

Swimming performance in juvenile shortnose sturgeon (*Acipenser brevirostrum*): the influence of time interval and velocity increments on critical swimming tests

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The most utilized method to measure swimming performance of fishes has been the critical swimming speed (UCrit) test. In this test, the fish is forced to swim against an incrementally increasing flow of water until fatigue. Before the water velocity is increased, the fish swims at the water velocity for a specific, pre-arranged time interval. The magnitude of the velocity increments and the time interval for each swimming period can vary across studies making the comparison between and within species difficult. This issue has been acknowledged in the literature, however, little empirical evidence exists that tests the importance of velocity and time increments on swimming performance in fish. A practical application for fish performance is through the design of fishways that enable fish to bypass anthropogenic structures (e.g. dams) that block migration routes, which is one of the causes of world-wide decline in sturgeon populations. While fishways will improve sturgeon conservation, they need to be specifically designed to accommodate the swimming capabilities specific for sturgeons, and it is possible that current swimming methodologies have under-estimated the swimming performance of sturgeons. The present study assessed the UCrit of shortnose sturgeon using modified UCrit to determine the importance of velocity increment (5 and 10 cm s⁻¹) and time (5, 15 and 30 min) intervals on swimming performance. UCrit was found to be influenced by both time interval and water velocity. UCrit was generally lower in sturgeon when they were swum using 5 cm s⁻¹ compared with 10 cm s⁻¹ increments. Velocity increment influences the UCrit more than time interval. Overall, researchers must consider the impacts of using particular swimming criteria when designing their experiments.

Key words: *Acipenser brevirostrum*, Critical swim speed test, exercise physiology, shortnose sturgeon, swimming methodology, UCrit

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Introduction

Of the two main methods to measure swimming performance in fish, the critical swimming test (UCrit) is still the tool most widely used by researchers (Hammer, 1995; Plaut, 2001; Kieffer, 2010). In this test, the fish is forced to swim against an incrementally increasing velocity of water until fatigue occurs. The methodology of the test has been critically evaluated (e.g. Farlinger and Beamish, 1977; Beamish, 1978; Hammer, 1995; Kolok, 1999; Plaut, 2001), and the test remains a widely used and relevant methodology of evaluating the effects of various biotic and abiotic factors on fish (Plaut, 2001; Farrell, 2008; Kieffer and Cooke, 2009). A significant literature exists on species-specific UCrits in fish (e.g. Beamish, 1978; Peake, 2004a, b; McKenzie *et al.*, 2007; Kieffer and Cooke, 2009, Table 1), and a large amount of research has focused on high performance fish, such as Salmonids, and other game fish. Most research involving fish exercise physiology is invested in Salmonids mainly due to their importance as a fishery species and the impact of dams on stock populations (Brett and Glass, 1973; Williams and Brett, 1987). Salmonids have become a physiological 'model species' in the context of cardiac and exercise physiology, as they frequently swim at UCrit and thus perform at or near maximum oxygen consumption (Jain *et al.*, 1997). Recently, studies using other fish are available (see Table 1 for references), such as sturgeons, mainly due to their conservation status. However, there still is a paucity of information regarding the swimming capabilities of sturgeons, when compared to the teleosts (reviewed by Peake, 2004a).

Most sturgeon species' populations are vulnerable (listed as either threatened or endangered) to many anthropogenic impacts on the environment, including over-fishing and dams blocking migration routes (Rochard *et al.*, 1990; Williot *et al.*, 2002; Mussen *et al.*, 2014; Verhille *et al.*, 2014; Jager *et al.*, 2016). Dam construction limits spawning grounds, causing larvae to hatch in less-ideal locations (e.g. higher salinity) in the river (Cheong *et al.*, 2006). In addition, dams also cause changes in river flows and temperature which can impact water quality (Secor *et al.*, 2002; Cai *et al.*, 2015) and thus affect swimming performance. To mitigate migration issues with respect to dams, fishways are built so migrating fish can overpass the dam. However, most fishway designs are built for Salmonids, which have different body morphologies and swim performances than sturgeons (Peake *et al.*, 1997a; Wang and Guo, 2005; Zheng *et al.*, 2010; Thiem *et al.*, 2011; Cai *et al.*, 2013). In order to encourage Salmonids and Clupeid fish to swim through the passage, fishways rely on mechanisms such as bends and obstructions to alter flow regimes (Jager *et al.*, 2016), with water velocity ranging from prolonged swimming speed, to as high as burst swimming speed (Cai *et al.*, 2015). However, sturgeons prefer swimming along a constant flow, as evident by pallid sturgeon (*Scaphirynchus albus* Forbes and Richardson, 1905) preferring migration routes with the lowest, constant flows for energy optimization (McElroy *et al.*, 2012). White sturgeon (*Acipenser transmontanus* Richardson, 1836) benefitted from fishway designs that implemented flow

straighteners to provide constant flow (Jager *et al.*, 2016). Therefore, with global sturgeon populations on the decline as a result from anthropogenic influences such as dam construction, fishways need to accommodate local sturgeon populations. Recent studies have specifically focused on exercise physiology of sturgeons to provide data that might improve fishway designs (Cai *et al.*, 2013; Braaten *et al.*, 2015; Jager *et al.*, 2016; Thiem *et al.*, 2016). Many of these studies focus on burst swimming, which may not be an important aspect of sturgeon physiology, as their anaerobic capabilities appear to be less than teleosts (Kieffer *et al.*, 2001). Peake *et al.* (1997a) found that Lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817; 12–132 cm total length; T_L) are incapable of high speed or burst swimming (compared to Salmonids), as evident by fatigue graphs that do not show a slope change between prolonged and burst swim speeds. A similar trend was found in juvenile shortnose sturgeon (7.07 ± 0.38 cm T_L), as there was no statistically significant change in slope as the fish transitioned from prolonged to burst swimming speeds (42 cm s^{-1} ; 6 BL s^{-1}) during an endurance test (Deslauriers and Kieffer, 2012a). In contrast, Adams *et al.* (1999) did note a slope change for juvenile Pallid sturgeon (13–20.5 cm Fork Length; F_L) during endurance tests, however, unlike many sturgeons, they are found in fast flowing rivers (>40 cm s^{-1}). In addition, sturgeons have retained their primitive notochord, which limits locomotor power output (Long, 1995). Recently, it has been suggested that sturgeon rely on aerobic swimming (Kieffer *et al.*, 2009), however, relative to other species of fish, it has been shown that sturgeons have low critical swimming speeds (Webb, 1986; Peake *et al.*, 1995; Kieffer *et al.*, 2009; Deslauriers and Kieffer, 2012a, b; Cai *et al.*, 2013, 2015; Verhille *et al.*, 2014; May and Kieffer, 2017). While this lower swimming capacity of sturgeon is partially related to its body morphology (presence of scutes, heterocercal tail; Webb, 1986; Peake, 2004a; Kieffer *et al.*, 2009; Deslauriers and Kieffer, 2011; Qu *et al.*, 2013), it is uncertain whether the methodology used to swim sturgeon might influence UCrit values, and thus the swim performance of these animals. Specifically, many swimming tests were initially developed for Salmonids (Brett, 1964), and various modifications to the procedure have been adopted (Kolok and Sharkey, 1997; Farrell, 2008), in part because of differences in fish size (age), size of flume, and reduction of time to complete tests (i.e. minimizing experimental time). Thus, standardized protocols for UCrit tests are not often adhered to, and are likely to be species specific. In particular, the magnitude of the velocity increment and prescribed time interval for a given swimming period vary (Table 1), which has been shown to affect the UCrit (Farlinger and Beamish, 1977; Beamish, 1978), and thus can greatly influence the value of comparisons between studies. For species such as sturgeon, which are benthic species that modify their swimming behaviour substantially at different swimming speeds (Kieffer *et al.*, 2009; Deslauriers and Kieffer, 2012a; May and Kieffer, 2017), the choice of velocity and time intervals might be important factors that influence the overall UCrit performance (Verhille *et al.*, 2014). To date, this is not known for any

