

Research article

Non-horizontal locomotion in blue and channel catfish

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Abstract

The purpose of this study was to examine the non-horizontal locomotion of blue and channel catfish. Ten blue and channel catfish were swum at each of nine angles (0° , $\pm 15^\circ$, $\pm 30^\circ$, $\pm 45^\circ$, $\pm 60^\circ$) using a critical swimming speed (Ucrit) protocol. Critical swimming speed, metabolic rate, cost of transport, and tail beat frequency were determined for each fish and regression curves were constructed. Blue catfish had a significantly lower Ucrit than channel catfish when swimming at -15° ($P=0.03$), 0° ($P=0.0002$), $+15^\circ$ ($P=0.0004$), $+30^\circ$ ($P=0.03$), and $+60^\circ$ ($P=0.05$). Both species demonstrated a linear decrease in Ucrit with a corresponding increase in swimming angle. However, blue catfish showed no significant differences in swimming performance compared to horizontal swimming when the angle of decline increased, while channel catfish demonstrated a non-linear swimming ability with an increasing decline angle. Significant differences between blue and channel catfish oxygen consumption (-60° , $p=0.002$; $+45^\circ$, $p=0.006$), total cost of transport (-60° , $p=0.0004$; -45° , $p<0.0001$; -30° , $p<0.0001$; -15° , $p<0.0001$; $+60^\circ$, $p=0.04$), net cost of transport (-30° , $p<0.0001$), and tail beat frequencies (-60° , $p=0.001$; 0° , $p<0.0001$; $+15^\circ$, $p=0.03$) also were found. Calculations of burst and glide swimming based on these data show a maximum possible energy savings of 49.5% and 42.6% for blue and channel catfish, respectively, at a 60° burst angle and a 15° glide angle. The results of this study indicate that measurable differences exist between swimming performance of these two closely related species relative to angles of incline or decline. **Copyright © www.acascipub.com, all rights reserved.**

Keywords: blue catfish, channel catfish, swimming, metabolism, respiration

Introduction

Non-horizontal locomotion has been studied in many terrestrial animals, and inclined locomotion has been shown to increase metabolic rate more so than level locomotion (19, 24, 45, 46). Most studies conducted on non-horizontal locomotion have been made using animals running horizontally or uphill, but rarely downhill. Thornton et al. (46) studied the effect on horses of horizontal and incline exercise with and without a load. Although, their study determined oxygen consumption increased with incline, speed and load, the biggest change in metabolic rate was

due to incline. The incline allowed them to obtain the same effect at slow speeds as the horizontal did at high speeds. For humans, energy expenditure over a range of angles and speeds appears to be linear (34). However, net cost of transport (cal/kg/km) has been found to be independent of speed, and only related to incline (34). Cerretelli et al. (20) also found the net cost of transport to be independent of speed for dogs.

In the few studies that tested locomotion on a decline, metabolic rate decreased to that of horizontal locomotion (5, 34, 37). Armstrong et al. (5) tested the effect of running up an incline and down a decline on rats and found that the slope of the regression line relating speed to oxygen consumption was significantly steeper for uphill runners than the slope of the regression line for downhill runners. All slopes were significantly different from horizontal locomotion.

Historically, studies to determine swimming performance, efficiency, and optimal speed in fishes have been conducted in swimming chambers that force fish to swim horizontally against a water flow (reviews in 8, 48). However, fish often swim in a manner other than horizontally during their daily activities. Fish swim non-horizontally for several reasons including: (1) prey capture or predator avoidance; (2) vertical migration; (3) ascending fish ladders, fishways, or waterfalls; and (4) burst and glide swimming to maximize swim efficiency (14) during migrations. Although the energetics and biomechanics of non-horizontal locomotion have been studied for terrestrial mammals (19, 20, 24, 34, 45, 46, 53), it has not been investigated for fishes.

Since studies on terrestrial mammals have shown the elevated cost of incline locomotion, non-horizontal swimming may represent a larger component of a fishes' activity output. Therefore, studying the energetics of non-horizontal swimming in fishes is important. The purpose of this study was to compare the following variables in blue, *Ictalurus furcatus* (Rafinesque) and channel, *I. punctatus* (Rafinesque), catfish: (1) critical swimming speed at each angle tested; (2) swimming energetics at each swim speed and angle tested; and (3) energy savings associated with burst and glide swimming.

Materials and methods

Animal Maintenance

One-year-old juvenile blue and channel catfish fingerlings used for this study were obtained from 0.10-ha ponds at the U.S. Department of Agriculture-Agriculture Research Service (USDA-ARS) Fish Genetics Unit in Stoneville, MS, USA. Fish selected for testing were held in laboratory tanks for a minimum of one week before swimming trials. Fish were hand-fed once daily until apparent satiation, as judged by cessation of feeding activity, using a nutritionally complete (35) commercial 32% protein catfish feed purchased from Delta Western Feed Mill, Indianola, MS, USA. Fish selected for testing were not fed for 36 h prior to the beginning of swimming trials to ensure a post-absorptive state (36). Water in the laboratory tank and swim chamber was maintained at ambient room temperature (19-21°C).

Swimming Protocol

A tilting tunnel swimming respirometer based on the design of Blazka et al. (15) and described in Beecham (9) was used to compare swimming energetics and performance. This swim tunnel could be set at inclining or declining angles from 0° to ± 90° (**Fig. 1**). The swim chamber water flow rate was calibrated using a Swoffer Instruments Current Sensor (Model 2100, Seattle, WA, USA).

