Calibration of accelerometer transmitters for estimating field metabolic rates in walleye *(Sander vitreus)*

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Abstract

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The Great Lakes represent nearly a fifth of the global freshwater surface supply, and support culturally, economically, and ecologically important fish species such as Walleye (*Sander vitreus*). With water temperatures projected to rise by several degrees in the coming century, understanding the energetic impacts on fishes is crucial for effective habitat and fisheries management. I measured the swimming performance, accelerometer-based activity, and metabolism of walleye in relation to body size, sex, and water temperature to assess potential responses to climate variability. Both acceleration and swim speed predicted metabolic rate with reasonable accuracy. Temperature had a positive effect on oxygen consumption whereas body mass had a negative effect. Critical swimming speed increased with temperature, and tailbeat frequency had positive relationships with swim speed and acceleration. My laboratory-based calibrations should enable remote field monitoring of energy use of walleye (via accelerometers) and help conserve an important species through bioenergetic modelling.

Keywords: walleye, metabolism, bioenergetics, accelerometry, respirometry, great lakes, climate change.

Dedication

This thesis is dedicated in loving memory of my dear friend Mohamad Fanous.

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Chapter 1: General Introduction

1.1 Physiological responses to climate change

Aquatic ecosystems represent complex networks of habitats that support substantial amounts of biodiversity and species that are invaluable to proper ecological functioning. Aquatic ecosystems experience dynamic temperature changes on both diel and seasonal bases, which influence ecological dynamics and processes (Nowell et al 2015; Matthews and Zimmerman 1990). Within the Great Lakes, climate change is expected to drive increases in water temperatures by several degrees over the next century (Zhang 2020). Increased temperature and altered precipitation patterns can disrupt thermal regimes and nutrient loading, resulting in fluctuations in individual growth, population dynamics, community structure, and production in large lake fisheries (Collingsworth et al. 2017; Jeppesen et al. 2010; Portner and Farrell 2008; Sheridan and Bickford 2011). Particularly for ectotherms, temperature is referred to as the "master factor" in ecophysiology due to its impact on biochemistry, physiology, and ultimately, behavior and life history (Brett 1971; Fry 1971). There is hence significant value for scientific managers and researchers to understand and predict how these changes will impact lakes and the species within them. Bioenergetic modelling offers a method to solving these key questions by quantifying energy use and the metabolic costs of climate change in fish and other species.

1.2 Quantifying fish metabolism

Energy is a fundamental currency of life that can be used to describe not only the behaviour and growth of individual animals, but also populations and entire ecosystems

(Brown et al 2004; Jobling 1995; Brownscombe et al 2022). Characterizing animal energy budgets is an effective approach to understanding how environmental and anthropogenic factors influence their energetic needs, growth, and population dynamics (Brownscombe et al. 2022). The energy budget of an organism is defined as the total intake and expenditure of energy (see Equation 1), including allocations to various physiological processes such as metabolic rate (Jobling 1994). In fish, measuring metabolic rate has mainly been achieved through laboratory-based studies using respirometry, including swim tunnel respirometers (Raby et al 2020; Hvas 2019; Brownscombe et al 2018). Swim tunnel respirometers expose fish to set water flow speeds to measure metabolic rate via gas exchange; also known as respirometry or indirect calorimetry (McKenzie 2011). Swim tunnel respirometry presents a unique opportunity to study swimming performance as it allows for control of factors such as temperature and oxygen availability, and how they result in differences in muscle use, aerobic and anaerobic metabolism, swimming gait, and ultimately, energy budgets.

Outside of a laboratory setting, it has historically been difficult for researchers to estimate metabolic rate in wild fishes. The measurement of energy expended by free-ranging animals in their natural environment, commonly referred to as field metabolic rate (FMR), has generally been achieved either through doubly labelled water (DLW) (Shaffer 2011) or estimation of heart rate (Gilman & Wells 1993). Researchers have also explored methods of measurement that rely on quantifying locomotory movement, often referred to as active metabolism (standard metabolic rate (maintenance metabolism) + energy allocated to activity), which is a major component of FMR and can be highly variable in fishes (Boisclair and Leggett 1989). Field estimation of active metabolism via telemetry was first made possible using electromyogram (EMG) transmitters (Hinch and Rand 1998; Cooke et al. 2004), which involve EMG sensors implanted into the white muscle of a fish to estimate swimming activity. Accelerometer loggers were later developed to study the activity of metabolic demands in many animals (Yoda et al 2001; Wilson et al 2006; Shepard et al 2008; Gleiss et al 2011; Halsey et al 2011), which provide useful insights into animal behaviour and bioenergetics in nature (Cooke et al 2016; Wilmers et al 2015; Hussey et al 2015; Brownscombe et al 2018). Accelerometer loggers are often externally attached, and record measurements at high frequencies (often >100 Hz) in up to three axes; providing data that has can be tightly correlated with $\dot{M}_{O2}$ (Wilson et al 2008; Wilson et al 2013; Brownscombe et al 2018).

More recently, the development of small acoustic transmitter tags has allowed for internal implantation and transmission of information through signals sent to receivers located meters to kilometres away (Pincock and Johnston 2012; Wilson et al 2013). Tri-axial accelerometers are the most used accelerometer device to quantify animal movement and body posture (Brownscombe et al 2017) and provide opportunities to better understand bioenergetics in wild fish in realistic ecological conditions. Estimates of the active metabolism component of a fish's energy budget can be substantial but are highly variable and often a poorly described in bioenergetics models (Madon and Culver 1993; Boisclair and Leggett 1989; Lucas et al 1991; Boisclair and Sirois 2011).

1.3 Swimming mechanics and muscle composition

In characterizing fish swimming performance and active metabolism, it is important to understand how fish move and use energy. Fish swim by exerting force against water. Generally, fish alternate contractions of complex muscles (myomeres) from one side of their body to the other that moves their body and tail in a wave-like motion (Preuschoft 2022). Different species have also evolved diverse swimming gaits to optimize performance and adapt to their environment depending on their ecological needs. Periodic propulsions are characterized by using body and caudal fins (BCF) to push through water in a wave-like manner produced at regular time intervals (Webb et al 1984). About 85% of fish exhibit BCF swimming for normal propulsion and tend to have a more slender and elongated body shape (Liu and Jiang 2002; Friedman et al 2021). BCF swimmers (along with most fish) also depend on intermittent swimming, which is exhibited through burst-and-coast mechanisms to optimize locomotion costs through a unique intrinsic cycle (Gellman et al 2019). Burst-and-coast is a two-step gait transition process that involves an active propulsion followed by an inertial passive glide due to momentum where red muscle function is supplemented with the contraction of white muscles to sustain the demanded swim speed (Li et al 2021; Webb 1994; McKenzie 2011; Clark et al 2013; Fry & Hart 1948; Steffensen 1989; Alexandre 1989).While some species consistently employ this behaviour as a means of locomotion, others use it sporadically during short periods of high-speed swimming to perform additional functions such as feeding and defense against predators (Price et al 2015; Li et al 2021).

Variation in swimming styles between species can be attributed to different morphological and evolutionary histories, and therefore involves additional differences in muscle composition as well. Fish typically use a combination of white and red muscle fibers to swim depending on the duration and intensity of the activity. White muscle fibers are primarily used for short bursts of high-intensity swimming by means of anaerobic metabolism, which consists of energy produced in absence of oxygen through glycolysis (McKenzie 2011). White muscle accounts for 90-95% of all muscle in most fishes (minimum 70% in all species; Sänger and Stoiber 2001), while red muscle is commonly located along the lateral line and generally constitutes less than 10% of total musculature (Kiessling et al 2006). Red muscles fibers are heavily vascularized (i.e., supplied with blood) and primarily used for sustained swimming by means of aerobic metabolism which relies on oxygen to generate energy through cellular respiration (Pinte et al 2021). Most physiological processes are in fact powered by aerobic metabolism (Brownscombe et al 2022), making the measurement of oxygen consumption a good proxy for energy expenditure in fishes.

1.4 Respirometry

Respirometry is the most widely accepted method for estimating metabolic rate when examining fish swimming physiology and biomechanics (Clark et al 2013; Fry and Hart 1948; Steffensen 1989; Nelson 2016). Respirometry measurements can be conducted in a static chamber, or when a fish is actively swimming in a swim tunnel while measuring the rate of oxygen consumption based on the decline of oxygen in the water surrounding the fish in a closed system. The measurement of swimming metabolism of fish was first reported by Fry (1947) using goldfish to explore the relationship between standard and maximum metabolic rates across a range of temperatures. Following, Blazka et al (1960) designed a swim tunnel that uses a tube-within-a-tube design where the flow of water within the inner tube of the respirometer is facilitated by a propeller-generated current that circulates the water towards the front of the respirometer through the space between the inner and outer tubes. Brett et al. (1964) later crafted a new design which involved placing a fish in a distinct segment of an oval flume with an inline pump to propel water past it. These two designs (Blazka and Brett) assembled the foundation for countless studies where oxygen consumption could be used as an indicator of physiological effort (Liao 2007, Metcalfe et al 2016; Sebert et al 2009; Tudorache et al 2008; Palstra et al 2008).

Swimming respirometry tests have been widely used to evaluate effects of various biotic and abiotic factors on fish (Plaut 2001; Farrell 2008). One of the main methods of measuring swimming performance in fish is via the critical swimming speed test (U_{crit}), which refers to the maximum speed a fish can sustain over a short time interval (e.g., 20-60 minutes) (Bellwood and Fisher 2001). Primarily quantified via aerobic metabolism, swimming speed is increased incrementally at specific intervals until the fish fatigues based on a given protocol (Brett 1964). U_{crit} has been reported to be associated with the capacity to cope with stress (Vandeputte et al 2016), cardiac functioning (Claireaux et al 2005), and disease resistance (Castro et al 2013). Notably, findings from critical swimming speed tests have had valuable applications in the field such as the establishment of appropriate water velocity criteria for fishways and culverts (Peake 2008; Watson et al 2019).

1.5 Bioenergetic modelling applications

Insights generated from swimming respirometry tests can be used to help ‘solve’ the bioenergetic equation of different species. This equation involves examining the gains, losses, and transfers of energy within an organism (Winberg 1956):

$$\mathbf{C = R + A + D + F + U + G}$$

Equation 1: Bioenergetic equation of an organism

C is the energy consumed, which is equal to R (resting metabolism) plus A (active metabolism (swimming)) plus D (energy used to digest food), plus F and U (energy lost via egestion and excretion), plus G (growth). Most elements of the bioenergetic equation have been well described for many species such as walleye, but active metabolism of wild fish is still largely unknown. Coupled with oxygen consumption measurements, fine-scale information on energy expenditures can be achieved using accelerometer sensors that measure locomotion and whole-body acceleration. These sensors have been positively correlated with swim speed, oxygen consumption ($\dot{M}_{\mathrm{O2}}$), and tail-beat frequency in the laboratory (Wilson et al 2013; Cruz-Font et al 2016) and in the field (Zupa et al 2021; Murchie et al 2011; Brownscombe et al 2017).

Bioenergetic modelling enables managers to review stocking numbers and thus ensure predator-prey systems remain stable. Species-specific estimations of oxygen consumption ($\dot{M}_{O2}$, mg O_2 kg^{-1} $hour^{-1}$) based on acceleration outputs can be converted to energy consumption (in calories) using an oxycalorific coefficient for bioenergetic Once modelling (Brett 1995). a model for a particular species is established, it can be applied on a stock or population level by multiplying the single fish dynamics by population size estimates and cohort mortality rate (Stewart et al 1983; Hartman and Margraf 1992; Hansen et al 1993). Stock- and population-level estimates are used to approximate food consumption based on observed growth rates over time or growth rates based on observed consumption over time (Kitchell et al 1977). This more complex model can then be further expanded when coupled with larger models to predict more complex interactions such as predation, nutrient cycling, and trophic efficiency (Stewart et al 1981). For example, in Lake Michigan, bioenergetic modelling simulations were used to predict the prey availability (alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*)) of key fish species (lake trout (*Salvelinus namaycush*) and introduced salmonids) in years to come (Stewart et al 1981). He et al. (1993) also used bioenergetics models to assess the effects of long-term phosphorus cycling and responses to random fish recruitment events within the food web.

When habitat data is available, researchers can investigate the temporal and spatial relationships amongst species and ecosystems using bioenergetic modelling (Brandt et al 1992; Brandt and Kirsch 1993; Bevelhimer 1990). Brandt and Kirsch (1993) developed models of fish growth based on acoustic measures of prey density to map regions of Chesapeake Bay and were able to predict the areas at which the seasonal growth of striped bass was highest. Bevelhimer et al (1985) used a bioenergetics model that simulated different stocking conditions to successfully predict the success of esocids in Ohio waters with different thermal regimes by measuring individual food consumption, growth, and metabolic rate. The power of bioenergetics modelling is particularly relevant in the face of climate change as managers attempt to predict how future changes in water temperature will impact the effects of pollutants (Lefevre et al 2011; Wood et al 2012), parasitic infestations (Brauner et al 2012; Hvas et al 2017a), aquaculture productivity and welfare (Anttila et al 2014; Hvas & Oppedal 2017), range shifts in ecological niches (Ficke et al 2007), and ultimately the management of wild populations as a whole (Cooke et al 2012; Farrell 2002, 2016; Lefevre 2016).