Table 1: The comparison of speed increment (cm s^{-1}), time interval (min) and resulting UCrit (BL s^{-1} and $\text{cm s}^{-1} \pm \text{SE}$) for various fish species

Species	T_L (cm)	n	Temperature ($^{\circ}\text{C}$)	Speed increment (cm s^{-1})	Time interval (min)	U_{crit}		Reference
						BL s^{-1}	cm s^{-1}	
Shortnose sturgeon (<i>Acipenser brevirostrum</i>)	19.4 ± 0.1	71	10–25	5	30	1.5 ± 0.1	29.5 ± 1.3	Deslauriers and Kieffer (2011)
	7.1 ± 0.1	6	15	3	20	3.2 ± 0.2	22.3 ± 0.6	Deslauriers and Kieffer (2012b)
	16 ± 0.7	8	15–16	5	30	1.8 ± 0.1	28.7 ± 1.1	May and Kieffer (2017)
	16.4 ± 0.7	8	15–16	5	30	1.7 ± 0.1	27.2 ± 2.1	
Siberian sturgeon (<i>Acipenser baerii</i>)	58.4 ± 0.6	4	24	10	10	1.8	105.5	Qu et al. (2013)
	64.3 ± 0.9	7	24	10	10	1.7	106.3	
Lake sturgeon (<i>Acipenser fulvescens</i>)	13.84 ± 0.2	24	14	5	10	28.56 ± 0.61	2.07 ± 0.05	Peake et al. (1995)
	39.32 ± 1.2	39				38.98 ± 0.88	1.02 ± 0.03	
	115 ± 4.72	3				107.67 ± 6.97	0.94 ± 0.5	
Amur sturgeon (<i>Acipenser schrenckii</i>)	18.8 ± 0.3	18	20	0.25*	30	1.96 ± 0.1	36.8 ± 1.9	Cai et al. (2013)
Chinese sturgeon (<i>Acipenser sinensis</i>)	13.7 ± 2	2	16–25	10	20	2.6 ± 0.1	36 ± 5	He et al. (2013)
	24.5 ± 2.4	2	10–25	10	20	2.3 ± 0.1	55.5 ± 2.5	
	35.3	1	10–16	10	20	2	70	
	40.5	1	10–16	10	20	2.1	85	
Pallid sturgeon (<i>Scaphirhynchus albus</i>)	21.4 ± 0.3	8	20	5	30	1.7 ⁺	35.9 ± 1.2	Adams et al. (2003)
Shovelnose sturgeon (<i>Scaphirhynchus platorynchus</i>)	57 ⁻	2	16	10	15	1.79 ± 0.2	102 ± 14	Adams et al. (1997, 2003)
	67.2 ± 1.4 ⁻	3	16	10	15	1.4 ± 0.2	90.9 ± 14.8	
	19.5 ± 0.73	6	20	5	30	1.9 ⁺	36.9 ± 3.5	
	20.9 ± 1.3	4	10			0.93 ⁺	19.5 ± 4.4	
Green sturgeon (<i>Acipenser medirostris</i>)	4.3 ± 0.2	32	18–19	5	5	8.5 ± 0.4	35.7 ± 1.7	Verhille et al. (2014)
	6.5 ± 0.2	40	18–19	5	10	7.1 ± 0.2	45.3 ± 1.5	
	15.4 ± 0.6	25	18–19	10	20	2.9 ± 0.1	43.2 ± 1.3	Allen et al. (2006)
	22.1 ± 0.4	27	18–19	10	20	2.2 ± 0.1	48.1 ± 1.3	Miller et al. (2014)
	49.4 ± 0.6	53	18–19	10	30	1.2 ± 0.5	57.5 ± 2.5	
	68.3 ± 2.7	11	19	10	20	1.2 ± 0.1	79.2 ± 4.9	Mayfield and Cech (2004)

(Continued)

Table 1: continued

Species	T_L (cm)	n	Temperature (°C)	Speed increment (cm s ⁻¹)	Time interval (min)	U_{crit}		Reference
						BL s ⁻¹	cm s ⁻¹	
White sturgeon (<i>Acipenser transmontanus</i>)	8 ± 0.4	44	18–19	5	10	4.6 ± 0.2	35.3 ± 1.4	Verhille <i>et al.</i> (2014)
	34.2 ± 1.6	14	11–12.5	5	15	1.6 ± 0.05	56.4 ⁺	Counihan and Frost (1999)
Coho salmon (<i>Oncorhynchus kisutch</i>)	61.1 ± 0.9 ⁻	12	7.6 ± 0.1	0.15*	5–20	1.61 ± 0.02	98.2 ± 1.8	Lee <i>et al.</i> (2003)
	57.7 ± 1.4 ⁻	13	8.2 ± 0.7			1.68 ± 0.05	96.5 ± 1.9	
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	31–33	9	8–10	0.5*	10	2.13 ± 0.08	68 ⁺	Gallaughier <i>et al.</i> (2001)
Sockeye salmon (<i>Oncorhynchus nerka</i>)	7.74 ± 0.06 (0.3 years)	10	15	9.1	60	6.65	51.5	Brett (1965)
	10.03 ± 0.17 (0.7 years)	9	15	9.1	60	5.94	59.8	
	12.78 ± 0.21 (0.9 years)	42	15	9.1	60	4.16	53.2	
	18.8 ± 0.8 (1.4 years)	10	15	9.1	60	4.12	77.4	
	41.8 ± 1.13 (3.4 years)	4	15	9.1	60	3	125	
	53.9 ± 0.67 (4.4 years)	14	15	9.1	60	2.65	143	
	64.2 ± 0.7 ⁻	20	18 ± 0.2	0.15*	5–20	2.08 ± 0.05	132.9 ± 1.7	Lee <i>et al.</i> (2003)
	57.9 ± 1.6 ⁻	6	13 ± 0.2	0.15*	5–20	2.36 ± 0.06	136.8 ± 3.4	
	62.4 ± 1.6 ⁻	12	15.9 ± 0.2	0.15*	5–20	1.74 ± 0.05	110.4 ± 2.7	
	64 ± 0.9 ⁻	12	12.2 ± 0.2	0.15*	5–20	1.41 ± 0.03	89.8 ± 1.7	
	16 ± 0.17	5	2	5	5	30	2.5 ± 0.13	39.98 ± 2.09
Pink salmon (<i>Oncorhynchus gorbuscha</i>)	49.3 ± 3.8	78	12–14	10–15	30	2.4 ± 0.75	118 ⁺	Williams and Brett (1987)
	46.8 ± 2.4	101	12–14	10–15	30	2.2 ± 0.87	103 ⁺	
Rainbow trout (<i>Oncorhynchus mykiss</i>)	38.9 ± 0.5	5	5.5–8	0.2*	30	1.72 ± 0.08	67 ⁺	Jain <i>et al.</i> (1997)
	42 ± 1	2	5.5–8	0.2*	30	1.5 ± 0.11	63 ⁺	
	33.3 ± 0.5	4	5.5–8	0.2*	30	2.1 ± 0.06	70 ⁺	
	10	56	6	2.5	5	4.3 ⁺	43.4	Peake <i>et al.</i> (1997b)
	10	48	18	2.5	5	5.4 ⁺	54.4	

