

How lipid content and temperature affect American shad (*Alosa sapidissima*) attempt rate and sprint swimming: implications for overcoming migration barriers

Shannon M. Bayse, Stephen D. McCormick, and Theodore Castro-Santos

Abstract: How seasonal effects such as temperature increases and reduced lipid content affect the ability of anadromous fishes to traverse high-velocity barriers and sprint swimming is poorly understood. We evaluated American shad (*Alosa sapidissima*) swimming performance in a flume against high flow velocities (2.5–3.7 m·s⁻¹) during the upstream migration period (April–May; temperatures 11.1–21.4 °C) to determine how their willingness to enter a velocity barrier (attempt rate) and their swimming endurance changed during migration. American shad did not make attempts at low temperatures, and attempt rate gradually increased throughout the migration as temperatures warmed. American shad displayed two distinct, nonsustained swimming modes (prolonged and sprint swimming), and endurance was different between sexes. At warmer temperatures, females swam at prolonged speeds more often and longer females displayed a lower endurance. Males primarily swam at sprint speeds and were affected by swimming speed, fork length, and lipid content. Our results indicate that American shad motivation and swimming endurance change over the course of the migration as conditions change, potentially limiting their ability to pass barriers.

Résumé : L'incidence d'effets saisonniers, comme l'augmentation de la température et la baisse du contenu lipidique, sur la capacité de poissons anadromes de franchir des obstacles de haute vitesse et sur leur vitesse de nage de pointe n'est pas bien comprise. Nous évaluons la performance de nage de l'aloise savoureuse (*Alosa sapidissima*) dans un canal jaugeur contre des vitesses d'écoulement élevées (2,5–3,7 m·s⁻¹) durant la période de montaison (avril–mai; températures de 11,1 °C à 21,4 °C), afin de déterminer l'évolution de leur volonté d'entrer dans un obstacle de haute vitesse (fréquence des tentatives) et de leur endurance de nage durant la migration. Les aloses savoureuses ne faisaient pas de tentative à faible température, et la fréquence des tentatives augmentait graduellement durant la migration au fil de l'augmentation de la température. Les aloses savoureuses présentaient deux modes de nage non soutenue distincts (prolongé et de pointe), et l'endurance n'était pas la même pour les deux sexes. Les femelles nageaient en mode prolongé plus souvent à température plus élevée et, à température élevée, les femelles plus longues avaient une moins bonne endurance. Les mâles nageaient principalement à des vitesses de pointe et leur nage était influencée par la vitesse de nage, la longueur et le contenu lipidique. Nos résultats indiquent que la motivation et l'endurance de nage des aloses savoureuses évoluent durant la migration au fil du changement des conditions, ce qui pourrait limiter leur capacité de franchir des obstacles. [Traduit par la Rédaction]

Introduction

Fishways exist to provide river connectivity and facilitate fish passage beyond barriers. In rivers with dams, passage via fishways is essential to provide fishes access to spawning, nursery, and feeding grounds. However, fishways may also act as a velocity barrier that approaches, or exceeds, the behavioral and physiological limits of the species they intend to pass (Haro et al. 2004). Many factors can affect the efficiency of fish passage through a fishway, including temperature, discharge, flow velocity, and swimming endurance (Castro-Santos 2004).

Typically, fishways are designed to pass specific species under current site conditions; however, passage efficiency is likely to change as temperature and flow regimes vary seasonally or are altered by climate change (Kemp et al. 2011) or anthropogenic thermal inputs (Webb 1996). Additionally, climate change is expected to alter precipitation rates (Trenberth 2011), and these shifts, either higher or lower, can affect fishway discharge, which

can in turn influence passage efficiency (Ovidio and Philippart 2002). Increases in temperature and changes in flow may affect a fish's endurance to traverse fishways, which can dramatically alter current passage efficiencies.

With few exceptions, fishes are obligate poikilotherms that cannot produce enough metabolic heat to compensate for rapid heat loss through the gills and epidermis (Fry 1968). This is contrary to the regulated homeostatic state that fishes can achieve with other environmental factors such as salinity, oxygen, and pH (Brett 1971). Temperature has a strong impact on all enzymatic reactions, and environmental temperature therefore has a profound effect on crucial fish physiological processes, including growth, energetics, and swimming (Brett 1971).

The effect of temperature on fish swimming capacity is well documented for nonsprint swimming speeds. At sustained swimming speeds, speeds that can be maintained for >200 min (Beamish 1978), fishes rely on aerobic processes to power their swimming. The influence of temperature on sustained swimming

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is directly related to oxygen consumption (Brett 1965), and at sustained swimming speeds, metabolic rate generally increases with higher temperatures until an optimum is reached, beyond which temperature negatively affects metabolic rate (Fry 1947; Beamish 1978). Prolonged-swimming speeds are thought to generally range from 20 s to 200 min (Beamish 1978) and rely on a combination of aerobic and anaerobic processes (Bilinski 1974), which can induce fatigue. Similar to metabolic rate during sustained swimming, prolonged-swimming capacity increases with temperature to an optimum level, beyond which temperature negatively affects swimming performance (Beamish 1978).

How temperature affects sprint swimming is less clear. Sprint swimming is a high-rate, steady mode of swimming that leads to fatigue, typically in less than 20 s (Beamish 1978; Webb 1975). Sprint swimming relies almost exclusively on anaerobic metabolism, which is sustained by glycogen, adenosine triphosphate, and phosphocreatine stored in white muscle (Milligan 1996), and is thought to be largely independent of temperature (Brett 1971), although few studies have investigated this relationship.

The sprint-swimming capacity of fishes has historically been studied in relatively short swimming chambers (Brett 1964; Videler 1993; Peake et al. 1997). Recent studies in large-scale flumes that allow fish to swim against greater flows, and with more volition, have found higher swim speeds, indicating that small swim chambers may limit detection of maximum sprint-swimming ability (Haro et al. 2004; Peake and Farrell 2006; Castro-Santos et al. 2013). For example, Castro-Santos et al. (2013) observed brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) swimming at speeds > 25 body lengths (BL)·s⁻¹, which was much higher than found in previous studies (<12 BL·s⁻¹; Bainbridge 1960; Peake et al. 1997). Additionally, previous studies in small fish chambers found no correlation between temperature and sprint swimming for performance or recovery (Brett 1964; Schreer et al. 2001), but very few studies have used large flumes and volitional swimming to investigate the impacts of temperature or other environmental factors.