1.6 Great Lakes walleye

Walleye (*Sander vitreus*) are a species that were central to the development of early bioenergetics models. Walleye are a cool water fish species that live in lakes and rivers throughout much of central and eastern North America, and are a popular sportfish throughout their range, thus generating millions of dollars a year to commercial fisheries in the Great Lakes region (Kinnunen 2003; Pandit et al. 2013). Commercial walleye fisheries were historically prolific, dating back to the 1800s when harvests in Lake Huron would produce 400 tonnes annually (Brown et al., 1999; Baldwin and Saalfeld, 1962). However, the top two walleye fisheries in Great Lakes (Huron and Erie) collapsed in the 1950s and 1960s when harvests reached peaks of 7000 annual tonnes in Lake Erie alone (Nepszy 1977; Schneider and Leach 1977). Collapsed populations in Lake Huron pointed to overfishing, habitat degradation, and poor water quality (Schneider and Leach, 1977) in addition to an increase in the predation of fry by the invasive alewife (Madenjian et al., 2008). Similarly, Lake Erie stocks were overexploited and impacted by alterations to spawning habitat, in addition to effects from pollution and eutrophication (Koonce et al 1996).

With fishing quotas enacted and habitats enhanced, walleye populations have since recovered in Lake Erie (Hatch et al., 1987; Ryan et al., 2003). Improvements in water quality and fingerling stocking in the 1980s (Schneider and Leach, 1977; Fielder and Baker, 2004) equally helped with the re-establishment of populations in Lake Huron. Eventually, the largest source of walleye stock within Lake Huron (Saginaw Bay) fully recovered in the 2000s after the non-native alewife (*Alosa pseudoharengus*) populations collapsed (Fielder and Thomas 2014; Madenjian et al. 2008).

1.7 Walleye in a changing climate

Walleye play an important role in the food web as key predators that shape aquatic communities through top-down (i.e., driven by predation) trophic cascades (Koenst and Smith 1975; Bowlby et al. 2010; Pandit et al. 2013). Yet, as previously mentioned, these fish are under pressure from harvest, invasive species, and the long-term threat of climate change (Holmlund and Hammer 1999; Fuller et al. 2002). As a result of climate change, suitable thermal habitat for certain freshwater species is declining, which is a consequence of increased surface water temperatures, increased thermal stratification, and decreased lake-mixing (Livingston and Lotter 1998; Adrian et al. 2009; Magnuson et al. 1990; Ficke et al. 2007). Effects from habitat degradation can result in population declines of species adapted to cooler waters if habitat availability continues to diminish. Additionally, increased surface water temperatures may cause an invasion of warmwater species to areas historically too cold to occupy (Sharma et al. 2007). Warming may therefore increase predation and competition in food-web interactions by invasive species that favor warmer waters as they begin extending their range (Van Zuiden and Sharma 2016). The consequences of such thermal range shifts could include lowered abundances of fishes, plants, and invertebrates, along with the potential to extirpate vulnerable species (MacRae and Jackson 2001; Kolar et al. 2007).

In optimal water temperature ranges (18 to 24oC), walleye undergo the most growth while possessing sufficient energy to allocate to gamete production for generating strong subsequent year classes (Christie and Regier 1988; Jeffrey et al 2020; McMahon et al 1984; Hokanson 1977). With water temperatures above this range, fish exhibit higher metabolic costs, decreased growth rates, and increased mortality rates, while lower temperatures are associated with lower metabolic costs and growth rates (Peat et al. 2015; Kershner et al. 1999; Clarke and Johnston 1999). While many impacts of temperature on the physiology of walleye are known, most data are based almost entirely on laboratory studies. Ecological realism is important to ensure that the estimates acquired under simulated conditions mimic those under natural conditions. Advances in technology, including the development of accelerometer transmitters, provide an opportunity to estimate the metabolic costs of activity across temperatures in walleye. Bioenergetic applications therefore present a unique opportunity to make important discoveries about an important species found within the Great Lakes.

1.8 Research objectives

The objective of my thesis is to establish laboratory-based bioenergetic parameters in captive walleye to estimate metabolic rates in the wild. Specifically, the objective was to determine the relationships between the output of implant transmitters (vectorial sum of acceleration (VeDBA)), swimming speed, and rate of oxygen ($\dot{M}_{O2}$) as a function of temperature, body size, and sex in adult walleye. This was accomplished through the measurement of active metabolic rates at a range of temperatures in adult walleye, using fish sourced from Lake Ontario, the St. Clair River, and White Lake Fish Culture Station (Ontario). It was predicted that walleye metabolic rates would increase predictably as a function of body size, water temperature, and activity level.

Chapter 2. Calibration of accelerometer transmitters for estimating field metabolic rates in walleye

2.1 Introduction

Bioenergetic modelling is highly applicable to fishes due to the variable nature of their aerobic metabolic scope and relevance to fisheries management and aquaculture (Jobling et al. 1995; Brownscombe et al. 2022). However, the measurement of bioenergetics in wild fish is challenging (Cooke et al. 2016). The study of movement in fish has been made possible through the development of telemetry techniques which allow for numerous variables to be monitored remotely for long periods of time in both freshwater and saltwater (Thorstad et al 2013a). Accelerometer loggers have enabled researchers to measure activity levels on fine scales (e.g., fin movement) in addition to generalized behaviours (e.g., foraging) in a manner that is quick and limits handling time (Gleiss et al 2011; Brown et al 2013; Brownscombe et al 2018). However, although the effects of electronic tags are species-specific, external attachment can pose limitations such as tissue damage, tag burden (decreased swimming ability, increased predation), entanglement, and premature tag loss (McCleave and Stred 1975; Jepsen 2015; Bridger and Booth 2010; Lewis and Muntz 1984). Internal tags are generally preferred due to placement near the gravitational center of the fish, reduced physical obstruction, and tag-associated drag (Jepsen et al 2015; Bridger and Booth 2010). Still, limitations of internal implantation must be considered such as species-specific restrictions (ex: body shape and size), altered behaviour, reduced feeding, and infection (Thorstad et al 2013a; Thorstad et al 2013b; Cooke et al 2011; Bridger and Booth 2003; Jepsen et al 2002).

Energy use in fishes has often been quantified using movement through the relationships between swimming speed (SS), tail-beat frequency (TBF), and metabolic rate, typically measured via the rate of $\dot{M}_{\mathrm{O2}}$ as a proxy (Webb 1986; Wilson et al 2013). The first study to calibrate internal accelerometer transmitters with energy expenditure using a model species was Wilson et al. (2013) who provided evidence of direct associations between tail beat frequency, swim speed, and $\dot{M}_{\mathrm{O2}}$ in captive Sockeye salmon (*Oncorhynchus nerka*). As swim speed increases, so does tail beat frequency and $\dot{M}_{\mathrm{O2}}$ (Brett 1964). This association between tail beat frequency and M_{O2} allows for the opportunity to estimate fish activity and bioenergetics in the field; however, the existing literature lacks proper standardization of implantation and calibration (Cruz-Font et al 2015).

Despite the recognized importance of bioenergetics to resolving ecological questions, for many fishes we lack the data for estimating key bioenergetic parameters from wild fish in natural environments and models often rely on lab-based estimates or those borrowed from other species (Brownscombe et al. 2022). The bioenergetics model for walleye (*Sander vitreus)* in the Great Lakes currently relies on parameters derived from a different species (European perch), and so until a specific model for walleye is developed, these research gaps will continue to limit our ability to predict species-specific responses as water temperatures continue to rise.

To generate bioenergetics estimates for wild fishes, we first require species-specific calibration in the lab. Therefore, the objectives of this study were to determine in adult walleye: (1) the relationship between accelerometer output (VeDBA) and swimming speed, (2) the relationship between accelerometer output and $\dot{M}_{O2}$ across a range of ecologically relevant temperatures, body sizes, and sexes, and (3) the degree of potential effects that acoustic tags have on swimming performance and $\dot{M}_{O2}$. This study expands upon previous calibration studies (Payne et al 2011; Wilson et al 2013; Cruz-Font et al 2015; Clark et al 2010) and presents new findings on the calibration of acoustic transmitter tags in adult walleye. The data from this study will underlie the application of accelerometer transmitters for estimating field metabolic rates in one of North America's ecologically and economically important fishes.

2.2 Methods

2.2.1 Fish collection

The animal handling procedures in this study were approved by the animal care committees of Fisheries and Oceans Canada (AUP #OPA-ACC-2022-15) and Trent University (Trent U AUP #26767) following guidelines set by the Canadian Council on Animal Care. Experiments took place at the Canadian Centre for Inland Waters in Burlington, Ontario, in the Aquatic Life Research Facility. Forty-seven adult walleye were used for this study: nineteen hatchery-reared fish from White Lake Fish Culture Station (11 males and 8 females; fork length (FL) = 38.6-45.7 and 43.6-50.5 cm, respectively), ten fall-caught wild fish (10 males; FL = 53.4-71.5 cm), nine spring-caught wild fish (9 males; FL= 63.1-69.1 cm) captured in Hamilton Harbour, Lake Ontario (44.295ºN, 79.801ºW), as well as nine summer-caught wild fish (8 males and 1 females; FL = 363-449 cm) captured in the St. Clair River, ON (around 42°55'1.17"N, 82°27'29.36"W and 43° 0'15.34"N, 82°25'1.70"W). Fish were kept indoors in circular tanks (800 L) with recirculated freshwater systems (Recirculating Aquaculture System (RAS)) containing dechlorinated municipal water when not undergoing swim tunnel respirometer trials. Upon introduction to the lab, fish were held in salt baths (5 g L^{-1} salinity) for five days to reduce potential for issues with disease and were held for at least one week prior to surgical implantation of transmitters. All fish were euthanized by immersion in tricaine methane sulfonate (MS-222) the end of experiments (250 mg L^{-1} buffered with 500 mg L^{-1} sodium bicarbonate), which also allowed for sex determination.

2.2.2 Acoustic tag surgery

We surgically implanted two types of acoustic transmitters into walleye for experiments (Innovasea, Nova Scotia, Canada) depending on the body size of the recipient fish. One tag type measured acceleration (model V13A, 12.5 Hz sampling frequency; tri-axial acceleration algorithm; 40-50 sec delay; 30 sec recording period; 3.43 m s^{-2} sensitivity; 13 mm diameter, 34 mm long, 4.8 g in water) and the other measured acceleration and temperature (model V16AT, 12.5 Hz sampling frequency; tri-axial acceleration algorithm; 90-180 sec delay; 87 sec recording period; 3.43 m s^{-2} sensitivity; 16 mm diameter, 95 mm long, 14.9 g in water). Selection of tag type was dependent on fish size to minimize tag burden by ensuring tag weight was <2% of the fish's body mass (Winter 1983; Jepsen et al 2005).

A suture was secured to each transmitter with a slip knot ¼ of the way from the back (where the sensor was located). Surgical tools, tags, and sutures were sanitized in

1% Virkon Aquatic before and between surgeries and rinsed in deionized water prior to reuse. Prior to surgery, fish were placed in an anesthetic bath containing 120 mg L^{-1} MS-222, pH buffered with 2:1 sodium carbonate. Once the fish reached stage 5 anesthesia (<5 minutes as exhibited by loss of equilibrium, slow ventilation rate, and no response to tail grab), it was placed ventral side up in a padded V-shaped trough. In the trough, the fish's gills were irrigated with aerated freshwater containing a buffered maintenance dose of 60 mg L^{-1} MS-222.

With the fish facing ventral side up, an incision was made 1 cm from the mid-ventral line with the most posterior point of the incision 3 cm anterior of the anus. The tag was inserted with sensor toward the posterior and was anchored at the posterior end of the incision with an anchor stitch. The anchor stitch was completed by puncturing the fish's body wall from the inside out, then back from outside in to create a small loop. The anchor stitch ensured that the placement of the tag was secure and standardized with each fish, i.e., with the sensor end of the transmitter being *ca*. 3 cm anterior of the anus, slightly off the ventral midline, in all individuals. The suture was then used to puncture the skin on the opposing side of the incision, creating a tag end, which was tied to the loop end (created on the other side) using a surgeon's knot (3x2x2 wraps). The incision was then closed with 2-3 interrupted sutures equidistant across the incision. After surgery, fish were weighed and measured for total length, width, and height, and subsequently held in a salt bath (5 g L^{-1}) to reduce the potential for infection.

