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CRITICAL SWIMMING SPEEDS OF YELLOW PERCH *PERCA FLAVESCENS*: COMPARISON OF POPULATIONS FROM A NATURALLY ACIDIC LAKE AND A CIRCUMNEUTRAL LAKE IN ACID AND NEUTRAL WATER

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Summary

The objectives of this study were to determine if environmental acidity reduces swimming performance in the acid-tolerant yellow perch (*Perca flavescens*) and to use swimming performance as an indicator of fitness in testing whether fish from naturally acidic environments perform better in acidic water. Perch from a naturally acidic lake (pH 4·4) or a nearby circumneutral lake were swum after either 5–7 months of laboratory acclimation to simulated soft, natural waters or after more than 2 years of acclimation to hard, circumneutral water. The performance test was a critical swimming speed (U_{crit}) determination, with $5\,cm\,s^{-1}$ velocity increments at 30 min intervals. Low environmental pH (4·0) produced significant decreases in average swimming performance in each of three experimental series. Acid decreased performance in most but not all fish. The two perch populations had similar mean U_{crit} values when swimming in acid water. Pre-acclimation to hard water significantly increased swimming performance. Gravid females acclimated to acid water had very low critical swimming speeds in acid water, whereas U_{crit} changed little in acid water when oogenesis occurred in neutral water.

Introduction

Performance has been advanced as an ecologically relevant way to assess organismal fitness (Arnold, 1986) and physiological compensation to the environment (Huey & Stevenson, 1979). Locomotor performance is easily measurable and can be considered as one component of a selection gradient (Arnold, 1983). Among lower vertebrates, individual differences in locomotor performance have heritable components (Garland, 1988; van Berkum & Tsujii, 1987; DiMichele &

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Powers, 1982). This suggests that exercise performance may be used as an integrated measure of an animal's physiological suitability to an environment, although studies successfully correlating locomotor performance to fitness in a natural environment are rare (Christian & Tracy, 1981; but see Walton, 1988).

For water-breathing osmoregulators, the energetic cost of activity and possibly swimming performance depend on environmental ion composition (Febry & Lutz, 1987; Glova & McInerny, 1977). It is suggested that as environmental ion composition deviates from the regulatory set point of the animal, basal osmoregulatory costs increase, reducing the animal's scope for activity (Beamish, 1978). Changes in gill perfusion (Neumann *et al.* 1983) and blood pressure (Randall & Daxboeck, 1982) may exacerbate net ion losses (Wood, 1988), increasing the cost of ion regulation during exercise and further reducing the scope for activity. Osmoregulatory costs during activity have usually been measured by varying the mineral ion content of the water (Farmer & Beamish, 1969; Febry & Lutz, 1987; Rao, 1968). Although results have generally supported the above hypothesis, the relationship is complex (Febry & Lutz, 1987) and discrepancies exist. Acid–base balance and osmoregulation are inextricably linked in teleosts (Evans *et al.* 1979; Heisler, 1986), and exercise disrupts acid–base balance (Holeton *et al.* 1983; Wood, 1988), so that energetic costs of acid–base regulation and osmoregulation during exercise need to be considered together.

The effect of manipulating environmental H^+ concentration on swimming capacity or cost of swimming has previously been studied only in rainbow trout (*Salmo gairdneri*) (Graham & Wood, 1981; Hargis, 1976; Waiwood & Beamish, 1978; West & Garside, 1986), a species which shows no particular acid tolerance (Audet & Wood, 1988) nor propensity for acidic environments. The yellow perch (*Perca flavescens*) used in this study is the most acid-tolerant Nearctic, perciform fish, as shown by its field distribution and by laboratory acid exposure (Rahel & Magnuson, 1983; Wiebe *et al.* 1934). Populations of this species isolated in naturally acidic, dystrophic lakes show an even greater tolerance to potentially lethal acidity than do perch living in circumneutral lakes (Rahel, 1983). The yellow perch I used originated in a very acid lake (mean pH = 4·4, range 3·5–5·1) and the acid swimming treatment was at an environmentally realistic, but extreme, pH 4·0.

Critical swimming speed (Brett, 1964; see Materials and methods for description) is the common measure of prolonged swimming performance for fish. This parameter has been used most often to determine critical levels of environmental controlling factors such as oxygen and temperature (Beamish, 1978), but effects of toxins and pathogens have frequently been the focus of investigations using critical swimming speed as a response variable (Beamish, 1978). Here I use critical swimming speed to answer three major questions. (1) Does environmental acidity and coincident soft water depress prolonged swimming performance of yellow perch? (2) Do the natural selection and acclimatory processes, which produced acid-tolerant populations of perch, also produce enhanced swimming performance at low pH? (3) Is prolonged swimming performance influenced by acclimation to waters of different hardness?