Fish were tested at 0°, ±15°, ±30°, ±45°, and ±60° angles. Ten channel and ten blue catfish were tested at each angle, no fish were swum more than once, and selection of species and test angle were randomized. Swimming in these tests was forced rather than voluntary and swimming capabilities rather than swimming preferences were measured. Mean (± s. e. m.) standard lengths (SL) were 19.3 ± 0.2 cm for blue catfish and 19.4 ± 0.2 for channel catfish; mean (± s. e. m.) weights were 95.6 ± 2.1 g for blue catfish and 100.2 ± 2.6 g for channel catfish. Fish were transferred from holding tanks with a dip net and quickly placed inside the swim tunnel, where they were allowed to acclimate for 2 h at 10 cm/s. After this acclimation period, the water velocity was increased by 10 cm/s every 30 min until the fish fatigued. Fatigue was defined as the point at which the fish could no longer maintain position in the chamber and became impinged on the rear grating of the swim chamber. Critical swim speed (Ucrit) was

calculated using Brett's (17) equation:

$$U_{crit} = u_1 + (u_2)(t_1/t_2)$$

Where u_1 is the highest velocity maintained for the prescribed period of time, u_2 is the velocity increment (10 cm/s), t_1 is the time (min) fish swam at fatigue velocity, and t_2 is the prescribed period of swimming (30 min). Because fish used in this study had a cross sectional area less than 10% of the cross sectional area of the working section of the swim tunnel, no corrections for solid blocking were necessary (17, 42).

Oxygen consumption and water temperature were measured at 1 min intervals using a calibrated model 52 DO meter (YSI, Inc., Yellow Springs, Ohio, USA) with a probe mounted in the swim chamber top. Ending dissolved oxygen concentrations were never < 5 mg/L. Oxygen consumption (VO_2 , mg O_2 /g/hr) was calculated for each speed at each angle and the metabolic rate (MR, cal/g/hr) was determined using the oxycaloric coefficient of 3.25 cal/mg O_2 (16). Standard metabolic rate (SMR) was estimated by plotting oxygen consumption against swim speed of each individual fish and extrapolating the lines for each fish at each angle to zero activity (3, 7, 13, 23, 26). SMR was then averaged for each fish at each angle. All SMR values for individual species were also averaged together. Active metabolic rate (AMR), or the highest metabolic rate observed, was determined for each individual fish at each angle. Scope for activity (SFA), defined by Fry (27) as the amount of energy available for swimming, was determined by subtracting the averaged estimate of SMR from the average observed AMR at each angle. Total cost of transport (TCOT) was calculated using the method of Schmidt Nielsen (38), where the metabolic rate was divided by the swim speed (cm/s). Net cost of transport (NCOT) was calculated by subtracting the SMR from each data point and then calculating COT using the method of Schmidt Nielsen (38). Swimming respiration and swimming performance tests were measured simultaneously. Standard length (SL) to the nearest 0.1 cm, weight (WT) to the nearest 0.01g, and sex were obtained for each fish at the conclusion of each test.

Burst and Glide Calculations

The amount of energy consumed by employing burst and glide swimming (14) at various angle combinations was compared to the amount of energy consumed swimming an equal horizontal distance. Burst swimming in this case does not imply anaerobic swimming. Calculations were only made on angle combinations where the burst swimming angle was greater than the glide angle. Fish were assumed to swim at their optimal swimming speed for each angle. The glide energy consumption was based on the SMR for the glide angle. The energy consumed (cal/g/km) was multiplied by the distance traveled. The total amount of energy consumed for the burst and glide phases was subtracted from the amount of energy needed to swim the horizontal distance and that energy savings was presented as a percent of the cost to swim horizontally.

Statistical Analysis

Regression analysis was used to describe the relationships between the species, angle tested, swim speed, and the dependent variables (U_{crit} and VO_2). Analysis of covariance (ANCOVA) was used to determine differences between the species, angle tested, and the following dependent variables: U_{crit} , VO_2 , SMR, AMR, SFA, TCOT, and NCOT. Data were analyzed with SAS 9.1 (SAS Institute Inc., Cary, NC, USA), significance testing was at the 0.05 probability level, and post hoc tests (LSMEANS) were used to determine differences.

Results

U_{crit}

Blue catfish had a significantly lower U_{crit} than channel catfish when swimming at -15° ($P=0.03$), 0° ($P=0.0002$), $+15^\circ$ ($P=0.0004$), $+30^\circ$ ($P=0.03$), and $+60^\circ$ ($P=0.05$). However, it is noteworthy that blue catfish mean U_{crit} was lower at all angles tested. As the angle of incline increased, the U_{crit} of channel and blue catfish decreased linearly from that when swimming horizontally (**Fig. 2**). For both species, the U_{crit} at $+15^\circ$ was the only U_{crit} at inclining angles that was not significantly different from horizontal. However, at declining angles, channel catfish demonstrated a non-linear decline in swimming ability (**Fig. 3**). For channel catfish, the U_{crit} at -15° ($P=0.0056$) was significantly lower than the U_{crit} while swimming horizontally, and reached a minimum at -30° ($P=0.0001$). After this minimum, the U_{crit} increased as angle of decline further increased. The U_{crit} of channel catfish

swimming at -60° showed no statistical difference ($P=0.36$) from the Ucrit of fish swimming horizontally. For blue catfish, Ucrits for all declining angles tested were not significantly different from horizontal swimming. A regression model was fit to the Ucrits for incline and decline swimming for both species. The relationship between Ucrit and inclining angles was linear and was expressed by: $Y = -0.27 X + 52.0$, $R^2 = 0.61$ for blue catfish; and $Y = -0.34 X + 59.32$, $R^2 = 0.62$ for channel catfish (**Fig. 2**). The relationship between Ucrit and declining angles was quadratic and was expressed by: $Y = 0.0050 X^2 + 0.22 X + 51.41$, $R^2 = 0.23$ for blue catfish; and $Y = 0.0078 X^2 + 0.48 X + 59.23$, $R^2 = 0.25$ for channel catfish (**Fig. 3**).

Oxygen Consumption and Metabolic Rate

Oxygen consumption rates were significantly different between species ($P<0.0001$), among swimming angles ($P<0.0001$), and speeds ($P<0.0001$), and there was a significant interaction between species and angle ($P<0.0001$). The VO_2 at speeds of 10 and 20 cm/s did not significantly differ, whereas all other speeds were significantly different and differed from each other. Overall, the VO_2 increased as the angle of incline increased for both blue and channel catfish with the exception of $+15^\circ$, which was less than the VO_2 of horizontal swimming for both species (**Fig. 4**). However, at declining angles, the VO_2 decreased as angle of decline increased only for the blue catfish. The VO_2 for channel catfish at declining angles was lowest for fish swimming horizontally.