2.2.3 Swim trials – measuring metabolic rate

Tagged walleye were given at least 72 hours to recover before performing a trial (allowing for salt bath treatment, proper wound healing, and water temperature acclimation). Swim trials were completed using a 185L swim tunnel respirometer (Loligo Systems Inc., Viborg, Denmark, https://www.loligosystems.com). The swim tunnel was housed in an environmental chamber such that the air (and therefore water) temperature could be controlled and filled with dechlorinated municipal water. The 'upstream' portion of the tank was covered with a darkening shade to encourage fish to swim, yet the posterior half of the fish was always visible from the downstream end of the tank ensuring tailbeats could still be observed. At the downstream end was a metal grid that could be momentarily electrified (8V) to encourage swimming if necessary (criteria for application described below).

Once a fish was sealed into the swim tunnel, it was given 5 minutes to rest before commencing a practice swim. Beginning at a resting swim speed of 10 cm s^{-1}, water velocity was gradually increased to 50 cm s^{-1} (equivalent to a mean of 0.984 body lengths (BL) s^{-1}) over the course of 3 minutes and then kept there for an additional 12 minutes with the flush pump turned off (to estimate $\dot{M}_{O2}$ via the decline in dissolved oxygen in the chamber). Once the 15-minute practice swim was complete, water velocity was brought back down to 10 cm s^{-1} with the flush pump turned on for 45 minutes to allow for both oxygen levels and the fish to recover. Fish then swam through a ramp protocol to quantify its critical swimming speed (U_{crit}) (Brett 1964; Jain et al. 1997; Lee et al. 2003; Wilson et al. 2013) at four different temperatures (5, 10, 16, and 21°C). These temperatures were chosen as they span most of the temperatures that walleye occupy over different seasons (Christie and Regier 1988; Lester et al. 2004; Hokanson 1977). By including the bottom and top few degrees, we can apply model estimates to the energy use of fishes throughout the course of the year with greater accuracy. The equation to determine U_{crit} was established by Brett (1964):

$$U_{\text{crit}} = \mathrm{V_f} + [(T/t)(\mathrm{dV})]$$

Equation 2: Critical swimming speed

where U_{crit} is expressed in cm s^{-1}, $\mathrm{V_f}$ is the last speed at which the fish completed a full time increment, t is the time increment duration that the fish swam at each speed, dV is the speed increment, and T is the duration of time that the fish swam at its final increment before exhaustion.

Water temperature in holding tanks was never raised by more than 2°C day^{-1} and fish had at least 2 days of acclimation at each temperature before completing a swimming trial. Some fish were used for multiple trials and temperatures when logistically required. To begin each U_{crit} trial, water velocity was increased from 10 to 40 cm s^{-1} and held for 20 minutes, and then increased incrementally by 10 cm s^{-1} every 20 minutes. This continued until the endpoint of our protocol was reached, which was when the fish needed to be shocked off the downstream grid three times in short succession, i.e., with the fish only coming off the grid for < 5s off the grid between shocks. In total, thirty-seven individuals (30 males and 7 females) were tagged with an accelerometer and ten non-tagged individuals (8 males and 2 females) were used as controls to complete a total of N = 71 U_{crit} trials. Originally, we had completed 92 trials; however, the warmest temperature group showed very inconclusive results. We attributed this to the time of year (21°C trials completed in early December) as well as duration of time spent in lab. Those fish have been excluded from our analyses and were replaced with new trials conducted in the spring (see Appendix Figure A1).

2.2.4 Acceleration and oxygen consumption measurements

Oxygen consumption ($\dot{M}_{\mathrm{O2}}$) was continuously recorded inside the swim tunnel (0.5 Hz) with two optical oxygen probes (Firesting-O2, PyroScience, Aachen, Germany) and appropriate software (Pyro Workbench, PyroScience, Aachen, Germany). The swim tunnel was sealed (flush pump turned off and valve closed) for the first 8-10 minutes of each U_{crit} trial increment so that M_{O2} could be estimated via the rate of decline of dissolved oxygen in the chamber. Concentrations of dissolved oxygen were kept above 85% air saturation, and blank runs without fish were also completed at least once weekly to account for microbial respiration (0.065 ± 0.026 O_2 L^{-1} hour^{-1}). An acoustic hydrophone was placed in the tank and connected to a receiver (VR100, VEMCO, Halifax, NS, Canada) which recorded the outputs of the transmitters. The acceleration signal is measured on three axes (in m s^{-1}) that contribute to an overall root mean square acceleration value that can be used as a measure of activity. Acceleration is sampled on each axis at 12.5 Hz (measurements per second) over a given period (77 and 87 seconds for V13A and V16AT, respectively), then stored until the tag delay time is complete (between 80 and 160 seconds for V13A tags and 90 to 180 seconds for V16AT tags) at which point the signal is transmitted. We also corrected for solid body blocking effects based on Bell and Terhune (1970) to ensure accurate measurements of water flow velocities experienced by a positionally stable fish were achieved (Kline et al 2015). Swim trials were also recorded with two simple USB cameras one placed above and the other to the side of the tank. Video was recorded for ~30 seconds one to two times per speed increment to generate estimates of tail beat frequency.

2.2.5 Data analysis and statistics

All statistical analyses were completed using RStudio (version 2022.07.2) with α set to 0.05. Data were tested for normality and homoscedasticity, with log transformation used as needed. Linear mixed-effects models were used to quantify the relationships between M_{O2}, acceleration, swimming speed, and tail beat frequency across different body sizes and temperatures as covariables when applicable and with fish ID as a random slope. Models were also tested for interactions between temperature, body mass, speed, acceleration, and sex.

To assess relationships between walleye swimming metrics, a series of linear mixed effects (LME) models were fit with the nlme R package (RStudio Version 1.2.5033). In each case, to account for repeated measures of individuals, fully parameterized models were initially fit in separate models with individual fish as a random intercept, slope, and intercept + slope, selecting the best model based on Akaike's Information Criterion (AIC) values. To assess the relationship between acceleration and metabolic rate, and LME was fit with M_{O2} as the response and acceleration, temperature, sex, and body mass as predictors, as well as their two-way interactions. To assess relationship between swim speed and metabolic rate, a second LME model was fit, substituting swim speed for acceleration. To assess predictors of walleye acceleration, an LME was fit with swim speed, temperature, sex, and body mass as predictors, as well as their two-way interactions. An LME was also fit with tail beat frequency as the response, acceleration, temperature, sex, and body mass as predictors, as well as their two-way interactions. Another was fit with tail beat frequency as the response substituting swim speed for acceleration as a predictor.

For U_{crit}, a second order polynomial regression was fit with temperature as a predictor. To test for tagging effects, an LME was fit with U_{crit} as the response, temperature, tagged (yes or no) as predictors, and their two-way interactions. Similarly, we fit a linear mixed effects model with M_{O2} as the response, speed, tagged (yes or no) as predictors, and their two-way interactions. In all cases, full models were compared to reduced models with backward model selection, and the best fitting models were selected using AIC. Model fits were assessed by plotting residuals against fitted values, as well as against each predictors following Zuur et al. (2009). In some cases, response or predictor variables were log transformed to improve model fit.

2.3 Results

2.3.1 Acceleration, swim speed, and tail beat frequency

As expected, we found that the rate of oxygen consumption (mg O_2 hour^{-1} kg^{-1}) in adult walleye increased with body acceleration as measured by the accelerometer transmitter (g s^{-1}). The strongest predictor of log transformed $\dot{M}_{O2}$ was a model with log transformed body mass ($p < 0.001$), and the interaction between acceleration and temperature ($p = 0.009$; Table 1). Temperature was also positively associated with $\dot{M}_{O2}$ (Figures 1, 2, 3). The relationship between $\dot{M}_{O2}$ and body mass had a negative association where the highest oxygen consumed was by small fish at high temperatures (Figure 4). Conversely, a linear mixed-effects model incorporating swim speed rather than acceleration as a predictor variable showed that swim speed ($p < 0.001$), temperature ($p < 0.001$), log transformed body mass ($p < 0.001$), and the interaction between swim speed and sex(M) ($p = 0.029$) were the clearest predictors of log transformed $\dot{M}_{O2}$ (Table 2). The associations between swimming speed and $\dot{M}_{O2}$ did not differ between tagged and untagged individual fish ($p = 0.52$; Table 3, Figure 5), suggesting the transmitter (and/or surgery) did not impact the relationships.

The relationship between acceleration and swim speed was best fit using a linear mixed-effects model with fish ID as a random slope (Table 4). Acceleration and swimming speed were positively correlated ($p < 0.001$) such that with every 10 cm/s increase in swim speed, transmitter-measured acceleration increased by 0.0065 g/s. The model also included an interaction between swimming speed and log transformed body mass included as a predictor variable ($p = 0.003$, $R^2 = 0.82$) whereby overall acceleration was lower for larger fish (Figure 6). The relationship between acceleration and tail beat frequency ($R^2 = 0.86$) was best fit using a linear mixed-effects model with fish ID as a random slope (Table 5). The best model for predicting log transformed tail beat frequency included acceleration ($p < 0.001$), temperature ($p < 0.001$), and log transformed body mass ($p < 0.001$). The relationship between acceleration and tailbeat frequency became stronger (steeper) with increasing temperature (Figure 7), while body mass had an inversely proportional effect (Figure 8) whereby an increase in body mass resulted in fewer tail beats per second. The highest tail beats per second therefore occurred among (small) individuals at high accelerations and high temperatures (Figure 9). Conversely, we note that when the linear mixed-effects model was fit using speed rather than acceleration to predict tail beat frequency, it delivered a higher correlation coefficient ($R^2 = 0.94$). The best predictors of tail beat frequency were found to be speed, temperature, and body mass (Table 6). Specifically, temperature ($p = 0.01$) and water speed ($p = 0.01$) were positively associated with tailbeats per second (Figure 10), while the association with body mass ($p = 0.003$) was negative (Figure 11).

2.3.2 Swimming performance (U_{crit})

U_{crit} was predicted with temperature ($p < 0.001$) using a linear polynomial regression (Table 7; $R^2 = 0.82$). Overall, critical swimming speed increased with temperature (Figure 12). Tagging did not impact U_{crit} among hatchery fish (Table 8, Figure 13). Sex was not a significant predictor of $\dot{M}_{O2}$ or U_{crit} and did not differ between males and females. The mean absolute speed of U_{crit} did not significantly differ between the eleven male and eight female hatchery fish (66.9 + 7.73 and 64.79 $\pm$ 7.01 cm s^{-1}, respectively: $t = 0.91$, $df = 37$, $p = 0.37$). However, there was a significant difference in U_{crit} velocity between males (1.61 + 0.20 BL s^{-1}) and females (1.40 + 0.11 BL s^{-1}) amongst hatchery fish ($t = 3.67$, $df = 24$, $p = 0.001$). Indeed, the mean length of females (47.80 $\pm$ 2.21 cm) were significantly larger than males (41.62 $\pm$ 1.67 cm) in hatchery fish ($t = -8.74$, $df = 26$, $p < 0.001$). Female hatchery fish showed no significant change in swimming capabilities between 10°C and 16°C temperatures for mean absolute U_{crit} speed (t = 1.56, df = 13, p = 0.14) or velocity (t = 1.45, df = 13, p = 0.17). However, male hatchery fish swam significantly better in 16°C water compared to 10°C in both speed (t = 3.22, df = 13, p < 0.001) and velocity (t = 2.46, df = 9, p = 0.036). There was an overall difference in absolute mean U_{crit} speed between 10°C and 16°C water (t = 3.11, df = 27, p = 0.004) while there was no difference in BL s^{-1} velocity between the two temperatures. Females therefore had a strong influence on the overall lack of significance between mean U_{crit} velocities between temperatures, and male fish had a strong influence on the significant difference observed in overall U_{crit} swimming speeds between the two temperatures.

When comparing individuals tested at the same temperatures (10°C and 16°C), wild fish were found to be larger than hatchery fish used (61.60 + 4.11 and 44.55 + 3.68 cm, respectively: t = 14.11, df = 34, p < 0.001). This translated to significantly lower U_{crit} velocities achieved among wild fish (1.07 + 0.16 BL s^{-1}) compared to hatchery fish (1.51 + 0.19 BL s^{-1}; t = -8.76, df = 44, p = 3.35) with no significant difference in absolute speeds at which U_{crit} was reached (65.63 + 7.76 and 66.82 + 6.46 cm s^{-1}, respectively: t = -0.61, df = 36, p= 0.55).