Brown trout (<i>Salmo trutta</i>)	–	6	5	30	15	1.95 ± 0.13	–	Beaumont <i>et al.</i> (1995)
	–	6	15	30	15	1.94 ± 0.1	–	
	7.8 ± 0.2	8	–	5	20	8.3 ⁺	65.43 ± 0.54	Tudorache <i>et al.</i> (2008)
Pumpkinseed (<i>Lepomis gibbosus</i>)	12.7 ± 0.27	12	20	–	60	3.01 ± 0.27	38	Brett and Sutherland (1965)
Common carp (<i>Cyprinus carpio</i>)	4.9 ± 0.1	8	–	5	20	8.8 ⁺	43.31 ± 2.15	Tudorache <i>et al.</i> (2008)
	10.7 ± 0.2	8	–	5	20	5.8 ⁺	62.3 ± 4.15	
	22.8 ± 3.9	8	–	5	20	3.8 ⁺	87.09 ± 5.24	
Gudgeon (<i>Gobio gobio</i>)	10 ± 0.3	8	–	5	20	5.4 ⁺	54.15 ± 2.01	
	12.3 ± 0.3	8	–	5	20	4.9 ⁺	60.17 ± 1.17	
Stone loach (<i>Barbatula barbatula</i>)	7.2 ± 0.5	8	–	5	20	3.9 ⁺	28.25 ± 0.32	
Common roach (<i>Rutilus rutilus</i>)	4.6 ± 0.2	8	–	5	20	10 ⁺	45.78 ± 2.1	
	7.3 ± 0.3	8	–	5	20	8.1 ⁺	59.45 ± 1.27	
	15.7 ± 1.5	8	–	5	20	7 ⁺	110.75 ± 6.71	
Arctic char (<i>Salvelinus alpinus</i>)	35.5 ± 1.2	11	–	10	10	2.8 ⁺	100.2 ± 3	Jones <i>et al.</i> (1974)
Mountain whitefish (<i>Prosopium williamsoni</i>)	30.4 ± 1.5	9	–	10	10	1.4 ⁺	42.5 ± 6.5	
Arctic cisco (<i>Coregonus autumnalis</i>)	42.1	4	–	10	10	1.9 ⁺	80	
Emerald shiner (<i>Notropis atherinoides</i>)	6.5	4	–	10	10	9.1 ⁺	59	
Trout spp.	7.2	3	–	10	10	7.6 ⁺	55	
Goldeneye (<i>Hiodon alosoides</i>)	22.5	2	–	10	10	2.7 ⁺	60	
Least cisco (<i>Coregonus sardinella</i>)	29.5	2	–	10	10	2 ⁺	60	
Zebra fish (<i>Danio rerio</i>)	4.4 ± 2.5	21	28	4	5	15.5	56 ± 4.8	Plaut (2000)
	5.2 ± 0.38	17	28	4	5	12.5	43.7 ± 6.8	
Iberian barbel (<i>Luciobarbus comizo</i>)	15.6–50.9	60	16–21	0.75*	30	3.1 ± 0.86	81 ± 11	Mateus <i>et al.</i> (2008)
Creek chub (<i>Semotilus atromaculatus</i>)	12.2 ± 0.9	7	21	3.5	2	4.3 ⁺	53.2 ± 1.8	Tritico and Cotel (2010)
Guppy (<i>Poecilia reticulata</i>)	1.75 ± 0.05	37	27–29	2.9	3	13.7	23.7 ± 0.96	Nicoletto (1991)
	1.76 ± 0.05	22	27–29	2.9	3	12.8	22.6 ± 0.79	
	1.73 ± 0.05	27	27–29	2.9	3	12.4	21.3 ± 0.65	
Atlantic silverside (<i>Menidia menidia</i>)	6.34 ± 0.23	10	20	0.5*	2	9.7	61 ⁺	Hartwell and Otto (1991)
	6.34 ± 0.23	10	20	0.5*	5	9.5	60 ⁺	
	6.34 ± 0.23	10	20	0.5*	10	9.7	61 ⁺	

(Continued)

Table 1: continued

Species	T_L (cm)	n	Temperature (°C)	Speed increment (cm s ⁻¹)	Time interval (min)	U_{crit}		Reference
						BL s ⁻¹	cm s ⁻¹	
Winter flounder (<i>Pseudopleuronectes americanus</i>)	6.34 ± 0.23	10	20	0.5*	15	9.2	58 ⁺	Joaquim <i>et al.</i> (2004)
	6.34 ± 0.23	10	20	0.5*	20	9.5	60 ⁺	
	6.34 ± 0.23	10	20	0.5*	30	8.6	54 ⁺	
	6.34 ± 0.23	10	20	0.5*	45	8.5	53 ⁺	
	6.34 ± 0.23	10	20	0.5*	60	9.1	58 ⁺	
Scalloped hammerhead (<i>Sphyrna lewini</i>)	35.8 ± 0.6	7	4	4	15	0.65 ± 0.06	23.2 ± 2.2	Lowe (1996)
	38.8 ± 0.8	8	10			0.73 ± 0.07	28.3 ± 2.4	
	55	11	21.6–28.6	10	30	1.17 ± 0.21	65 ± 11	

Note: ‘-’ indicates that information is not provided in study. The length of the fish (T_L ; cm ± SE), sample size (n) and water temperature (°C) is also provided. An asterisk (*) represents a speed interval that increases per BL s⁻¹. A minus sign (-) represents the length of the fish in fork length. A plus sign (+) represents converted UCrit values (cm s⁻¹ to BL s⁻¹, or vice versa) by the authors of this paper.

sturgeon species, and understanding this may help improve design of fishways specifically for sturgeons.

