

Effect of water temperature on laboratory swimming performance and natural activity levels of adult largemouth bass

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Abstract: Although locomotory performance in vertebrates is related to fitness, most performance tests are conducted in a laboratory setting, or in a manner that forces the organism to move not of their own volition. Biotelemetry offers the possibility to measure voluntary activity in a natural setting and provides the opportunity to combine laboratory-derived data with field studies on wild fish. In this study, it was found that laboratory- and field-based measurements of swimming performance and voluntary activity resulted in similar general seasonal trends, though each measurement assessed a different swimming type. In the field, all swimming metrics were lower at cooler water temperatures and were lowest during early winter (mean daily activity = 0.016 BL/s; mean voluntary swimming activity = 0.04319 BL/s; maximum swimming speed = 0.17 BL/s). In the laboratory, fish acclimatized to 25.0, 14.0, and 7.5 °C decreased swimming performance (U_{crit}) with water temperature (25.0 °C (2.17 BL/s); 14.0 °C (1.69 BL/s); 7.5 °C (1.17 BL/s)). Although some species and tissues have been shown to exhibit different degrees of thermal adaptation, these results show that swimming, one of the most important functions in fish, is largely dependent on environmental temperature, at least in largemouth bass (*Micropterus salmoides* (Lacepède, 1802)).

Résumé : Bien que la performance de locomotion chez les vertébrés soit reliée à la fitness, la plupart des tests de performance sont faits dans un milieu de laboratoire ou dans une situation qui force les animaux à se déplacer, donc pas de leur propre volonté. La biotélémetrie permet de mesurer l'activité volontaire dans un milieu naturel et fournit l'occasion de combiner les données obtenues en laboratoire et les études sur le terrain de poissons sauvages. Dans notre travail, les mesures en laboratoire et sur le terrain de performance de nage et d'activité volontaire montrent les mêmes tendances saisonnières générales, bien que chaque mesure évalue un type de nage différent. En nature, toutes les métriques de nage sont plus basses aux températures d'eau plus fraîches et sont minimales au début de l'hiver (activité journalière moyenne = 0,016 BL/s; activité volontaire moyenne de nage = 0,04319 BL/s; vitesse de nage maximale = 0,17 BL/s, où BL est la longueur du corps). En laboratoire, les poissons acclimatés à 25,0, 14,0 et 7,5 °C diminuent leur performance de nage (U_{crit}) en fonction de la température de l'eau (25,0 °C (2,17 BL/s); 14,0 °C (1,69 BL/s); 7,5 °C (1,17 BL/s)). Bien qu'on ait démontré que certaines espèces et certains tissus présentent des degrés divers d'adaptation thermique, nos résultats établissent que la nage, une des fonctions les plus importantes chez les poissons, est en grande partie dépendante de la température du milieu, au moins chez les achigans à grande bouche (*Micropterus salmoides* (Lacepède, 1802)).

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Introduction

Locomotion is a frequently studied response variable because it is crucial for many ecologically relevant activities such as predator avoidance, prey capture, territorial defense,

and migration (Swingland and Greenwood 1983). Locomotion is also commonly studied to relate performance to individual fitness in animals (Irschick 2003). Because of logistical difficulties associated with measuring field performance in free-ranging animals, much of the research as-

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sessing animal locomotor performance has been conducted in controlled laboratory settings where animals are evaluated using manufactured apparatus (e.g., swimming tunnels, tread mills, and flight cages) in which they are often “forced” to perform. Recently, some scientists have argued that these laboratory-based measurements of locomotion are not representative of the performance of wild, free-ranging animals (Irschick and Garland 2001). Thus, there is a need to develop metrics that can accurately assess animal performance in the field (Hertz et al. 1988; Pough 1989; Irschick 2003).