2.4 Discussion

Bioenergetic modelling enables researchers to predict species-specific responses to environmental changes and has been used extensively with walleye (Madenjian et al 2018; Kitchell et al 1977; Harris and Snodgrass 1993). However, the bioenergetics model for walleye in the Great Lakes currently relies on parameters from laboratory-based studies or derived from a different species, leaving uncertainty in model outputs. This study calibrated a highly relevant new tool for quantifying bioenergetic parameters in adult walleye that measured swimming activity (via accelerometers) and body temperature, thus supporting the use of sensor-equipped telemetry transmitters to estimate field metabolic rates of wild fishes.

Here I found that mass-specific metabolic rates in adult walleye increased with higher acceleration values, higher temperatures, and lower body masses. These findings are consistent with similar studies and fundamental biological principles (Brody and Lardy 1946, Fry 1947, Brett and Groves 1979, Peters 1986, Jobling 1993, Brafield 1985). The strongest predictors of oxygen consumption were body mass and the interaction between acceleration and temperature. Related to this interaction, the slope of the line for the relationship between acceleration and $\dot{M}_{O2}$ changed substantially with temperature, reflecting a higher rate of increase in metabolic rate with activity levels at higher temperatures. These results suggest that temperature and activity may be having a synergistic effect, where more activity becomes more costly at higher temperatures. Numerous studies have found that increased temperatures do in fact result in increased MMR for fish (Fry & Hart 1948; Brett 1965; Norin et al 2014; Eliason et al. 2011; Claireaux et al 2006; Clark et al 2011).

Oxygen consumption rates decreased with increasing body mass, which has generally been a well described finding whereby metabolism decreases with increasing mass (Brown et al 2004; Beamish 1964; Schmidt-Nielsen 1975). Brett (1964) observed oxygen consumption decreasing with increasing sockeye salmon size (Oncorynchus nerka), similar to Doulos and Kindschi (1990) who noted oxygen consumption declined with increasing trout size. The slope of the relationship between log transformed body mass and oxygen consumption of walleye was found to be -0.18. This means that every 1-gram increase in fish body mass will result in an overall decrease of oxygen consumption by 0.18 mg O_2 hr^{-1} kg^{-1}. Further, the logarithmic slope falls within the normal range (-0.5 to 0) proposed by Fry (1971). Cait and Summerfelt (1991) also observed declines with increasing body mass in walleye when plotted logarithmically, which suggests that energetic costs of locomotion at certain speeds are not affordable beyond a certain size threshold (Ferrón et al 2018; Makarieva et al 2006).

Oxygen was not only highest among smaller body sizes, but also at higher temperatures (Figure 4). One possible explanation for this lies within sampling limitations, where smaller fish happened to swim at the highest temperature (which require more oxygen) while the lowest temperature was solely comprised of larger fish. The 10°C and 16°C trials had a mix of hatchery (small) and wild (large) fish, however the 5°C trials exclusively consisted of large wild harbour fish, and the 21°C trials consisted of small wild river fish. Our study was limited by the numbers and sizes of fish available for experimentation by differing temperatures, which, unfortunately is not an ideal study design. For example, the interaction between body size and temperature was not included in the models as there wasn't a sufficient range of body sizes to assess this. However, our model outputs successfully incorporated the data to capture general patterns in swimming activity, temperature, body size, and metabolism. Despite the above-mentioned discrepancies, size standardized model predictions across temperatures demonstrated that all body sizes have an exponential increase in oxygen consumption with temperature which is consistent with pre-existing literature. For example, Tirsgaard et al (2015) observed that the thermal dependence of MMR changed between size classes of trout. In their study, metabolic rates of smaller fish (50g) increased with a broad range of temperatures (2 – 20°C), while the larger fish (200 – 450g) plateaued after 10°C. This suggests a size-dependent thermal limitations of MMR, which complements the findings in our study where the highest observed mass-specific metabolic rates in adult walleye were observed to increase with temperature while decreasing with body mass. This aligns with our findings where the critical swimming speeds of females (larger size class) did not increase from 10°C to 16°C whereas the critical swimming speed of males (smaller size class) did increase.

The greatest predictor of oxygen consumption in our model was the interaction between acceleration and temperature. A fish's ability to swim at faster speeds is limited by the temperature's direct controlling effect of maximum metabolic rate. The model incorporating swim speed ($R^2 = 0.86$) explained slightly more variance than acceleration alone ($R^2 = 0.83$) when predicting $\dot{M}_{O2}$. Indeed, on its own, swim speed had a strong relationship with acceleration ($R^2 = 0.82$), which demonstrates that these tags can give reasonable estimations of swim speeds in the wild. We also observed a relationship between speed and body mass, indicating that smaller fish were reaching higher acceleration values when compared to larger fish at the same speed. Once again, it is important to consider fish body size in attempting to predict swimming speed from acceleration in field data. Larger walleye required fewer tail beats per second to maintain the same speed compared to smaller fish, much like research by Webb et al (1984) where tail beat frequency decreased with increasing size in trout. The relationship between size, acceleration, and tail beat frequency likely contributed to lower acceleration values generated by larger individuals when swimming at the same speeds as smaller fish.

We found linear correlations between tail beat frequency and acceleration across all temperatures and body masses. The correlation coefficient obtained ($R^2 = 0.86$) was similar to those of previous studies (Wilson et al 2013; Cruz-Font et al 2016). Warmer temperatures allow for faster muscle contraction time which results in increased tail beats (Nofrizal and Arimoto 2020). Bainbridge (1958) found that maximum attainable frequency decreases with increasing size of fish among trout (slightly) as well as dace and goldfish (more distinct). As with acceleration, tail beat frequency increased with swim speed ($R^2 = 0.94$). These findings agree with Cruz-Font et al (2016), where lake trout tail beat frequency increased linearly with water flow (thus swim speed) in the swim tunnel ($R^2 = 0.87$).

Wild fish and hatchery fish achieved similar absolute U_{crit} speeds (cm s^{-1}). Hatchery fish did however achieve higher relative speeds (BL s^{-1}) due to their significant size difference. One shortcoming of this study was that there were insufficient females to rigorously test for sex differences. Given that we were not able to catch many wild female walleye, sex comparisons were done using only hatchery fish. Amongst hatchery fish, female U_{crit} was not affected by the thermal increase of 10 to 16°C while male U_{crit} increased with temperature. Similarly, although the absolute U_{crit} speeds (cm s^{-1}) between males and females were similar, males ultimately achieved higher velocities (BL s^{-1}) due to their significant reduction in size. Walleye are sexually dimorphic, meaning that females tend to attain larger sizes than males (Henderson 2003; Purchase et al 2005). We therefore believe that size is likely to be a more important factor than origin (hatchery vs wild) or sex (male vs female) in determining metabolic rate and that differences between groups are due to size, not inherent phenotypic differences. For example, Mateus et al (2008) found that sex had no effect on the swimming capacity of Iberian barbel (*Barbus bocagei*), but significant differences in U_{crit} were found across sizes. However, it has been documented that males may expend energy at a higher rate than females, which could explain why the critical swimming speed of males was more influenced by temperature increases than for females (Madenjian 2013). Another potential biological reason for increased male swimming performance may be the need to maximize swimming power over body size in the competition for fertilizations on spawning shoals (Henderson 2003).

It is important to note however that according to the Arrhenius equation, although metabolic capability typically increases with temperature, there are upper limits to this relationship (DeLong et al 2017). For example, in walleye consumption capacity starts to decline above 24°C (McMahon et al., 1984), with their critical thermal maximum (CTmax) understood to be around 30°C (Wismer and Christie 1987). High temperatures have been shown to result in reduced activity, condition, consumption, and growth (Quist et al 2002).Our findings show that U_{crit} increased with temperature for walleye from 5 to

21°C. These temperatures are biologically relevant as they correspond to thermal habitat ranges that walleye successfully occupy for optimal growth (20-24°C) and spawning (2-15°C) (Christie and Regier 1988; Lester et al. 2004; Hokanson 1977). As temperature increased, so did activity and thus swimming performance (U_{crit}) indicating that the temperature range of this study did not exceed thermal performance thresholds. However, applying these calibrations to field data at temperatures outside of the scope of this study should be done with consideration. One can utilize available databases and programs (see: Fish Bioenergetics 4.0) to compare species-specific outputs of relationships already established within existing models (Deslauriers et al 2017).

Anchoring sensor tags to the body cavity of fish ensured placement would not influence the acceleration outputs used to estimate swimming speed. To ensure tag burden was minimized, we compared the swimming data of tagged and untagged fish. Based on our results, we found no evidence to suggest that these tags would have affected swimming capabilities of the study fish (Table 3; Figure 5). In fact, tagged fish achieved similar or higher U_{crit} values and showed better metabolic capabilities at associated swim speeds compared to untagged fish (Table 8; Figure 13). Given our assessment of tag validation, we recommend similar techniques be employed with wild fishes in the field.

In conclusion, this study has advanced our understanding of the bioenergetics and swimming performance of adult walleye in response to different environmental conditions. Our findings confirm and expand upon established biological principles, demonstrating that mass-specific metabolic rates in walleye are influenced by factors such as acceleration and temperature. The results also shed light on size-based differences in swimming performance, emphasizing the significance of this factor in determining metabolic rates. While caution is advised in extrapolating beyond the study's temperature range, the methodology and insights provided in this study lay the groundwork for future investigations into the thermal limitations of fish metabolism. Finally, this study successfully validated the use of sensor tags and ensured their impact on swimming capabilities was minimal. Overall, this research advances the field of fish bioenergetics and provides valuable insights into species-specific responses to climatic changes.

Chapter 3. General Discussion

Our study evaluated the use of accelerometry and respirometry to calibrate novel technology with the goal of acquiring energetics estimates from wild walleye fish in natural ecosystems. These calibrations enable field deployments, where accelerometers, along with measures of temperature and body size, can estimate field metabolic rates of walleye. This can give insights into how fishes make energetic trade-offs based on physiological demands as well as increased environmental stressors through bioenergetic modelling. Bioenergetic modelling has enabled researchers to evaluate the influence of diet and environmental conditions on growth (Bevelhimer and Adams 1993), predator-prey interactions (Stewart et al 1981) and feeding and growth of fishes (Post 1990; Moden and Culver 1993; Beauchamp 2009). Additionally, effects from pollutants (Stafford and Haines 2001), impacts from invasive species (Cooke and Hill 2010), effects of habitat alterations (Rose et al 2013), and investigations of whole-life growth patterns of fish (Hayes et al 2000) can now be evaluated. Understanding how fish use their energy budgets in the wild is invaluable from a fisheries management standpoint because it provides insights into how growth (body size) and reproductive output will change as the climate continues to change (Peterson and Kitchell 2001); therefore, adding to our understanding of adaptation and evolution of fishes.

3.1 Findings and Implications

Temperature increases lead to higher metabolic rate (Clarke and Johnston 1999). While greater temperatures increase swimming capabilities, they also mean higher demands for dissolved oxygen (DO) and caloric (food) intake which can then result in changes in feeding habits. Decreased DO impacts all aspects of aquatic ecosystems and often results in lower food supplies. This makes it difficult for fish to meet their increased metabolic requirements when operating at higher temperatures. The need for more DO by fish at higher temperatures, coupled with the decreased availability of DO under said conditions are reducing growth (Kershner et al 1999) and increasing natural mortality rates (Houde 1989) among individuals unable to cope with the stress or adapt fast enough to change. Such may be predicted to be the case for walleye within the Delta Marsh, which is the largest coastal wetland on Lake Manitoba (Jeffrey et al 2020).

Physiological consequences of high temperatures and low DO include population-level effects such as decreased fitness due to prolonged stress, in addition to alterations to the genetic composition of future populations if unintended selection of hypoxia or heat tolerant fish occurs (Jeffrey et al 2020). The life history of walleye is greatly affected by temperature, influencing behaviour (Reynolds 1977), condition (Kocovsky & Carline 2001), spawning (Collette et al 1977), growth (Kelso, 1972; Momot et al 1977), and recruitment (Busch et al 1975; Momot et al 1977; Hansen et al 1998). Optimal temperature ranges exist at which fish require to reproduce. If these conditions are not met, fish will either migrate away searching for more suitable habitat or simply fail to reproduce.

Failure to reproduce will consequently result in significant reductions among populations. Reductions in population sizes can not only have devastating ecological impacts but can cause economic downfalls as well. Temperatures exceeding optimal ranges are associated with higher metabolic costs and declines in food availability, which negatively impacts growth and reproduction rates; hence reducing the fishery productivity and maximum sustainable yield. Increased accuracy of metabolic rate estimates will enable us to predict and manage stock projections based on future anticipated changes in climate.

