Swimming Performance of Lake Sturgeon, Acipenser fulvescens

S. Peake, F.W.H. Beamish, R.S. McKinley, C. Katopodis, and D.A. Scruton

Department of Fisheries and Oceans Science Branch P.O. Box 5667 St. John's, Newfoundland A1C 5X1

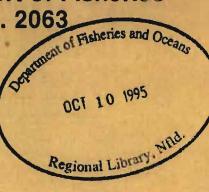
September 1995

Canadian Technical Report of Fisheries and Aquatic Sciences No. 2063



Fisheries and Oceans

Pêches et Océans



Canadä

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of the Department of Fisheries and Oceans, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in *Aquatic Sciences and Fisheries Abstracts* and indexed in the Department's annual index to scientific and technical publications.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and the Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page. Out-of-stock reports will be supplied for a fee by commercial agents.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques du ministère des Pêches et des Océans, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications complètes. Le titre exact paraît au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la revue *Résumés des sciences aquatiques et halieutiques*, et ils sont classés dans l'index annual des publications scientifiques et techniques du Ministère.

Les numéros 1 à 456 de cette série ont été publiés à titre de rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre. Les rapports épuisés seront fournis contre rétribution par des agents commerciaux.

(at # 188306

i

Can. Tech. Rep. Fish. Aquat. Sci. No. 2063

September 1995

Swimming Performance of Lake Sturgeon, Acipenser fulvescens

S. Peake¹, F.W.H. Beamish¹, R.S. McKinley², C. Katopodis³ and D.A. Scruton⁴

- ¹ Department of Zoology, University of Guelph Guelph, Ontario N1G 2W1
- Department of Biology University of Waterloo Waterloo, Ontario N2L 3G1
- ³ Department of Fisheries and Oceans Freshwater Institute
 501 University Crescent Winnipeg, Manitoba
 R 3T 2NS
- Department of Fisheries and Oceans Science Branch
 P.O. Box 5667
 St. John's, Newfoundland
 A1C 5X1

Funding for this study was provided by the U.S. Department of the Interior, Fish and Wildlife Service, Fort Snelling, MN and the Wisconsin Department of Natural Resources. ©Minister of Supply and Services Canada 1995 Cat. No. Fs 97-6/2063E ISSN 0706-6457

Correct citation for this report is:

S. Peake, F.W.H. Beamish, R.S. McKinley, C. Katopodis and D.A. Scruton. 1995. Swimming Performance of Lake Sturgeon, *Acipenser fulvescens*. Can. Tech. Rep. Fish. Aquat. Sci. 2063, iv + 26 pp.

Table of Contents

C

đ

1

| Abstract ii |
|---|
| Introduction |
| Materials and Methods 2 |
| Results |
| Discussion |
| Practical Application of the Model Describing Endurance of Lake Sturgeon 12 |
| Acknowledgements |
| References |
| Tables |
| Figures |

Abstract

S. Peake, F.W.H. Beamish, R.S. McKinley, C. Katopodis and D.A. Scruton. 1995. Swimming Performance of Lake Sturgeon, *Acipenser fulvescens*. Can. Tech. Rep. Fish. Aquat. Sci. 2063, iv + 26 pp.

Fishways have traditionally been designed to provide safe passage for jumping fish and only recently have non-jumping species been considered. Concern over dwindling populations of lake sturgeon (*Acipenser fulvesens*) has focused attention on fishway designs that accomodate its swimming abilities. The objective of this study was to derive models that describe swimming endurance and critical speed (5 cm/s increment, 10 minute interval) for lake sturgeon. Critical speed increased with temperature (7-21° C) and with total length (12-132 cm). Endurance at sustained and prolonged swimming speeds (those maintainable for more than 20 seconds) increased with temperature but was independent of temperature at higher burst speeds. Endurance increased with total length at all speeds. Swimming performance of lake sturgeon, relative to body length, is inferior to that of salmonids. Fishway designers need to consider swimming ability, space requirements and behavior of lake sturgeon to ensure them safe passage of migratory obstructions.

S. Peake, F.W.H. Beamish, R.S. McKinley, C. Katopodis and D.A. Scruton. 1995. Swimming Performance of Lake Sturgeon, *Acipenser fulvescens*. Can. Tech. Rep. Fish. Aquat. Sci. 2063, iv + 26 pp.

Jusqu'a à présent, les passes migratoires étaient conçues dans le but d'assurer le libre passage des poissons sauters; ce n'est pas que récemment qu'on s'est penché sur la situation des espèces non sauteuses. En raison de la diminution des populations d'esturgeons de lac (*Acipenser fulvescens*), on cherche à concevoir des passes qui correspondent à ses capacités natatoires. La présente étude avait pour objet de formuler des modèles pour decrire l'endurance et la vitesse critique (incréments de 5 cm/min., intervalles de 10 minutes) de l'esturgeons de lac. La vitesse limite augmente avec la température (7 a 21 °C) et avec la longeur totale (12 a 132 cm). L'endurance dans le cas de vitesses soutenues et prolongées (plus de 20 secondes) augmente avec la température, mais demeure indépendante de la température à des vitesses de pointe. À toutes les vitesses, le niveau d'endurance augmente avec la longeur totale. Le rendement natatoire de l'esturgeon de lac, relativement à sa longeur, est inférieur à celui des salmonidés. Les concepteurs de passes migratoires doivent tenir compte des capacités natatoires, des besoins d'espace et des comportements de l'esturgeon de lac s'ils veulent qu'il puisse franchir de façon sécuritaire des obstacles à sa migration.

Introduction

Since the mid 1800's, populations of lake sturgeon, *A cipenser fulvescens*, have decreased dramatically due to commercial exploitation, loss of habitat and an increasing sport fishery (Rochard *et al.* 1990). Slow growth, late sexual maturity and infrequency of spawning all contribute to their vulnerability to exploitation (Brousseau 1987). In large rivers hydroelectric installations can impede migrations and cause instability in flow rates, decreasing the quality of spawning and feeding habitat (Harkness and Dymond 1961; Priegel and Wirth 1971; Parks 1978). Although fishways have been constructed on some rivers to allow safe passage of migratory fish, designs have primarily facilitated the swimming capabilities of salmonids (Collins *et al.* 1962, 1963; Weaver 1963). Only recently have fishways been designed to accomodate other species (e.g. Katopodis *et. al.* 1991).