For fish, there are three types of swimming performance metrics that are commonly measured in the laboratory, each with differences in muscle recruitment and duration for which the activity can be sustained (Beamish 1978; Hammer 1995; Blake 2004). First, sustained swimming uses aerobic red muscle and can last for over 200 min (theoretically for indefinite periods), and is typically used by fish to move long distances (i.e., during migration) or when moving voluntarily throughout their surroundings (Beamish 1978). Prolonged swimming also uses aerobic red and white muscles and typically lasts for less than 200 min and results in depletion of tissue energy stores (Beamish 1978). It is difficult to assess whether fish use prolonged swimming speeds in the wild, but it has been shown to correlate with routine activity and metabolic rates (Plaut 2001). Lastly, burst swimming, or exhaustive swimming, uses only white muscle and requires anaerobic respiration for fuel (Beamish 1978). Burst swimming is often used when capturing prey, when being chased by a predator, or when transiting through difficult flow conditions. All types of swimming performance have been shown to be linked to water temperature (Beamish 1978; Randall and Brauner 1991). Because each swimming type is distinct (Blake 2004), numerous methods and protocols have been developed to assess swimming performance, mostly within a laboratory setting (reviewed in Hammer 1995), and include using laser gates to assess burst swimming (Nelson et al. 2002) and quantifying prolonged and burst swimming performances using swim tunnels (Brett 1964; Farrell et al. 1998; Gregory and Wood 1998).

Recently, however, there has been debate as to what constitutes ecologically relevant swimming tests and metrics. Critical swimming speed (or U_{crit}), measured using a swim tunnel, has long been regarded as the best metric of swimming performance because it indicates maximal aerobic swimming capacity (Beamish 1978). More recently, researchers have argued that U_{crit} tests have been used arbitrarily (Plaut 2001; Nelson et al. 2002) and methods such as laser gaits and swimming flumes that result in the fish moving more freely or voluntarily are a more representative metric (Nelson et al. 2002; Peake and Farrell 2004; Swanson et al. 2004, 2005; McDonald et al. 2007). One method that measures voluntary activity is field-based telemetry.

Field-based telemetry is the use of manual or automatic tracking systems to remotely locate transmitters attached to free-ranging individuals (Lucas and Baras 2000), and this method has been used to study swimming abilities of fish in their natural setting (Cooke et al. 2004a, 2004b; Hanson et al. 2007). The majority of these field studies measuring swimming ability cover large spatial and temporal scales, often using hydrophone or antenna arrays distributed along the length of a river (e.g., Hanson et al. 2008). For many lake telemetry

studies, the distance between subsequent points and the time interval between the points are used to assess activity (e.g., Cooke et al. 2001; Hanson et al. 2007). Often, the time intervals can be multiple days and the points can be hundreds of metres apart, meaning that only coarse assessments of activity can be made (e.g., Bauer and Schlott 2004). However, new innovations in telemetry, which include near real time positioning of multiple individual fish using submerged fixed acoustic hydrophone systems and code division multiple access (CDMA) enabled transmitters, have provided the ability to assess fine-scale swimming ability (Niezgoda et al. 2002; Cooke et al. 2005; Hanson et al. 2007). Thus, CDMA-based telemetry may offer a more appropriate means for measuring swimming performance in fish in the wild.

The aim of this study was to examine seasonal changes in swimming performance measured in the field and the laboratory. To do so, we examined the effect of water temperature and seasonality on the swimming performance of free-swimming largemouth bass (*Micropterus salmoides* (Lacepède, 1802)), as well as largemouth bass held in the laboratory and forced to swim in a swim tunnel.

Materials and methods

Biotelemetry study

Warner Lake (8.3 ha), located entirely within the property of the Queen’s University Biological Station, is a freshwater lake with a maximum depth of 7 m. Warner Lake is equipped with a fixed-station, submerged acoustic telemetry array consisting of a CDMA-based telemetry system that is able to monitor the three-dimensional position of telemetered fish. The system consists of 2 multipoint MAP 600 receivers (one for each basin) and 13 hydrophones moored approximately 2 m below the water surface (Lotek MAP 600; Lotek Wireless Inc., Newmarket, Ontario) (Cooke et al. 2005). Each hydrophone has a cable extending to a central location on shore where it is connected to a receiver. Receivers are connected to a desktop computer controlled by MAP 600 PC HOST software (version 3.09; Lotek Wireless Inc., Newmarket, Ontario). Fish position data are stored on flash cards and are later transferred to personal laptops for interpretation and positioning in BioMAP (version 2.1.12.1; Lotek Wireless Inc., Newmarket Ontario). Filters within BioMAP process raw position data, remove erroneous positions using wavelet-based analysis (Hess-Nielsen and Wickerhauser 1996; Akay and Mello 1997), and provide daily estimates of both mean and maximum swimming speeds for each fish (Niezgoda et al. 2002).