Temperature can play a large role in the ability or willingness of important species to pass through fishways. The role of temperature in limiting fish passage is important to understand from a management perspective to improve current passage efficiency and to be prepared for potential changes as temperatures increase via climate change. Few studies have directly examined how temperature affects the willingness and ability of a fish to pass a velocity barrier (a zone where fishes must swim at unsustainable speeds to pass upstream; Castro-Santos et al. 2013). Castro-Santos (2004) quantified how several covariates, including temperature, affect the attempt rate of white sucker (*Catostomus commersonii*) and walleye (*Sander vitreus*) against a velocity barrier with water velocities of 1.5–4.5 m·s⁻¹ through an open-channel flume. This study found that increasing temperatures increased the attempt rate for both species. Haro et al. (2004) included temperature when investigating the sprint-swimming performance of several fish species. These authors found a positive correlation between temperature and maximum distance traversed while sprint swimming for both blueback herring (*Alosa aestivalis*) and walleye and a negative correlation for American shad (*Alosa sapidissima*).

American shad present an interesting species to investigate how temperature can affect the attempt rate and swimming endurance of a diadromous fish and the subsequent implications for fish passage. American shad is a numerous, anadromous species on the east coast of North America and a commercially and ecologically important species throughout its range (Greene et al. 2009). The species is distributed from Florida (USA) to Newfoundland (Canada), and individuals across that range may experience wide seasonal and geographical variations in temperature. For example, American shad in the Connecticut River (USA) experience a large change in temperature over the course of their spawning migration, from approximately <5 °C at the beginning stages in

April to >25 °C at the end stages in late July (Castro-Santos and Letcher 2010), and have been shown to be sensitive to rising temperatures for both swimming endurance (Haro et al. 2004) and passage delays (Castro-Santos and Letcher 2010).

Coupled with the seasonal increase in temperature is a gradual reduction in fish lipid content. American shad do not feed during the freshwater portion of their migration, which can be greater than 228 km in the Connecticut River. In fresh water, lipid stores are gradually reduced below 0.5% of their total somatic content (Bayse et al. 2018), and total energetic depletion can range from 35% to 60% over the course of the migration (Leonard and McCormick 1999). The level of lipid reserves may influence both motivation and swimming endurance and likely changes over the course of the migration as temperatures rise and lipid resources become reduced.

Seasonally, increased temperatures and reduced lipid content could potentially decrease the passage ability of American shad. This would likely increase passage delay length, further exposing American shad to deleterious temperatures and using up energetic resources, all of which could amplify current passage difficulties. We investigated the effects that seasonal temperature increases (natural, not manipulated) and loss of lipid content have on motivating American shad to pass fishways and how these factors affect American shad sprint-swimming endurance over the course of their spawning migration.

Materials and methods

Flume

Swimming performance was measured in a flume at the S.O. Conte Anadromous Fish Research Laboratory (US Geological Survey (USGS)) in Turners Falls, Massachusetts, USA (Fig. 1). The flume was similar to the one used in previous studies (Haro et al. 2004; Castro-Santos et al. 2013; Duguay et al. 2019). It was 35 m long, 0.64 m wide, and 0.64 m deep and was set with a 1% slope. It was constructed from transparent acrylic sheeting supported within aluminum and steel framing and a downstream staging area (53 m² × 1 m deep). During trials, fish volitionally entered the flume from the low-velocity staging area.

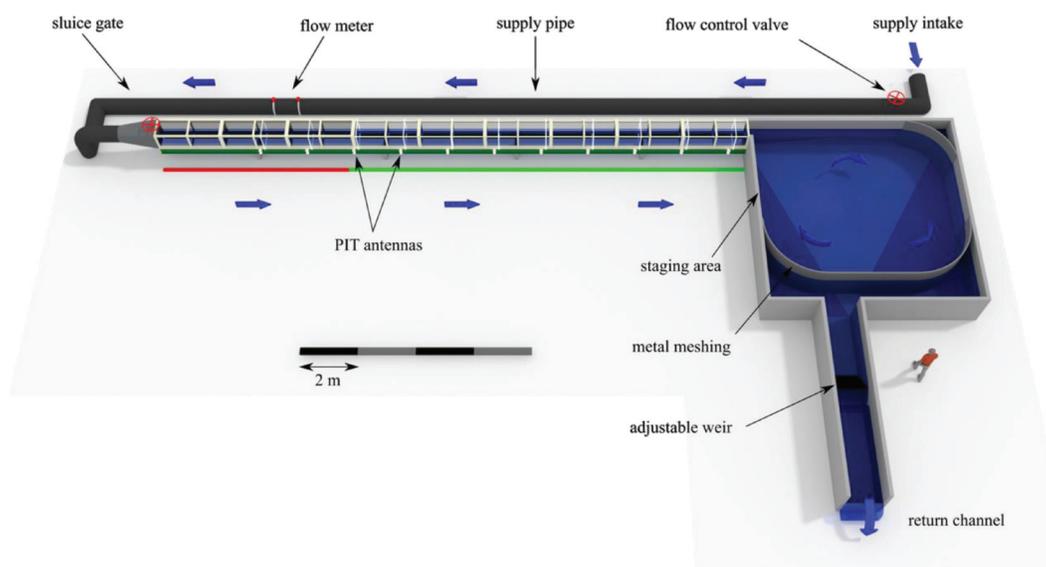
Flow to the flume was supplied by gravity and adjusted by an intake valve connected to a 76.2 cm supply pipe from the adjacent hydroelectric power canal. Flow entered the flume under an adjustable sluice gate and continued down the flume to the staging area, with a clockwise recirculatory pattern providing a low-velocity zone. Flow exited the staging area through a semicircular wall (10.4 m²) of perforated steel plate (50% open) into a channel equipped with an adjustable-height weir, which was used to regulate the water surface level in the staging area (Fig. 1).

Water depth and velocity within the flume were regulated by adjusting the valve opening, height of the sluice gate, and depth of the staging area. Flow rates were monitored using a GF Signet 2552 Magmeter (Schaffhausen, Switzerland) within the supply pipe. Water surface levels were manually measured every 1.8 m up the length of the flume for each trial. Flume water temperatures were measured at the start of each treatment using a Taylor 9841 Extended Range Thermometer (Oak Brook, Illinois, USA).

Instrumentation

Fish movements within the flume were monitored using a passive integrated transponder (PIT) telemetry system. The PIT system consisted of 16 antennas spaced every 1.8 m for the first 23.4 m of the flume and every 3.6 m for the remaining 11.6 m. Each antenna was tuned to detect tags over a 0.5 m range and interfaced to a separate half-duplex PIT reader (TIRIS Series 2000 system, Texas Instruments, Dallas, Texas, USA). Readers were configured to charge and read tags at 10 Hz and interfaced through a multiport serial-to-USB converter (Edgeport/16, Digi International, Inc., Minnetonka, Minnesota, USA) to a personal computer that recorded

Fig. 1. Experimental flume and staging area (aquatic biomechanics and kinematics station, or ABiKiS) used for sprinting performance studies. Figure is modified from Duguay et al. (2019) and is approximately to scale. PIT, passive integrated transponder. [Colour online.]