Swimming ability among species can vary with differences in anatomy, metabolism and behaviour. Fishways designed to allow passage of one species can select against others of lesser swimming ability (Schwalme *et al*,1985). One difference that exists between sturgeon and salmonids is tail morphology. Salmonid tails are broad and symmetrical, while the lower lobe of the lake sturgeon tail is smaller than the upper lobe. The small lower lobe gives the tail less depth, making its contribution to total thrust less than that of salmonids (Webb 1986). Sturgeon also experience more drag per unit area than trout, presumably due to the presence of their bony plates or scutes (Webb 1986). Finally, metabolism of sturgeon has been found to be significantly lower than that of teleost fishes (Singer *et al*, 1989).

Swimming activities of fish in general have been described by three categories: sustained, prolonged and burst. Sustained occurs at relatively low velocities and represents speeds which can be maintained for a period greater than 200 minutes (Beamish 1978), making use of energy derived exclusively from aerobic processes. The velocity at which endurance falls below 200 minutes is referred to as the maximum sustained speed. Prolonged swimming covers a spectrum of speeds between sustained and burst. Burst represents high velocities which can be maintained for less than 20 seconds, using energy entirely generated by anaerobic processes (Hoar and Randall 1978).

Swimming ability of fish is often evaluated by determining the endurance and the critical swimming speed of a species. Endurance is defined as the amount of time a fish can swim at a particular velocity. Sustained, prolonged and burst speeds can be identified by

measuring endurance over a range of swimming velocities. Critical speed is a measure of prolonged swimming that was first described by Brett (1964). It represents the maximum velocity a fish can maintain for a prescribed time period.

Ideally, fishways should be able to successfully pass all migratory species inhabiting the river on which the dam is built. Water velocities within the fishway should be less than the maximum attainable speed of all indigenous species and the distance a fish must swim to pass the fishway should not exceed its endurance. The present study investigated endurance and critical swimming speed of lake sturgeon in relation to body size and ambient temperature. Performance was compared to that of salmonids, and recommendations for future fishway designs capable of accommodating both species are offered.

Materials and Methods

Lake sturgeon swimming performance was determined for individuals 12.0 to 132.0 cm in total length. A total of 58 sturgeon, 12 to 55 cm, were obtained as progeny of wild stock from the Moose River basin in northern Ontario. Five large fish, 106 to 132 cm, were captured in trap nets from southeastern Lake Huron. Fish were held in the laboratory in tanks supplied with running non-chlorinated well water, the quality of which is summarized in Table 1. Sturgeon were subjected to a 16/8 hour light/dark photoperiod. Small sturgeon (\leq 15 cm) were fed live earthworms to satiation 3 times per week, intermediate fish (23 to 55 cm) received daily feedings of dry pellet formula, while large fish (\geq 100 cm) were fed live crayfish (*Orconectes* sp.) to satiation three times per week.

Prior to experimentation water temperature was adjusted to 7.0, 14.0 or $21.0 \pm 0.5^{\circ}$ C by an increase of 1.0 or a decrease of 0.5° C/ day. Before fish were used in experiments they were held at the selected temperature for at least 7 days and were not fed for 36 hours immediately prior to testing to ensure a post absorptive state.

Swimming performance of small sturgeon was measured in 3.2 L swimming flumes (Waiwood and Beamish 1978). Intermediate fish were tested in a 200 L swimming flume (Farmer and Beamish 1969) modified by the addition of a vertical chimney at the downstream end of the swim chamber through which fish were introduced and removed. Water velocity within the flumes was measured using a recently calibrated current meter and

controlled by rheostats. Water flow within the 3.2 and 200 L swim flumes was essentially rectilinear in profile. Water from aerated and thermally controlled reservoirs was added at a rate of approximately 120 and 600 ml/min for the 3.2 and 200 L flumes, respectively, to assure oxygen content in excess of air saturation and a constant temperature.

Performance of large sturgeon was measured in a black PVC pipe approximately 2.5 m long with a diameter of 56 cm. The tube was equipped with a fixed plastic retaining screen at the upstream end and a removable rubber mesh screen at the downstream end. Fish were introduced and removed at the downstream end of the tube. Two windows (15 by 25 cm) were cut in the apparatus approximately 0.5 m from each end to facilitate viewing of fish. Flow was found to be approximately rectilinear in profile and flow rates were calibrated. Windows were covered from the inside with heavy gauge, clear vinyl to minimize internal turbulence. Strips of white tape were applied to the inside of the tube, in the window regions, to allow fish to be seen against the dark interior. After assembly, the entire apparatus was submerged and secured within a large aquatic flume (3 by 5 m) located at the University of Guelph. Maximum cross-sectional areas of all lake sturgeon used in this study were less than 10% of that in their respective swimming flumes, eliminating the need to adjust for blocking effect (Smit et al. 1971).

Swimming performance was evaluated by measuring critical swimming speed and fish endurance. Prior to measuring endurance, fish were transferred from the holding tank to a flume and forced to swim at approximately 0.45 body lengths/ second (bl/s) for one hour, after which velocity was abruptly increased to the desired test velocity. Endurance was measured at 20, 40, 45 and 50 cm/s for fish less than 15 cm, at velocities ranging from 30 to 90 cm/s for sturgeon between 23 and 52 cm and at 90, 120, 150 and 180 cm/s for fish greater than 100 cm. Small fish were tested at 7.0 and 14.0, intermediate sturgeon at 7.0, 14.0 and 21.0, and large fish at 14.0 ± 0.5 C. Endurance data were statistically analyzed to produce a model describing endurance of lake sturgeon of a prescribed length at a given temperature and velocity. Velocities corresponding to endurance greater than 200 minutes were considered to represent sustained swimming and were not included in data used to derive the model. Sturgeon that swam in excess of 200 minutes were allowed to continue for an additional 280 minutes after which experimentation was terminated.

Critical speed was determined after lake sturgeon had swam one hour at approximately 0.45 bl/s, after which velocity was increased in a constant, stepwise

progression. Critical speed was calculated for each fish using the formula described by Brett (1964),

$$C = u_{crit} = V + (t \circ \Delta t^{-1}) \Delta v,$$

where C is the critical speed, cm/s; Δt is time increment, minutes; Δv is velocity increment, cm/s; t is time elapsed at final velocity, minutes; and V is the highest velocity maintained for the prescribed time period, cm/s. A ten minute time interval and a five cm/s velocity increment was used in this experiment. This time interval was considered more relevant to fishway design (*i.e.* passage time) than the more commonly used 30 or 60 minute intervals in swim speed trials.