Materials and methods

The yellow perch populations originated from a dystrophic, naturally acidic lake (Wharton) and a mesotrophic, circumneutral lake (Trout) in Vilas Co., Wisconsin (Table 1; morphometry in Nelson *et al.* 1988). The experiment consisted of three experimental series with two different pre-treatments (Table 2). Fish were transported 360 km to Madison (Dane Co.), Wisconsin, where, for the first experimental series, they were kept in Madison tap water (Table 1). In subsequent series, fish were acclimated to an artificial water designed to mimic their native lake water (Table 1). Perch were swum in artificial lake water at pH 4·0 and 7·8 in a flumé designed to minimize turbulence (Vogel, 1981).

The 17 l laminar-flow swim tunnel (Fig. 1) was modified from the designs of Vogel & LaBarbera (1978) and Vogel (1981). The rectangular working section was constructed of 0·63 cm thick polyvinyl chloride (PVC) 'flat stock', and the return circuit was made from 7·6 cm diameter PVC piping. The working flume was 1 m long, 10 cm high and 10 cm wide; 50 cm of the 1 m length was available to swimming fish. An opaque cover with a shuttered window reduced surface waves and external disturbance while allowing access to the fish. Flowing water was straightened with an 'egg crate' fiberglass collimator preceding the propeller, and by a soda straw array (Vogel & LaBarbera, 1978) at the upstream end of the working section. A nylon bushing embedded in the downstream collimator eliminated wobble of the propeller shaft. Metal surfaces either did not leach or were painted with epoxy paint to eliminate leaching. An 18·7 W Heller motor drove the 7·6 cm diameter stainless-steel propeller. Motor control was provided by a Heller GT-21 controller which maintained a steady rate when encountering line current or viscosity fluctuations.

Calibration of the swim tunnel and visualization of flow was by cinematography. Dye suspension was released at the upstream end of the tank and photographed at

Table 1. *Chemical composition of water types*

Water type	Ion concentrations (mequiv l^{-1})						Alkalinity (mequiv l^{-1})	pH
	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}		
Wharton Lake	0·017	0·009	0·05	0·027	0·004	0·031	0	4·4
Trout Lake	0·07	0·018	0·584	0·255	0·037	0·031	0·54	7·6
Artificial Wharton	0·016	0·001	0·015	0·020	0·006	0·238	NM	*
Artificial Trout	0·048	0·003	0·354	0·313	0·019	0·021	NM	7·8
Madison tap	0·0522	0·051	4·32	2·72	0·138	0·177	5·72	7·8

* pH varied; 4·0 during swimming, 4·7–4·9 during acclimation.

NM, not measured.

Water chemistry data were provided by Doug Lindelof, University of Wisconsin, Department of Geology.

Cation concentrations were determined by atomic absorption spectrophotometry and anion concentrations by ion chromatography.

Data for Madison tap water were provided by the Madison Public Utility.

Table 2. *Experimental series description: capture characteristics, acclimation conditions, and experimental procedure summarized for each of the experimental series*

Treatment	Experimental series					
	Series I		Series II		Series III	
	Trout Lake	Wharton Lake	Trout Lake	Wharton Lake	Trout Lake	Wharton Lake
Capture						
Date	June 1984; August 1985		June 1987	May 1987	September 1987	
Lake temperature (°C)	13·7; 18	15·4; 17	18·9	15·0	16·8	17·0
Fish mass range	22·1–96·5 g	21·5–75·8 g	20·5–69 g	31–70 g	30–132 g	24·5–66 g
Laboratory acclimation						
Duration	2–3 years		4 months	5 months	7 months	
Average temperature (°C)	Seasonally fluctuating 2–20 then: 15·0	15·2	15·0	14·9	14·8	14·8
Photoperiod (L:D)	Natural then 12 h:12 h		12 h:12 h		12 h:12 h	
Water type	Madison tap water		Artificial lake water		Artificial lake water	
Experimental conditions						
Date	July–September 1987		November–December 1987		April–May 1988	
Temperature (°C)	15		15		15	
Sex	Mixed		Mixed		Mostly female	

