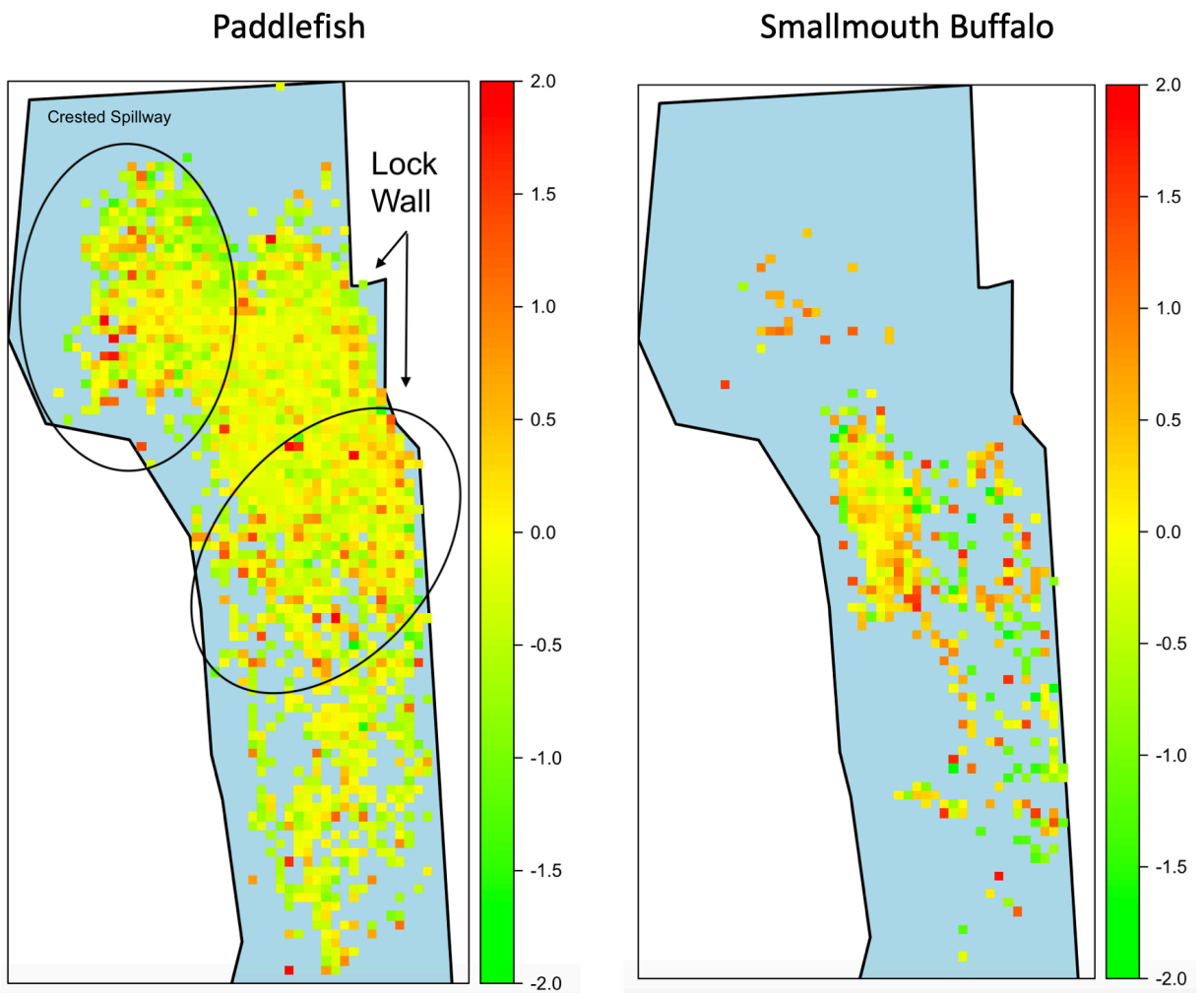
Figure 12. A map showing the spatial distribution of EMG activity Z scores in the tailrace of Claiborne Lock and Dam, separated by species. Cells with a reddish hue represent areas where fish's EMG transmitters emitted higher than average activity code values, while green indicates below average activity levels. Circled areas on the left show "hot" areas for paddlefish, where muscle activity readings seemed to be higher than average for the individuals tracked in those locations.