When the SMR, AMR, and SFA of each species at each angle was analyzed, significant differences between the species (SMR, $P<0.0001$; AMR $P<0.0001$), the angles (SMR, $P=0.025$; AMR, $P=0.02$; SFA, $P=0.009$), and a species*angle interaction was observed ($P=0.0003$, **Table 1**). A significant difference in the overall mean (\pm s.e.m.) SMR for blue (0.149 ± 0.02 mg O_2 /g/hr) and channel (0.299 ± 0.04 mg O_2 /g/hr) catfish was found ($P=0.04$). A significant difference in overall mean (\pm s.e.m.) AMR for blue (0.461 ± 0.02 mg O_2 /g/hr) and channel (0.696 ± 0.05 mg O_2 /g/hr) catfish was found ($P=0.0001$). A significant difference in overall mean (\pm s.e.m.) SFA for blue (0.311 ± 0.03 mg O_2 /g/hr) and channel (0.423 ± 0.04 mg O_2 /g/hr) catfish was found ($P=0.0014$).

The TCOT was significantly different for species ($P<0.0001$), angle ($P<0.0001$), and speed ($P<0.0001$), and two-way interactions were found for species*angle ($P<0.0001$), species*speed ($P<0.0001$), and angle*speed ($P=0.0017$). There were no significant differences in TCOT between speeds of 20 and 30 cm/s or 30 and 40 cm/s, but all other speed combinations were significantly different. Overall, the TCOT increased as the angle of incline increased for both blue and channel catfish (**Fig. 5**). However, the TCOT at $+15^\circ$ was less than the TCOT of 0° (horizontal) swimming for both species. At declining angles the TCOT decreased as the angle of decline increased for the blue catfish. The TCOT for channel catfish swimming at declining angles was lowest at -60° , but the TCOT at -60° was only lower than 0° (horizontal) at speeds of 35-50 cm/s. For channel and blue catfish, $+15^\circ$ was the most efficient inclined swimming angle and -60° was the most efficient declined swimming angle. Overall, channel catfish had a lower TCOT than blue catfish at 0° (horizontal) and $+15^\circ$, but blue catfish had the lowest TCOT at -60° .

The NCOT was significantly different for species ($P=0.0001$), angle ($P<0.0001$), and speed ($P<0.0001$), and a two-way interaction between species and angle ($P=0.0006$) was found. The NCOT at speeds of 10 cm/s was significantly different than all other speeds, but no other differences were observed. Overall, the NCOT increased as the angle of incline increased for both blue and channel catfish (**Fig. 6**). However, the NCOT at $+15^\circ$ was less than the NCOT of 0° (horizontal) swimming for both species. At declining angles the NCOT was lowest at -60° for blue catfish and -15° for channel catfish at speeds of 25-40 cm/s. For both channel and blue catfish, $+15^\circ$ was the most efficient inclined swimming angle. The most efficient declined swimming angle was -60° for blue catfish and -15° for channel catfish. Overall, channel catfish had a lower NCOT than blue catfish at 0° (horizontal) and $+15^\circ$, but blue catfish had the lowest NCOT at -60° .

Burst and Glide Swimming

Burst and glide swimming provided energy savings for both blue and channel catfish (**Table 2**). Burst swimming at 60° and gliding at 15° was found to be the most efficient combination for both blue and channel catfish, providing 49.5% and 42.6% energy savings, respectively. Negative values in the tables represented an energetic cost to the fish by using those angle combinations. No calculations were made for burst swimming at 30° because no minimum TCOT was determined.

Discussion

Swimming and Metabolism

Locomotion both on land and in water requires energy to support the animals' mass and to provide forward movement. However, the physical properties of water are different than air and the interactions between fish and their environment are different than those for terrestrial organisms. Underwater, a fishes' buoyancy counteracts its mass, and these, in turn, are acted on by gravity (47). Alexander (4) states that the center of mass of a fish is typically above the center of buoyancy in many species causing stability control problems because the stable equilibrium position in these fish is belly-up. However, Videler (47) stated that being unstable provides a higher degree of maneuverability. For the catfish to hold its body horizontal, energy is required because it is not the natural equilibrium position. Moving at an inclining or declining angle means changing the fishes' equilibrium position, thus changing the relative position of the center of buoyancy and mass. The results of this study indicate that blue or channel catfish fingerlings could use the angles of 0° or $+15^\circ$ for fast-start escape responses without a reduction in swimming performance. The choice of escape angle could be partly determined by the fish's position in the water column. Assuming a near-surface location, the fish would be more likely to choose a declined angle over an inclined angle for escape. While a shallower angle could be used, data in this study demonstrate that at angles of decline from -30° to -60° (largest angle tested) performance increases as indicated by an increasing U_{crit} . A fish might choose an angle even $>-60^\circ$ if this trend of increasing U_{crit} with increasing angle of decline past -30° were to continue.

Non-horizontal locomotion studies on terrestrial mammals have shown that inclined locomotion increases metabolic rate (19, 24, 45, 46). Fish are capable of passing around dams through fishways up to 28% slope ($+16^\circ$) (2, 18, 28, 39, 40, 41, 44). Adams et al. (2) found that the angle of incline did seem to affect the distance that brook trout, *Salvelinus fontinalis*, could travel. At higher angles, brook trout swam shorter distances than at lower angles. Haro et al. (28) found that the percentage of fish that were able to pass through a fishway depended on species. For American shad, *Alosa sapidissima*, increasing the fishway slope decreased the percent passage, but for blueback herring, *A. aestivalis*, a higher fishway slope did not decrease fish passage in a standard Denil fishway (increased angle did decrease fish passage in an Alaska steep pass fishway). Bunt (18) found no differences in the passage efficiencies for white suckers, *Catostomus commersoni*, and smallmouth bass, *Micropterus dolomieu*, swimming through fishways with slopes of 10 and 20% ($+5.7^\circ$ and $+11.3^\circ$ respectively). The ability to swim efficiently at inclined angles may be species specific. These studies indicate that swimming at angles $>+15^\circ$ or more may have significant physiological, behavioral, and survival importance for many species of fishes. These studies also indicate that many species of fishes have evolved the ability to swim at angles of $+15^\circ$ or less without metabolic implications.