The present study was undertaken to examine the relationship between the effects of time and velocity increments on the critical swimming speed of shortnose sturgeon (*Acipenser brevirostrum* LeSueur, 1818), and these studies complement some of our earlier research on swimming performance and behaviour in sturgeon (Kieffer *et al.*, 2009; Deslauriers and Kieffer, 2011, 2012a; Downie and Kieffer, 2017; May and Kieffer, 2017). The shortnose sturgeon is found along the eastern seaboard of North America, from Saint John River, New Brunswick (only Canadian population) down to the St. John’s River, Florida, and was listed as an endangered species in 1973 under the US Endangered Species Act (Kynard, 1997) and according to DFO (Department of Fisheries and Oceans, Canada) is a species at risk (Kynard *et al.*, 2016). Several field studies have noted the negative impacts of dams on shortnose sturgeon spawning sites in South Carolina (Cooke and Leach, 2004; Finney *et al.*, 2006), North Carolina (Moser and Ross, 1995) and Connecticut (Buckley and Kynard, 1985). While the recommendation from these studies is to construct fishways in order to improve migration over dams, field studies are limited in understanding the swim performance of these animals. The use of lab-based UCrit tests that follow a standard protocol for sturgeon may better improve the conservation strategies and construction of proper fishways for these at-risk species. It is hypothesized that UCrit values will be impacted both by swimming time and velocity increments, with the prediction that large velocity increments will lead to higher critical swimming speeds, as has been shown in a previous study by Farlinger and Beamish (1977) for largemouth bass (*Microperus salmoides* Lacépède, 1802).

Methods and materials

Animal husbandry

Juvenile shortnose sturgeon were obtained from Acadian Sturgeon and Caviar, Inc. (New Brunswick, Canada; <http://www.acadian-sturgeon.com>), and housed in 208 l holding tanks (50–80 individuals per tank) which was continuously supplied with a flow-through of fresh, well aerated, dechlorinated, city water (salinity = 0 ppt; temperature = 15 ± 1°C; pH = 7) at a rate of 1 l min⁻¹. Fish were fed daily to satiation with commercial Salmonid pellets (1.5 mm optimum salmonid feed; 52% crude protein, 18% crude fat, 1.2% crude fibre; www.coreyaqua.ca) each day, but were fasted for 24 h prior to the swim trials (Deslauriers and Kieffer, 2011). A photoperiod of 14 h:10 h (day:night) was maintained throughout the holding period.

Experimental flume

The experimental flume (Aquabiotech Inc., Coaticook, Canada) measured 732 cm (length) × 50 cm (height) × 50 cm (width). The swimming test area was 155 cm length × 17 cm height of the water × 50 cm width. An acrylic flow

channel was set up ahead of the swimming area to ensure laminar flow. A mesh screen was placed at the downstream end of the flume. Flume velocity was calibrated using a FLO-MATE Marsh-McBirney portable flowmeter (Model 2000) (Deslauriers and Kieffer, 2012a, b; May and Kieffer, 2017; Downie and Kieffer, 2017). Water temperature within the flume was maintained at 15°C. Dechlorinated fresh water was used for the swim trials; after every second fish swim, approximately a third of the water was drained from the flume and replaced to replenish water oxygen levels (always >9.0 mg l⁻¹).

Swimming protocol

Fish were gently removed from the holding tank using a wet net and quickly measured under water, so they were the target length for the study (18–20 cm T_L ; total length; tip of rostrum to tip of caudal fin). A single fish was swum in the flume at a time. Fish were placed in the flume and allowed to recover from handling from their holding tank, at flow speeds of 5 cm s⁻¹ for 30 min (following methods described in Deslauriers and Kieffer, 2012a). Following this habituation period, velocity was increased in a constant stepwise progression (Brett, 1964). Time increments used were 5, 15 and 30 min; velocity increments were 5 and 10 cm s⁻¹. Eight ($n = 8$) fish were used for each set of UCrit tests. Once the swimming trial was complete, the weight of the fish was recorded and it was subsequently placed in a different holding tank, so they could not be swum more than once. Critical swimming speed (UCrit) was calculated using the following formula:

$$\text{UCrit (cm s}^{-1}\text{)} = V_f + [(T1/t) \times dv],$$

where V_f is the speed of the last completed interval (cm s⁻¹), $T1$ is the time swum at the final velocity before it fatigued (min), t is the time increment (5, 15 or 30 min) and dv is the velocity increment (5 or 10 cm s⁻¹) (Brett, 1964). UCrit is then converted to body length per second (BL s⁻¹).

Statistical analysis

Data were graphed and presented as means \pm SE. The UCrit values (BL s⁻¹) were compared between velocity increments (5 or 10 cm s⁻¹) and time increments (5, 15 or 30 min) using two-way ANOVAs ($\alpha = 0.05$). Data were log₁₀ transformed to better approximate normality and equal variance. A Tukey's post hoc test was used if significant differences were found. All statistics were performed using Sigma Stat 3.5 with $\alpha = 0.05$.

Results

There were no significant differences in mass or length in fish between treatment groups (two-way ANOVA; $P > 0.05$, for both mass and length). On average, fish were 19.2 ± 0.1 cm (SE) and 22.6 ± 0.6 g (SE) across the groups. It was also observed during the swim trials that at slower water

velocities (<15 cm s⁻¹), sturgeon spent more time in the water column. At faster speeds (>20 cm s⁻¹), sturgeon remained on the bottom of the flume (generally substrate skimming), particularly at the front of the flume. Results of a two-way ANOVA on log₁₀ transformed data indicated that critical swimming (BL s⁻¹) was affected by velocity increment ($P = 0.025$) and time interval ($P = 0.046$) (increment \times interval interaction, $P = 0.135$; Fig. 1). Overall, the UCrit was about 20% higher in fish swum using a 10 cm s⁻¹ versus 5 cm s⁻¹ increment at 15 and 30 min intervals (Fig. 1). This contrasted the situation for fish swimming at 5 min intervals, where the UCrit values were nearly identical (~ 2.3 BL s⁻¹) at both speed increments. When the velocity increment was set at 5 cm s⁻¹, critical swimming speed decreased curvilinearly with increases in time interval. In contrast, UCrit values were similar (~ 2.2 BL s⁻¹) in fish tested at 10 cm s⁻¹ regardless of the interval used.