For ectotherms, standard metabolic rate represents the baseline, or minimum metabolic rate at a resting, non-active state (Secor 2009). Current bioenergetics models use standard metabolic rate estimates as a measure of quantifying the metabolic costs of fish kept in a laboratory (Jorgensen et al 2016). We observed high metabolic rates in our study, which are related to higher activity levels, energy expenditures, competition, and territorial aggression (Careau et al 2008; Auer et al 2017; Biro and Stamps 2010). This higher cost of living is beneficial for survival when food availability is high but is a major disadvantage when food is limited (Bochdansky et al. 2005; Armstrong et al. 2011; Burton et al. 2011; Killen et al. 2011). The elevated metabolic rates we observed in our study may have potentially been as a result of stress from the artificial environment in which they were held. The implication of using high standard metabolic rate estimates than what would otherwise be assumed is that it may lead managers to underestimate field costs, food needs, responses to temperature, and overall repercussions to fisheries. The within-species variation of SMR is largely related to temperature and body size (Clarke and Johnston 1999), and so underestimating SMR of organisms that are subjected to temperature variations is underestimating the ultimate effects of climate change.

Swim tunnel respirometry is a powerful tool that can provide a reliable, ecologically relevant measurement of metabolic rates and swimming abilities that has been used for decades. Critical swimming speed data is repeatable, reflects maximum aerobic capacity, and generates comparable data on the overall swimming capabilities of fish (Plaut 2001). However, as with any artificial system, this is not without limitations. For example, the design of swim tunnels may not always be appropriate for certain fish species or swimming behaviors. There is an optimal range where the size of a fish must be large enough to get accurate $\dot{M}_{O2}$ measurements, while ensuring the fish is not too large where natural swimming becomes compromised (1:100 fish mass to water mass ratio (Clark et al 2013)). Hence why solid-blocking effects must be accounted for when the cross-sectional area of a fish exceeds 10% of the total cross-sectional area of the tunnel (Bell and Terhune 1970). Additionally, acceleration measurements are achieved through implantation of a tag, which poses the risk of burden and bias. While we accounted for solid-blocking effect and demonstrated that tagging did not impact our study, fish are being swam in laminar, consistent flowing water in a straight line which is not an accurate representation of natural swimming behaviors in the wild. For example, turning has high metabolic costs (Meskendahl et al 2019). Therefore, given that certain behaviors cannot be accounted for when measuring metabolic rates within swim tunnels, this should be kept in mind when extrapolating findings in the lab to the field.

3.2 Future directions

Swim tunnels have been used extensively to provide a window into the relationships that exist between swim speed and metabolism (Claireaux & Lagarde 1999, Steinhausen et al. 2010, Gleiss et al. 2010).Despite the high applicability, there has also been criticism that data acquisition from bioenergetic modelling in swim tunnels is over complicated and leads to errors in estimations when there are extensive parameters to account for (Ney 1990; Bartell et al 1986; Boisclair and Leggett 1989). Laboratory-based methods may not always reflect the natural swimming behaviors or conditions that a fish would experience in the wild. For example, the restrictive nature of a tunnel compared to what an individual would experience in the wild could lead to abnormal behavior for prolonged period. Such abnormal behavior could then result in increased oxygen intake (Wendelaar Bonga 1997) and limited movement due to tank size and design (Tang and Boisclair 1993; Peake and Farrell 2004). One option could be to increase the swim tunnel length, as this has been shown to increase U_{crit} due to less restricted burst-and-coast swimming behavior (Tudorache et al 2007; Peake and Farrell 2006; Haro et al 2004; Castro-Santos 2004, 2005). However, downsides to increasing the length of the tunnel could include financial and logistical restraints as well as greater size requirements to acquire accurate oxygen consumption measurements.

Given experiments are conducted within the lab, ensuring sufficient acclimation periods and gentle handling to minimize stress are encouraged and will improve the realism of experiments. Additional sources of error may arise from effects from flow, water chemistry and presence of other organisms. For these reasons, we should perform tests in the field using the latest equipment when possible (e.g., Brett-type swim tunnel respirometers purpose built for mobility and use in the field (Farrell et al 2003)) where fish can be evaluated at ambient temperatures and photoperiods (Jones et al 1974; Williams 1986; Farrell et al 2001). Physiological telemetry is also recommended as it bridges the gap between lab and field measurements (Priede and Young 1977; Armstrong

1986; Lucas and Armstrong 1991; Lucas et al. 1993) by validating previous data as well as providing a more comprehensive understanding of fish swimming in nature (Brodie et al 2016; Hansen et al 1993).

In conclusion, this study presents a significant advancement in the field of fish energetics, particularly in the context of wild walleye populations. The successful calibration of accelerometry and respirometry techniques opens new opportunities for estimating field metabolic rates in natural environments. By utilizing bioenergetic modeling, we gain valuable insights into the intricate energetic trade-offs that fish, particularly walleye, make in response to physiological demands and environmental stressors. This knowledge is crucial for effective fisheries management, particularly in the face of ongoing climate change. Swim tunnel respirometry proves to be a powerful tool for acquiring bioenergetic estimates in fishes and future research should aim to refine experimental conditions and incorporate physiological telemetry to bridge the gap between lab and field measurements.

Tables

Table 1: Linear mixed effects model of oxygen consumption using acceleration in adult walleye (Marginal $R^2 = 0.72$, Conditional $R^2 = 0.83$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
$\log(\dot{M}_{O2})$	(Intercept)	5.94	0.36	142	16.31	0.0000
	Acceleration	-0.65	11.20	142	-0.05	0.9535
	Temperature	0.02	0.009	142	2.04	0.0433
	log(Body mass)	-0.18	0.04	142	-4.37	0.0000
	Acceleration*Temperature	1.88	0.71	142	2.65	0.0091

Table 2: Linear mixed effects model of oxygen consumption using swim speed in adult walleye (Marginal $R^2 = 0.86$, Conditional $R^2 = 0.86$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
log($\dot{M}_{O2}$)	(Intercept)	5.80	0.26	142	16.31	0.0000
	Swim Speed	0.013	0.0018	142	7.80	0.0000
	Temperature	0.037	0.0035	142	10.75	0.0000
	log(Body mass)	-0.26	0.032	142	-8.20	0.0000
	Sex(M)	0.21	0.11	25	1.94	0.0627
	Swim Speed*Sex(M)	1.88	0.71	142	2.65	0.0275

Table 3: Linear mixed effects model of oxygen consumption using swim speed to assess tagging effects in adult hatchery walleye (Marginal $R^2 = 0.37$, Conditional $R^2 = 0.50$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
$\dot{M}_{O2}$	(Intercept)	21.82	35.92	102	0.61	0.5448
	Speed	3.90	0.59	102	6.59	0.0000
	Tagged(Yes)	30.66	46.96	18	0.65	0.5221
	Speed*Tagged(Yes)	-0.72	0.75	102	-0.95	0.3427

Table 4: Linear mixed effects model of acceleration using swim speed in adult walleye (Marginal $R^2 = 0.82$, Conditional $R^2 = 0.82$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
Acceleration	(Intercept)	0.005	0.008	143	0.69	0.4939
	Swim Speed	<0.001	<0.001	143	4.55	0.0000
	log(Body mass)	<-0.001	0.001	143	-0.81	0.4207
	Swim Speed*log(Body mass)	<-0.001	<0.001	143	-3.06	0.0026

Table 5: Linear mixed effects model of tail beats frequency (TB s^{-1}) using acceleration in adult walleye (Marginal $R^2 = 0.74$, Conditional $R^2 = 0.86$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
log(TBF)	(Intercept)	0.89	0.27	89	3.26	0.0016
	Acceleration	34.39	3.08	89	11.16	0.0000
	Temperature	0.01	0.003	89	4.22	0.0001
	log(Body mass)	-0.11	0.03	89	-3.57	0.0006

Table 6: Linear mixed effects model of tail beats frequency (TB s^{-1}) using swim speed in adult walleye (Marginal $R^2 = 0.80$, Conditional $R^2 = 0.94$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
log(TBF)	(Intercept)	1.23	0.59	87	2.09	0.0394
	Speed	0.02	0.009	87	2.51	0.0139
	Temperature	0.02	0.009	87	2.49	0.0146
	log(Body mass)	-0.22	0.07	87	-3.1	0.0026
	Speed*Temperature	<-0.001	<0.001	87	-1.4	0.1652
	Speed*log(Body mass)	-0.001	0.001	87	-1.24	0.2170

Table 7: Linear polynomial regression of U_{crit} and temperature in adult walleye (Marginal $R^2 = 0.24$, Conditional $R^2 = 0.82$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
U_{crit}	(Intercept)	68.47	1.16	141	59	0.0000
	poly(temp, 2)1	48.59	6.07	141	8	0.0000
	poly(temp, 2)2	-11.60	5.75	141	-2.02	0.0456

Table 8: Linear mixed effects model of U_{crit} to assess tagging effects in adult hatchery walleye (Marginal $R^2 = 0.30$, Conditional $R^2 = 0.85$)

Variable	**Factor**	**Value**	**SEM**	**d.f.**	**t-Value**	**P-Value**
U_{crit}	(Intercept)	64.53	1.97	89	32.78	0.0000
	Temperature (10C)	-1.38	1.25	89	-1.11	0.2711
	Tagged(Yes)	7.76	2.55	18	3.04	0.0070
	Termperature(10C)*Tagged(Yes)	-4.22	1.39	89	-3.03	0.0032

Figures

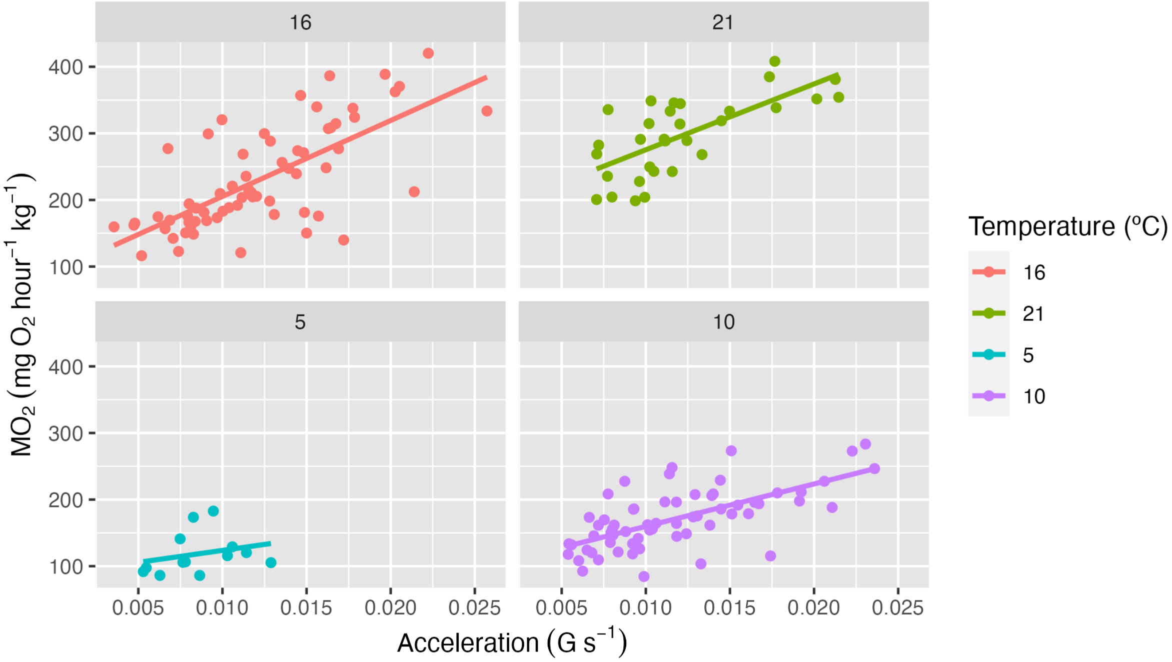

Figure 1: Relationship between oxygen consumption and acceleration at different temperatures ($R^2 = 0.83$)

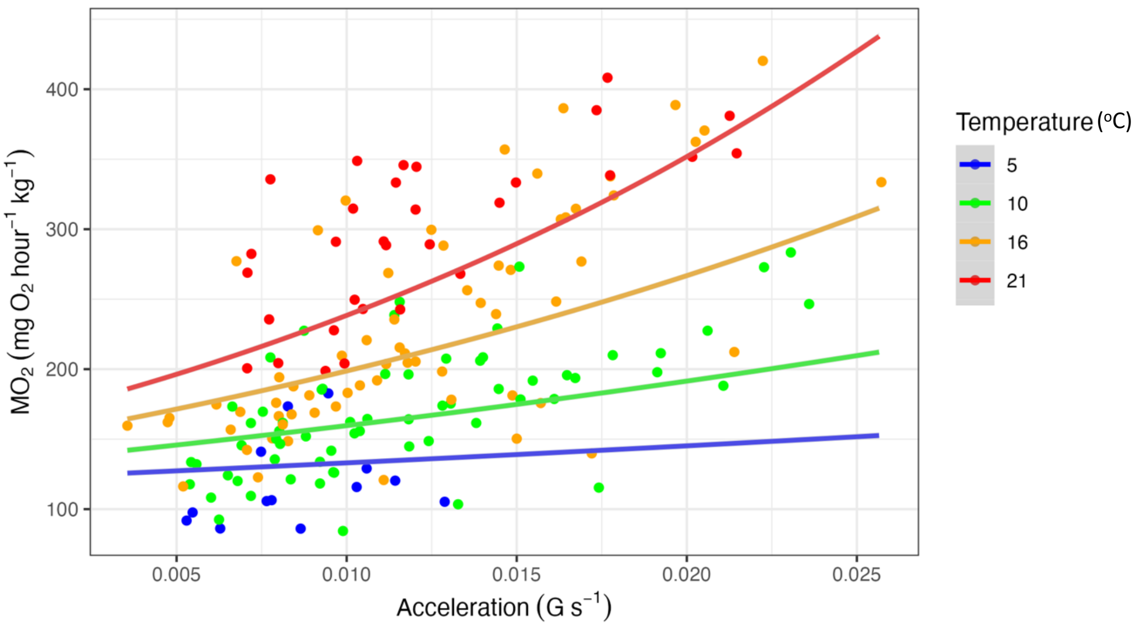

Figure 2: Relationship between acceleration, oxygen consumption, and temperature in adult walleye. Solid lines represent predicted oxygen consumption rates based on relative acceleration values at four different temperatures ($R^2 = 0.83$).