The present study revealed that blue and channel catfish experience an increased metabolic rate during inclined locomotion. As catfish swam on an incline, their VO_2 and TCOT increased as the angle increased. Also, the critical swimming speed of the catfish decreased as the swimming angle increased. Since there was no significant difference in U_{crit} , VO_2 , TCOT, and NCOT between $+15^\circ$ and 0° , it appears that the fish are physiologically compensating through changes in buoyancy or other mechanisms for inclined angles of $+15^\circ$ or less.

At declined angles, fish were expected to have U_{crit} s higher than the U_{crit} at horizontal, but this was not necessarily the case. Both species showed a non-linear change in U_{crit} with declining angle. For channel catfish, as the angle of decline increased they expended more energy to swim (higher metabolic rate at -15° , -30° , & -45° , higher TCOT at all negative angles, higher NCOT at -30° and -60°). However, the slope of the VO_2 curve at -15° was negative. A negative respiration curve slope may have been caused by an insufficient amount of time to acclimate to the new angle (2 hr). The fish may have been expending increased energy initially, as they tried to adjust their body to this particular angle. The fish may have still been too agitated when the initial swimming bout was performed. For blue catfish, the VO_2 (except at -60°) and the TCOT and NCOT at declining angles are not significantly different than the rates and costs at horizontal. This indicates that swimming at declining angles is not metabolically more or less expensive. Swimming is most efficient for blue catfish swimming at -60° (the largest declining angle). These data demonstrated that the changes from horizontal U_{crit} were less metabolically demanding for blue catfish than for channel catfish.

Unlike the studies of Margaria et al. (34) and Ceretelli et al. (20) wherein the NCOT of humans and dogs, respectively, was observed to be independent of speed, this study did show that NCOT of blue and channel catfish was dependent on speed. Net cost of transport values at 10 cm/s were different from all other speeds, but the NCOT values at other speeds were not significantly different from each other.

Studies have shown that fish, both neutrally and negatively buoyant, will often “tilt” their bodies at some angle relative to the direction of locomotion (29, 33, 49) when swimming at low speeds. This tilting mechanism is viewed as a method of increasing stability at low swimming speeds (49). This was considered as an explanation for decreasing U_{crit} with increasing incline and at low declining angles. However, after examining videos of the fish swimming at all angles, it was determined that this was not a plausible explanation because there was no detectable difference in fish angle relative to tunnel angle. The fish aligned themselves with the bottom of the tunnel with their head directed into the current. The fish did not attempt to swim at an angle other than the tunnel angle.

Comparative studies on the habitat usage of blue and channel catfish, have found blue catfish to be more prevalent in mid and open water habitats than channel catfish, and have found channel catfish more commonly in shallow near-shore benthic areas (1, 21, 22, 25, 31, 32). Blue catfish may be more adapted to ascending and descending in the water column, which may require a higher U_{crit} and lower energetic costs at swimming angles.

Calculations for the SMR of channel catfish may have been inflated because values for channel catfish SMR at -15° , -30° , and -45° were extremely high and they had a very high standard error. The elevated value for SMR at -15° is evidenced by the negative respiration curves. Because the respiration curves had negative slopes, back-extrapolation to the zero speed resulted in high SMR estimates. The elevated values for SMR at -30° and -45° could have been caused by the stress of swimming at these angles. When these elevated values for SMR were removed, mean SMR for channel catfish was 0.19 ± 0.017 mg O_2 /g/hr, and no differences in SMR between blue and channel catfish were found ($P=0.0931$). This information demonstrates the problems associated with estimating SMR from data on non-horizontal swimming. Care should be taken when estimating SMR and decline locomotion should likely not be used in this estimation.

There are potential pitfalls associated with comparing the TCOT of two species. Comparisons of TCOT are affected by the SMR of the species (47). Channel catfish were found to have a higher TCOT than blue catfish at all negative angles and $+60^\circ$. The fact that the TCOT is higher for channel catfish is important because it means that channel catfish require more energy to conduct their daily activities and will either have less energy to put into growth or require more energy input to maintain the same activity levels as blue catfish. However, if the NCOT is calculated, comparisons between the species are based solely on the amount of energy required for swimming at a particular speed because SMR is subtracted from the oxygen consumption values. The NCOT at -30° was significantly higher for channel catfish than blue catfish. This higher NCOT means that at any speed it takes channel catfish more energy to swim at -30° . Differences seen in the TCOT are caused by the higher SMR at those angles. Furthermore, no differences in the SFA between the species were found.

Studies examining the swimming performance and energetics are few for channel catfish and nonexistent for blue catfish. Hocutt (30) determined the U_{crit} for channel catfish to be 58.5 cm/s at $25^\circ C$ and 14.0-15.4 cm TL (20 min bouts; no rest). Sylvester (43) reported an average U_{crit} of 55.2 cm/s (range of 52.9 to 58.7 cm/s) for channel catfish with a mean weight of 191.5 g at $20^\circ C$ (30 min bouts; 15 min rest). Bartlett (6) found the average U_{crit} to be 52.1 cm/s at $25^\circ C$ and 8.0 mg/L O_2 for catfish between 16 and 27 cm SL (131.0 g mean weight) (1 hr bouts; 30 min rest). The results of the above studies compare favorably with the U_{crit} of 59.28 ± 2.31 cm/s for channel catfish and 51.57 ± 1.27 cm/s for blue catfish at $19-21^\circ C$ as determined in the present study (swimming horizontally; 30 min bouts; no rest).