Critical speed was determined for small sturgeon at 7.0 and 14.0, for intermediate fish at 7.0, 14.0 and 21.0, and for large fish at 14.0 ± 0.5 C. Data were statistically analyzed to generate a model describing critical speed for fish of a prescribed length at a given temperature.

Measurements of critical speed and endurance depend on accurate and consistent recognition of fish fatigue. Electric shocking was not used in this study and fish were occasionally stimulated to maintain swimming by various methods, depending on the flume in which they were tested. Small fish were completely enclosed in the flume and were stimulated by short and sharp fluctuations in velocity followed by an immediate return to the test velocity. Intermediate fish, in the 200 L flume, were stimulated by gentle prodding with a plastic rod and by the velocity fluctuations described for small fish. Large sturgeon were also gently prodded to keep them from resting against the downstream retaining screen. In all cases, fish were considered fatigued when they failed to leave the downstream screen despite repeated attempts to stimulate them. In most cases, onset of fatigue was obvious. After experimentation fish were measured, weighed and returned to their holding tanks. All fish were allowed to recover for at least 8 hours prior to subsequent experimentation. Statistical significance was determined by multiple regression analysis (Draper and Smith, 1966).

Results

Lake sturgeon swimming performance was found to increase with total length at all swimming speeds and temperatures tested. Large fish could swim for longer periods of time and attain higher speeds than smaller fish. Large sturgeon swam for approximately 50 minutes at 90 cm/s, while intermediate sturgeon could maintain this velocity for only a few seconds. Small sturgeon were not able to swim at 90 cm/s.

Sturgeon that swam longer than 200 minutes generally continued to swim until they were stopped. It is assumed that these fish would have continued to swim indefinitely if they had not been interrupted. Speeds that result in swimming for indefinite periods are considered sustained. The velocity at which a sturgeon was not able to continue sustained swimming represents the maximum sustained speed of that fish.. This speed, for observed fish, can only be approximated, but was found to increase with fish length, from about 10 cm/s for small sturgeon, to 25 cm/s for intermediate fish, to over 80 cm/s for large sturgeon at 14 $^{\circ}$ C.

Velocities greater than maximum sustained speed caused endurance to fall below 200 minutes and represent prolonged swimming. For small sturgeon an increase in speed to 20 cm/s caused fatigue after approximately 120 minutes, and for intermediate fish an increase to 30 cm/s resulted in fatigue after approximately 185 minutes of swimming, at 14 °C. As velocity continued to increase, endurance declined rapidly. For small fish, an increase in speed to 50 cm/s resulted in fatigue after only a few seconds of swimming. Intermediate fish quickly fatigued when speed was increased to 90 cm/s, and large fish swam less than 30 seconds at 180 cm/s.

Sustained swimming performance was enhanced by increasing temperature between 7 and 21° C. Maximum sustained speed of intermediate fish increased from 25 to just under 40 cm/s at 7 and 21° C. The inevitable result was that, in some cases, prolonged swimming changed to sustained with the increase in temperature. Intermediate sturgeon, swimming at 30 cm/s, fatigued after less than 90 minutes at 7°C. Fish swimming at the same speed, but at 21° C, swam indefinitely, indicating that increased temperature had caused a shift from prolonged to sustained swimming at 30 cm/s.

Sturgeon swimming at prolonged speeds displayed enhanced endurance at higher

temperatures. Intermediate sturgeon, swimming at a speed of 45 cm/s in 7° C water, fatigued in less than 4 minutes, but at 21° C, swam for as long as 24 minutes. The magnitude of the enhancing effect of increased temperature lessened as velocity increased and disappeared altogether at high swimming speeds. Intermediate fish, at 90 cm/s, swam for approximately 25 seconds at both 7 and 21° C.

The relationship among endurance, temperature, fish length and swimming speed is described by the regression:

$$log(E) = 1.40 + (2.26 \times 10^{-2} \cdot L) + (5.47 \times 10^{-2} \cdot T) - (4.55 \times 10^{-2} \cdot V) - (5.36 \times 10^{-4} \cdot T \cdot V) + (1.85 \times 10^{-4} \cdot L \cdot V),$$

Equation 1

where E is swimming endurance, min; L is total length, cm; V is swimming speed, cm/s; and T is temperature, $\binom{0}{C}$. The model has a critical F-value of 274.6 (P< 0.05) an adjusted r^2 of 0.854 (Table 2) and has 233 degrees of freedom. Interaction between temperature and velocity and between temperature, velocity and length were not found to be significant.

Fatigue curves generated by the model take the form of a single straight line with no changes in slope. The line represents endurance for lake sturgeon, of a prescribed length at a given temperature, at velocities up to maximum sustained speed. It is not valid for endurance responses greater than 200 minutes. A vertical line must be added, at maximum sustained speed, to reflect demonstrated ability of lake sturgeon to swim indefinitely at sustained velocities. This model is also invalid for determining endurance for fish greater than 55 cm at temperatures other than 14 C. With these limitations considered, patterns in model generated curves agreed well with those observed from the data.

The model confirms that large sturgeon have the ability to swim longer and at higher speeds than smaller fish (Fig. 1a). Sturgeon 120 cm in length, at 14° C, can swim for 127.5 minutes at 90 cm/s, while a 35 cm fish can maintain this speed for just 3.5 seconds. Maximum sustained speed can be accurately estimated, using the model, and is equivalent to that velocity corresponding to an endurance of exactly 200 minutes. Maximum sustained speed, at 14° C, increases with length, from 4.0 cm/s for 15 cm sturgeon to 83.7 cm/s for 120 cm fish.

Endurance declines rapidly, for fish of all sizes, at velocities greater than their maximum sustained speed. A sturgeon 55 cm in length, at 14° C, can swim for 133.0 minutes at 30.0 cm/s, but will fatigue after 8.0 seconds at 100.0 cm/s. The model showed the same temperature effects, for sturgeon 55 cm or less, as those observed in the data (Fig. 1b). Maximum sustained speed, for a 55 cm sturgeon, increases with temperature, from 18.5 cm/s at 7°C to 32.0 cm/s at 21°C. This allows swimming categories for the same fish to change with a fluctuation in water temperature. A 55 cm sturgeon, swimming at 30.0 cm/s at 7°C, fatigues after 71.38 minutes, indicating prolonged swimming, but at 21°C, the same fish can maintain 30.0 cm/s indefinitely, indicating sustained swimming.