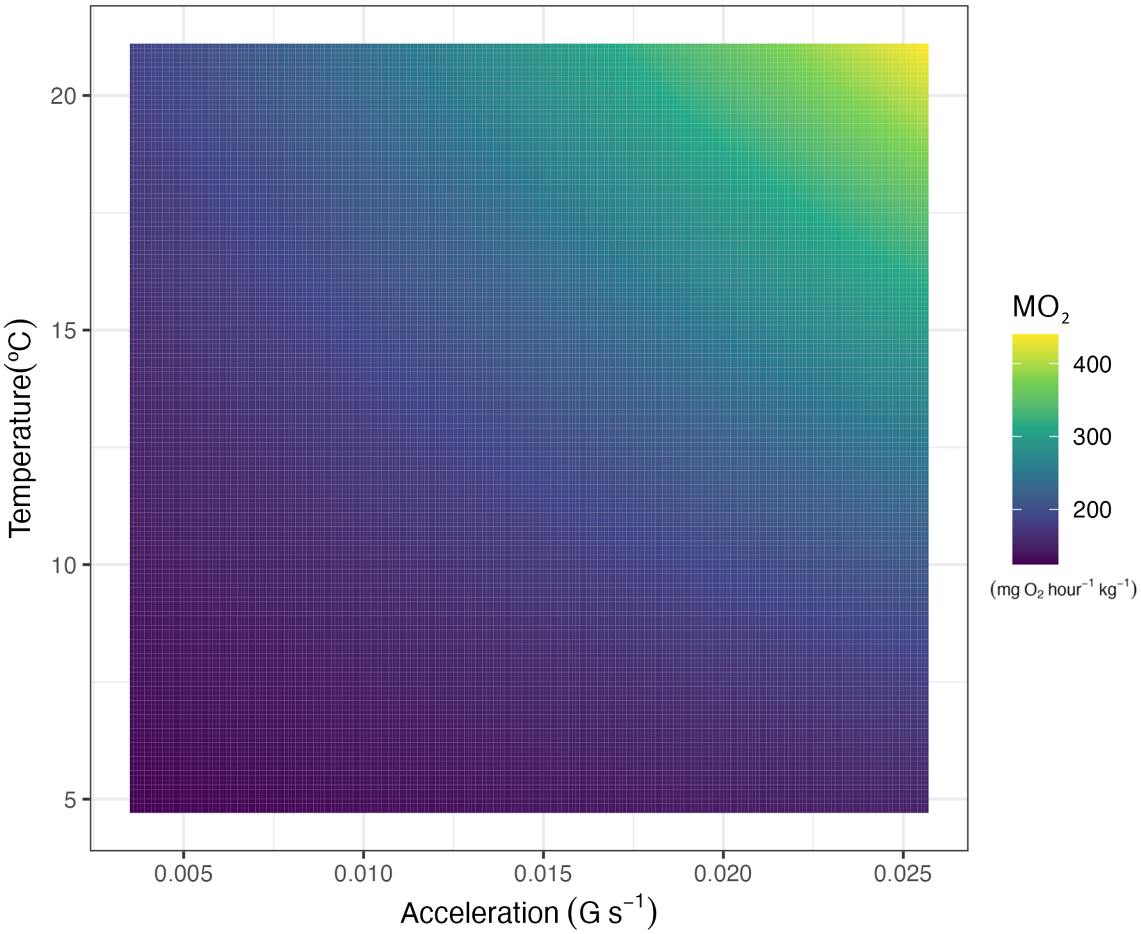

Figure 3: Heatmap illustrating the predicted relationship between oxygen consumption and the interaction between acceleration and temperature.

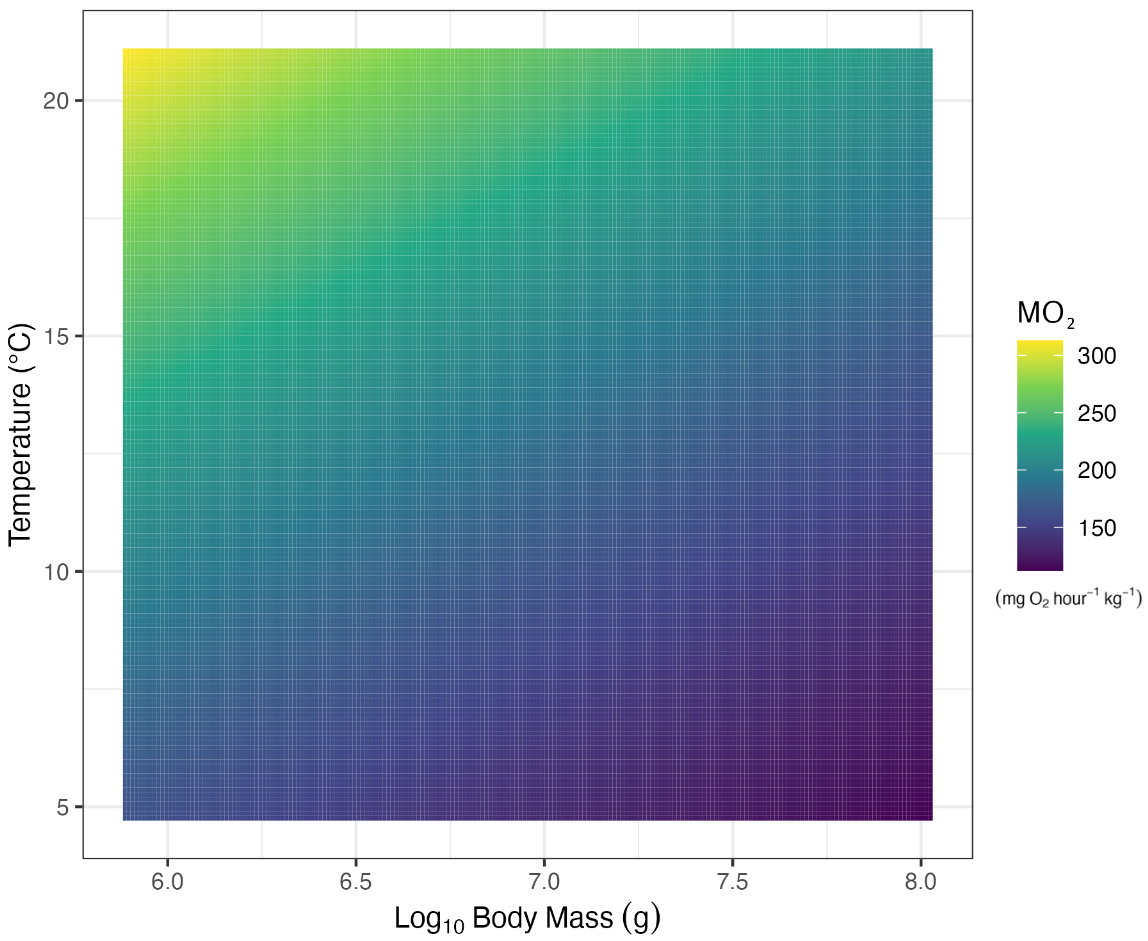

Figure 4: Heatmap illustrating the predicted relationship between oxygen consumption at given temperature and body mass

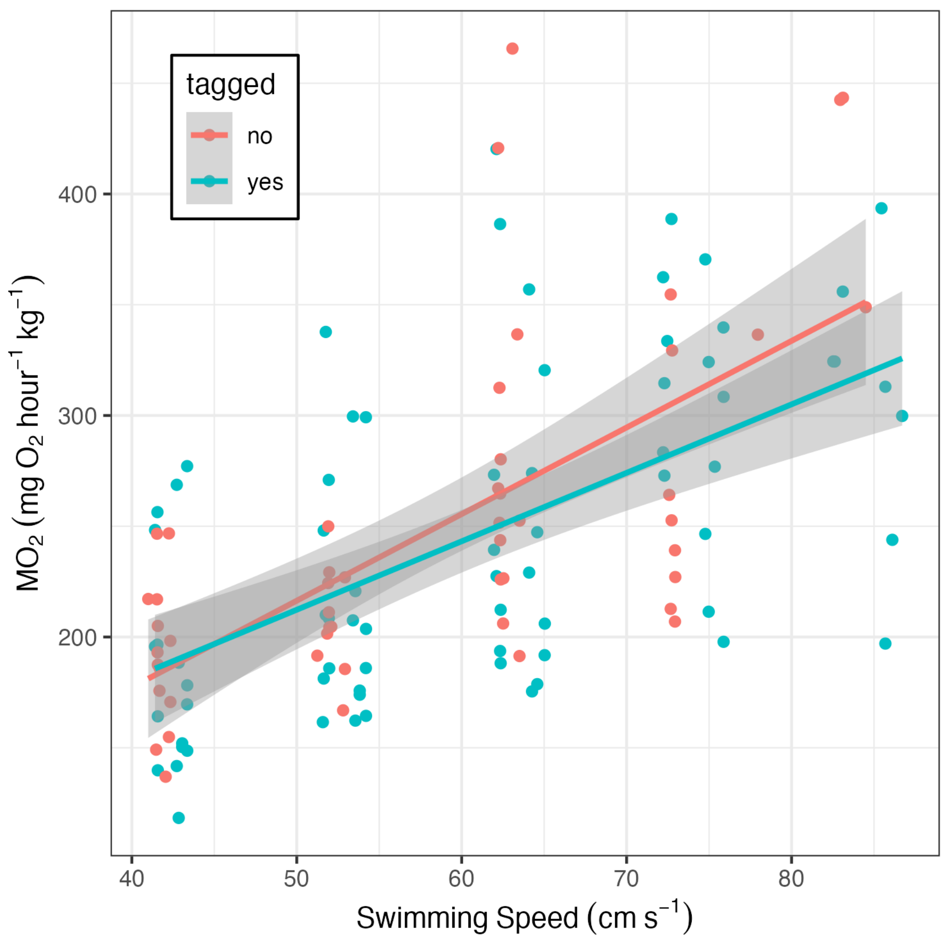

Figure 5: Relationship between swim speed and oxygen consumption for control (untagged) hatchery fish and tagged (V13A) hatchery fish ($R^2 = 0.50$).