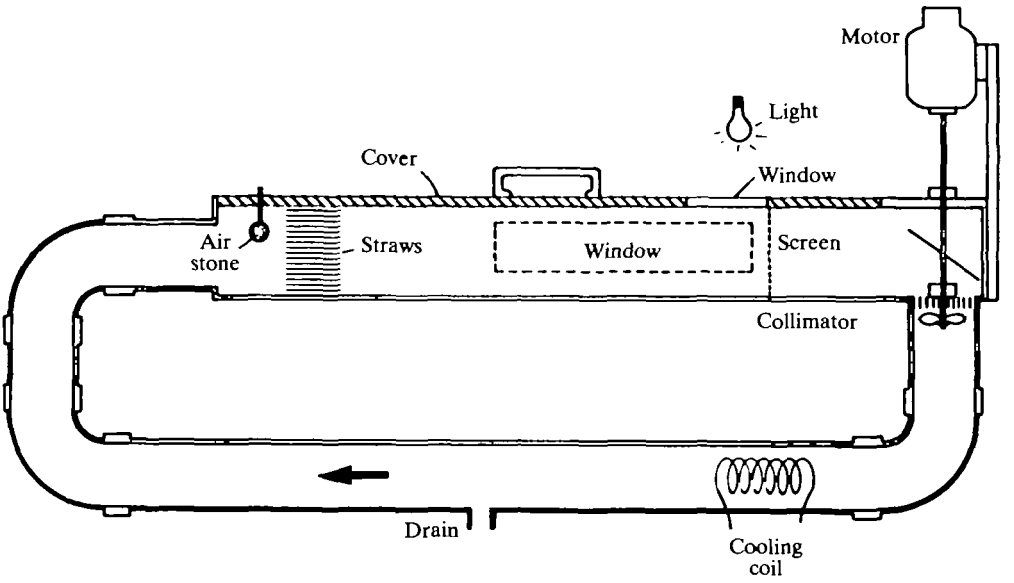

Fig. 1. Schematic diagram of the swim chamber designed after Vogel & LaBarbera (1978). Arrow shows direction of water flow.

64 frames s^{-1}. Film frames were counted to calculate water velocity. Water velocity was calibrated to the revolutions of the propeller shaft measured with a Cole-Parmer model 8211 digital tachometer. Flow appeared laminar at all speeds over the entire working section of the tank, and increased linearly with motor revolutions over the range bracketing perch swimming speeds:

$$\text{velocity (cm s}^{-1}) = 0{\cdot}028R - 4{\cdot}3 \qquad r^2 = 0{\cdot}92\ ,$$

where R is the propeller rate in revs min^{-1}.

Critical swimming speed (Brett, 1964) was determined with 5 cm s^{-1} step increases of water velocity every 30 min. Motivation was provided by a light gradient requiring the fish to swim into the current to remain at low light levels (Fig. 1). This was sufficient for most fish at low to intermediate current speeds, but an 8 V electric field was placed across the back of the flume to prevent uncooperative fish from resting there. The electric field was switched off before speeds close to exhaustion were reached (25 cm s^{-1}). Manual prodding with a blunt probe was used to exhaust most fish completely. Exhaustion was defined by the inability of a fish to keep off the downstream retaining screen when prodded. Each fish was swum to exhaustion once, whereupon it was allowed to return to the front of the working section at a reduced velocity before resuming exercise (Smit *et al.* 1971). For fish continuing to swim after returning to their original velocity, the second time exhaustion was reached was taken as an endpoint. Most fish went into a burst locomotor phase 30–45 min before exhaustion. In this phase, fish drifted back with the current and then rapidly swam upstream upon reaching the light

source. Timing the onset of this behavior was not possible because some fish used this form of locomotion throughout their swim and others, that attempted to use fins as depressors to maintain station, mimicked this locomotor style.

Temperature was regulated about 15 ± 1 °C throughout the 16 h acclimation and the swim, and was measured before and after each acclimation and at 30 min intervals during swimming periods. The pH was measured before and after each acclimation, exercise or recovery period with an Orion 399A ion analyzer and Ross electrode. Adjustments of pH were always made with analytical grade H_2SO_4 and NaOH.