Beecham et al. (12) and Beecham et al. (10) tested the time-to-fatigue of blue and channel catfish at individual speeds from 30 to 110 cm/s and found that channel catfish swam longer without fatigue than blue catfish of similar size (19 cm, 91 g) and in a similar water temperature ($19-22^\circ C$) at all speeds tested above 40 cm/s. The mean fatigue time for pond-raised channel catfish was 186 min at 50 cm/s and 41 min at 60 cm/s while blue catfish fatigued in 84 and 6 min, respectively at those speeds. Both fatigued in < 3 min at 80 cm/s and < 60 s at 110 cm/s.

This information is similar to this study wherein blue catfish had a lower U_{crit} than channel catfish. Beecham et al. (10) also found no significant differences between cultured and wild-caught channel catfish at speeds between 30 and 110 cm/s.

Beecham et al. (11) found no significant difference in the time course recovery of plasma lactate, glucose, cortisol, and muscle lactate in juvenile blue and channel catfish following exhaustive swimming at 60 cm/s in a swim tunnel. These results suggest that the two species respond similarly to swimming-related stresses. Although the blue catfish fatigued faster (mean, 7.2 min \pm 0.8) than the channels (mean, 27.6 \pm 2.8 min) as they did in the present study, both recovered from fatigue in 2-4 h.

Burst and Glide Swimming

Burst and glide swimming can be defined as alternating periods of active swimming with periods of passive gliding. For humans, chimpanzees, and mice, data show that they require more energy to run uphill followed by running downhill than if they covered the same distance running horizontally (34, 45). However, the energy savings for a fish using burst and glide swimming (14, 50, 51), a form of locomotion in which fish burst swim at an incline and then passively glides back to its original level, suggests significant energy savings. This differs from terrestrial animals running on an incline followed by running on a decline because the fish can return to their original level using little energy (only SMR) thanks to the buoyancy provided by water. Theoretical models have indicated that an energy savings of 50% are possible for glide angles on the order of 10° (14, 50, 52). Weihs (52) created energy savings curves for different burst and glide angles. He determined that as the glide angle increases the maximum energy savings decreases. He also determined that when glide angles exceed 30°, negative values of energy savings occur for high burst angles. His calculations show maximum energy savings to be at a 70° burst angle and a 5.7° glide angle. His next highest energy savings was found at a 60° burst angle and an 11.3° glide angle. This information coincides closely with the maximum energy savings of 49.5% & 42.6% calculated for blue catfish and channel catfish swimming at a 60° burst angle and a 15° glide angle. Furthermore, this study also found negative values of energy savings for glide angles of 45° or greater.

Both costs and benefits are associated with non-horizontal locomotion. However, a fish may maximize its locomotion efficiency by swimming at its optimal swimming angle and/or its optimal swimming speed. Wickler et al. (53) supported this hypothesis when he found that the preferred speed of trotting horses was very near the minimum cost of transport (COT) both on a horizontal surface and on an incline. They also determined that the preferred trotting speed of horses decreased from 3.29 \pm 0.24 m/s on a horizontal to 3.05 \pm 0.30 m/s on an 11.8° (+6.7°) incline. It would probably be incorrect to assume that one particular mechanism is solely responsible for the differences in swimming abilities of blue and channel catfish for inclining or declining swimming. The physiological systems of fish are extremely complicated and act together for more than one purpose, but the evolution of a fish's locomotory pattern is probably dictated by its life history. Physiological mechanisms used in locomotion are diverse and the overall survival and growth of each fish is influenced by the environment in which it lives and the variability of food, productivity, hydrostatic pressure, and water currents.

List of symbols and abbreviations

Critical Swimming Speed (U_{crit})
Standard length (SL)
Oxygen consumption (VO_2)
Metabolic rate (MR)
Standard metabolic rate (SMR)
Active metabolic rate (AMR)
Scope for activity (SFA)
Total cost of transport (TCOT)
Net cost of transport (NCOT)
Weight (WT)
Analysis of covariance (ANCOVA)