Discussion

Farlinger and Beamish (1977) state: 'Ideally, critical performance should be measured under conditions in which fatigue is the result of swimming, not of the method applied.' Results from the current study show that both velocity increment and time interval affect UCrit values in shortnose sturgeon. In general, swimming fish at 10 cm s⁻¹ yield higher UCrit values compared with fish swimming at 5 cm s⁻¹. However, at 10 cm s⁻¹, sturgeon were able to maintain consistent critical swimming speeds regardless of the time interval used. This consistency across time intervals was not evident in fish swum at 5 cm s⁻¹ intervals, where the UCrit decreased curvilinearly with increases in time interval. The reason(s) for this finding may be related to cost of transport at different water velocities and/or

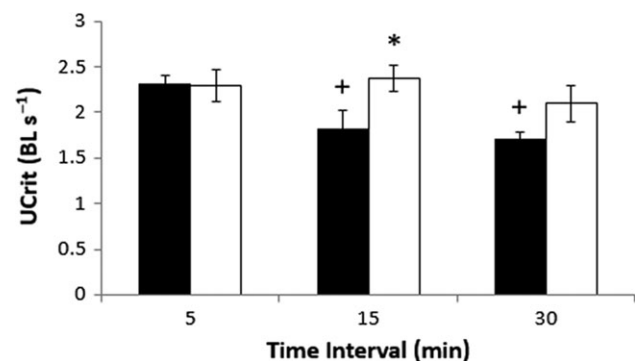


Figure 1. The critical swimming speed (UCrit) of juvenile shortnose sturgeon (*Acipenser brevirostrum*) swum at different speed (5 cm s⁻¹; black bars and 10 cm s⁻¹; open bars) and time intervals (5, 15 and 30 min). UCrit is expressed as body lengths per second (BL s⁻¹). A plus sign (+) indicates a significant difference ($P < 0.05$) in UCrit values from the corresponding 5 min interval. An asterisk (*) indicates a significant difference ($P < 0.05$) in UCrit values between the different velocity increments at any given time interval. Values are means \pm standard error (SE).

some behavioural adjustments that might be required to swim at various speeds in sturgeon. For example, *Cai et al.* (2013) recently found that the cost of transport in juvenile Amur sturgeon (*Acipenser schrenckii* Brandt, 1869) decreased slowly with increased swimming speed, and concluded that this species of sturgeon was an efficient swimmer. Although not quantified in the present study, we noted in previous studies that sturgeon modify their behaviour when swum at various speeds during the UCrit test. *Kieffer et al.* (2009) and *May and Kieffer* (2017) specifically noted that shortnose sturgeon modify their swimming behaviour at various speeds by using a combination of behaviours such as station-holding, substrate skimming, and burst-and-glide behaviours. Some of these behavioural modifications have also been noted for other species of sturgeon (*Adams et al.*, 1997; *Chan et al.*, 1997; *Peake*, 2004a; *Hoover et al.*, 2011). To sufficiently allow a species to use specific swimming behaviours during a swimming challenge, it is essential to match swimming style with the type (e.g. flat bottom) and size of flume (*Deslauriers and Kieffer*, 2011). In the present study, the size of the flume was large relative to the fish size to allow for fish to modify their behaviour to match the swimming velocity and challenge, which may allow for weaker swimmers to swim at speeds approaching the UCrit values (as suggested by *Deslauriers and Kieffer*, 2011). Therefore, it may be possible that it takes a particular velocity (noted by *May and Kieffer*, 2017) and/or period of time for the fish to switch from one swimming behaviour to another. This is important as *Braaten et al.* (2015) noted that flow regimes in fishways built along the Yellowstone River (Western USA) vary throughout (flows are 1.2–2.4 m s⁻¹ along the ramp of the fishway and >2.4 m s⁻¹ at the crest (top) of the fishway), and thus sturgeon may or may not be able to switch swimming behaviour to cope with the change in water velocity as they swim through the passage. Coupled with this, it was noted, but not quantified, that fish swum at 5 cm s⁻¹ intervals appeared to spend more time swimming in the water column, compared to fish swimming at 10 cm s⁻¹. How time spent swimming in the water column versus closer to the bottom of the flume influences swimming performance (i.e. cost of transport between swimming in the water column vs swimming on the benthos) in sturgeon is not fully understood, but may be worthy of further study.

In general, our findings support earlier conclusions of *Farlinger and Beamish* (1977) and *Beamish* (1978) that a velocity increment of 10 cm s⁻¹ appears to be satisfactory for swimming performance studies; however, the selection of the time interval in the various publications may be reflective of the study objectives (see Table 1). As noted by *Farrell* (2008), the UCrit test can be time consuming; depending on what the endpoint UCrit is used for, a shorter or modified UCrit test might be sufficient for testing the effects of abiotic and biotic factors on swimming performance. However, if the goal of the research is to couple swimming performance with metabolic costs (i.e. oxygen consumption rates), a longer time interval

(greater than 20 min) is needed to ensure that the swimming fish is in steady state, and to provide enough time for multiple measurements of the oxygen consumption of the fish during swimming at each speed. However, this may be less relevant because of the enhanced oxygen measuring technology now available to researchers.

From a conservation perspective, consistent UCrit protocols will enable the aerobic swim performance of sturgeon to be accurately measured and be representative of the species under field conditions. While many swim experiments investigate swim speeds that fish can maintain over time, water velocity inside a fishway must be set at a speed that fish can make progress against (*Peake et al.*, 1995). *Cai et al.* (2013) mentioned the importance of accurate UCrit results in constructing the dimensions of fishway openings, flow of water through the passage and the number of resting pools. For threatened/endangered species, such as sturgeons, the proper construction of such structures will support local populations impacted by anthropogenic structures, such as dams. Shortnose sturgeon populations continue to be threatened by many factors, including the construction of dams which block off ideal spawning sites that cause larvae to hatch in conditions (such as salinity or temperature), which leads to lower recruitment to the adult population (*Boreman*, 1997; *Kynard*, 1997). The construction of fishways designed for the proper swim performance of these sturgeon may enable adults to over-pass dams and return to these ideal spawning sites and prevent larvae and juveniles from growing under less-ideal conditions (e.g. temperature and salinity). For example, in Connecticut, fishways have been used successfully to allow adult shortnose sturgeon to pass over the Holyoke Dam (*Kynard*, 1998). However, *Kynard* (1998) notes that most adults enter during specific flow rates into the fishway (water flow: 200–400 m³ s⁻¹), and thus the fishways' design have to accommodate the sturgeon's swim performance, so the appropriate flow rates/water velocities are not too strong for the fish. Results from this study suggest that the opening of the fishway and the current flowing through it should not exceed the UCrit speed (2.2 BL s⁻¹) for juvenile shortnose sturgeon (18–20 cm T_L) based on the time and velocity intervals prescribed in this study.