Temperature thermochrons (DS1921Z, iButton; Maxim Integrated Products and Dallas Semiconductor, Sunnyvale, California) were deployed to record ambient temperature at 4 h intervals from November 2005 to November 2006. The thermochrons were attached to floating ropes and anchored at numerous depths (0–5 m) and at multiple locations to ensure complete coverage of the lake.

In October 2005, nine largemouth bass (39.9 ± 0.65 cm) were angled from Warner Lake and implanted with CDMA temperature–pressure sensing acoustic transmitters (Lotek MA-TP 16-25, 16 mm \times 65 mm, repetition rate 59.5 s, life expectancy of 3 years, weighing 30.0 g in air; Lotek Wireless Inc., Newmarket, Ontario), using surgical approaches

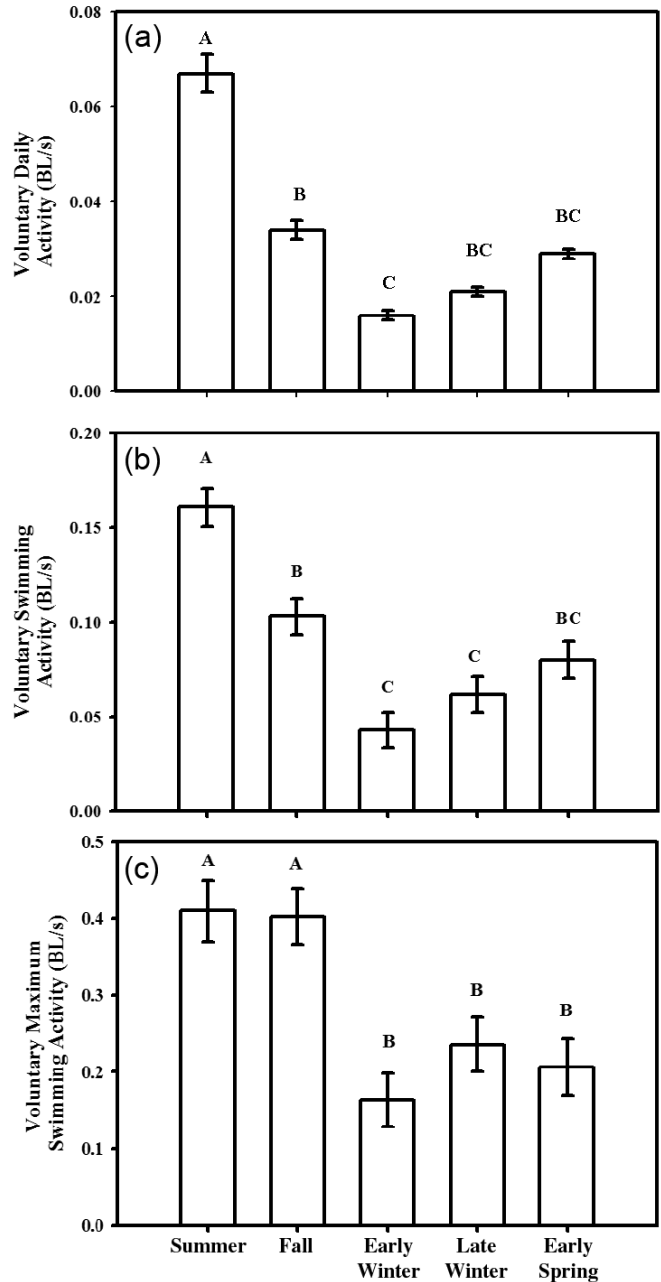
outlined in Cooke et al. (2003). Each fish was released following surgery and tracking by the telemetry system began immediately. Tracking of all fish continued into the following summer, with the exception of one fish that was no longer being tracked after April 2006.