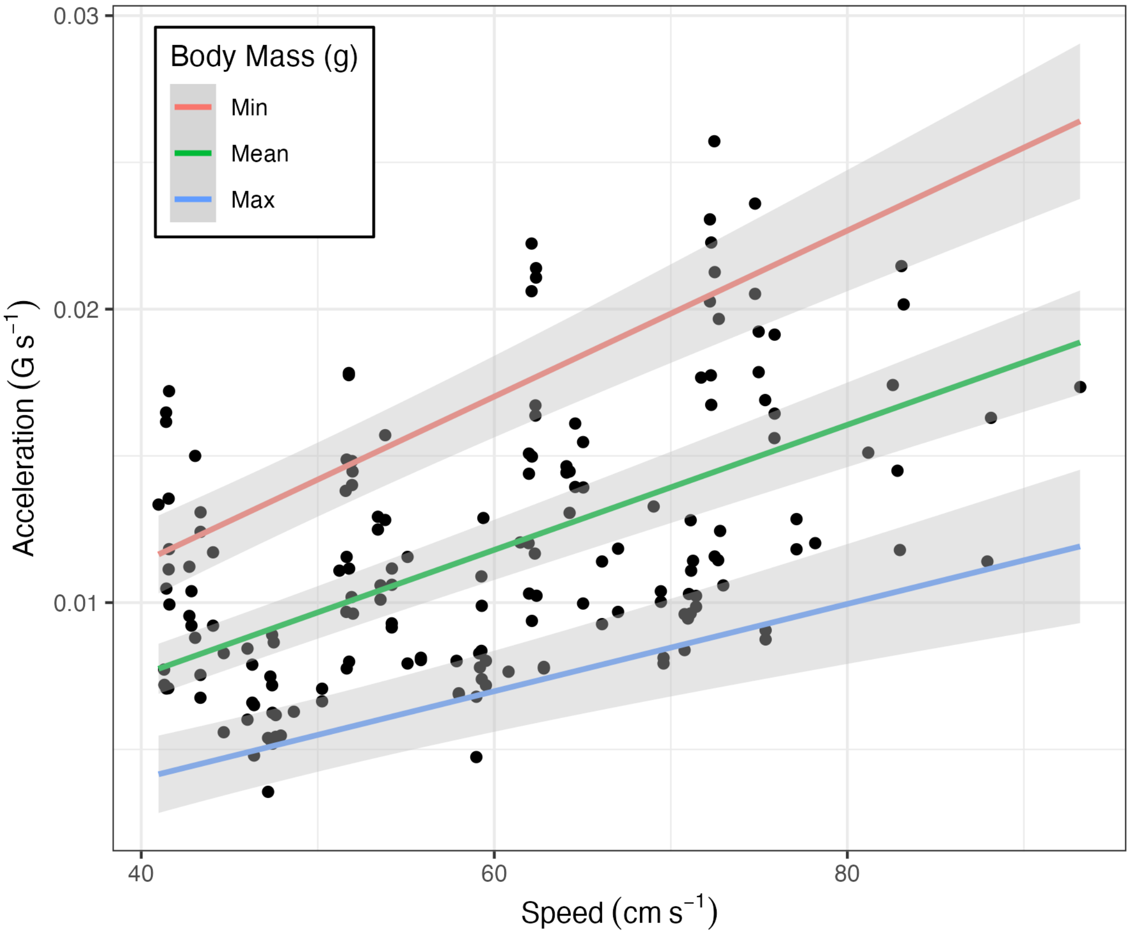

Figure 6: Relationship between swim speed and acceleration in adult walleye. Solid lines represent the predicted acceleration values relative to swim speed at mean, minimum, and maximum body mass classes (R^2 = 0.82).

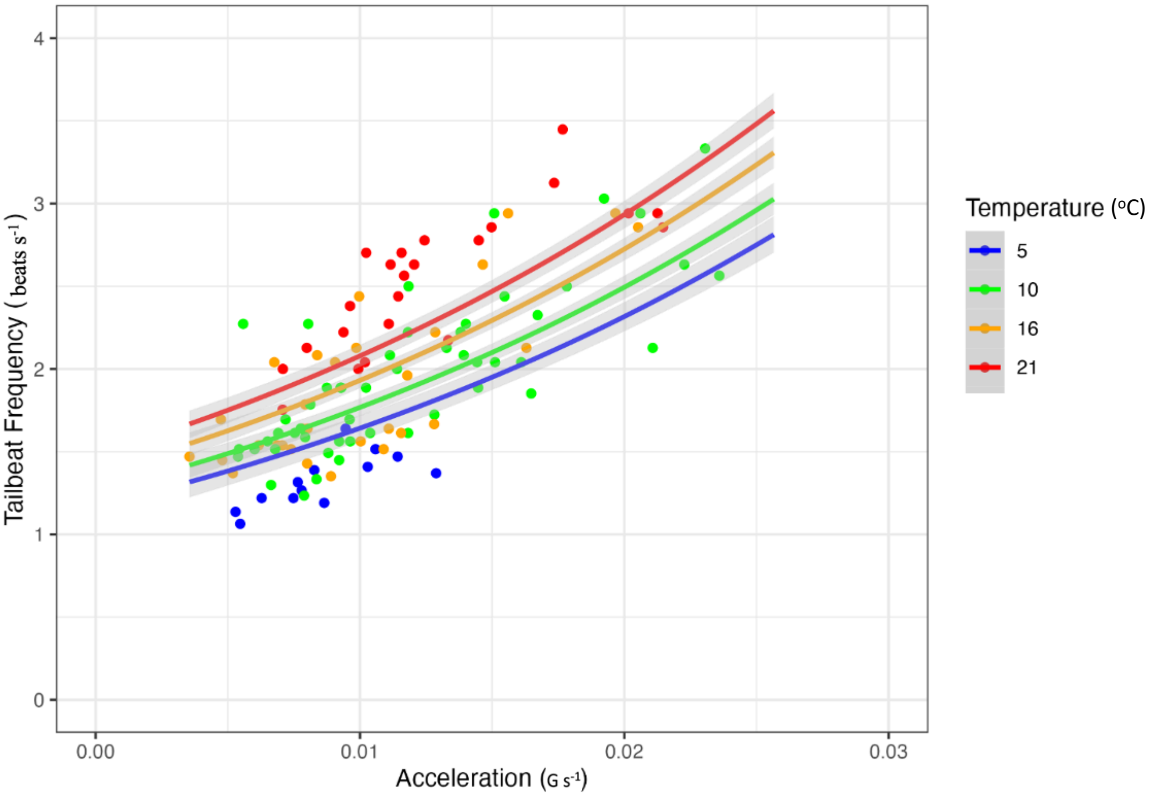

Figure 7: Relationship between acceleration and tail beat frequency in adult walleye. Solid lines represent the predicted tail beats per second relative to acceleration at four different temperatures ($R^2 = 0.86$)

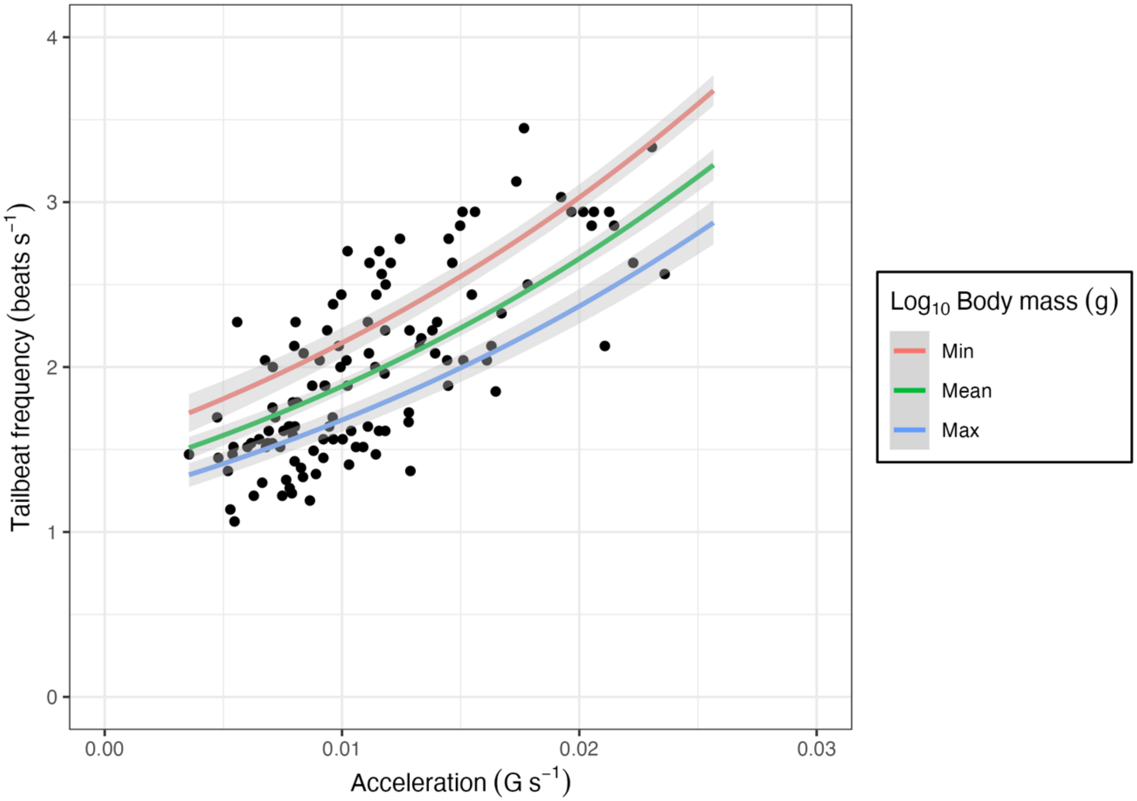

Figure 8: Relationship between tail beat frequency and acceleration in adult walleye. Solid lines represent the predicted tail beats per second relative to acceleration at mean, minimum, and maximum body mass classes (R^2 = 0.86)

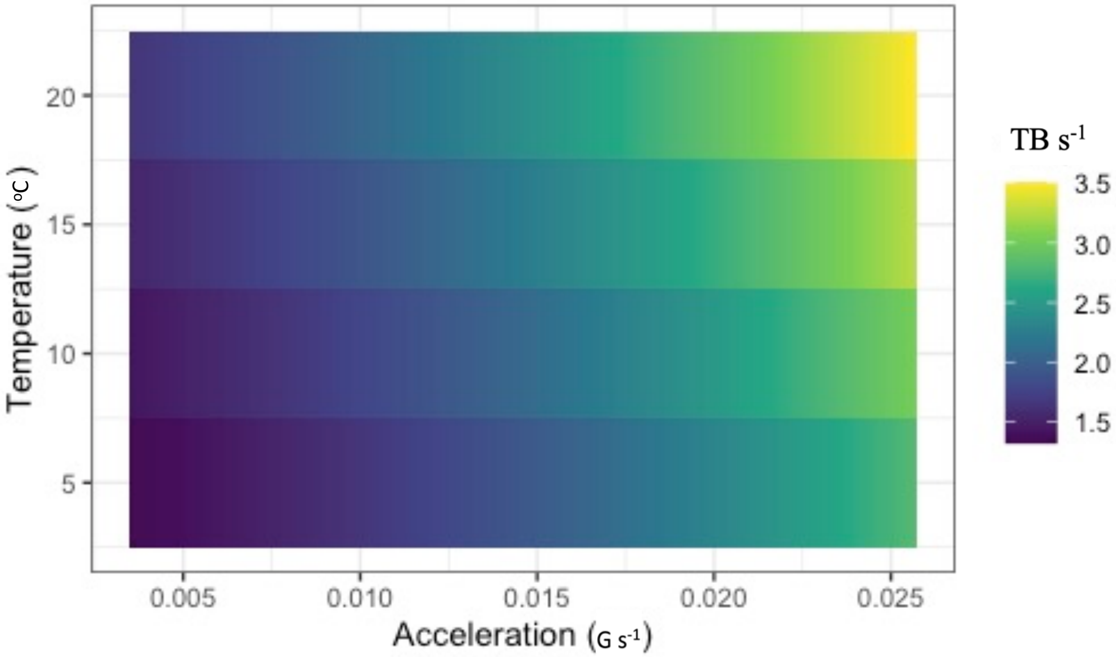

Figure 9: Heatmap of relationship between predicted tail beats per second at given temperatures and acceleration values in adult walleye

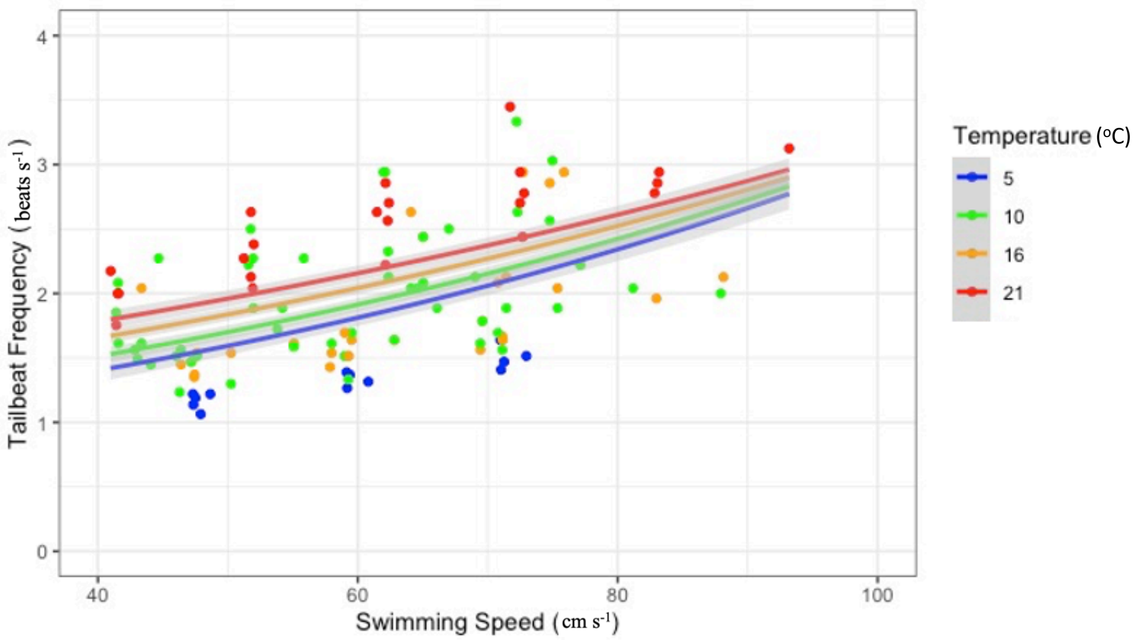

Figure 10: Relationship between swim speed and tail beat frequency in adult walleye. Solid lines represent the predicted tail beats per second relative to swim speed at different temperatures ($R^2 = 0.94$)