Life stage and how swim ability changes over ontogeny are also important criteria to consider in fishway design. Juvenile green sturgeon increase UCrit from hatch until they reach a critical size when they enter seawater (*Allen et al.*, 2006). From this point onward, UCrit will either decrease or increase as the fish continues to grow, depending on season, age or thyroid hormone levels (*Allen et al.*, 2006). *He et al.* (2013) found that UCrit is higher among younger juvenile Chinese sturgeon (aged 2.5, 4.5 and 6.5 months) than older juveniles (aged 8.5, 10.5 and 12.5 months). *He et al.* (2013) hypothesized this may be because younger fish have increased muscle mass, available energy reserves and metabolic rate relative to their size early in life. *Peake et al.* (1995) investigated the UCrit of Lake sturgeon over ontogeny using three size classes (small fish: 12–22 cm, intermediate fish: 23–55 cm and large fish: 106–132 cm T_L)

and found that relative critical swimming speed is higher among the smaller fish than the larger size classes. Peake *et al.* (1995) hypothesized that small fish invest more energy into growing lengthwise than girth (muscle) and as fish grow, length growth rate decreases and larger fish develop muscle mass to reduce drag. However, critical swimming speed in larger fish decreases with length as the sturgeon cannot increase enough muscle mass to overcome drag (Peake *et al.*, 1995). While studies have investigated the impact of ontogeny on behaviour of shortnose sturgeon (Richmond and Kynard, 1995; Kynard and Horgan, 2002), changes in swim speed as fish grew were not measured. Most studies investigating the swim performance of sturgeon have focused on smaller life stages (e.g. juveniles), and thus future research should also investigate the swim performance of larger juveniles or adult sturgeons, so fishways can accommodate a wider range of sizes and developmental stages. While it has been previously difficult to assess the swim speed and metabolism of large juvenile and adult sturgeon in nature, newer technology (e.g. biotelemetry) is now available to allow for such studies to be conducted (Cooke *et al.*, 2004). This is important as Braaten *et al.* (2015) state that the current fishways in use along the Yellowstone River are designed for adult pallid sturgeon (112–164 cm T_L ; average swimming speed in nature is 0.77–1.95 m s^{-1} ; flow velocity through passage is 1.2–2.4 m s^{-1}) and not suitable for juveniles (average size of juvenile pallid sturgeon are 13–21 cm T_L ; average U_{crit} is 0.1–0.25 m s^{-1} ; average burst swimming is 0.4–0.7 m s^{-1}) (Adams *et al.*, 1999). Overall, life history stage is an important metric when evaluating swim ability and sure also be considered when constructing fishways, especially near nursery grounds.

In conclusion, these findings for shortnose sturgeon support the earlier recommendations of Farlinger and Beamish (1977) and Beamish (1978) that velocity increments should range between 5 and 10 cm s^{-1} , and time intervals between 10 and 30 min for U_{crit} tests. In a similar manner to Beamish (1978), we recommend that preliminary studies should be conducted when swimming new fish species. Once the swimming parameters have been determined for that species, researchers should adhere to them for future studies. In addition, while U_{crit} is a more representative measurement of Acipenserid swimming capabilities, the importance of burst swimming should also be further investigated to construct fishways that accommodate a range of swim speeds across ontogeny.

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References

- Adams SR, Parsons GR, Hoover JJ, Killgore KJ (1997) Observations of swimming ability in shovelnose sturgeon (*Scaphirhynchus platorhynchus*). *J Freshw Ecol* 12(4): 631–633. doi:10.1080/02705060.1997.9663578.
- Adams SR, Hoover JJ, Killgore KJ (1999) Swimming endurance of juvenile pallid sturgeon, *Scaphirhynchus albus*. *Copeia* 3:802–807.
- Adams SR, Adams GL, Parsons GR (2003) Critical swimming speed and behaviour of juvenile shovelnose sturgeon and pallid sturgeon. *Trans Am Fish Soc* 132:37–41. doi:10.1577/1548-8659(2003)1322.0.CO;2.
- Allen PJ, Hodge B, Werner I, Cech JJ Jr (2006) Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (*Acipenser medirostris*). *Can J Fish Aquat Sci* 63: 1360–1369. doi:10.1139/f06-031.
- Beamish FWH (1978) Swimming capacity. In Hoar WS, Randall DJ, eds, *Fish Physiology*, Vol 7. Academic Press, London, pp 101–187.
- Beaumont MW, Butler PJ, Taylor EW (1995) Exposure of brown trout, *Salmo trutta*, to sub-lethal copper concentrations in soft acidic water and its effect upon sustained swimming performance. *Aquat Toxicol* 33:45–63. doi:10.1016/0166-445X(95)00007-Q.
- Boreman J (1997) Sensitivity of North American sturgeons and paddlefish to fishing mortality. *Environ Biol Fish* 48(1):399–405. doi:10.1023/A:1007345806559.
- Braaten PJ, Elliott CM, Rhoten JC, Fuller DB, McElroy BJ (2015) Migrations and swimming capabilities of endangered pallid sturgeon (*Scaphirhynchus albus*) to guide passage designs in the fragmented Yellowstone River. *Restoration Ecol* 23:186–195. doi:10.1111/rec.12161.
- Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *J Fish Res Bd Can* 21:1183–1226. doi:10.1139/f64-103.
- Brett JR (1965) The relation of size to oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J Fish Res Bd Can* 22(6):1491–1501. doi:10.1139/f65-128.
- Brett JR, Glass NR (1973) Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J Fish Res Bd Can* 30:379–387. doi:10.1139/f73-068.
- Brett JR, Sutherland DB (1965) Respiratory metabolism of pumpkinseed (*Lepomis gibbosus*) in relation to swimming speed. *J Fish Res Bd Can* 22(2):405–409. doi:10.1139/f65-039.
- Buckley J, Kynard B (1985) Yearly movements of shortnose sturgeons in the Connecticut River. *Trans Am Fish Soc* 114(6):813–820. doi:10.1577/1548.8659(1985)114<813:YMOSSI>2.0.CO;2.