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Figures

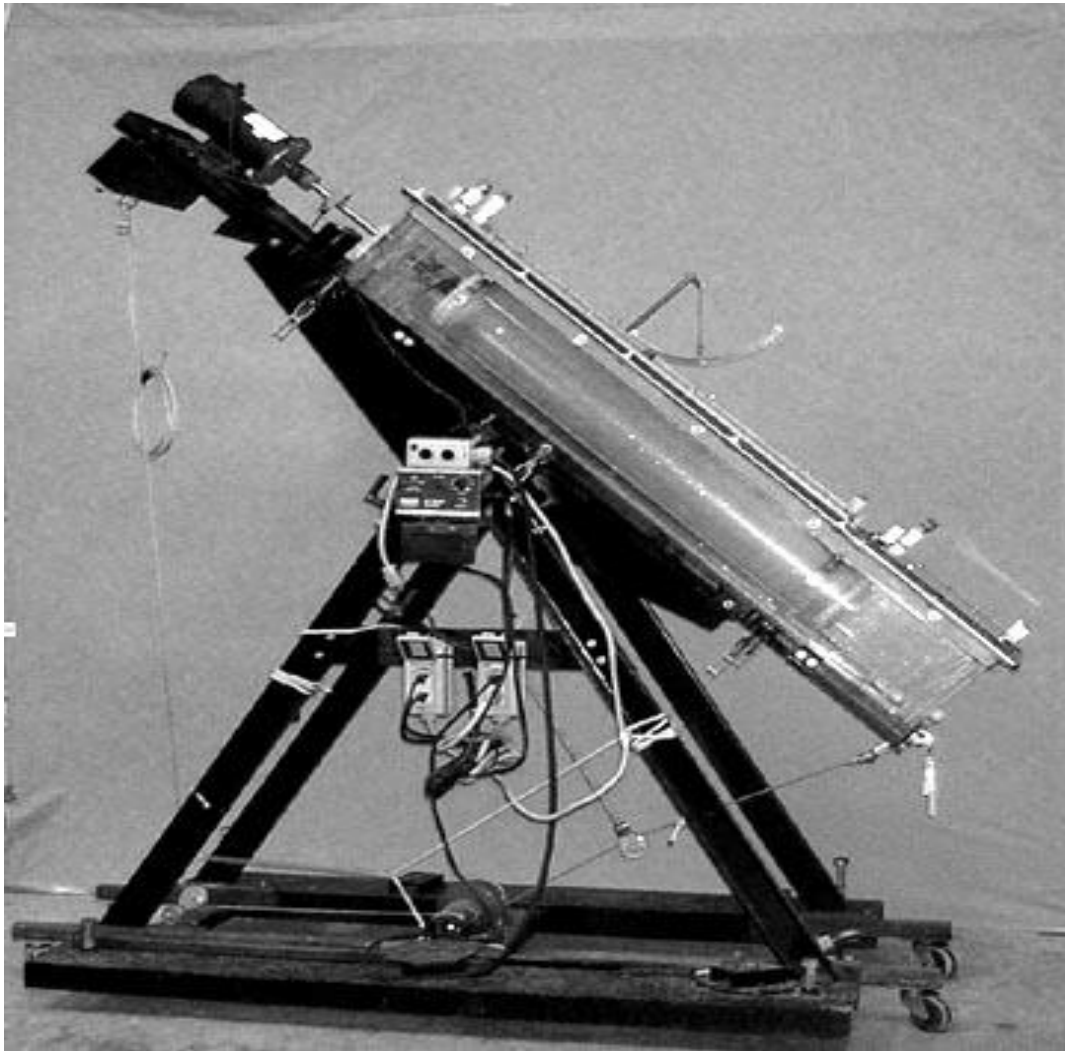


Figure 1: Photograph of the tilting tunnel respirometer.

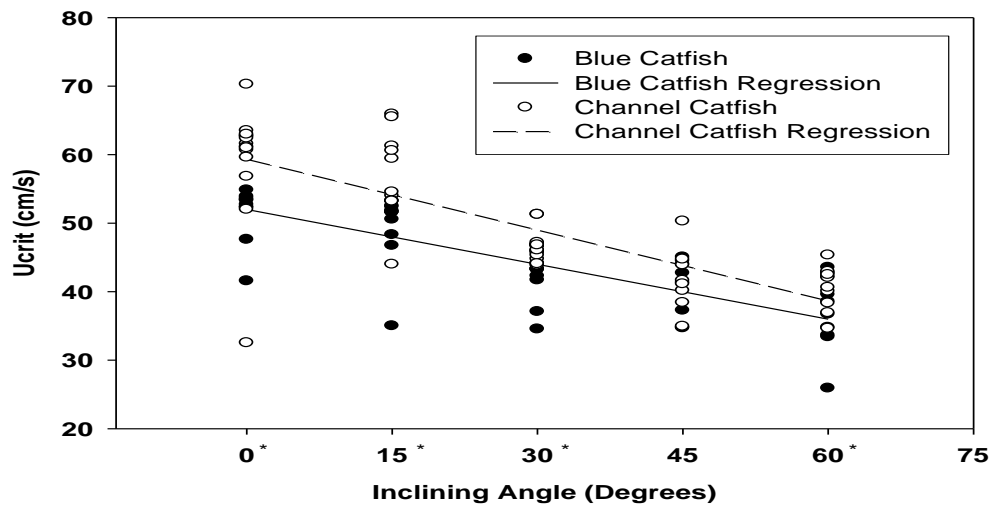


Figure 2: Linear regressions of juvenile blue and channel catfish critical swimming speed at inclining angles. The “*” indicates a significant difference between blue and channel catfish at that angle.

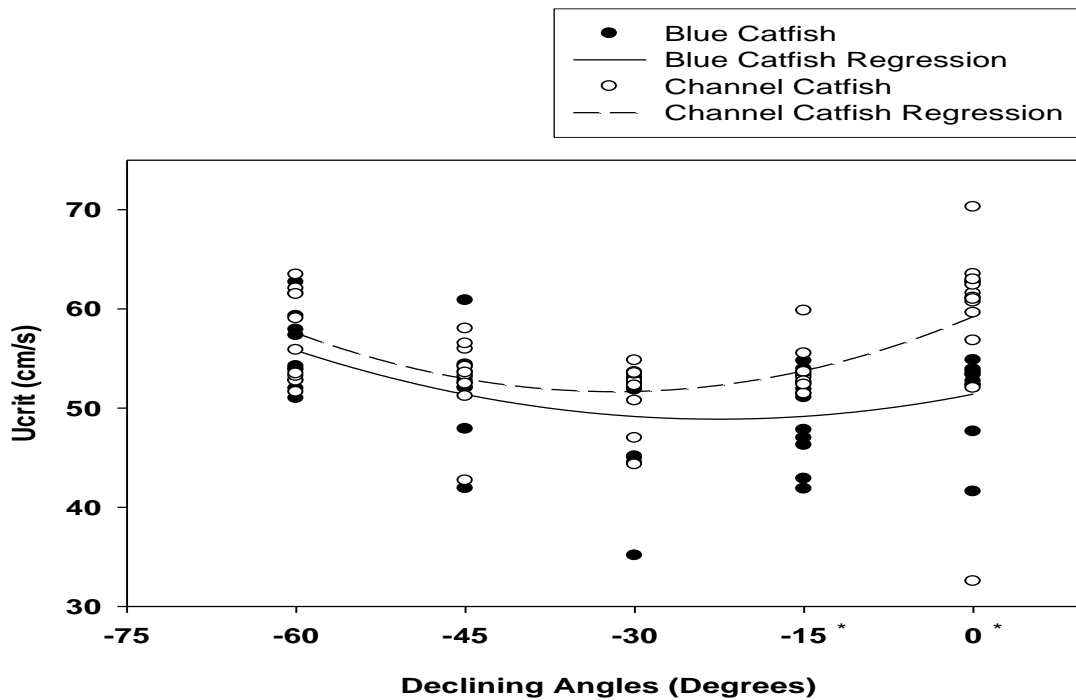


Figure 3: Quadratic regressions of juvenile blue and channel catfish critical swimming speed at declining angles. The “*” indicates a significant difference between blue and channel catfish at that angle.