Endurance of sturgeon is also enhanced by temperature at prolonged speeds. Endurance of a 55 cm sturgeon, swimming at 35 cm/s, increases with temperature, from 45.5 to 145.0 minutes at 7 and 21° C. The magnitude of the temperature effect is most pronounced at speeds just above maximum sustained, and decreases as velocity increases, eventually becoming insignificant at high speeds. A 55 cm sturgeon swimming at 100 cm/s will fatigue after 7.9 seconds at 7° C, and after 8.2 seconds at 21° C.

Critical swimming speed tended to increase with sturgeon length and water temperature. The relationship between critical speed, fish length and temperature is described by the regression:

Ucrit =
$$16.0 + (0.479 \cdot L) + (0.0138 \cdot T \cdot L)$$
, Equation 2

where Ucrit is critical swimming speed, cm/s; L is total length, cm; and T is temperature, ^o C. The critical F-value of the regression is 182.8 (P< 0.05), it has an adjusted r^2 of 0.844 (Table 3) with 67 degrees of freedom. Temperature alone was not significant (P = 0.07) and was not retained in the model. Critical speed increases with length, from 26.1 for 15 cm sturgeon, to 96.7 cm/s for 120 cm fish at 14^oC (Fig. 2a), and with temperature, from 36.1 cm/s at 7^oC, to 42.9 cm/s at 21^oC for 35 cm fish (Fig. 2b).

Studies of fish locomotion often express swimming speed in relation to body length. This allows performance of different sized fish to be compared. Velocities expressed in body lengths/second (bl/s) are called specific swimming speeds and this approach will be used to describe velocity in the ensuing paragraphs.

Effects of sturgeon body length on endurance and critical speed are sometimes altered when specific speeds are used. Maximum sustained speed, in bl/s, increases with fish length as before, from 0.27 to 0.70 bl/s for 15 and 120 cm sturgeon at 14 $^{\circ}$ C (Fig. 3), but at speeds greater than 0.8 bl/s, this relationship reverses. Endurance for small fish becomes greater than that of larger fish at the same specific speed. A 15 cm fish can swim for 56.4 minutes at 1.0 bl/s, while a 120 cm fish can maintain this speed for just 15.2 minutes, at 14 $^{\circ}$ C. The performance advantage is most pronounced at high velocities. A 15 cm sturgeon can swim for 18.6 seconds at 4.0 bl/s, but a 120 cm fish can swim, for the same time period, at just 1.46 bl/s.

The relationship between length and critical swimming speed, measured in bl/s, is also reversed. Small sturgeon have higher specific critical speeds than large fish, with a 120 cm sturgeon having a critical speed of 0.81 bl/s and a 15 cm fish showing a critical speed of 1.74 bl/s at 14 $^{\circ}$ C.

Discussion

The swimming ability of fish depends on the amount of thrust that it can produce to overcome the drag its body causes, thus variations in performance among species tend to be the result of mechanisms that increase thrust and/or decrease drag. Drag increases with the square of velocity in proportion to wetted surface area. Low velocities, such as those associated with maximum sustained speed, generate relatively little drag, and larger fish use their increased muscle mass to outperform small fish at these speeds (Fig. 3). As velocity increases, drag for large sturgeon increases at a faster rate than for small fish, making small sturgeon better high speed swimmers than large fish in relative terms. This may explain why sturgeon tend to grow flesh over their scutes as they mature (Harkness and Dymond 1961), with drag reduction becoming increasingly more important than protection from predators.

Critical swimming speed is a measure of prolonged swimming performance and, in this study, represents the speed at which a sturgeon can swim for a period of ten minutes. Critical speed, measured in bl/s, initially declines dramatically with increasing sturgeon length, but decreases at a much slower rate for fish larger than 50 cm. This may occur

because, during the first few years of life, sturgeon tend to grow much faster in length than in weight (Harkness and Dymond 1961). As time goes on, growth in length slows and the sturgeon begin to gain weight. A small sturgeon that grows 5 cm in length might increase its weight by a few grams, but similar growth in a large fish could be accompanied by a weight increase of several kilograms. The cost of any growth is an increase in drag, and with only a marginal increase in muscle mass, critical speed of small fish, relative to the increased body length, decreases. Larger fish slow this decline by shifting from length to weight oriented growth, increasing muscle mass to compensate for increased drag. In spite of this, critical speed for large sturgeon continues to decline slowly with increased length, suggesting that sturgeon cannot increase muscle mass sufficiently to completely overcome the accompanying increase in drag.

Fatigue curves are important tools in studies of fish swimming performance, and are typically reported for species of a certain length tested at a particular temperature. Fatigue curves are generated by plotting log endurance against speed and, for salmonids, are characteristically resolved into three straight lines connected by two changes in slope. The first line is vertical and is located at maximum sustained speed. Swimming speeds to the left of this line are considered sustained. The change in slope that occurs at maximum sustained speed marks the beginning of the second line which represents prolonged swimming. The slope change is caused by a shift in metabolism, from strictly aerobic to a mixture of aerobic and anaerobic processes. The second inflection typically occurs at an endurance of 15 to 20 seconds and is caused by another shift in metabolism, from combined aerobic and anaerobic, to exclusively anaerobic processes. This slope change marks the beginning of the third line representing burst swimming speeds.

Patterns in lake sturgeon fatigue curves resemble those found for salmonids with some noteworthy exceptions. Curves representing sturgeon endurance do not show the second inflection corresponding to burst swimming. Endurance, at high speeds, simply continues to decline at the same rate as for prolonged speeds. Consequently, lake sturgeon are not capable of attaining the high burst speeds shown by salmonids of similar size (Fig. 4a).

This is not to say that lake sturgeon do not possess burst swimming capability. Salmonid species, whose performance has been shown to be affected by temperature, show the effect most profoundly at sustained and prolonged speeds, but not at burst. Lake sturgeon endurance is similarly influenced by temperature, showing significantly enhanced sustained and prolonged performance at higher temperatures, but an independence to temperature at speeds that can be maintained for less than 20 seconds. It is therefore probable that, at the metabolic level, these velocities represent burst swimming for lake sturgeon.