- Cai L, Taupier R, Johnson D, Tu Z, Liu G, Huang Y (2013) Swimming capability and swimming behaviour of juvenile *Acipenser schrenkii*. *J Exp Biol* 319A:149–155. doi:10.1002/jez.1780.
- Cai L, Johnson D, Mandal P, Gan M, Yuan X, Tu Z, Huang Y (2015) Effect of exhaustive exercise on the swimming capability and metabolism of juvenile Siberian sturgeon. *Trans Am Fish Soc* 144: 532–538. doi:10.1080/00028487.2015.1007163.
- Chan MD, Dibble ED, Killgore KJ (1997) A laboratory examination of water velocity and substrate preference by age-0 Gulf sturgeon. *Trans Am Fish Soc* 126:330–333. doi: 10.1577/1548-8659(1997)126<0330:ALEOWV>2.3.CO;2.
- Cheong TS, Kavvas ML, Anderson EK (2006) Evaluation of adult white sturgeon swimming abilities and applications to fishway design. *Environ Biol Fish* 77:197–208. doi:10.1007/s10641-006-9071-y.
- Cooke DW, Leach SD (2004) Implications of a migration impediment on shortnose sturgeon spawning. *N Am J Fish Manage* 24(2): 1460–1468. doi:10.1577/M03-141.1.
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* 19(6): 334–343.
- Counihan TD, Frost CN (1999) Influence of externally attached transmitters on the swimming performance of juvenile white sturgeon. *Trans Am Fish Soc* 128:965–970. doi:10.1577/154-8659(1999)128<0965:IOEATO>2.0.CO;2.
- Deslauriers D, Kieffer JD (2011) The influence of flume length and group size on swimming performance in shortnose sturgeon (*Acipenser brevirostrum*). *J Fish Biol* 79:1146–1155. doi:10.1111/j.1095-8649.2011.03094.x.
- Deslauriers D, Kieffer JD (2012a) Swimming performance and behaviour of young-of-the-year shortnose sturgeon (*Acipenser brevirostrum*) under fixed and increased velocity swimming tests. *Can J Zool* 90:345–351.
- Deslauriers D, Kieffer JD (2012b) The effects of temperature on swimming performance of juvenile shortnose sturgeon (*Acipenser brevirostrum*). *J Appl Ichthyol* 28:176–181. doi:10.1111/j.1439-0426.2012.01932.x.
- Downie AT, Kieffer JD (2017) A split decision: the impact of substrate type on the swimming behaviour, substrate preference and UCrit of juvenile shortnose sturgeon (*Acipenser brevirostrum*). *Environ Biol Fish* 100: 17–25. doi:10.1007/s10641-016-0548-z.
- Farlinger S, Beamish FWH (1977) Effects of time and velocity increments on the critical swimming speed of largemouth bass (*Micropterus salmoides*). *Trans Am Fish Soc* 106(5):436–439. doi:10.1577/1548-8659(1977)106<436:EOTAVI>2.0.CO;2.
- Farrell AP (2008) Comparisons of swimming performance in rainbow trout using constant acceleration and critical swimming speed tests. *J Fish Biol* 72:693–710. doi:10.1111/j.1095-8649.2007.01759.x.
- Finney ST, Isely JJ, Cooke DW (2006) Upstream migration of two pre-spawning shortnose sturgeon passed upstream of Pinopolis Dam, Cooper River, South Carolina. *Southeast Nat* 5(2):369–375. doi:10.1656/15287092(2006)5[369:UMOTPS]2.0.CO;2.
- Gallaughan PE, Thorarensen H, Kiessling A, Farrell AP (2001) Effects of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transport and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *J Exp Biol* 204:2861–2872.
- Hammer C (1995) Fatigue and exercise tests with fish. *Comp Biochem Physiol A: Physiol* 112:1–20. doi:10.1016/0300-9629(95)00060-K.
- Hartwell SI, Otto RG (1991) Critical swimming capacity of the Atlantic silverside, *Menidia menidia* L. *Estuaries* 14(2):218–221. doi:10.2307/1351696.
- He X, Lu S, Liao M, Zhu X, Zhang M, Li S, You X, Chen J (2013) Effects of age and size on critical swimming speed of juvenile Chinese sturgeon at seasonal temperatures. *J Fish Biol* 82:1047–1056. doi:10.1111/j.1095-8649.2012.12015.x.
- Hoover JJ, Collins J, Boysen KA, Katzenmeyer AW, Killgore KJ (2011) Critical swimming speeds of adult shovelnose sturgeon in rectilinear and boundary layer flow. *J Appl Ichthyol* 27:226–230. doi:10.1111/j.1439-0426.2011.01707.x.
- Jager HI, Parsley MJ, Cech JJ Jr, McLaughlin RL, Forsythe PS, Elliott RF, Pracheil BM (2016) Reconnecting fragmented sturgeon populations in North American rivers. *Fisheries* 41(3): 140–148. doi:10.1080/03632415.2015.1132705.
- Jain KE, Hamilton JC, Farrell AP (1997) Use of a ramp velocity test to measure critical swimming speed in rainbow trout (*Oncorhynchus mykiss*). *Comp Biochem Physiol A Physiol* 117(4):441–444. doi:10.1016/S0300-9629(96)00234-4.
- Joaquim N, Wagner GN, Gamperl AK (2004) Cardiac function and critical swimming speed of the winter flounder (*Pleuronectes americanus*) at two temperatures. *Comp Biochem Physiol A* 138:277–283. doi:10.1016/j.cbpa.2004.03.016.
- Jones DR, Kicenuik JW, Bamford OS (1974) Evaluation of the swimming performance of several fish species from the Mackenzie River. *J Fish Res Bd Can* 31(10):1641–1647. doi:10.1139/f74-206.
- Kieffer JD, Wakefield AM, Litvak MK (2001) Juvenile sturgeon exhibit reduced physiological responses to exercise. *J Exp Biol* 204(24): 4281–4289.
- Kieffer JD, Cooke SJ (2009) Physiology and organismal performance of centrarchids. In Cooke SJ, Philipp DP, eds, *Centrarchid Fishes: Diversity, Biology, and Conservation*. Wiley-Blackwell, West Sussex, pp 207–263.
- Kieffer JD, Arsenault LM, Litvak MK (2009) Behaviour and performance of juvenile shortnose sturgeon *Acipenser brevirostrum* at different water velocities. *J Fish Biol* 74: 674–682. doi:10.1111/j.1095-8649.2008.02139.x.
- Kieffer JD (2010) Exercise in Fish: 50+ years and going strong. *Comp Biochem Physiol A Physiol* 156:163–168. doi:10.1016/j.cbpa.2010.02.009.