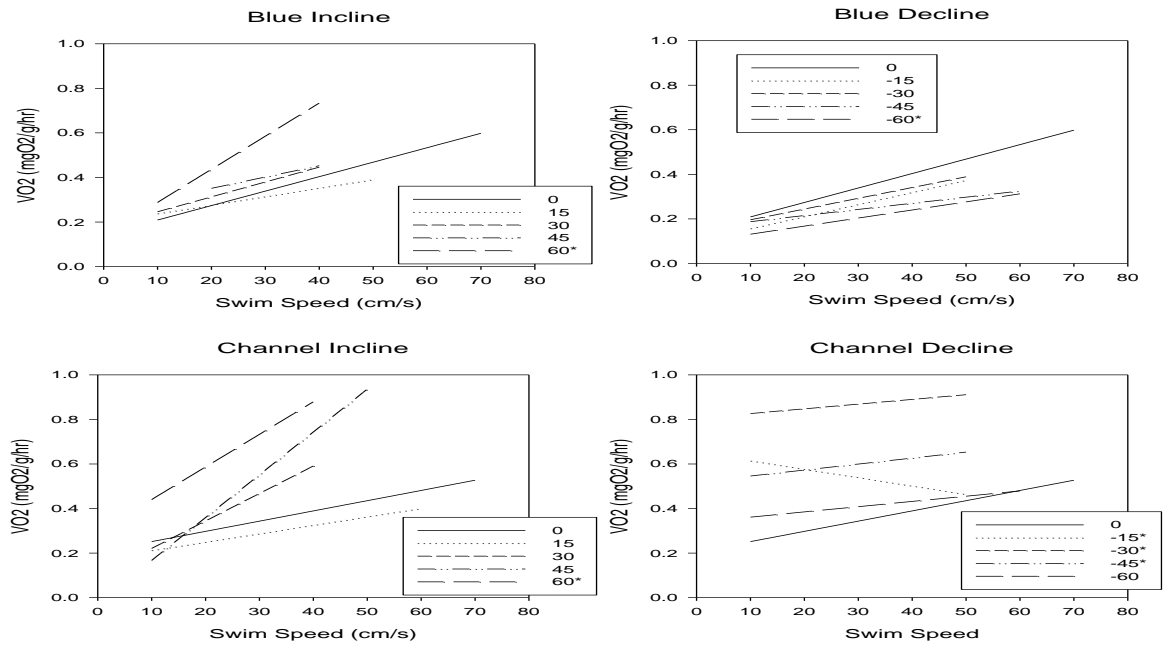


Figure 4: Linear regressions of juvenile blue and channel catfish oxygen consumption (VO_2) at inclining and declining angles. The “*” indicates a significant difference between that angle and horizontal (0°).

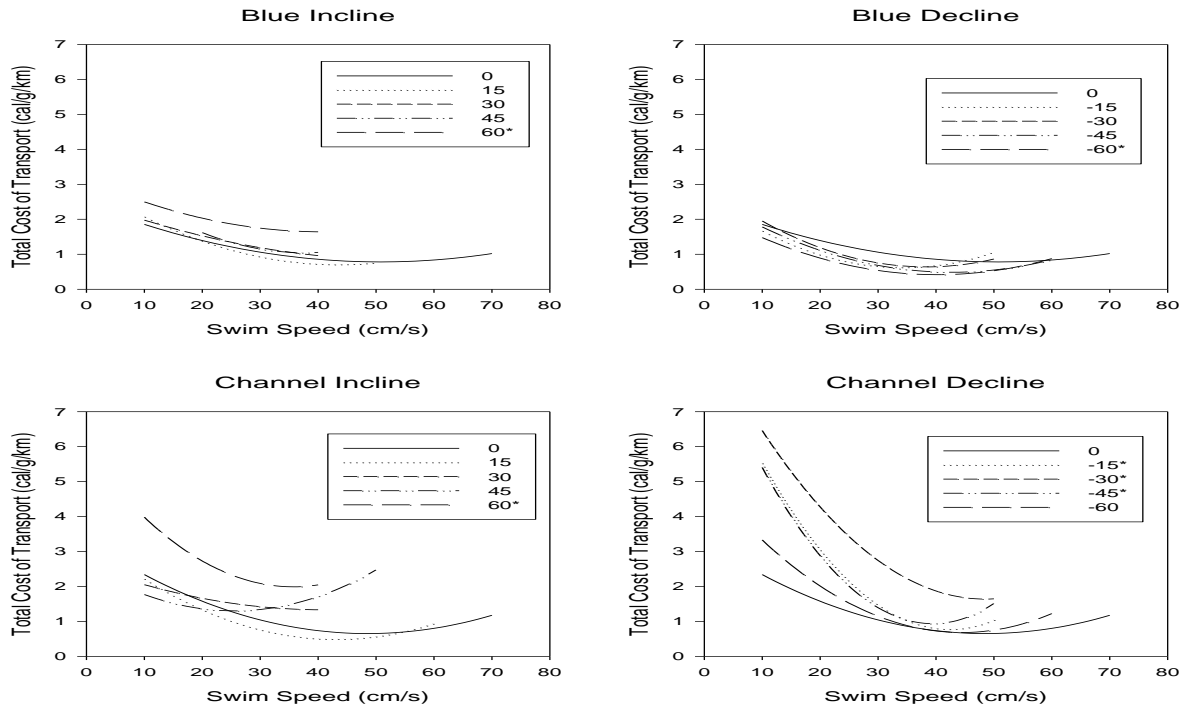


Figure 5: Quadratic regression of total cost of transport (TCOT) at each angle for juvenile blue and channel catfish. The “*” indicates a significant difference between that angle and horizontal (0°).