Perch from Wharton and Trout Lakes were captured with fyke nets and by angling and transported to Madison in their native lake water containing antibiotics. Fish were kept in 500 l fiberglass aquaria (Frigid Units–Living Streams) in dechlorinated, slowly moving Madison tap water (Table 1). Immediate placement of fish into the simulated lake waters after transport resulted in large mortality in earlier attempts, so fish for series II and III were initially held in Madison tap water for 5 (series II) or 10 (series III) weeks. The perch were then gradually changed to artificial lake water. Artificial Wharton Lake water for holding purposes was a 100:1 dilution of Madison tap water with distilled water, acidified to pH 4·7 ± 0·43 (S.D., series II) or 4·9 ± 0·80 (series III). Artificial Trout Lake water was a 10:1 dilution of Madison tap water, pH 7·8. Water conditions were kept relatively constant by a 20 % water change each day (100 l). Series III differed from series II in utilizing mostly ripe, gravid females.

For the first experimental series, photoperiod and temperature were kept approximately natural until the 1987 vernal equinox, when fish were switched to a constant 12 h:12 h L:D photoperiod and gradually raised to 15 °C (15·0 ± 0·46, Trout; 15·2 ± 0·68, Wharton; Table 2) for the remaining 110 or more days of acclimation. For series II and III, holding tank temperatures were: 14·9 ± 0·5 °C, (Wharton) and 15·0 ± 0·5 °C (Trout) for series II and 14·8 ± 0·85 °C (Trout) and 14·8 ± 0·73 °C (Wharton) for series III, and were measured daily along with pH. The photoperiod was 12 h:12 h L:D throughout. Fish were fed a regular diet of live bluntnose and fathead minnows (*Pimephales* sp.) and were supplemented seasonally with fresh zooplankton. Feeding live food and keeping the perch in a current were attempts to minimize captivity-induced changes in activity metabolism (Somero & Childress, 1980).

Treatment order was selected randomly. Perch were acclimated in the swim tunnel at 3 cm s^{-1} for 16 h before swimming. They were swum in either artificial Wharton Lake water at pH 4·0 or artificial Trout Lake water at pH 7·8 between 06.00 h and 15.00 h Central Standard Time, and 40–88 h after feeding. Artificial lake waters were always mixed at least 24 h before use and continuously aerated until use, during acclimation and the swimming treatments. Intermittent checks of oxygen content and carbon dioxide tension always showed an oxygen saturation greater than 80 % (Orion 97-08 O_2 electrode) and P_{CO_2} less than 0·133 kPa (Radiometer BMS-3).

Data were analyzed using the general linear models (GLM) procedure of the

statistical analysis system (SAS, 1982). The general model was a two-way unbalanced analysis of covariance (ANCOVA), with population and swimming treatment as the class variables and size as the covariate. Trout Lake perch in series III were also analyzed separately by sex and maturity, pooling males and immature females. Tukey's multiple-comparison test was used to compare means, the recommended test for unbalanced designs (SAS, 1982).

Results

General effects

Body size was intentionally limited in this study, contributing to the small size effect on critical swimming speed (Fig. 2). Critical swimming speed was positively and significantly ($P < 0{\cdot}05$) related to body mass:

$$U_{crit} = 0{\cdot}102m + 30{\cdot}3\ ,$$

where m is the mass in grams and U_{crit} is measured in $cm\,s^{-1}$. However, the regression explained only 4 % of the variance in critical swimming speed. The order in which a fish swam in a given series did not significantly influence its critical swimming speed, explaining less than 1 % of the variance.

Treatment effects

Regardless of population or acclimation conditions, swimming in acid water reduced the critical swimming speed of yellow perch (Fig. 3). This effect was significant for all cases (ANCOVA, $P < 0{\cdot}0001$), for both Trout and Wharton Lake

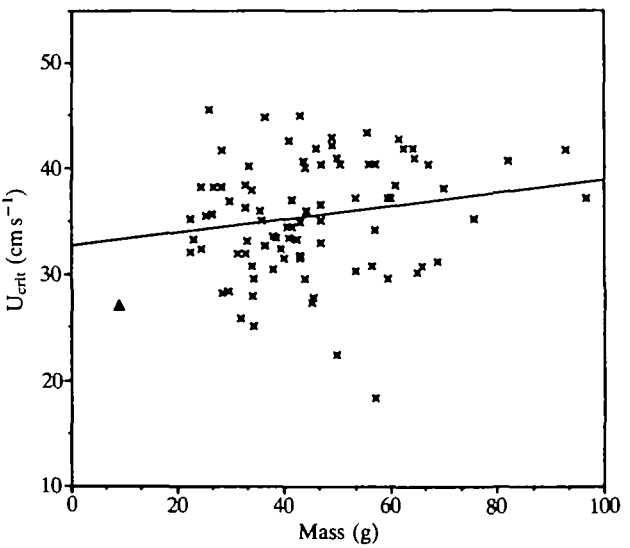

Fig. 2. Critical swimming speed (U_{crit}) as a function of body mass in yellow perch. Fish from all treatments are presented. An estimated U_{crit} from Otto & Rice (1974) is also included (▲).