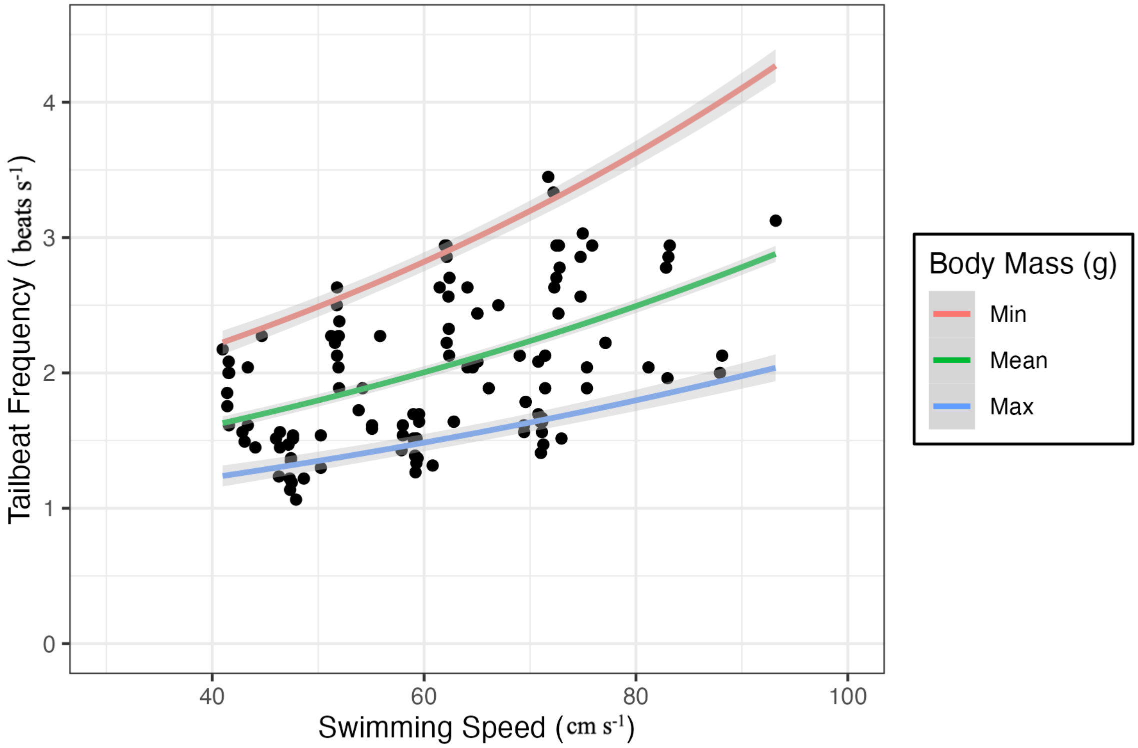

Figure 11: Relationship between swim speed and tail beat frequency in adult walleye. Solid lines represent the predicted tail beats per second relative to swim speed at mean, minimum, and maximum body mass classes (R2 = 0.94).

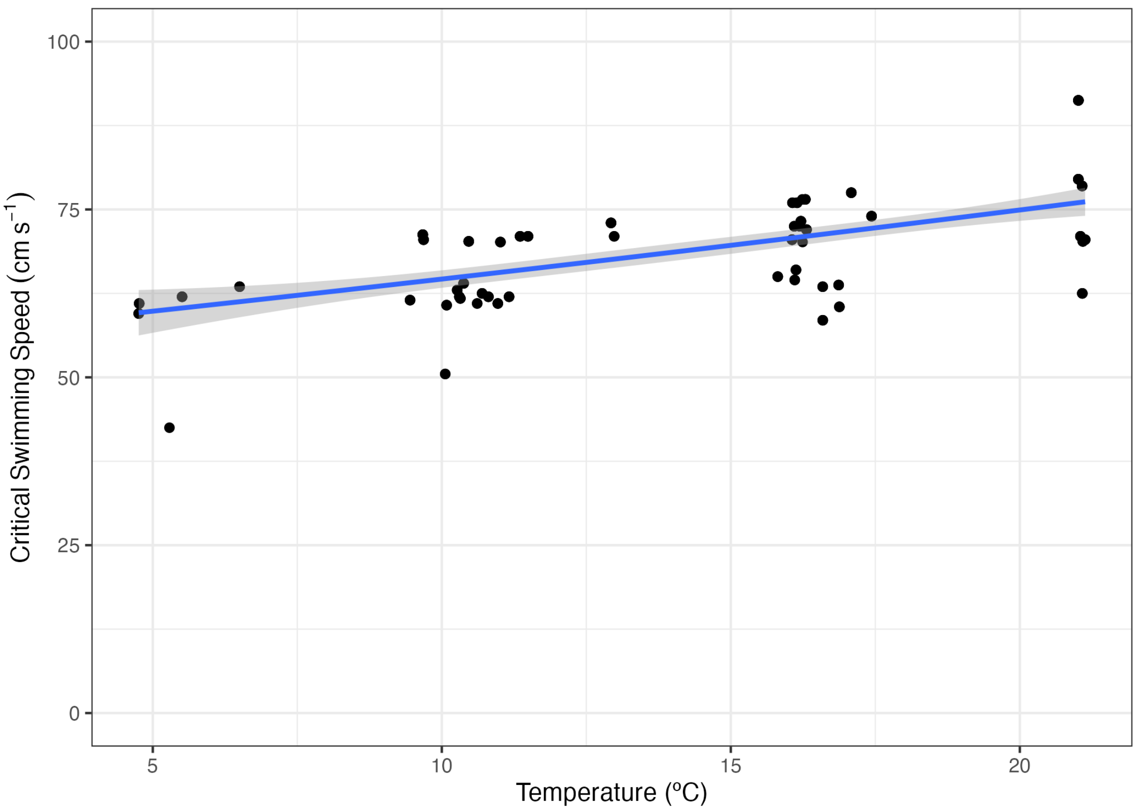

Figure 12: Relationship between predicted U_{crit} *values and temperature in adult walleye (*$R^2 = 0.82$*).*

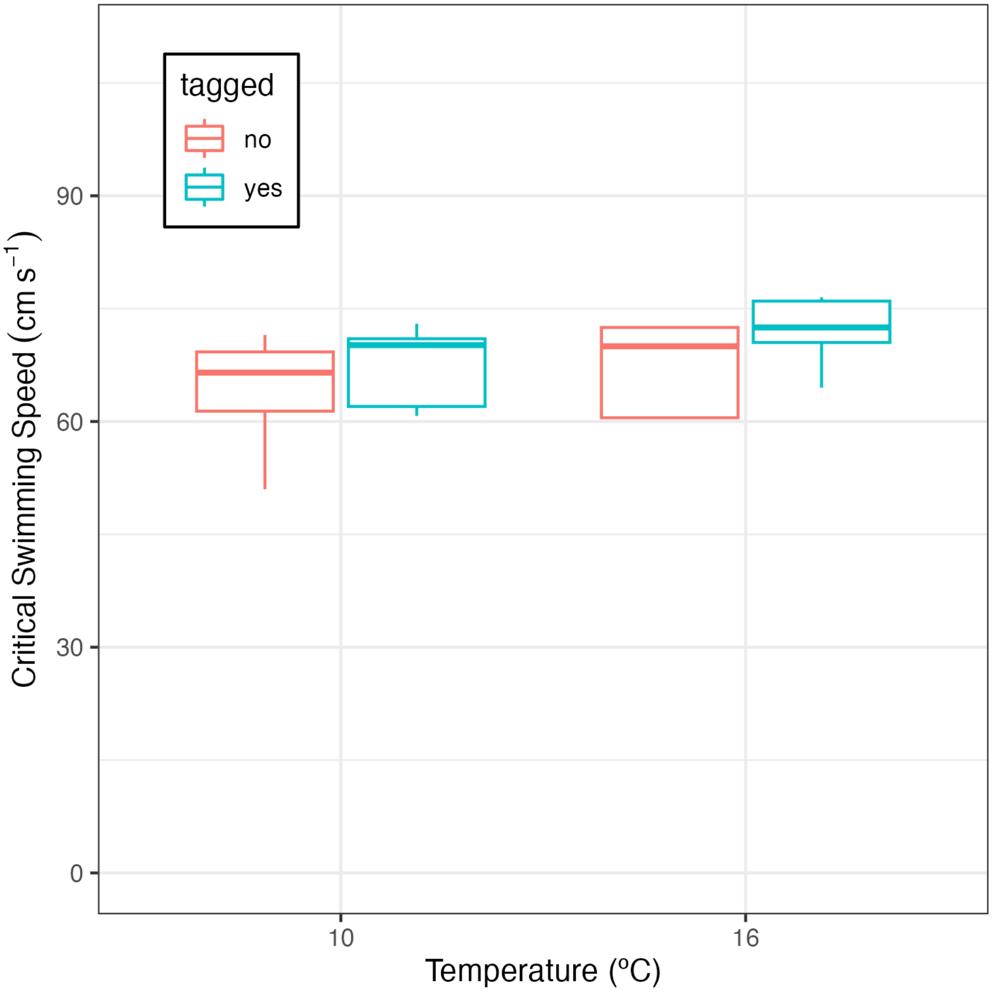

Figure 13: Relationship between critical swimming speed and temperature between tagged and untagged adult hatchery walleye (R^2 = 0.85).

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Appendix

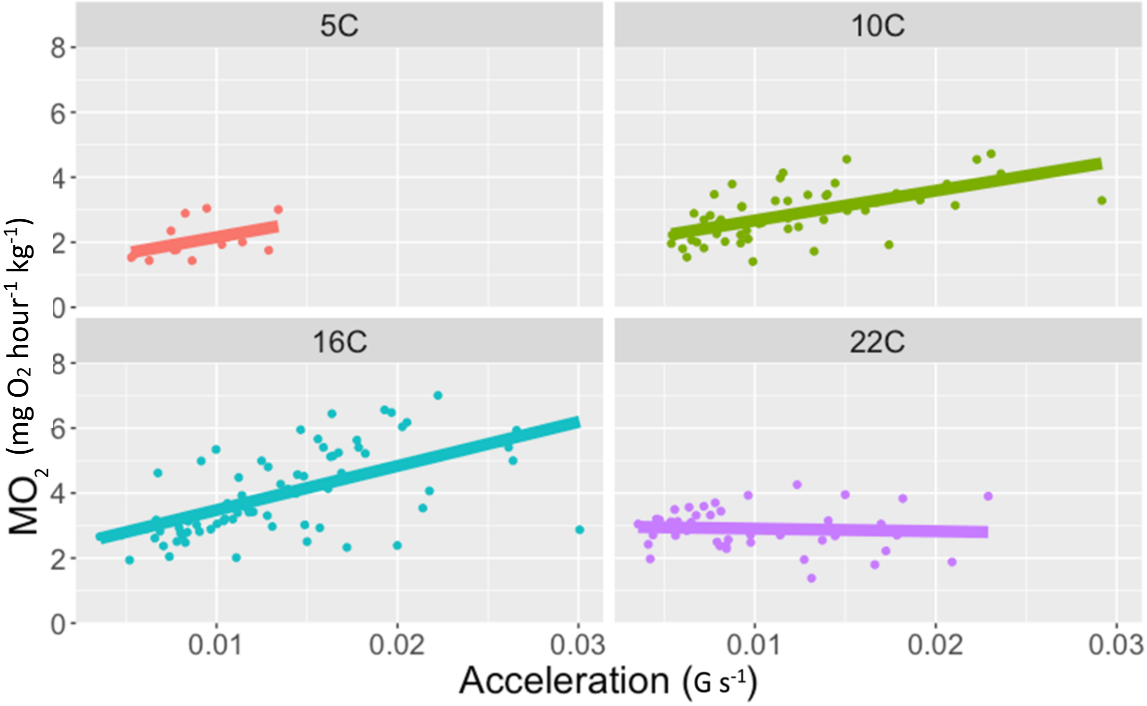

Figure A1: Relationship between acceleration and oxygen consumption that include the original 22°C trials excluded from our results.