- Kolok, AS 1999. Inter-individual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Can J Fish Aquat Sci* 56: 700–710. doi:10.1139/f99-026.
- Kolok AS, Sharkey D (1997) Effect of freshwater acclimation on the swimming performance and plasma osmolarity of the euryhaline Gulf killifish. *Trans Am Fish Soc* 126:866–870. doi:10.1577/1548-8659(1997)126<0866:E0FAOT>2.3.CO;2.
- Kynard B (1997) Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Environ Biol Fishes* 48: 319–334. doi:10.1023/A:1007372913578.
- Kynard B (1998) Twenty-two years of passing shortnose sturgeon in fish lifts on the Connecticut River: what has been learned? In Jungwirth M, Schmutz S, Weiss S, eds, *Fish Migration and Fish Bypasses*. Fishing News Books, London, pp 255–264.
- Kynard B, Horgan M (2002) Ontogenetic behaviour and migration of Atlantic sturgeon, *Acipenser oxyrinchus*, and shortnose sturgeon, *Acipenser brevirostrum*, with notes on social behaviour. *Environ Biol Fish* 63(2): 137–150.
- Kynard B, Bolden S, Kieffer M, Collins M, Brundage H, Hilton EJ, Litvak M, Kinnison MT, King T, Peterson D (2016) Life history and status of shortnose sturgeon (*Acipenser brevirostrum* LeSueur 1818). *J Appl Ichthyol* 32: 208–248. doi:10.1111/jai.13244.
- Lee CG, Farrell AP, Lotto A, MacNutt MJ, Hinch SG, Healey MC (2003) The effect of temperature on swimming performance and oxygen consumption in adult sockeye salmon (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J Exp Biol* 206:3239–3251. doi:10.1242/jeb.00547.
- Long JH (1995) Morphology, mechanics and locomotion: the relation between the notochord and swimming motions in sturgeon. *Environ Biol Fish* 44: 199–211.
- Lowe CG (1996) Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. *J Exp Biol* 199:2605–2610.
- Mateus CS, Quintella BR, Almeida PR (2008) The critical swimming speed of Iberian barbell *Barbus bocagei* in relation to size and sex. *J Fish Biol* 73:1783–1789. doi:10.1111/j.1095-8649.2008.02023.x.
- May L, Kieffer JD (2017) The effect of substrate type on aspects of swimming performance and behaviour in shortnose sturgeon *Acipenser brevirostrum*. *J Fish Biol* 90:185–200.
- Mayfield RB, Cech JJ Jr (2004) Temperature effects on green sturgeon bioenergetics. *Trans Am Fish Soc* 133:961–970.
- McElroy B, DeLonay A, Jacobson R (2012) Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* 93:29–34.
- McKenzie DJ, Steffensen JF, Korsmeyer K, Whiteley NM, Bronzi P, Taylor EW (2007) Swimming alters responses to hypoxia in the Adriatic sturgeon *Acipenser naccarii*. *J Fish Biol* 70:651–658. doi:10.1577/T02-144.1.
- Miller EA, Froehlich HE, Cocherell DE, Thomas MJ, Cech JJ Jr, Klimley AP, Fangue NA (2014) Effects of acoustic tagging on juvenile green sturgeon incision healing, swimming performance, and growth. *Environ Biol Fishes* 97:647–658. doi:10.1007/s10641-013-0167-x.
- Moser ML, Ross SW (1995) Habitat use and movements of shortnose and Atlantic sturgeons in the lower Cape Fear River, North Carolina. *Trans Am Fish Soc* 124(2): 225–234. doi:10.1577/1548-8659(1995)124<0225:HUAMOS>2.3.CO;2.
- Mussen TD, Cocherell D, Poletto JB, Reardon JS, Hockett Z, Ercan A, Banden H, Kavvas ML, Cechu JJ Jr, Fangue NA, et al. (2014) Unscreened water-diversion pipes pose an entrainment risk to the threatened green sturgeon, *Acipenser medirostris*. *PLoS ONE* 9(1):e86321.
- Nicoletto PF (1991) The relationship between male and female ornamentation and swimming performance in the guppy, *Poecilia reticulata*. *Behav Ecol Sociobiol* 28:365–370. doi:10.1007/BF00164386.
- Peake S, Beamish FWH, McKinley RS, Katopodis C, Scruton DA (1995) Swimming performance of lake sturgeon (*Acipenser fulvescens*). Canadian Technical Reports of Fisheries and Aquatic Sciences; Report # 2063.
- Peake S, Beamish FWH, McKinley RS, Scruton DA, Katopodis C (1997a) Relating swimming performance of lake sturgeon, *Acipenser fulvescens*, to fishway design. *Can J Aquat Sci* 54:1361–1366.
- Peake S, Barth C, McKinley RS (1997b) Effect of recovery parameters on critical swimming speed of juvenile rainbow trout (*Oncorhynchus mykiss*). *Can J Zool* 75: 1724–1727. doi:10.1139/z97-800.
- Peake S (2004a) Swimming and Respiration. In Lebreton TD, Beamish FW, McKinley RS, eds, *Sturgeons and Paddlefish of North America*. Kluwer Academic Publishers, Dordrecht, pp 147–166.
- Peake S (2004b) An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. *Trans Am Fish Soc* 133:1472–1479. doi:10.1577/T03-202.1.
- Plaut I (2000) Effects of fin size on swimming performance, swimming behaviour and routine activity of zebra fish *Danio rerio*. *J Exp Biol* 203:813–820.
- Plaut I (2001) Critical swimming speed: its ecological relevance. *Comp Biochem Physiol A: Physiol* 131:41–50. doi:10.1016/S1095-6433(01)00462-7.
- Qu Y, Duan M, Yan J, Feng G, Liu J, Zhang P (2013) Effects of lateral morphology on swimming performance in two sturgeon species. *J Appl Ichthyol* 29:310–315. doi:10.1111/jai.12131.
- Richmond AM, Kynard B (1995) Ontogenetic behaviour of shortnose sturgeon, *Acipenser brevirostrum*. *Copeia* 1: 172–182.
- Rochard E, Castelnaud G, Lepage M (1990) Sturgeons (Pisces: Acipenseridae); threats and prospects. *J Fish Biol* 37: 123–132.
- Secor DH, Anders PJ, Van Winkle W, Dixon DA (2002) Can we study sturgeons to extinction? What we do and don't know about conservation of North American sturgeons. *American Fisheries Society Symposium*. 183–189.
- Thiem JD, Binder TR, Dawson JW, Dumont P, Hatin D, Katopodis C, Zhu DZ, Cooke SJ (2011) Behaviour and passage success of

- upriver-migrating lake sturgeon *Acipenser fulvescens* in a vertical slot fishway on the Richelieu River, Quebec, Canada. *Endangered Species Res* 15:1–11.
- Thiem JD, Dawson JW, Hatin D, Danylchuk AJ, Dumont P, Gleiss AC, Wilson RP, Cooke SJ (2016) Swimming activity and energetic costs of adult lake sturgeon during fishway passage. *J Exp Biol* 219: 2534–2544. doi:10.1242/jeb.140087.
- Tritico HM, Cotel AJ (2010) The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *J Exp Biol* 213:2284–2293. doi:10.1242/jeb.041806.
- Tudorache C, Viaene P, Blust R, Vereecken H, DeBoeck G (2008) A comparison of swimming capacity and energy use in European freshwater fish species. *Ecol Freshw Fish* 17: 284–291. doi:10.1111/j.1600-0633.2007.00280.x.
- Verhille CE, Poletto JB, Cocherell DE, DeCourten B, Baird S, Cech JJ Jr, Fangue NA (2014) Larval green and white sturgeon swimming performance in relation to water-diversion flows. *Conserv Physiol* 2 (1):1–14. doi:10.1093/conphys/cou031.
- Wang X, Guo J (2005) Brief review on research and construction of fishways at home and abroad. *J China Inst Water Resour Hydropower Res* 3:222–228.
- Webb W (1986) Kinematics of lake sturgeon, *Acipenser fulvescens*, at cruising speeds. *Can J Zool* 64:2137–2141. doi:10.1139/z86-328.
- Williams IV, Brett JR (1987) Critical swimming speed of Fraser and Thompson river pink salmon (*Oncorhynchus gorbuscha*). *Can J Fish Aquat Sci* 44:348–356. doi:10.1139/f87-043.
- Williot P, Arlati G, Chebanov M, Gulyas T, Kasimov R, Kirschbaum F, Patriche N, Pavlovskaya LB, Poliakova L, Pourkazemi M, et al. (2002) Status and management of Eurasian sturgeon: an overview. *Internat Rev Hydrobiol* 87:483–506.
- Zheng J, Han D, Hu W, Wang X, Zhang X (2010) Fish swimming performance related to fishway design. *J Hydroecol* 3: 104–110.