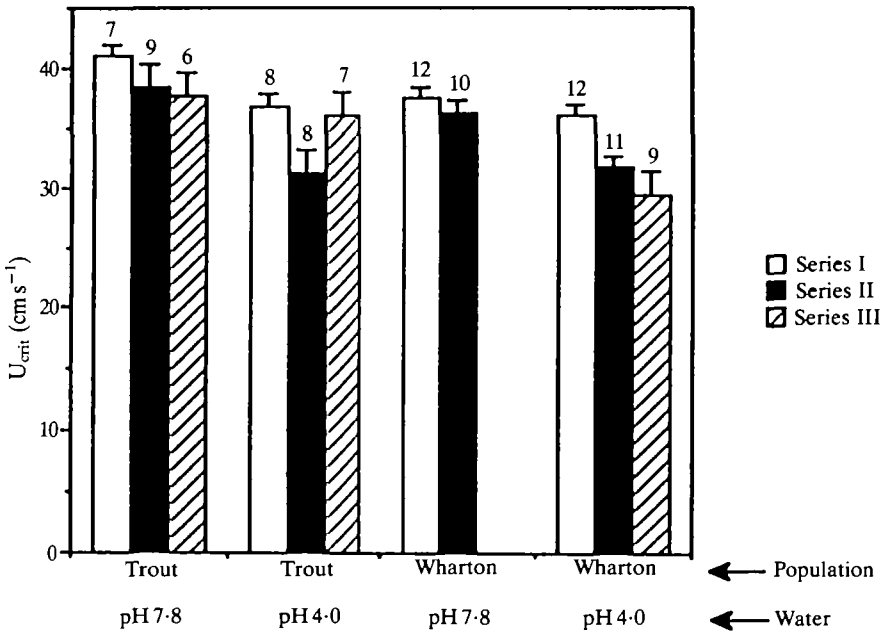

Fig. 3. Critical swimming speeds of perch. Means ± 1 S.E. of U_{crit} and N are shown for each combination of population and swimming treatment. Series I: perch acclimated to Madison tap water for a minimum of 2 years. Series II: perch acclimated for a minimum of 4 months in an artificial water designed to mimic their native lake conditions (Table 1). Series III: perch acclimated for a minimum of 7 months in an artificial water designed to mimic their native lake conditions (Table 1). Fish were mostly gravid females and no fish from Wharton lake were swum at pH 7·8.

populations considered individually ($P < 0{\cdot}001$), and for each experimental series in isolation ($P < 0{\cdot}01$). Within-population depression of critical swimming speed by soft, acid water was significant for Trout Lake perch in series II ($P < 0{\cdot}05$).

Results from population mean comparisons are presented in Table 3. Few differences in the size-adjusted critical swimming speeds between populations of perch from Wharton and Trout Lakes were apparent in acid water, but Trout Lake perch swam significantly better than Wharton Lake perch in pH 7·8 water for the

Table 3. *Size-adjusted statistical significance of swimming treatments*

Entire experiment	Tr, 7·8^{a}	Wh, 7·8^{a}	Tr, 4·8^{b}	Wh, 4·0^{b}
Series I	Tr, 7·8^{c}	Wh, 7·8^{c,d}	Tr, 4·0^{c,d}	Wh, 4·0^{d}
Series II	Tr, 7·8^{c}	Wh, 7·8^{c,d}	Wh, 4·0^{d,e}	Tr, 4·0^{d,e}
Series III	Tr, 7·8^{c}	Tr, 4·0^{c,d}	Wh, 4·0^{e}	

Treatments marked with the same letter are not different at the $P < 0{\cdot}05$ level (ANCOVA).

Population is listed first, followed by the swimming water pH. Tr, Trout Lake; Wh, Wharton Lake.

Treatments are listed from left to right in order of decreasing U_{crit}.