The poorer swimming performance of lake sturgeon, relative to that of salmonids, is not confined to burst speeds but is evident in all categories of swimming. Reduced prolonged performance is supported by the relatively low critical swimming speeds found for lake sturgeon (Fig. 4b). Studies of sturgeon physiology have found that metabolism is intermediate between the more primitive elasmobranch and the more advanced teleost fishes (Singer *et al* 1989). A lower overall metabolism could, partially, account for the depressed swimming ability of lake sturgeon. Disproportionately poor performance at burst swimming speeds may also indicate that anaerobic processes utilized by sturgeon are less efficient at providing usable energy than those in salmonids. Further, the absence of a change in slope, at burst speeds, may indicate a more gradual shift to exclusive anaerobic metabolism than that demonstrated by salmonids.

Morphology, and specifically that of the tail, can significantly influence swimming capabilities among fish species. The salmonid tail is symmetrical, with upper and lower lobes producing similar thrust; however the lower lobe of the sturgeon tail is smaller than the upper and consequently generates 66% less thrust than the lower tail lobe of similarly sized trout. The net effect is that the sturgeon tail, as a whole, generates 18% less thrust than that of trout over sustained and prolonged speeds (Webb 1986).

The performance consequence of impaired thrust is further complicated by morphological differences in body form between sturgeon and salmonids. Salmonids tend to have smooth, streamlined bodies, while sturgeon have a rough skin texture riddled with bony scutes. Studies have found that sturgeon experience approximately 3.5 times more drag than trout, per unit of surface area (Webb 1986). This means that a sturgeon must generate more thrust, with its less efficient tail, than a trout of similar size, and will require more energy to maintain the same swimming speed. Anaerobic metabolism, at burst speeds, provides a limited amount of energy, which the sturgeon will use up faster than the more efficient trout. This translates into reduced swimming performance, especially at burst, relative to that of trout of similar size. Traditionally, fishways have been installed on dams to provide safe passage for salmonids, with little regard for other migratory species, such as the lake sturgeon. Fish can successfully pass fishways in a few minutes or seconds, making prolonged and burst swimming capabilities of primary importance in establishing optimal water velocities within the structure. Unfortunately the inferior nature of lake sturgeon swimming, relative to similar size salmonids, is most pronounced at burst speeds. For both species to use the fishway, water velocities must be maintained within the swimming performance characteristics of sturgeon and salmonid.

It must be stressed that most studies, including this one, determine performance for fish swimming in flumes. The swimming speed of the fish is, correctly, taken to equal the water velocity within the flume. This is true only because the fish has zero velocity relative to the ground. Fish passing a fishway, obviously, must have a positive velocity relative to the ground. To accomplish this, the fish must swim faster than the speed of the water flowing through the fishway. Thus, water velocity cannot simply be set at a speed that a fish can maintain, it must be set at a speed that a fish can make progress against. The maximum water velocity, within a fishway of given proportions, that can be expected to pass sturgeon of given length, at a given temperature, can be determined using the method outlined in the next section (Practical Application of the Model Describing Endurance of Lake Sturgeon).

It is also important to note that mature sturgeon can be much larger than salmonids utilizing the same fishway. Performance comparisons made thus far have been between sturgeon and salmonids of the same size. A 55 cm sturgeon enters burst swimming at a speed of about 1.7 bl/s, which only represents sustained swimming for a trout of the same size. Burst swimming speeds for large sturgeon would be more comparable to burst swimming for smaller salmonids. A 150 cm sturgeon might enter burst at 1.4 bl/s, but this speed corresponds to an absolute velocity of 210 cm/s. A smaller 60 cm trout swimming for the species. Therefore, if emphasis is to be placed on passing only spawning size sturgeon, it may be that space is more important than slowing the water velocity within the fishway. Fishway designs requiring fish to jump from step to step are not generally conducive to the passage of large sturgeon. If, however, the goal in establishing the fishway is to provide safe passage for sturgeon, regardless of size, then slowing water velocity becomes as important to successful passage as space. If sturgeon populations are to rebound in the future, they must be given access to the type of spawning habitat they utilized prior to construction of hydroelectric dams and other river impediments. If fishways are to accomplish this, new designs must reflect the unique swimming capabilities of the lake sturgeon.

Practical Application Of The Model Describing Endurance Of Lake Sturgeon

In order to provide safe passage to migrating lake sturgeon, the water velocity within a fishway must be lower than the maximum attainable speed of the fish, and the distance this fish must swim to clear the fishway must not exceed its endurance. It has been shown that endurance can be estimated for sturgeon of a given length at a given water temperature and swimming speed. If the distance that the sturgeon must swim is known, and the minimum size of fish to be passed is decided on, the highest flow allowable within the fishway can be determined using the following formula:

$$V_f = V_s - (d / E_{Vs} * V_s),$$
 Equation 3

where V_f is the water velocity within the fishway, cm/s, V_s is the swimming speed of the sturgeon, cm/s, d is the distance the fish must swim to pass the fishway, cm, and E_{Vs} is the endurance of the sturgeon swimming at V_s . E_{Vs} must be determined using the formula describing endurance for lake sturgeon (Equation 1). The fish length used should reflect that of the smallest sturgeon that the fishway is required to pass. A similar performance analysis was proposed by Bainbridge (1960).

The maximum water velocity that will allow a sturgeon to pass a fishway can be determined using the second derivative method on Equation 3. It can also be determined graphically by solving Equation 3 for various values of V_s , and plotting a graph with V_s on the x axis and V_f on the y axis. An example of this method is given in figure 5. The maximum velocity within a fishway will correspond to the maximum value of V_f shown on the graph. If the velocity is set at maximum V_f , the fish must swim at the speed corresponding to this maximum value. If the velocity is set lower than maximum V_f , the fish will be able to pass the fishway at a range of speeds. Sturgeon may not be able to pass the fishway if velocities exceed the maximum value.

Maximum velocity will not change significantly at different temperatures, however it will change for fish of different size, or for fishways of different length.

Acknowledgements

Э

The authors would like to acknowledge the valuble assistance of the U.S. Fish and Wildlife Service (Region 3), the S.O. Conte Anadromous Fish Research Center of the U.S. National Biological Service, and the Wisconsin and Michigan Departments of Natural Resources for funding this research and facilitating this international collaboration. Technical assistance of Mr. Tyler Hoar and Mr. Robert Frank was appreciated.

References

Bainbridge, R. 1960. Speed and stamina in three fish. J. Exp. Biol. Vol. 37(1):129-153.