PIT identification number, antenna number, and time to the nearest 0.01 s. Further details of the PIT system can be found in Castro-Santos et al. (2013).

Fish collection

Migrating adult American shad were collected from the Connecticut River at the fish lift at Holyoke Dam (Holyoke, Massachusetts, USA; rkm 139 — the first river barrier) between 28 April and 30 May 2016. Collections were timed to be representative of the entire upstream migration season and cover the extent of the temperature regime that fish encounter while still migrating upstream. Fish collection was subject to availability and began at the start of passage at Holyoke Dam until the migration began to decline.

Collected American shad were transported to the flume via a fish transport truck (1000 L) supplied with recirculating, oxygenated Connecticut River water. Upon arrival, fish were measured for fork length and lipid content (see Lipid content section) and their sex was determined. Fish were then externally PIT tagged and released into the flume staging area. Tags were half-duplex Oregon RFID 12 mm PIT tags attached to fish hooks and were placed in the cartilage at the base of the dorsal fin (Castro-Santos et al. 1996). Drag incurred by the tags was considered negligible because of their extremely small size (0.17 g; 12 mm) relative to an adult American shad (~3 kg; 430 mm). Additionally, Castro-Santos (2002) observed no difference in swimming performance for American shad with or without tags. The gate to the flume was closed to prevent entry, and the fish were kept overnight in the staging area at a discharge rate of $0.08 \text{ m}^3 \cdot \text{s}^{-1}$.

Lipid content

Lipid content was measured for each American shad with a fat meter (Distell Model 692 Fish Fat Meter, Distell, Inc., West Lothian, Scotland, UK). The meter is a handheld device that uses microwave technology to determine lipid content. The meter actually measures water content in fish tissue and relates this to lipid content via the inverse relationship of lipid and water contents (Craig et al. 1978). Measurements followed the methods described by Bayse et al. (2018), which involved two readings directly under the dorsal fin, targeting white muscle just above the midline. Both replicate measurements were taken on the left side and totaled a duration of <10 s. The meter used the manufacturer setting “herring-1”, and the readings were adjusted with the re-

gression formula provided by Bayse et al. (2018) to be used in conjunction with American shad.

Trials

The experiment alternated between a moderate-velocity ($2.5 \text{ m} \cdot \text{s}^{-1}$) treatment and a high-velocity ($3.5 \text{ m} \cdot \text{s}^{-1}$) treatment for each trial, alternating the initial velocity on each day to prevent order effects. High velocities were chosen to focus results on factors affecting sprint swimming. Previous research has shown that American shad typically swim volitionally at sprint-swimming speeds against flow velocities $> 2.2 \text{ m} \cdot \text{s}^{-1}$ (Castro-Santos 2005). To capture a broad range of sprint speeds, we tested flow velocities from 2.5 to $3.7 \text{ m} \cdot \text{s}^{-1}$. Each trial began at approximately 0800 the morning following collection, and each treatment lasted approximately 3 h, typically with two treatments per day.

Statistical analysis

Attempt rate

Individual attempts were defined as entry past the initial gate and into the flume. These were counted and compared among treatments, and the associated attempt rate was quantified using time-to-event analysis (or survival analysis) (Allison 1995; Castro-Santos 2004). Attempt rate was measured as the “hazard”: the proportion of the available fish staging attempts at any given time (Hosmer and Lemeshow 1999). Time was included from the start of each trial until the first attempt, and the intervals elapsed between attempts. Fish that did not initiate attempts were included in the analysis as censored observations, with the trial duration substituted for event time. This allowed all available fish to contribute to the rate calculation, whether or not an attempt was staged. Additionally, for fish that staged attempts, the time elapsed between their last attempt time and the end of the trial was included as a censored observation.

How temperature, lipid content, velocity, fork length, and sex affected attempt rate was modelled using a Cox proportional hazards regression (coxme function in the coxme package (Therneau 2015) in R (R Development Core Team 2009) (Allison 1995; Castro-Santos and Perry 2012). Individual fish and trial were included as random effects on the intercept (Goerig and Castro-Santos 2017). A positive coefficient value indicated that a positive change in the covariate increased attempt rate (see Castro-Santos et al. (2013) for more details).

Table 1. Trial date, subtrial number, mean flow velocity (U_f), temperature at start of trial, and sample sizes for sprinting performance experiments.

Trial date (2016)	Subtrial No.	U_f (m·s ⁻¹)	Temperature (°C)	Number available	Number attempting	Total attempts
29 April	1	2.9	11.1	30	0	0
29 April	2	3.7	11.3	30	0	0
2 May	1	3.6	11.1	30	0	0
2 May	2	2.8	11.2	30	0	0
9 May	1	3.5	11.2	42	1	1
9 May	2	2.6	11.5	42	3	3
9 May	3	3.5	11.6	42	1	1
10 May	1	2.6	12.0	42	5	5
10 May	2	3.5	12.2	42	13	14
16 May	1	2.6	13.9	43	3	4
16 May	2	3.4	14.3	43	25	42
20 May	1	3.4	14.6	35	9	11
20 May	2	2.5	15.0	35	13	14
31 May	1	3.3	20.6	41	20	25
31 May	2	2.6	20.9	41	30	54
31 May	3	3.7	21.4	41	20	23

Note: Sample sizes include number of fish available (Number available), number of fish that made an attempt (Number attempting), and total attempts made (Total attempts).

Swimming endurance

Swimming endurance was defined as the relationship between swim speed (U_s) and fatigue time and was quantified using survival analysis (Castro-Santos 2005). For each swimming speed, swim speed–fatigue times were calculated for the attempt in which maximum distance of ascent was achieved. Any ascent that reached the upper end of the flume (considered antenna 15 for this study; 27.5 m from the flume entrance) was included as a censored observation. Regression models were fit using the survreg function in the survival package in R (Therneau 2004). Moving-point regression models were used to investigate mode shifts (Brett 1964; Castro-Santos et al. 2013). This was modelled following the moving-point regression methods of Castro-Santos et al. (2013), using the model

$$\ln(T) = \beta_0 + \beta_1 C_{ps} + \beta_2 U_s + \beta_3 C_{ps} U_s + \varepsilon$$

where fatigue time (T) is determined by an intercept term ($\beta_0 + \beta_1 C_{ps}$) and a slope term ($\beta_2 U_s + \beta_3 C_{ps} U_s$). The β terms are regression coefficients, and C_{ps} is a binary categorical variable that is 0 for observations less than an incrementing hypothetical swim-speed threshold (U_{ps}) where fish change swimming modes and 1 for observations greater than this value. Hence, two intercept values (β_0 and $\beta_0 + \beta_1$) and two slope values (β_2 and $\beta_2 + \beta_3$) were calculated, one for each side of the mode shift (if there were two modes). Separate regression models were considered for each value of U_{ps} , and the best model was selected based on the minimum Akaike's information criterion (AIC; Burnham and Anderson 2002). Each fitted model had a unique AIC value, allowing the examination of individual model variability, and the error term (ε) had a Weibull distribution (see Castro-Santos et al. (2013) for more details).