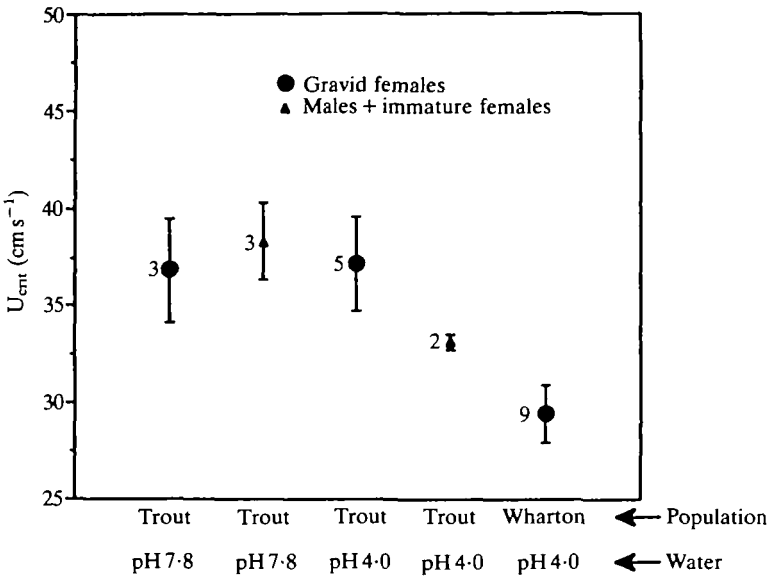

Fig. 4. Experimental series III separated by sex and reproductive condition. Means ± 1 S.E. of U_{crit} and N are shown for each combination of sex, population and swimming treatment.

entire experiment ($P < 0{\cdot}05$). Egg production decreased swimming performance only in Wharton Lake perch maturing eggs in acid water. Paradoxically, swimming performance in gravid females from Trout Lake was unaffected by acid water. This was noticeable both when comparing series II with series III (Fig. 3) and when gravid fish were compared with the two non-gravid fish from this treatment in series III (Fig. 4).

Fish acclimated to hard, circumneutral tap water had significantly higher critical swimming speeds than fish acclimated to soft, artificial lake water ($P < 0{\cdot}05$). This effect was particularly noticeable when fish swam in acid water (Fig. 3).

Discussion

Estimates of perch critical swimming speeds and the variability in those estimates agree well with values reported in the literature. The ranges and mean values of critical swimming speeds correspond to speeds determined by Beamish (1970), who used a similar protocol with largemouth bass (*Micropterus salmoides*) of similar total length. Otto & Rice (1974) report U_{crit} values of 33 cm s^{-1} for yellow perch acclimated to 20°C and 21 cm s^{-1} for perch acclimated to 10°C. Linear interpolation of their results yields estimated U_{crit} at 15°C of 27 cm s^{-1} for 8 g yellow perch, well within the confidence limits of my results (Fig. 2). Unfortunately, Otto & Rice (1974) report no measure of variability. Sandstrom (1983) reports an average range (±3 S.D.) of 18 % of the mean for European perch swimming against a rotating flow. This value is nearly identical to the ranges I

Table 4. *Variation in critical swimming speeds ($cm\,s^{-1}$)*

	pH 7·8					pH 4·0				
Series	*N*	Low	High	Mean	Coefficient of variation	*N*	Low	High	Mean	Coefficient of variation
Series I	19	30·7	45·5	38·8	10·4	20	31·4	44·8	36·3	9·7
Series II	19	30·2	42·8	37·3	11·6	19	18·3	40·0	31·4	15·6
Series III	6	33·4	42·0	37·6	9·8	16	22·3	43·3	32·3	17·4

The populations are pooled under the pH in which they swam.
Ranges, means, and coefficients of variation are reported.

report for yellow perch swimming in neutral water (Table 4), suggesting that a coefficient of variation around 10 is representative for perch.

Spending more than 2 years in laboratory aquaria had no effect on U_{crit} of yellow perch. Fish held in Madison tap water for 2–3 years showed improved performance ($P < 0{\cdot}05$; Fig. 3). Garland *et al.* (1987) and Gleeson (1979) reported a similar lack of decline in endurance performance in captive lizards.

Acid effects

This study confirms that levels of hydrogen ions encountered *in situ* can act to limit prolonged swimming capacity of yellow perch. Using Fry's (1971) paradigms, critical swimming speed in fish is controlled by factors such as temperature (Beamish, 1978) and morphology (Webb, 1975), and limited by factors such as oxygen, carbon dioxide, pollutants and disease (Beamish, 1978). Presumably, hydrogen ion levels and salinity can also act as limiting factors, but these have not been adequately tested.