- Beamish, F.W.H. 1980. Chars salmonid fishes of the genus *Salvelinus*. Perspectives in Vertebrate Science. ed. E. K. Balon. Dr. W. Junk by Publishers, pp 739-747.
- Beamish, F.W.H. 1978. In W.S. Hoar and D.J. Randall, eds. Fish Physiology. Vol. 7. Academic Press, Inc., New York, N.Y.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183-1226.
- Collins, G.B., C.H. Elling, and J.R. Gauley. 1962. Ability of salmonids to ascend high fishways. Trans. Am. Fish. Soc. 91: 1-7.
- Collins, G.B., C.H. Elling, J.R. Gauley, and C.S. Thompson. 1963. Effect of fishway slope on performance and biochemistry of salmonids. U.S. Fish Wildl. Serv. Fish. Bull. 63: 221-253.
- Draper, N.R., and H. Smith. 1966. Applied Regression Analysis. John Wiley and Sons, Inc., London. 407 pp.
- Farmer, G.L., F.W.H. Beamish. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. J. Fish. Res. Board Can. 26: 2807-2821.
- Harkness, W.J.K., and J.R. Dymond. 1961. The lake sturgeon: the history of its fishery and problems of conservation. Ontario Department of Lands and Forests, Fish and Wildlife Branch. Toronto.
- Katopodis, C., A.J. Derksen and B.L. Christensen. 1991. Assessment of two Denil fishways for passage of freshwater species. American Fisheries Society Symposium 10:306-324.
- Parks, N.B. 1978. The Pacific northwest commercial fishery for sturgeon. Maritime Fishery Review 40: 17-20.
- Priegel, G.R., and T.L. Wirth. 1971. The lake sturgeon. Its life history, ecology and management. Wisconsin Department of Natural Resources, Madison, Wisconsin. Publication 270-70.
- Rochard, E., G. Castelnaud, and M. Lepage. 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. Journal of Fish Biology. 37: 123-132.

Schwalme, K., W.C. Mackay, and D. Lindner. 1985. Suitability of vertical slot and Denil

fishways for passing north-temperate, non-salmonid fish. Can. J. Fish. Aquat. Sci. 42: 1815-1822.

- Singer, T.D., V.G. Mahadevappa, and J.S. Ballantyne. 1990. Aspects of the energy metabolism of lake sturgeon, *A cipenser fulvescens*, with special emphasis on lipid and ketone body metabolism. Can. J. Fish. Aquat. Sci. 47: 873-881.
- Smit, H., J.M. Amelelink-Koutstaal, J. Vijverberg, and J.C. von Vaupel-Klein. 1971. Oxygen consumption and efficiency of swimming goldfish. Comp. Biochem. Physiol. A39: 1-28.
- Weaver, C.R. 1963. Influence of water velocity upon orientation and performance of adult migrating salmonids. U.S. Fish Wildl. Serv. Fish. Bull. 63: 97-121.
- Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. Bull.Fish. Res. Board Can. 190:1-159.
- Webb, P.W. 1986. Kinematics of lake sturgeon, *Acipenser fulvescens*, at cruising speeds. Can. J. Zool. 64: 2137-2141.

Table 1.Selected chemical and physical properties of Guelph well water used in
holding tanks and swimming flumes. All wter used was non-chlorinated.
Temperatures used to determine sturgeon performance were 7.0, 14.0 and
 21.0 ± 0.5 °C.

| Parameter | Amount |
|------------------|---------------------|
| phosphate | 0.02 mg/L |
| nitrite | < 0.05 mg/L |
| nitrate | 0.18 mg/L |
| alkalinity | 250 mg/L |
| ammonia | 0.10 mg/L |
| conductivity | 948 <i>µ</i> mho/cm |
| calcium hardness | 411 mg/L |
| pH | 8.0 |
| sulphate | 131 mg/L |
| chloride | 52 mg/L |
| sodium | 24.1 mg/L |
| organic carbon | < 1.0 mg/L |

Table 2:Regression coefficients, F-values and levels of significance for parameters in
the model describing endurance of lake sturgeon. Total length must be
measured in cm, temperature in C, and velocity in cm/s. Level of
significance was p< 0.05.</th>

| Parameter | Regression Coefficient | F-value | P-value |
|----------------------|-------------------------------|---------|---------|
| total length | 2.26×10^{-2} | 55.7 | < 0.05 |
| temperature | 5.47×10^{-2} | 14.5 | < 0.05 |
| velocity | -4.55×10^{-2} | 194.9 | < 0.05 |
| temperature velocity | -5.36×10^{-4} | 5.2 | < 0.05 |
| length velocity | 1.85×10^{-4} | 72.9 | < 0.05 |

à

Table 3:Regression coefficients, F-values and significance for parameters in the model
describing critical swimming speed of lake sturgeon. Total length must be
measured in cm, and temperature in C. Level of significance was p < 0.05.</th>

| Parameter | Regression | F- value | P-value |
|--------------------|-----------------------|----------|---------|
| length | 4.79×10^{-1} | 33.9 | < 0.05 |
| length temperature | 1.38×10^{-2} | 7.2 | 0.009 |

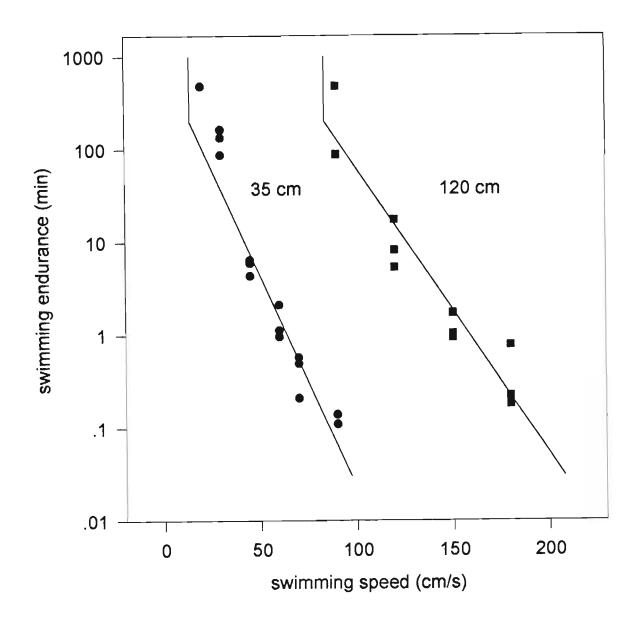


Figure 1a. The relationship between endurance and swimming speed for lake sturgeon. Circles and squares represent data from fish 30 to 40 and 117 to 122 cm in total length respectively. The lines are determined using lengths of 35 and 120 cm, a temperature value of 14 °C, and a range of swimming speeds (0 - 220 cm/s) substituted into equation [1] (p.7). Swimming speed of lake sturgeon increases with increased body length.