To assess the swimming performance of fish in the biotelemetry field study, three metrics were used: (1) daily voluntary activity, (2) voluntary swimming activity, and (3) maximum voluntary swimming activity. For each metric, movement data were generated during six different time periods: 10 days at water temperature 11.5 °C (fall: 16–25 October 2006), 10 days at 4.5 °C (early winter: 1–10 January 2006), 10 days at 5 °C (late winter: 10–19 March 2006), 10 days at 7.5 °C (early spring: 27 March – 5 April 2006), and 10 days at 25 °C (summer: 30 July – 8 August 2006). Daily voluntary activity quantified the amount of movement each fish undertook throughout the period and was calculated using all filtered data points. The distance and time between two subsequent points were calculated (using the Pythagorean theorem) and the instantaneous velocity between these two points was generated. Voluntary swimming activities were calculated in a similar manner, but only instantaneous velocities above the 75th quartile were included in the mean value. This was done so that periods when the fish were stationary were excluded from the assessment and produced a metric most closely associated to actual swimming potential. The third metric used to assess swimming performance in the biotelemetry study was maximum voluntary swimming activity. This metric was calculated as the mean of the maximum instantaneous velocities for each fish on each day during the 10-day sampling periods. Maximum voluntary swimming activity provided a metric that was the most closely linked to the highest speed at which a telemetered fish was observed to be swimming in the wild.

Swim-tunnel experiments

A 54 L Blazka-type swim tunnel (120 cm in length and 24 cm in diameter) (Blazka et al. 1960; Beamish 1978) was used to measure the U_{crit} and burst swimming ability of multiple largemouth bass (angled from Lake Opinicon; located approximately 1 km from Warner Lake) at three different seasonal temperatures throughout the year: 15 fish at 25.0 °C (summer: July–August; tail length (TL): 29.2 ± 1.4 cm), 7 fish at 14.0 °C (fall: October; TL: 27.8 ± 1.6 cm), and 10 fish at 8.5 °C (early spring: April; TL: 28.1 ± 1.5 cm) (Brett 1964). Lake Opinicon water was used to fill the swim tunnel, and the water in the tunnel was held at ambient Lake Opinicon temperature by allowing a small flow of lake water into and out of the swim tunnel throughout all swimming trials. For the U_{crit} protocol (Beamish 1970; Kolok 1992), each fish was acclimated to the swim tunnel at speeds of 0.5 body length per second (BL/s) for 1 h, after which the speed was increased in a stepwise fashion by 0.5 BL/s every half-hour until exhaustion (one fish in each trial). The fish was considered exhausted once it rested on the back of the swim tunnel with no reaction to disturbance from the observer, or when it was overwhelmed by the current and forced against the grate. At that point, the motor speed was decreased to stimulate the fish to begin swimming again and quickly brought back to the exhaustion

Fig. 1. Mean (\pm SE) voluntary daily activity (a), mean (\pm SE) voluntary swimming activity (b), and mean (\pm SE) maximum voluntary swimming activity (c) of free-swimming telemetered largemouth bass (*Micropterus salmoides*) during summer (25 °C), fall (11.5 °C), early winter (4.5 °C), late winter (5.0 °C), and early spring (7.5 °C). Bars not sharing the same letter are statistically different (repeated-measures ANOVA and Tukey’s HSD post hoc test; $P < 0.05$).



speed. The time measurement ended when the fish rested against or was forced against the grate for a second time. Fish were allowed 20 min to recover before the stepwise test was repeated and results from the second swimming test were used for analysis; the use of the second swimming test is recommended, as previous studies have shown it to be more indicative of swimming ability than the first replicate (Farrell et al. 1998).

Table 1. Seasonal percent change, relative to summer values, of voluntary daily activity, voluntary swimming activity, voluntary maximum swimming activity, laboratory-based prolonged swimming, and laboratory-based burst swimming ability for largemouth bass (*Micropterus salmoides*) monitored during both biotelemetry and laboratory studies.