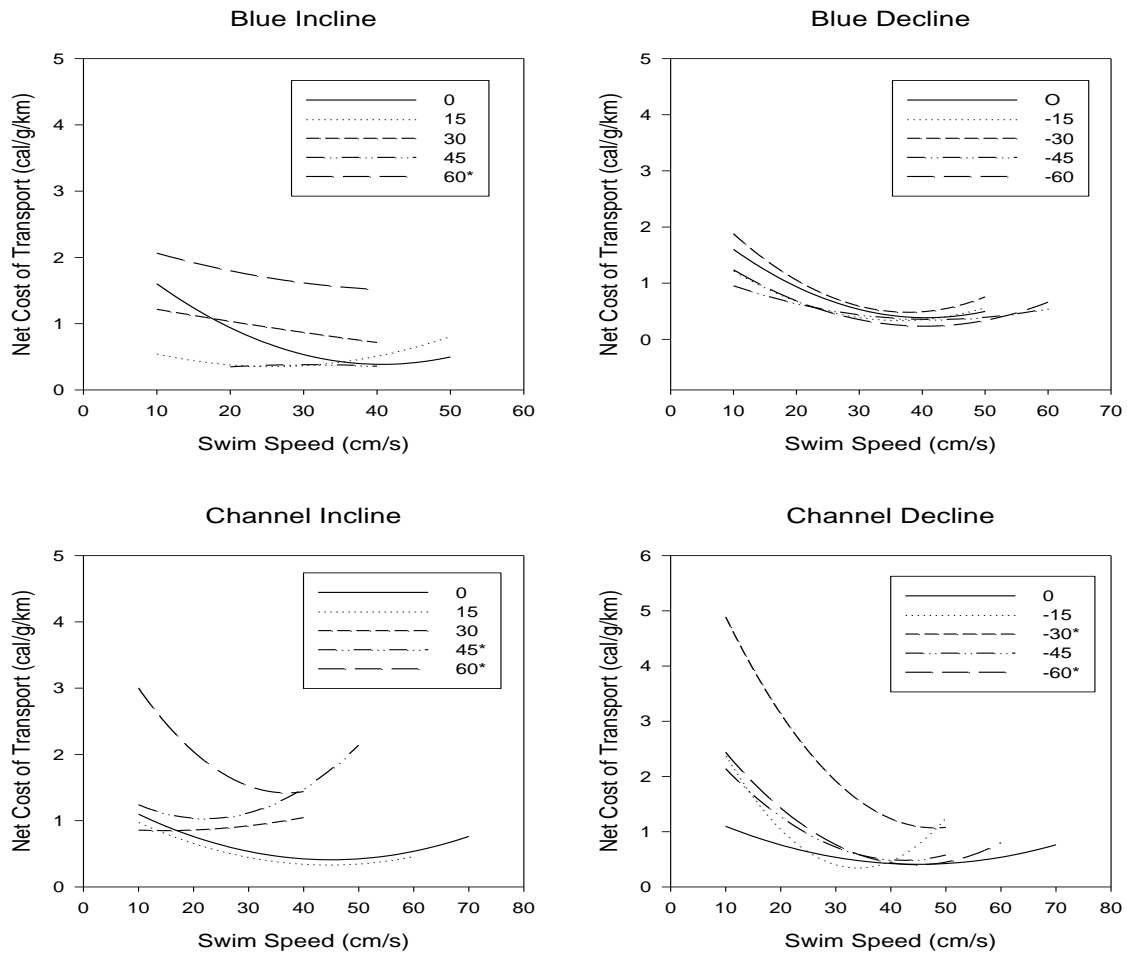


Figure 6: Quadratic regression of net cost of transport (NCOT) at each angle for juvenile blue and channel catfish. The “*” indicates a significant difference between that angle and horizontal (0°).

Tables

Table 1: Mean and standard error of the standard metabolic rate (SMR), active metabolic rate (AMR), and scope for activity (SFA) for juvenile blue and channel catfish swum at various angles. Different letters within each column indicate differences for individual species compared to the value at an angle of 0°.

Angle (degrees)	SMR		AMR		SFA	
	Channel	Blue	Channel	Blue	Channel	Blue
-60	0.248 ± 0.7 z	0.1402 ± 0.03 z	0.656 ± 0.07 z	0.349 ± 0.04 y	0.441 ± 0.08 z	0.209 ± 0.05 y
-45	0.629 ± 0.1 y	0.0954 ± 0.03 z	0.84 ± 0.1 z	0.447 ± 0.03 z	0.385 ± 0.1 z	0.351 ± 0.05 z
-30	0.453 ± 0.1 y	0.062 ± 0.03 z	1.152 ± 0.3 y	0.531 ± 0.1 z	0.698 ± 0.2 y	0.469 ± 0.1 z

-15	0.635 ± 0.27	y	0.126 ± 0.04	z	0.756 ± 0.2	z	0.418 ± 0.06	z	0.121 ± 0.1	y	0.292 ± 0.07	z
0	0.161 ± 0.02	z	0.169 ± 0.08	z	0.594 ± 0.09	z	0.671 ± 0.08	z	0.434 ± 0.1	z	0.502 ± 0.1	z
15	0.168 ± 0.03	z	0.188 ± 0.02	z	0.434 ± 0.03	z	0.428 ± 0.03	z	0.266 ± 0.05	z	0.239 ± 0.03	y
30	0.173 ± 0.03	z	0.108 ± 0.02	z	0.569 ± 0.8	z	0.378 ± 0.05	z	0.396 ± 0.07	z	0.27 ± 0.05	z
45	0.135 ± 0.07	z	0.31 ± 0.05	z	0.872 ± 0.3	z	0.424 ± 0.06	z	0.738 ± 0.2	y	0.114 ± 0.06	y
60	0.238 ± 0.1	z	0.049 ± 0.03	z	0.844 ± 0.07	z	0.705 ± 0.1	z	0.606 ± 0.1	z	0.656 ± 0.2	z

Table 2: Energy savings (%) of blue/channel catfish employing burst and glide swimming at various angle combinations. No calculations were made for burst swimming at 30° because no minimum TCOT was determined. No calculations were made where glide angle exceeded burst angle.

Burst Angle (degrees)	Glide Angle (degrees)			
	15	30	45	60
15	33.4 / 32.3	X / X	X / X	X / X
30	X / X	X / X	X / X	X / X
45	40.52 / 21.6	21 / -18.3	-22.2 / -49.8	X / X
60	49.5 / 42.6	34 / 12.7	-14.8 / -13.4	-14.5 / -65.2