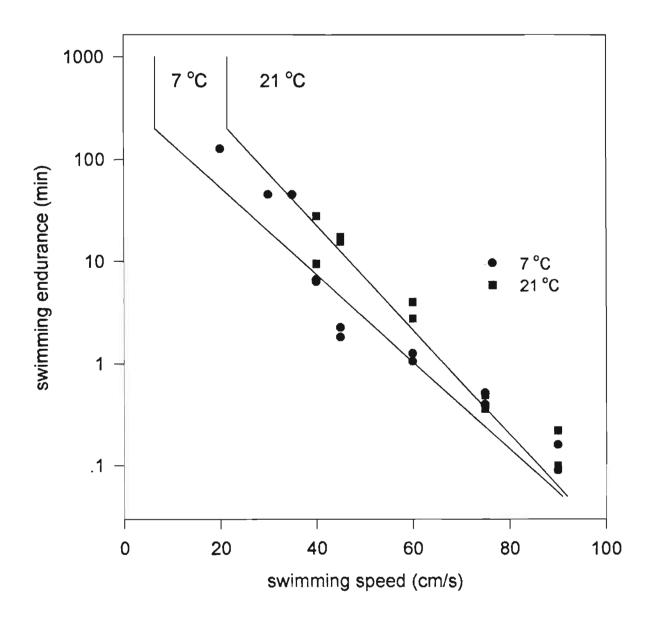


Figure 1b. The relationship between endurance and swimming speed for lake sturgeon (26 - 40 cm). Circles and squares represent data from fish tested at 7 and 21 °C respectively. Lines are determined using a total length of 35 cm, temperatures of 7 and 21 °C, and a range of swimming speeds (0 - 90 cm/s) substituted into Equation [1] (p.7). Increased temperature has an enhancing effect on swimming performance which is most evident at sustained speeds (0 - 20 cm/s), diminishes as prolonged speeds (20 - 70 cm/s) increase and has a negligible effect on burst speeds (70 - 90 cm/s).

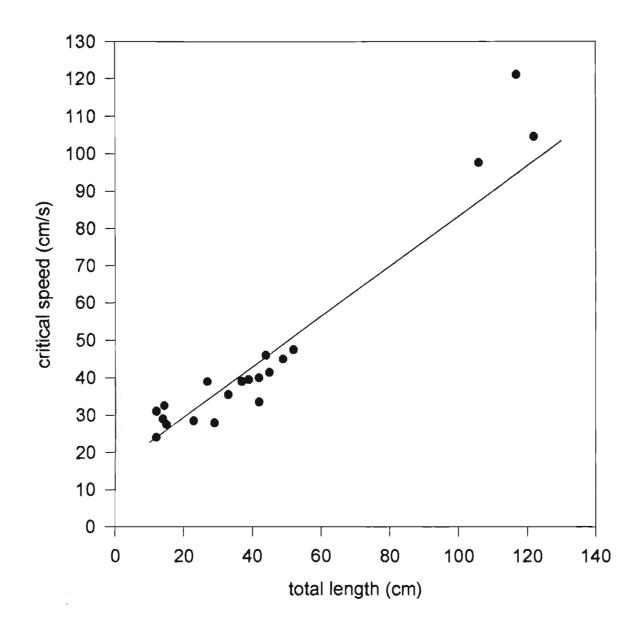


Figure 2a. The relationship between total length and critical swimming speed for lake sturgeon at 14 °C. Circles represent data from fish 15 to 22 cm in total length. The line is determined using a range of length values (10 - 125 cm) and a temperature of 14 °C substituted into Equation [2] (p.9). Critical speed for lake sturgeon increases with body length.

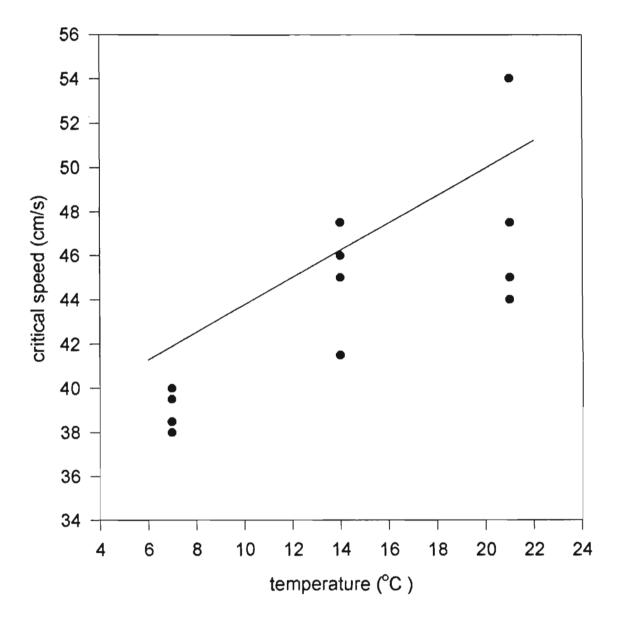


Figure 2b. The relationship between critical swimming speed and temperature for lake sturgeon. The circles represent data from fish 30 to 52 cm in length and tested at 7, 14 and 21 °C. The line is determined using a total length value of 45 cm and a range of temperatures (7 - 21 °C) substituted into Equation [2] (p.9). Critical speed for lake sturgeon increases with ambient temperature over the range of temperatures tested.