Type	Season	Percent change relative to summer values
Voluntary daily activity (cm/s)	Fall	-46.4
	Early winter	-75.6
	Late winter	-67.3
	Early spring	-55.3
Voluntary swimming activity (cm/s)	Fall	-37.2
	Early winter	-73.5
	Late winter	-62.1
	Early spring	-51.4
Voluntary maximum swimming activity (cm/s)	Fall	-12.6
	Early winter	-63.3
	Late winter	-47.3
	Early spring	-54.4
Laboratory-based prolonged swimming (U_{crit} ; cm/s)	Fall	-23.4
	Early spring	-52.8
Laboratory-based burst swimming ability (s)	Fall	-1.7
	Early spring	-86.3

After a 24 h recovery period, a test of burst swimming ability was performed using the same fish from the U_{crit} swimming test (Gregory and Wood 1998). For the burst swimming protocol, the fish was first acclimated to the swim tunnel for 5 min at 0.5 BL/s. In a stepwise fashion, the speed was increased by 0.5 BL/s every 30 s until 3.0 BL/s was reached. The fish was timed to determine how long it could maintain a swimming speed of 3.0 BL/s, and the trial was concluded using the same end points as described above. This portion of the study was only carried out during the summer and early-spring periods, and not during the fall period.

Data analysis

To standardize total length between the two studies, all rates are expressed in body lengths per second (BL/s). Biotelemetry-derived voluntary activity metrics were compared across temperatures using a repeated-measures one-way analysis of variance (ANOVA) and a Tukey's HSD post hoc test. Laboratory measurements of U_{crit} swimming performance were compared across temperatures using ANOVA and a Tukey's HSD post hoc test. Burst swimming versus temperature was compared using an unpaired Student's t test. To directly compare seasonal changes in the different metrics used, the percent change across temperatures for all activity assessments was determined by calculating the ratio of the seasonal value of each metric to the summer value of the same metric. All tests were performed using JMP version 6.0.2 (SAS Institute Inc., Cary, North Carolina), with the level of significance (α) for all tests being 0.05. Values reported are means \pm SE.

Results

Field study

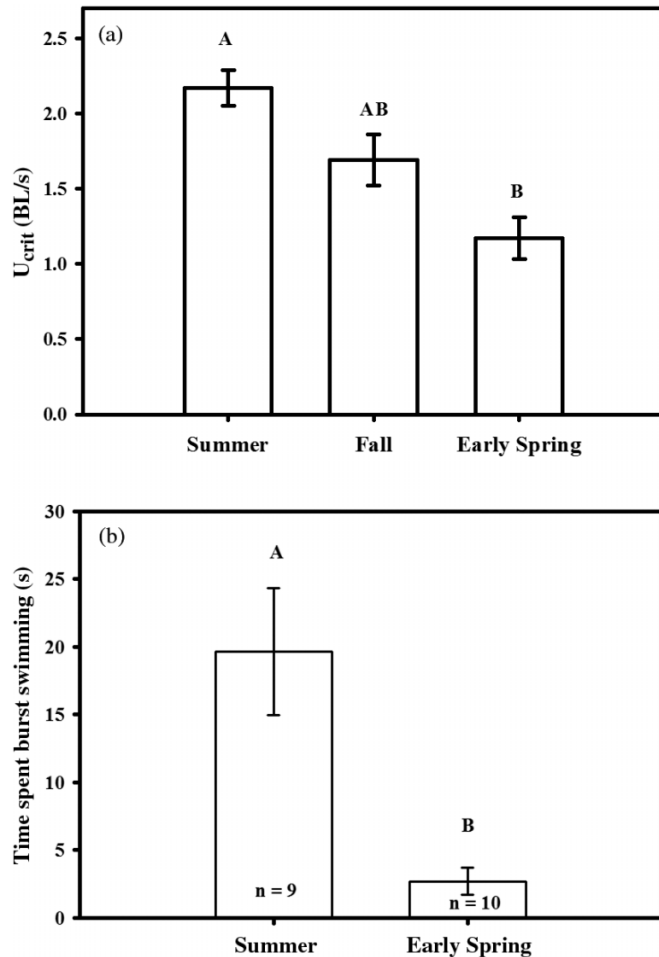
The voluntary daily activity of largemouth bass monitored using biotelemetry decreased significantly as the seasons