Temperature changes followed the natural increase in temperature during spring, and it was not possible to manipulate temperature because of the need for very large volumes of water in the flume. As such, the temperature-related effects we describe are also closely linked to seasonal changes over time. Originally, ordinal date (day of the year, 1–365) was investigated as an independent variable to represent the change of time over the course of the migration for both attempt rate and swimming endurance models. However, ordinal date was correlated with temperature, having a Pearson's product-moment correlation coefficient (Pearson 1948) of 0.99 (0 indicates no correlation, and –1 or 1 indicates complete correlation). Additionally, the variance

inflation factor (VIF) was >10 and rendered the slope of fit models illogically, which is common when multicollinearity is present. The VIF quantifies the severity of multicollinearity, and a value > 5 indicates a problematic amount of collinearity (James et al. 2013). Additionally, models that included ordinal date but did not include temperature had poor model fits. Best fit models that included ordinal date and excluded temperature retained several variables that were not significant ($p > 0.05$) and were illogical, which is a sign of multicollinearity. Models that included temperature and excluded ordinal date were logical, with several significant variables included. Thus, we excluded ordinal date from the analysis and retained temperature, with the understanding that temperature was a “temperature-related” effect that also had a seasonal component.

Results

Over the course of the migration, temperatures ranged from 11.1 to 21.4 °C. Five collections of American shad were made, with between 30 and 43 fish per collection, totaling 191 fish. The first two collections were performed on 28 April and 8 May 2016, and fish in these collections made zero and very few attempts to enter the flume, respectively. These fish were tested an additional day, either 48 (28 April collection) or 24 h (8 May collection) later to ensure that a long enough time had passed to generate attempts. Similar results were observed for repeated tests: both trials for the 28 April collection had zero attempts, and the 8 May collection had 5 and 19 attempts for the 9 May and 10 May trials, respectively (Table 1).

Of the fish collected, 52.1% were female and 47.9% were male. Fork length ranged from 35.2 to 50.9 cm, with females (mean \pm standard deviation (SD) = 45.2 \pm 2.4 cm) being significantly longer than males (40.2 \pm 2.6 cm) (analysis of variance (ANOVA), $F = 191.4$, degrees of freedom (df) = 1, $p < 0.001$; Table 2), which is typical for migrating American shad (Leonard and McCormick 1999). Lipid content measurements ranged from 0.6% to 9.4%, with males (mean \pm SD = 6.3% \pm 2.1%) having a significantly higher percentage of lipid content than females (4.1% \pm 2.1%) (ANOVA, $F = 40.7$, df = 1, $p < 0.001$; Table 2).

The fat meter was unavailable for the last trial date (31 May 2016); therefore, all model results (in the following sections) contain two separate model data sets: data set 1 includes all fish and all trials without lipid-content measurements, and data set 2 includes all fish and all trials except the trial and fish tested on 31 May 2016 and includes lipid-content measurements. A stipula-

Fig. 2. American shad attempt rate (attempts·individual⁻¹·day⁻¹) for each day that a trial occurred in 2016 (bars), and temperature at the beginning of each trial (solid line). Error bars indicate standard error of the mean for attempt rate on each trial day.

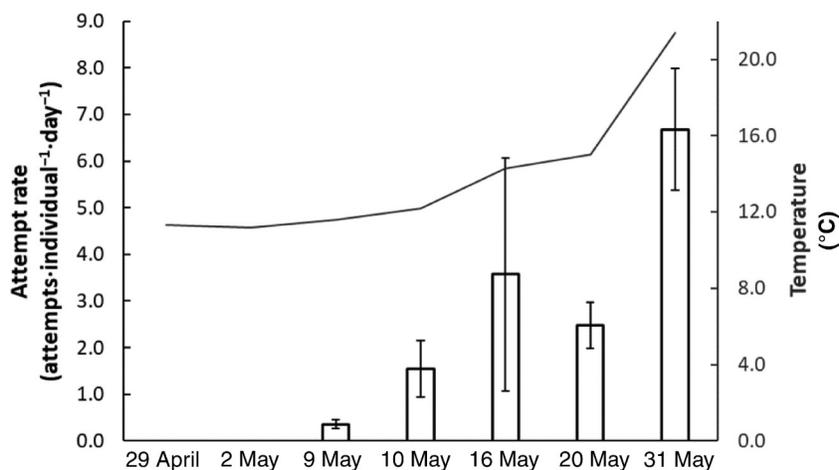


Table 2. Fork length and lipid content of American shad used in swimming studies.

Measurement	Female	Male	F value	p value
Mean length ± SD (cm)	45.2±2.4	40.2±2.6	191.4	<0.001
Mean lipid content ± SD (%)	4.1±2.1	6.3±2.1	40.7	<0.001

Note: Fork length includes all collected fish (female, $n = 100$; male, $n = 92$), and lipid content includes all fish excluding the collection from 30 May 2016 (female, $n = 72$; male, $n = 79$). p values < 0.05 are considered significant. SD, standard deviation.

tion of analyses using AIC is that models from different data sets cannot be compared.

Attempt rate

A total of 197 attempts were observed (Table 1). Several attempts ($n = 54$) had a missed reading at the first antenna due to equipment malfunction. To include these attempts in the swimming-endurance analysis, we extrapolated the time value at the first antenna with a linear model for each attempt. The time values at the next three antennas were used if they had a linear trend and extrapolated with the predict function (stats package) in R (R Development Core Team 2009). Attempts with zero slope or irregular relationships between time and distance were not extrapolated, and these attempts ($n = 13$) were removed from swimming-endurance analysis. The remaining extrapolations were reasonable: each model had a coefficient of determination (R^2) ≥ 0.99 .

American shad made more attempts as temperatures increased (Fig. 2). Attempts more than doubled as temperatures rose above 14.0 °C, with a total of 28 attempts at temperatures below 14.0 °C and 67 attempts between 14.0 and 15.0 °C (139.3% increase; Table 1). As temperatures continued to increase from 15.0 to 21.4 °C, 102 attempts were made (52.2% increase; Table 1). Attempt rate increased from 0.6 attempts·individual⁻¹·day⁻¹ at temperatures < 14.0 °C to 3.8 attempts·individual⁻¹·day⁻¹ at temperatures between 14.0 and 15.0 °C (533.3% increase; Fig. 2). As temperatures rose up to 21.4 °C, attempt rate continued to increase to 6.9 attempts·individual⁻¹·day⁻¹, which is an 81.6% increase from the attempt rate between 14.0 and 15.0 °C.