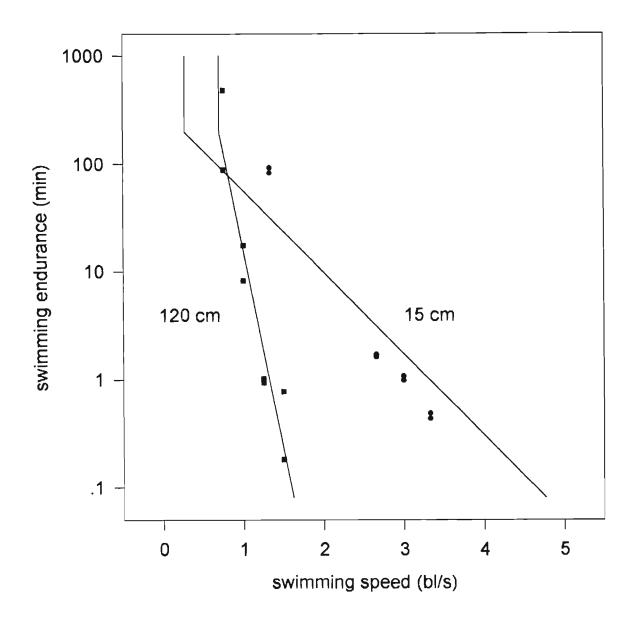


Figure 3. The relationship between endurance and swimming speed relative to body length for lake sturgeon at 14 °C. Circles and squares represent data from fish 12 to 15 and 117 to 122 cm in total length respectively. The lines are determined using total length values of 5 and 120 cm, a temperature of 14 °C, and a range of swimming speeds (0.25 - 5.0 bl/s) substituted into Equation [1] (p.7). Larger sturgeon have a higher maximum sustainable swimming speed than small fish, relative to their body length, however swimming performance of small sturgeon exceeds that of larger fish throughout most of prolonged and all of the burst swimming speeds.

c

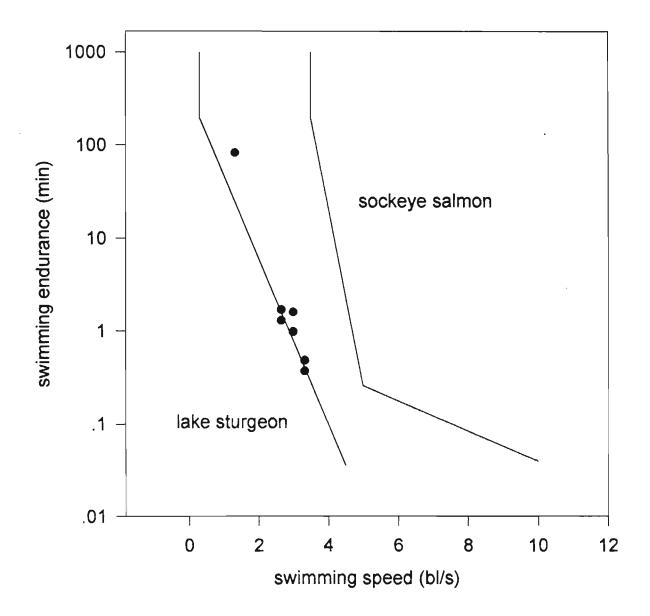


Figure 4a. A comparison of fatigue curves for lake sturgeon and sockeye salmon (15 - 18 cm fish, after Brett 1964). Circles represent data for sturgeon 12 to 15 cm in length at 14 °C. The line for sturgeon is determined using a length value of 18 cm, a temperature of 14 °C, and a range of swimming speeds (0.25 - 4.5 bl/s) substituted into Equation [1] (p.7). Performance of lake sturgeon is lower than that for sockeye salmon in all areas of swimming and particularly so for sustained and burst speeds.

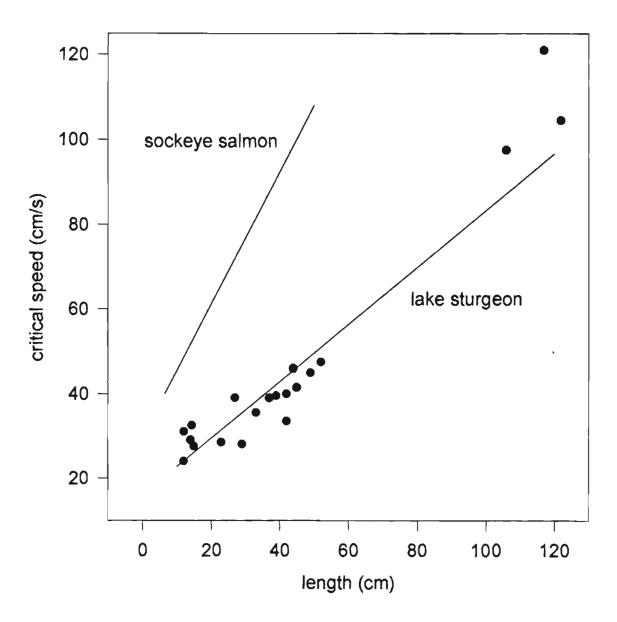


Figure 4b. A comparison of critical speed curves for lake sturgeon and sockeye salmon (6 - 50 cm fish, after Brett 1973). Circles represent data for sturgeon critical speeds and was collected from fish (15 - 122 cm in total length) at 14 °C. The line for sturgeon is determined using total length values of 10 to 122 cm and a temperature of 14 °C substituted into Equation [2] (p.9). Critical speed for lake sturgeon is inferior to that of sockeye salmon at 14 °C.

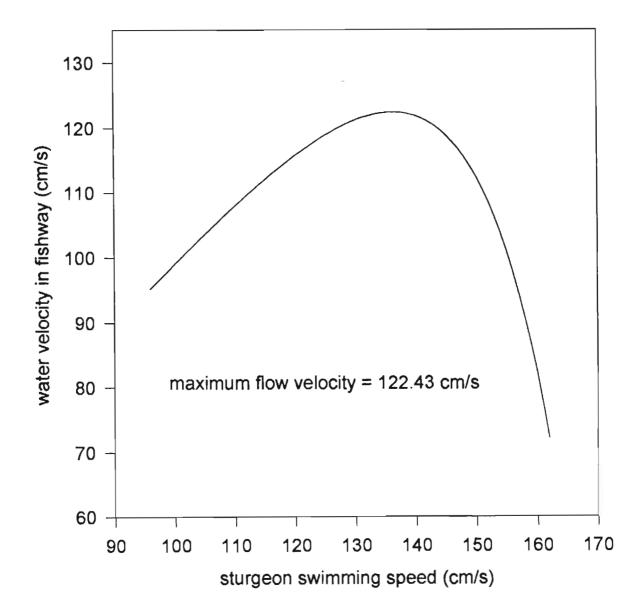


Figure 5. A curve describing the swimming requirements for a 100 cm lake sturgeon to successfully pass a 10 m fishway at 14 °C. This curve was developed by substituting the appropriate values into Equation [3] (p. 14) to obtain the maximum speed the fish can attain, relative to the water velocity, and still successfully pass the fishway. Under these circumstances, fish would not be expected to pass the fishway if flows exceeded 122.43 cm/s. Different values of fish length, temperature, and fishway length would yield different maximal values.