progressed from summer to early winter, and then there was a recovery in activity in the late winter and early spring (repeated-measures ANOVA; $F_{[4,35.3]} = 18.0$, $P < 0.0001$) (Fig. 1a). The voluntary daily activity of the fish during the summer (25 °C) was 0.067 ± 0.004 BL/s ($n = 7$), and there was a 46.4% reduction in mean daily activity during the fall when water temperature was 11.5 °C (Table 1). A further 45% reduction in mean daily activity, relative to the fall, was found during the early winter when water temperature was 4.5 °C (Fig. 1a). During late winter and early spring when water temperatures were 5 and 7.5 °C, respectively, mean voluntary daily activity tended to increase (nonsignificantly) 29% and 46% relative to the early-winter sample period and were no longer statistically different from the fall sample period (least means differences Tukey's HSD post hoc test; $P > 0.05$) (Fig. 1a, Table 1).

When periods of resting were eliminated, largemouth bass voluntary swimming activity again decreased significantly as the seasons progressed (repeated-measures ANOVA; $F_{[4,34.11]} = 19.6$, $P < 0.0001$) (Fig. 1b). The voluntary swimming activity of fish during the summer (25 °C) was 0.1608 ± 0.0108 BL/s ($n = 7$), and there was a 37.2% reduction in voluntary swimming activity during the fall when water temperature was 11.5 °C compared with during the summer (Table 1). There was a further 58% reduction, relative to the fall, in voluntary swimming activity when water temperature was 4.5 °C (early winter). No change in voluntary swimming activity was found in the late winter, but voluntary swimming activity in the early spring was 7% greater than during the late winter (least means differences Tukey's HSD post hoc test; $P > 0.05$) (Fig. 1b).

Voluntary maximum swimming activity of telemetered largemouth bass decreased significantly as the seasons progressed (repeated-measures ANOVA; $F_{[4,35.3]} = 17.9$, $P < 0.0001$) (Fig. 1c). The voluntary maximum swimming activity during the summer was 0.41 ± 0.23 cm/s ($n = 7$), and there was no significant difference between summer and fall

Fig. 2. (a) Critical swimming speeds (U_{crit} ; mean \pm SE) and (b) time spent burst swimming (3.0 BL/s; mean \pm SE) of wild largemouth bass (*Micropterus salmoides*) captured from Lake Opinicon when lake temperatures were 25.0, 14.0, and 8.5 °C (fish were not tested for burst swimming when the lake temperature was 14.0 °C). Fish were sampled using a swim tunnel. Sample sizes for each group are shown in bars in b. Bars not sharing the same letter in either a or b are statistically different (one-way ANOVA and Tukey's HSD post hoc test; $P < 0.05$).



values. There was a 63.3% reduction in voluntary maximum swimming activity during the early-winter period (Table 1). Voluntary maximum swimming activity during the late winter and early spring were not significantly different from the early-winter period (least means differences Tukey's HSD post hoc test; $P < 0.05$) (Fig. 1c).

Swim-tunnel experiments

As ambient water temperature declined, the prolonged swimming speed (U_{crit}) of largemouth bass forced to swim in a swim tunnel also declined (one-way ANOVA; $F_{[2,29]} = 14.6$, $P < 0.0001$) (Fig. 2a). Specifically, fish tested in the summer (25.0 °C) swam at 2.17 ± 0.12 BL/s. Fish tested in the fall (14.0 °C) were 23.4% slower than fish tested in the summer, and fish tested in the early spring (8.5 °C) were 52.8% slower than fish tested in the summer (least means differences Tukey's HSD post hoc test; $P < 0.05$) (Fig. 2a, Table 1). The ability of fish to perform burst swimming

(3.0 BL/s) also decreased in concert with declining ambient water temperature (unpaired Student's t test; $t_{[12,93]} = -3.1$, $P < 0.008$). Fish could burst swim for 19.7 ± 4.7 s during the summer period ($n = 9$) but only 2.7 ± 2.7 s ($n = 10$) during the early-spring period (Fig. 2b).