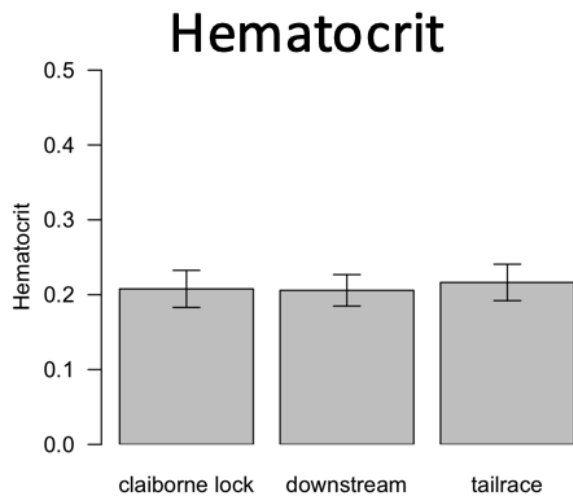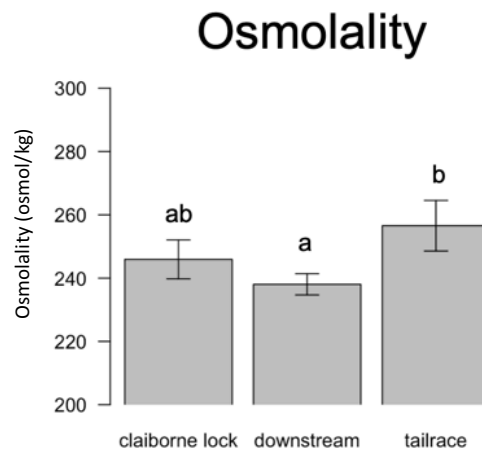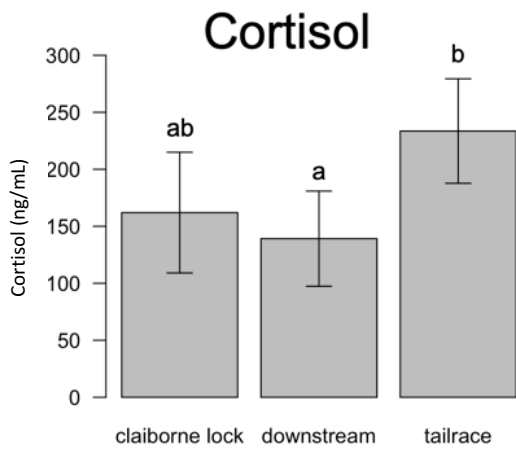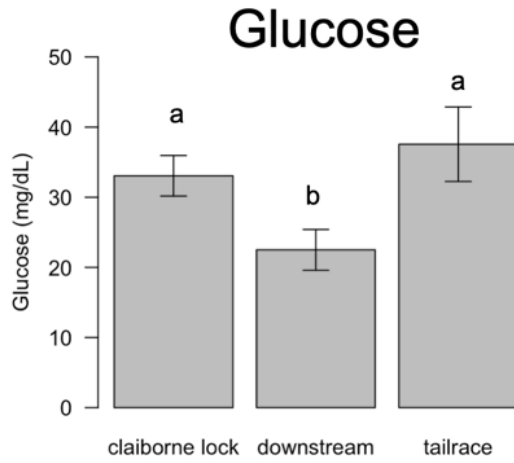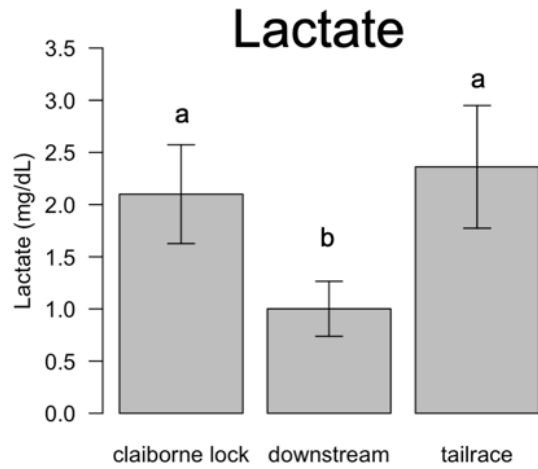
Figure 13. Bar plots ($\bar{x} \pm 1.96*SE$) showing blood parameter concentrations across sample locations for paddlefish.
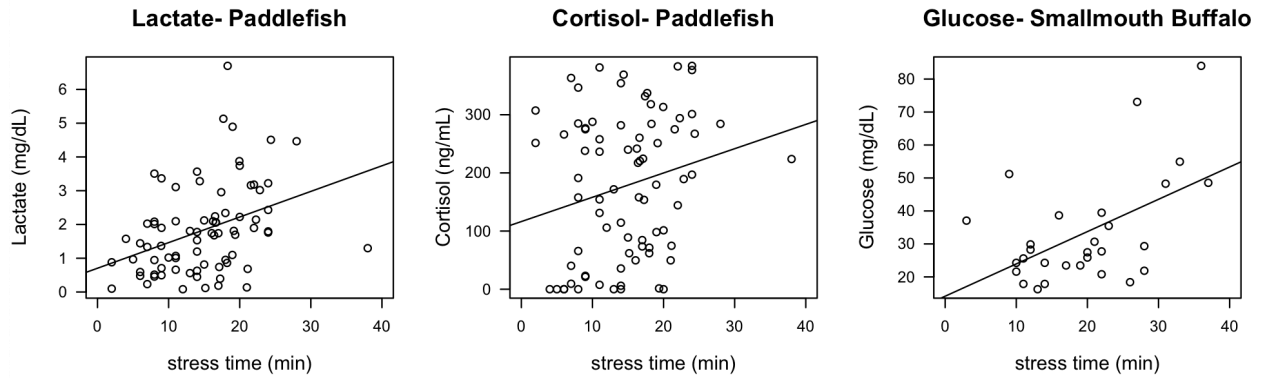
Figure 14. Scatterplots showing the significant effect of stress time (the number of minutes from the time that the gillnet was set to the time that blood was drawn from each individual) on the concentrations of the measured blood parameters.

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