Mean swimming performance of two yellow perch populations is significantly reduced in soft, pH 4·0 water. Using rainbow trout (*Salmo gairdneri*), Graham & Wood, (1981), Waiwood & Beamish (1978) and West & Garside (1986) investigated how reduced environmental pH influenced swimming capacity. Waiwood & Beamish (1978) found no effect on U_{crit} when the pH was reduced to 6·0, but West & Garside (1986) found a significant depression of U_{crit} at pH 5·6. Graham & Wood (1981) also found a linear decrease in U_{crit} as pH was progressively depressed below pH 4·6. Holeton & Stevens (1978) found that mildly acidic 'black' water from the Rio Negro, Brazil (pH 5·9–6·3) apparently increased relative swimming speed in a group of *Triportheus angulatus* compared with fish swimming in 'white' circumneutral water from the Rio Solimões. Conversion of their results into absolute velocities (using a mass *vs* length regression for yellow perch) and correcting for temperature differences [using a U_{crit} *vs* temperature regression from Beamish's (1970) results] reveals that *Triportheus angulatus* acclimated to white water and swum in black water had reduced critical swimming speeds (from 53·5 to 43·5 $cm\,s^{-1}$; $N = 11$), whereas fish acclimated to black water and swum in

black water had roughly similar U_{crit} values to controls (from 53·5 to 54·8 cm s^{-1}; $N = 5$).

Soft, acid water reduces mean critical swimming speed in perch by affecting only some individuals (Table 4). In two of the three experimental series, the range of critical swimming speeds approximately doubled and the coefficient of variation increased similarly when fish swam in acid water, whereas maximal velocities were roughly equal for fish in acid and neutral water. This means that isolated individuals were capable of performing at the same level in acid water as top performers in neutral water, yet many individuals had their swimming ability impaired in acid water, producing significant reductions of mean U_{crit} for the population. Interestingly, when fish were acclimated to hard, Madison tap water (Table 1; Fig. 3), the ranges of swimming speeds were identical in acid and neutral water, and acid water only affected swimming performance in Trout Lake perch. This result immediately implicates ionoregulatory problems as a source of reduced swimming ability in acid water, although perhaps spuriously. Series I was conducted in mid-summer (Table 2), whereas the other series were conducted in spring and autumn. Sandstrom (1983) reported a circannual rhythm of locomotor capacity, independent of temperature, in European perch. A similar rhythm in yellow perch could have caused the higher critical swimming speeds in series I, although Graham & Wood (1981) also found that harder water slightly increased U_{crit} at low pH levels.

The available evidence suggests that diminished swimming speeds in acid water resulted from increased osmoregulatory and/or acid–base regulatory costs during exercise. Measurements of standard or routine oxygen consumption at reduced environmental pH have spanned the range from reduced to increased O_2 consumption (reviewed in Wood & McDonald, 1982). Extremely low pH values that foster branchial mucus secretion clearly cause oxygen consumption to decline (Ultsch *et al.* 1980; Packer & Dunson, 1972), yet oxygen delivery is not the main factor limiting prolonged swimming performance by yellow perch. If it were, the higher hemoglobin concentration (Nelson *et al.* 1988) and lower P_{50} (G. A. Slater & J. A. Nelson, unpublished observation) in the blood of Wharton Lake perch would enhance their swimming performance at low pH. This was not observed. Whether an increase in resting osmoregulatory or acid–base regulatory costs results from mild levels of acid exposure should be examined further.

During exercise, measurements of increased costs from mild acid exposure are less equivocal. Hargis (1976) measured metabolic rate and ventilation frequency in young rainbow trout at two swimming speeds, and reported that both tended to be higher at pH 6 than at pH 7 or 8. Waiwood & Beamish (1978) reported that rainbow trout swimming at pH 6·0 showed significantly greater oxygen consumption than trout swimming at pH 7·75 over a range of swimming speeds from 20 to 50 cm s^{-1}. These studies suggest that perch swimming in acid water have relatively greater costs during the determination of critical swimming speed and possibly also the 16 h acclimation at low swimming speed, contributing to earlier fatigue.

Differences in ionic strength between the two water types could also have

reduced the scope for activity in perch. Febry & Lutz (1987) found that resting metabolic rates of tilapia were lower in fresh water than in isosmotic or full strength sea water. However, the cost of swimming gradually increased in fresh water relative to the other two conditions until, at higher swimming speeds, swimming in fresh water was most expensive. Extrapolating this result to the different ionic strength fresh waters used here suggests that the cost of swimming in artificial Wharton Lake water would gradually have increased relative to that in the artificial Trout Lake water as swimming speed increased.