Flow velocities ranged from 2.5 to 2.9 m·s⁻¹ for the moderate-velocity condition and 3.3 to 3.7 m·s⁻¹ for the high-velocity condition (Table 1). American shad made more attempts against higher flow velocities (117 in high velocity versus 80 in moderate velocity); however, the attempt rate was 0.1 attempts·individual⁻¹·day⁻¹ for both conditions.

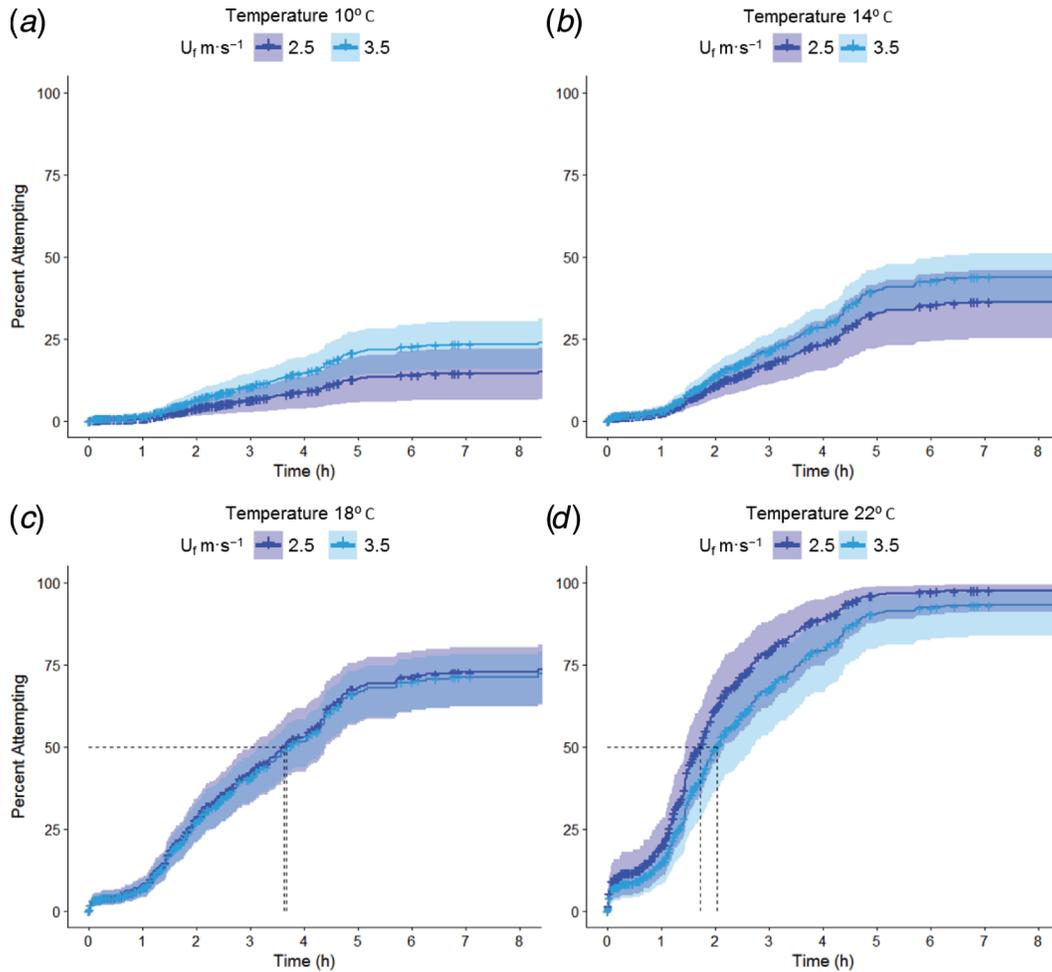
Table 3. Output of the Cox proportional hazards model of time between attempts for American shad stratified by attempt number.

Data set 1 (all attempts; $n = 197$)				
Parameter	Coefficient	SE	z value	p value
Temperature	0.937	0.230	4.080	<0.001
Velocity	2.531	0.861	2.940	0.003
Temperature × velocity	-0.148	0.047	-3.150	0.002
Random effects		Variable	SD	Variance
Individual		Intercept	0.810	0.657
Trial		Intercept	1.412	1.995
Data set 2 (attempts with lipid measurement; $n = 95$)				
Parameter	Coefficient	SE	z value	p value
Temperature	1.227	0.342	3.580	0.061
Velocity	0.519	0.277	1.870	<0.001
Lipid content	-1.799	0.830	-2.170	0.030
Length	-0.026	0.012	-2.270	0.023
Lipid content × length	0.004	0.002	2.070	0.038
Random effects		Variable	SD	Variance
Individual		Intercept	1.074	1.154
Trial		Intercept	1.112	1.237

Note: p values < 0.05 are considered significant. ×, interaction; SE, standard error; SD, standard deviation.

The best fit attempt-rate model for data set 1 (all data except lipid content) included an interaction between the temperature and velocity parameters (Table 3). This interaction term had a negative coefficient value, indicating that as one parameter increases and the other decreases, attempt rate changes. To visualize this relationship, the model was plotted with the survfit function from the survival package in R (Therneau 2004). This function is unable to plot models with random effects; therefore, random effects were removed to enable plotting (note that trends between the two models were consistent and aid in demonstrating model interpretation; Table 3; Fig. 3). At low temperatures (10 and 14 °C; Figs. 3a and 3b), attempt rate was higher at high flow velocity (3.5 m·s⁻¹) versus moderate flow velocity (2.5 m·s⁻¹). At 18 °C, attempt rate was about the same between flow velocities (Fig. 3c). At high temperatures (22 °C), attempt rate was higher for moderate flow velocity (Fig. 3d), which was the opposite of the lowest temperatures. Conversely, within a given flow treatment, the relative effect of temperature remained consistent, with greater rates associated with higher temperatures (Fig. 4).

Fig. 3. Percentage of American shad staging attempts as a function of time (data set 1), estimated from a Cox model, in which flow velocity (U_f) is constant and temperature increases (*a–d*). The solid lines represent the mean curves, shaded areas are the 95% confidence intervals, and the dashed lines indicate the times at which 50% of the fish had attempted to swim up the flume. [Colour online.]



The best fit model for data set 2 (includes lipid content) similarly contained temperature and velocity parameters as the main factors affecting attempt rate, but the interaction between temperature and velocity was no longer retained, and an interaction between lipid content and length was included (Table 3). This interaction term had a positive slope, indicating that as lipid content increases, longer fish have a higher attempt rate, whereas shorter fish have higher attempt rates at low lipid-content levels. The effect of the interaction between lipid content and length, even though significant ($p < 0.05$), was slight, with a slope of 0.004.