Direct laboratory and field comparisons

When the relative changes were compared between the laboratory and field studies, the trends in swimming speed were similar. Specifically, as the seasons progressed and water temperature decreased, so did the values of all five metrics (Table 1). Comparing the percent changes across metrics revealed that percent change to laboratory-derived U_{crit} measurements during the early spring, relative to the summer, was -52.8% and similar percent changes were found in voluntary daily activity (-55.3%), voluntary swimming activity (-51.4%), and voluntary maximum swimming activity (-54.4%). Both laboratory-derived burst swimming speed and voluntary daily activity during the fall were closest in magnitude to summer values, but these metrics still decreased by 1.7% and 12.6%, respectively. Activity levels for all other time periods were at least 23% lower than summer values (Table 1). During the early winter, only biotelemetry-derived observations were made. Activity metrics decreased between 63.3% and 75.6% during the early winter, which is the highest degree of change from summer values observed in the study (Table 1).

Discussion

Both laboratory- and field-based performance tests showed that daily activity and swimming performance of largemouth bass decrease with seasonal declines in water temperature. In the biotelemetry study, the daily activity of largemouth bass decreased during the fall compared with the summer and a further reduction was measured during the winter. Likewise, swimming speeds (U_{crit}) of largemouth bass tested in the swim tunnel decreased in the fall and early spring compared with summer swimming speeds. Locomotor capacity in ectotherms is directly correlated with ambient temperature, as body temperature influences many physiological processes because of the dependence of enzyme activity on temperature coefficients (Q_{10} values; Hochachka and Somero 1984; Bennett 1990). There are many reasons for the decrease in performance of fish at low temperatures, including reductions in cardiac performance (Brett 1971) and muscle contraction efficiency (Bennett 1984). The activities and speeds measured in both the biotelemetry study and the swim-tunnel study demonstrated progressively reduced movement and performance as the ambient temperature fell below summer temperatures. Thus, it is likely that a reduction and (or) slowing of a number of physiological processes were occurring as temperature decreased, resulting in a concomitant reduction in seasonal swimming performance.

Previous studies in both laboratory and field settings have documented a reduction in realized swimming speed and activity rates for several fish species during winter (Kolok 1991; Adams and Parsons 1998; Hanson et al. 2007). However, while smallmouth bass (*Micropterus dolomieu* Lacepède, 1802; a congener of largemouth bass) exhibited near dormancy during winter (Kolok 1991), the activity rates of

several key metabolic enzymes did not change during cold acclimation, suggesting that smallmouth bass might exhibit increased swimming performance if challenged and that winter dormancy was facultative. Thus, until our study, it was unclear as to whether bass exhibited reduced activity at cold water temperatures because they were incapable of increased performance owing to thermal constraints or because they chose to swim slowly to conserve energy stores. Results from our study show that largemouth bass are not capable of maintaining summer performance levels during winter. Both prolonged and burst swimming tests, as well as voluntary daily activity, swimming activity, and maximum swimming activity, showed a reduction with temperature, indicating that the bass were not able to swim at an equal speed across temperatures. The metrics cover all swimming types typically measured in fish, and the general reduction in all types of swimming, indicates that there is a hindrance in swimming ability at cold temperatures. However, it is likely that some of the decrease in swimming ability is facultative, as fish that were forced to swim during cold temperature did so at a much higher rate than telemetered fish.

In addition to the changes in swimming performance across seasons, our study also documented a substantial difference between laboratory-based prolonged swimming and field-based sustained swimming values. In the early spring, for example, laboratory-based prolonged swimming was found to be 10 times greater than voluntary swimming activity in the wild during the early spring. Although it is challenging to compare the absolute values of each independent test, it appears that free-ranging largemouth bass have the potential for increased swimming performance beyond what was observed in the wild. Undoubtedly, there are many factors that determine swimming activity in the wild (e.g., dissolved oxygen, prey abundance, food requirements). To determine these factors, and to what degree each factor influences swimming activity, many more experiments are needed that use both field- and laboratory-based tests. Although there is debate as to whether it is more accurate to use field-based estimates rather than laboratory-based estimates (Irschick and Garland 2001), it is important to fully understand the individual factors and their influence on swimming performance (through laboratory-based experiments) before field-based observations can be used to assess population- and community-level responses.