A likely alternative to the hypothesis that cost of activity increased in acid water is that hydrogen ions directly limit exercise performance. Proton uptake or decreased proton excretion may have increased the fixed acid load in perch swimming in soft, acid water. In support of this, Van den Thillart *et al.* (1983) caused H^+ excretion to decrease in swimming coho salmon (*Oncorhynchus kisutch*) by lowering seawater pH from 8 to 7·1. Although no additional extracellular acidosis is found in perch swimming in acid water (J. A. Nelson, unpublished observation), additional acidification of intracellular fluid could have inhibited glycolytic flux (Jones *et al.* 1977; but see Dobson *et al.* 1986), contributing to the limited swimming performance.

Egg production and water acidity interacted to influence critical swimming speed in series III. Gravid females from Wharton Lake had significantly worse swimming performance in acid water than gravid females from Trout Lake in this series (Figs 3, 4), probably reflecting the physiological strain of producing eggs in acid water (Chulakasem, 1987; Lee & Gerking, 1980), and the greater allocation of body reserves to reproduction in Wharton Lake perch (J. A. Nelson & J. J. Magnuson, unpublished observation). The lack of diminished exercise performance in gravid Trout Lake perch swimming in acid water is currently unexplained.

Population differences

The second purpose of this study was to assess exercise performance as an integrated measure of physiological fitness. Exercise performance has been suggested as a relevant laboratory assessment of Darwinian fitness (Arnold, 1986; Huey & Stevenson, 1979). Ware (1982) has argued that fish are selected for maximization of surplus available energy. Critical swimming speed is a possible way to assess available energy. In addition, locomotor performance has been shown to correlate with competitive advantage in fish (Castleberry & Cech, 1986). In this context, I tested whether fish in naturally acidic waters showed evidence of compensating to their environment by exhibiting enhanced swimming performance in soft, acidic water.

Perch from the naturally acidic Wharton Lake never had a higher critical swimming speed in acid water than did perch from the circumneutral Trout Lake. The only significant interpopulation difference in critical swimming speeds at low pH occurred in series III: swimming performance of gravid females from Wharton Lake was poorer in acid water. The relatively lower critical swimming speed of Wharton Lake perch in neutral water (Fig. 3) offers some evidence for adaptation

of exercise performance. The mean decrease in swimming performance in these two series from neutral to acidic water was less for Wharton Lake perch ($-1{\cdot}47\,cm\,s^{-1}$ series I; $-4{\cdot}59\,cm\,s^{-1}$ series II) than for Trout Lake perch ($-4{\cdot}46\,cm\,s^{-1}$ series I; $-7{\cdot}19\,cm\,s^{-1}$ series II).

These results do not overwhelmingly support the use of locomotor performance to assess physiological compensation to natural acidity in fish. Using white muscle buffering capacity, Nelson & Magnuson (1987) suggested that burst locomotor capacity was also identical between populations. However, the increased tolerance of Wharton Lake perch to lethal acidity (Rahel, 1983), their increased blood oxygen-carrying capacity (Nelson *et al.* 1988), various muscle metabolite and blood acid–base and ion differences (J. A. Nelson, unpublished results), and the weak evidence for resilience of swimming performance, all attest to some degree of acclimatization or adaptation in the Wharton Lake population.

In conclusion, the results show that acidic, but environmentally realistic, water reduces prolonged swimming performance of yellow perch. The impaired performance may have several causes. In individuals affected by acid water, substrate availability could determine fatigue time. Increased osmoregulatory and/or acid–base regulatory costs exhaust the limiting resource sooner, lowering U_{crit}. The effect of hard-water acclimation can be explained if the gill were to bind greater amounts of Ca^{2+} in hard water. Then the leaching of Ca^{2+} from the gills in acid water (Marshall, 1985; McWilliams, 1983) would be less important, and calcium could exert its ameliorating effect on ion flux rate and permeability upsets at low pH (McDonald, 1983; Wood & McDonald, 1982). In the perch minimally influenced by acid water, substrate is not limiting and fatigue is determined by other factors (such as intracellular acidosis or lactate accumulation) and is not affected by the increased costs of acid–base or ion regulation in acid water. The best alternative to this explanation is that those perch whose swimming performance is insensitive to soft, acid water are individuals with minimal changes in branchial permeability or ion transport kinetics in acid water.

A perch population isolated for 2000–3000 generations in a naturally acidic lake in northern Wisconsin did not have higher absolute swimming speeds in acid water, but their swimming performance was less affected by soft, acid water than conspecifics from a circumneutral lake.

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