Swimming endurance

Because of differences in length and body shape between female and male American shad, swimming endurance was investigated separately for each sex. Female American shad swam at speeds from 6.2 to 12.8 BL·s⁻¹, and a moving-point regression on the relationship between swim speed and fatigue time showed a significant breakpoint (a change in slope of the relationship between swim speed and fatigue time) between the two swimming modes at 8.0 BL·s⁻¹ (Fig. 5; Table 4). Therefore, swimming speeds ≤ 8.0 BL·s⁻¹ were considered mode 1, or prolonged swimming, and speeds > 8.0 BL·s⁻¹ were considered mode 2, or sprint swimming. Males swam at speeds from 6.9 to 15.1 BL·s⁻¹ (Fig. 6; Table 5), and a moving-point regression indicated a significant breakpoint between the two modes at 9.5 BL·s⁻¹.

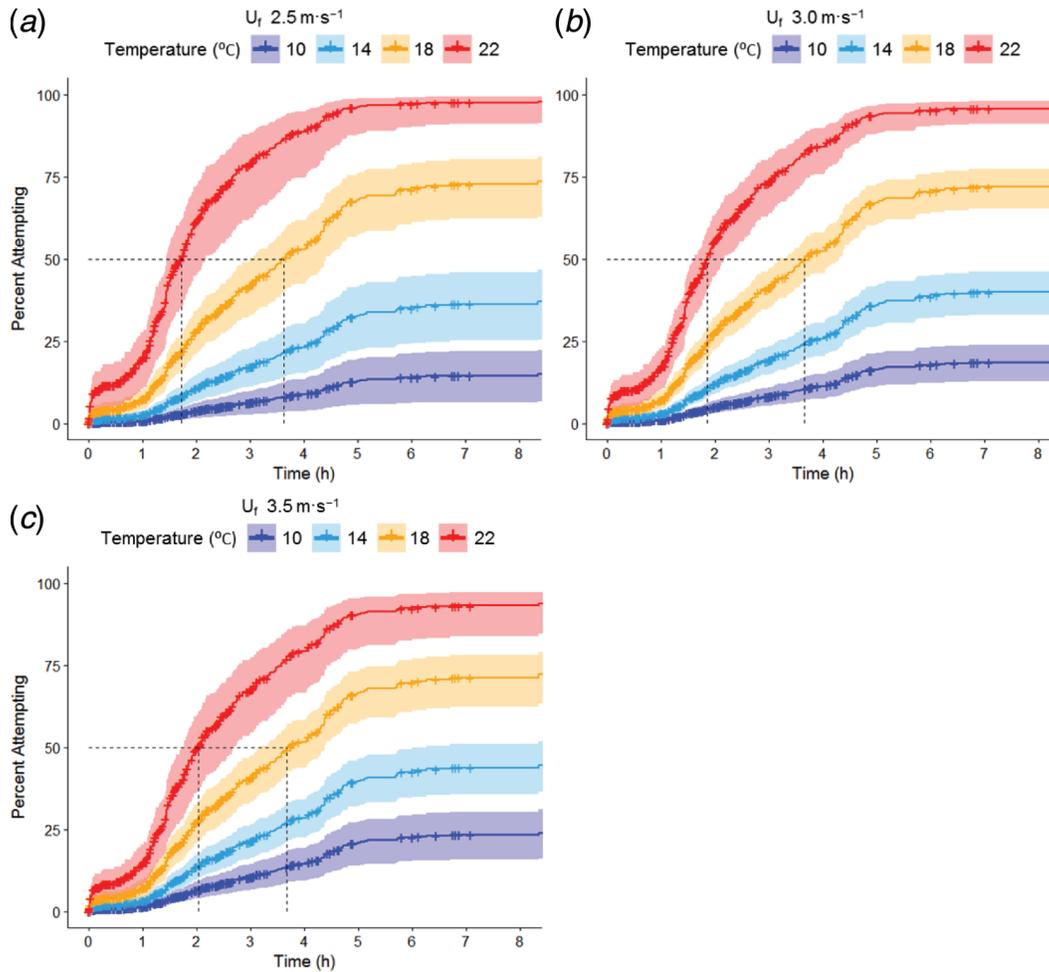
To further examine the existence and effect of a break between nonsustained swimming speeds (prolonged and sprint), the best

fit model was investigated for each sex and included both speeds, and if the break was significant, each speed was modelled separately. For data set 1, the best fit model with both swimming speeds for female American shad included significant parameters: break, swim speed, length, and an interaction between break and swim speed (Table 4). Length had a negative coefficient, indicating that smaller fish had greater endurance at a given relative swim speed. The interaction between break and swim speed had a positive coefficient, meaning that the slope of the relationship between swim speed and fatigue time was steeper for prolonged-swimming speeds than for sprint-swimming speeds (Fig. 5).

Among females, the best fit model for prolonged-swimming speeds in data set 1 included temperature, length, swim speed, and an interaction between temperature and length. Swim speed had a negative coefficient, meaning that fatigue time was greater at lower swim speeds. The interaction term had a negative coefficient and is illustrated in Fig. 5. For long fish (+1 SD of mean length), fatigue time was lower at high temperatures (20 °C) (Fig. 5, solid red line) than at cold temperatures (12 °C) (Fig. 5, solid blue line). For short fish (–1 SD of mean length), the opposite relationship was shown. At high temperatures, fatigue time was higher for short fish (Fig. 5, dashed red line), and at cold temperatures, fatigue time was lower for long fish (Fig. 5, dashed blue line).

The best model for females at sprint-swimming speeds in data set 1 included swim speed and length, both with a negative coef-

Fig. 4. Percentage of American shad staging attempts as a function of time (data set 1), estimated from a Cox model, in which temperature is constant and flow velocity (U_f) increases (a–c). The solid lines represent the mean curves, shaded areas are the 95% confidence intervals, and the dashed lines indicate the times at which 50% of the fish had attempted to swim up the flume. [Colour online.]



efficient, indicating greater endurance at lower swim speeds and for shorter fish. The relationship of fish length to sprint-swim speed and fatigue time was illustrated in Fig. 5 for short fish (dashed black line) versus long fish (solid black line).

Only 10 observations were made at a prolonged-swimming speed for male American shad. This indicated that the tested flow velocities were appropriate to concentrate male swimming at sprint speeds. Consequently, we did not further model prolonged swimming for males. The best fit model for sprint swimming for data set 1 included swim speed and length, both with negative coefficients (Table 5). Figure 6 shows the relationship between swim speed and fatigue time for sprint swimming, with short fish (dashed black line) having a higher swim speed and fatigue time relationship than long fish (solid black line).

For data set 2, prolonged-swimming attempts for female American shad dropped to only six observations that also had a lipid content measurement, and data set 2 was not further analyzed. Sprint swimming was investigated for both female and male attempts. For females, only swim speed was included in the best fit model, with a negative slope indicating that the relationship between swim speed and fatigue time decreased as swimming speed increased. The male model included swim speed and length with almost the same slope as without lipid content (data set 1); however, lipid was included in this model, with a positive slope indicating that endurance increased with higher lipid content (Table 5).

Discussion

Few studies have investigated the impacts of temperature or lipid content on American shad swimming endurance, and to our knowledge, no studies have addressed how both factors influence swimming endurance for any fish. Leonard et al. (1999) swam American shad in a respirometer at two temperatures, and a higher standard metabolic rate and swim speed (sustained swimming speeds) were observed in the high-temperature group. Castro-Santos (2002, 2005) and Haro et al. (2004) tested American shad sprint swimming in a flume similar to the one in this study and observed a negative correlation with temperature, distance traversed, and passage performance. Male American shad actually traversed greater distances at higher temperatures on their first attempt, whereas females travelled shorter distances (Castro-Santos 2002).

Several studies have addressed how adult salmon (Salmonidae) migrations will be affected by changing temperatures and energy content (Rand and Hinch 1998; Young et al. 2006; Hanson et al. 2008; Lennox et al. 2018). These studies considered performance over the entire migration period, focusing on migration speed, successful passage, and bioenergetic models; they differed from our design, which focused on sprint-swimming performance in a controlled flume. Generally, these studies found that fish size, swimming activity, and temperature greatly influenced energy demand, spawning success, mortality, and rates of iteroparity.

Fig. 5. Relationship between swim speed and fatigue time for female American shad (data set 1). The vertical dashed line indicates the location of a breakpoint between mode 1 (left) and mode 2 (right) swimming speeds. Triangles indicate fatigue, and circles indicate censored observations. Modelled relationships are demonstrated for mode 1: long fish (+1 standard deviation (SD) fork length) at cold temperatures (12 °C) (solid blue line), long fish at hot temperatures (20 °C) (solid red line), short fish (–1 SD fork length) at cold temperatures (dashed blue line), and short fish at hot temperatures (dashed red line). Models for mode 2 include short fish (dashed black line) and long fish (solid black line). BL, body length. [Colour online.]

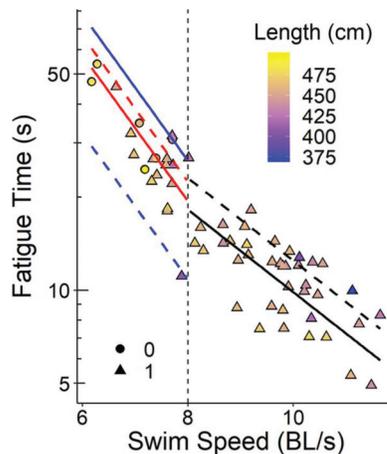


Table 4. Relationship between swim speed (U_s , $m \cdot s^{-1}$) and fatigue time ($\ln(T)$) for female American shad.

Parameter	Coefficient	SE	z value	p value
Mode 1 and mode 2 (n = 59)				
Intercept	11.016	1.371	8.034	<0.001
Break	-3.228	0.989	-3.264	0.001
U_s	-0.716	0.128	-5.586	<0.001
Length	-0.005	0.002	-3.272	0.001
Break $\times U_s$	0.409	0.130	3.149	<0.002
Mode 1 (n = 20)				
Intercept	-18.326	5.871	-3.122	0.002
Temperature	1.361	0.271	5.027	<0.001
Length	0.056	0.012	4.628	<0.001
U_s	-0.544	0.133	-4.095	<0.001
Temperature \times length	-0.003	0.001	-4.897	<0.001
Mode 2 (n = 39)				
Intercept	7.915	0.992	7.979	<0.001
U_s	-0.308	0.034	-8.967	<0.001
Length	-0.005	0.002	-2.842	0.004
Mode 2 with lipid (n = 22)				
Intercept	4.656	0.534	8.712	<0.001
U_s	-0.220	0.054	-4.087	<0.001

Note: Mode 1 represents prolonged swimming, and mode 2 represents sprint swimming. p values < 0.05 are considered significant. \times , interaction; SE, standard error.

When compared with this study, similar results were found in relation to fish size, with smaller animals performing better at warmer temperatures (temperature-size rule; Kingsolver and Huey 2008). Increased temperature was shown to increase energetic costs, but energetic cost was more sensitive to fish size and swimming speed (Lennox et al. 2018). Hanson et al. (2008) observed a negative correlation between migration speed and high energetic status in the ocean and a positive correlation between migration speed and temperature once in the river. Additionally, Young et al. (2006) found that low energetic content led to higher mortality for early-run sockeye salmon (*Oncorhynchus nerka*). Simi-

Fig. 6. Relationship between swim speed and fatigue time for male American shad at mode 2 swimming speeds (data set 1). Triangles indicate fatigue observations. Modelled relationships are demonstrated as short fish (–1 standard deviation (SD)) (dashed black line) and long fish (+1 SD) (solid black line). BL, body length. [Colour online.]

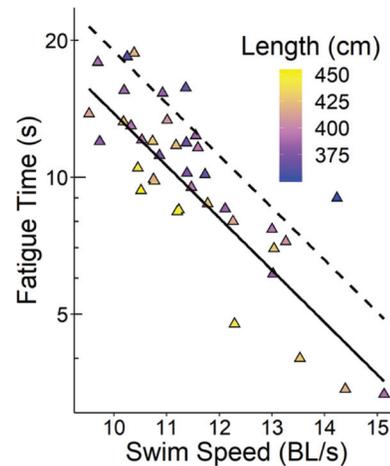


Table 5. Relationship between swim speed (U_s , $m \cdot s^{-1}$) and fatigue time ($\ln(T)$) for male American shad.

Parameter	Coefficient	SE	z value	p value
Mode 2 (n = 39)				
Intercept	7.797	0.653	11.943	<0.001
U_s	-0.264	0.025	-10.768	<0.001
Length	-0.006	0.001	-5.057	<0.001
Mode 2 with lipid (n = 29)				
Intercept	7.462	0.741	10.075	<0.001
U_s	-0.269	0.028	-9.532	<0.001
Length	-0.006	0.001	-4.455	<0.001
Lipid	0.038	0.014	2.754	0.006

Note: Mode 2 represents sprint swimming. p values < 0.05 are considered significant. SE, standard error.

lar conditions of increased temperatures and lower lipid content could similarly affect American shad migrations, increasing mortality and reducing spawning success and iteroparity, as suggested in a simulation model for American shad in the Connecticut River (Castro-Santos and Letcher 2010).

Lipid content and fork length were different for female and male American shad, which potentially affected motivation and endurance. In the Connecticut River, large fish expend 2%–21% more energy (mostly lipid) during migration compared with smaller fish (Leonard and McCormick 1999), and lipid and length together affected attempt rate in this study. Sex was not included in any attempt rate final model, but length perhaps slightly masked a sex effect, as females were longer. Additionally, migration to upriver spawning areas was considered to be 50%–100% more energetically expensive for females (Leonard and McCormick 1999), and increased temperatures (or longer periods of exposure to high temperatures) will further increase the metabolic rate of American shad. Each of these factors could prove more challenging to large females that have the combination of decreased relative swimming capacity and increased depletion of lipid reserves in higher temperatures. During prolonged-swimming attempts, higher temperatures decreased the swimming endurance of longer females, indicating that temperature negatively affects their performance. Unfortunately, not enough prolonged-swimming attempts had an associated lipid-content measurement, as low lipid content of these fish may have played a role in their decreased capacity. If an increased amount of work is required to pass barriers (additional failed

attempts) due to reduced endurance during prolonged swimming, a further reduction in available lipid is likely to ensue.

Our results are informative to management for determining how temperature changes affect American shad passage at fishways and other zones of high-velocity flow, which is an increasing concern with the realities of climate change affecting temperature and water flows (Silva et al. 2018). Other anthropogenic increases in temperature, including those caused by surface runoff, reservoir heating, and discharge from power plants, further exacerbate these effects and may be both more acute and greater in magnitude than climate-driven changes (Webb 1996; Mustard et al. 1999). Both direct and indirect anthropogenic effects, as well as natural climate cycling, can be expected to affect both motivation and ability of American shad to pass barriers.

American shad commonly experience migration delays, which can be up to 1 week or more at individual fishways (Sullivan 2004; Castro-Santos and Letcher 2010) and can be affected, at least partially, by temperature. Fish were collected for this study in a fish lift at a dam 139 km from the river mouth. These fish were motivated to migrate from the ocean and upriver, but were unwilling to enter the experimental flume (velocity barrier) until temperatures reached 14 °C, above which attempt rates increased several fold, with individual fish making multiple attempts. These results imply that at temperatures < 14 °C, American shad in the Connecticut River are clearly motivated to migrate to spawning grounds but are behaviorally and perhaps physiologically limited from passing high-flow regions. A constructed velocity barrier such as a dam could directly limit early-season migration range, which would in turn reduce spawning success of some individuals and decrease the overall population fecundity of a spawning season. However, as temperatures increase with climate change, perhaps warmer temperatures earlier in the year will promote a higher passage motivation at this stage. It should be noted, however, that we were unable to measure the effects of high temperature (>22 °C) on motivation and endurance because it did not occur during the upstream migration but may in the future. Based on previous research on prolonged swimming in other species, it seems likely that high temperature (above an optimal) will decrease swimming capacity at prolonged-swimming speeds, either by directly limiting delivery of metabolic substrates or by reducing aerobic scope, which would increase the time of recovery required between attempts (Brett and Glass 1973). This could directly affect female American shad that preferentially swam at prolonged speeds at high temperatures. Thus, any benefits of elevated temperature early in migration may result in a trade-off if temperatures are also elevated at the end of the migratory period.

However, fatigue events resulting from prolonged-swimming speeds were low in number for male American shad and were excluded from analysis. The study design was to target flow velocities that would only produce sprint swimming, but that objective was not met for female American shad, which had a very distinct separation between swimming modes. This approach was partially successful for male American shad, with 10 fatigue events at prolonged-swimming speeds. Therefore, our results for female American shad were split, lowering the number of attempts at sprint speed and leaving an unknown effect of temperature and lipid content for male American shad at prolonged-swimming speeds.

Although the two nonsustained swimming modes described in this study included speeds greater than typically associated with prolonged speeds, it is interesting to note that the break in the relationship between swim speed and fatigue time happened at 20 s, which is identical to what Brett (1964) described as the threshold between prolonged and sprint swimming. In this way, our terminology differs somewhat from the Sprint1 and Sprint2 modes described by Castro-Santos et al. (2013), who described a break at speeds > 19 BL·s⁻¹ and endurance times < 10 s. Recognizing this, Castro-Santos et al. (2013) did not refer to their observations as prolonged speeds. In the present study, however, the

mode switch at 8.0 BL·s⁻¹ is more consistent with the literature, so the lower speeds likely correspond with what is traditionally considered prolonged speeds. This is important because prolonged swimming is generally believed to comprise both aerobic and anaerobic musculature and metabolic processes (Brett 1964; Jayne and Lauder 1994). Thus, the observed temperature effects during prolonged swimming are consistent with the expectation that temperature has a stronger effect on aerobic metabolism than anaerobic metabolism and that sprinting ability is relatively independent of temperature.

In this study, we normalized swim speeds to BL·s⁻¹, which is standard practice for numerous and well-established biomechanical and metabolic reasons (Alexander 2005). However, the approach implicitly assumes an isometric relationship of speed, which is also known to be inaccurate. Over a large range of body sizes, this imposes error caused by allometries in swimming ability that are currently poorly understood. Because of this, we found a significant effect of body length, with smaller fish having greater endurance at relative swim speeds than larger fish. These effects, however, were less than the overall greater absolute performance of larger fish. For example, a 45 cm male American shad would fatigue at 10 s when swimming at 11.3 BL·s⁻¹ (5.1 m·s⁻¹), and a 40 cm male would have the same endurance when swimming at 12.4 BL·s⁻¹ (5.0 m·s⁻¹), thus the improved endurance at relative swim speeds is not sufficient to offset the overall speed advantages afforded by greater length. It does, however, reduce the magnitude of the benefit of added size and may in part account for why some researchers have failed to detect significant length effects on swimming performance when measured in the International System of Units (SI units; Peake and Farrell 2006). Nevertheless, this study was not designed to explicitly quantify length effects, and more work is needed to improve our understanding on this important driver of swimming performance.

These results raise significant concerns regarding models of swimming performance currently used in engineering manuals and guidelines for fish passage (Beach 1984; Bell 1991; Larinier 2002), all of which assume that temperature has a strong limiting effect on sprinting ability. These data suggest that a more nuanced view is required and further emphasize the need for empirical data on sprinting ability for migratory fishes in general and temperature effects in particular.

We have shown that attempt rate was directly affected by temperature and lipid content and that swimming endurance at prolonged-swimming speeds was affected by temperature for female American shad. As temperatures increase with climate change and other anthropogenic effects, a mix of impacts can be expected for American shad. An improvement in early-season passage could be a benefit of higher temperatures (and lipid resources that are not yet extinguished), ultimately perhaps selecting for earlier migrations. Limits to swimming motivation and (or) endurance, however, could prove detrimental to American shad's ability to pass barriers, preventing access to important spawning grounds, which could reduce spawning success, spawning at upriver sites, and potentially the rate of iteroparity.

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