Fish are known to fall on a spectrum of being well adapted for thermal change (i.e., eurythermal) to not being able to adapt to thermal change (i.e., stenothermal) (Hochachka and Somero 1984). Many physiological and biochemical changes can occur in fish exposed to cold temperature that may alter swimming ability (e.g., aerobic enzyme activities (Rome et al. 1985; Johnston and Dunn 1987; Guderley and Blier 1988), mitochondrial density (Eginton and Sidell 1989; Guderley 1990; Battersby and Moyes 1998)). Our field-based data show that largemouth bass have some ability to acclimatize to persistent cold temperature, as swimming performance in the late winter was higher than during the early winter. However, all swimming metrics determined using field-based telemetry during the winter were over 60% reduced compared with summer values. Thus, although the telemetered fish demonstrated a ten-

dency to be more eurythermal than stenothermal, they are by no means completely eurythermal. When five closely related centrarchid species were acclimated to cold temperatures, largemouth bass were the species least able to acclimate (Tschantz et al. 2002), and forced swimming performance of largemouth bass was greatly reduced by cold temperature (Kolok 1992). In general, although field-tested largemouth bass exhibited some recovery of swimming speed during late winter, largemouth bass were not found to be well adapted for maintaining high swimming activity. Future studies should attempt to link physiological and biochemical changes to swimming activity.

Laboratory- and field-based assessments of swimming performance are often studied separately, and few direct comparisons of these techniques exist in the literature. In our study, laboratory-assessed prolonged and burst swimming were assessed in combination with field-based telemetry measurements of voluntary daily and swimming activity. General trends in seasonal changes to performance were conserved across metrics. In general, it was found that as temperature decreased, so did swimming performance. However, field-based swimming activity was not equivalent to laboratory-based swimming, suggesting that there are multiple factors influencing swimming in the wild. In addition, largemouth bass in the winter were found to have some tendency to increase activity as cold temperatures persisted, indicating possible acclimatization. Because largemouth bass are regarded as ambush predators, it may also be worthwhile to study these issues in fish that spend more time actively swimming.

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References

- Adams, S.R., and Parsons, G.R. 1998. Laboratory-based measurements of swimming performance and related metabolic rates of field-sampled smallmouth buffalo (*Ictiobus bubalus*): a study of seasonal changes. *Physiol. Zool.* **71**(4): 350–358. doi:10.1086/515419. PMID:9678496.
- Akay, M., and Mello, C. 1997. Wavelets for biomedical signal processing. *Proc. IEEE*, **6**: 2688–2691. doi:10.1109/IEMBS.1997.756888.
- Battersby, B.J., and Moyes, C.D. 1998. Influence of acclimation temperature on mitochondrial DNA, RNA, and enzymes in skeletal muscle. *Am. J. Physiol.* **275**(3): R905–R912. PMID: 9728090.
- Bauer, C., and Schlott, G. 2004. Overwintering of farmed common carp (*Cyprinus carpio* L.) in the ponds of a central European aquaculture facility — measurement of activity by radio telemetry. *Aquaculture*, **241**(1-4): 301–317. doi:10.1016/j.aquaculture.2004.08.010.

- Beamish, F.W.H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. *Can. J. Zool.* **48**(6): 1221–1228. doi:10.1139/z70-211. PMID:5503024.
- Beamish, F.W.H. 1978. Swimming capacity. In *Fish physiology*. Vol. 7. Edited by W.S. Hoar and D.J. Randall. Academic Press, Inc., New York. pp. 101–172.
- Bennett, A.F. 1984. Thermal dependence of muscle function. *Am. J. Physiol.* **247**(2): R217–R229. PMID:6380314.
- Bennett, A.F. 1990. Thermal dependence of locomotor capacity. *Am. J. Physiol.* **259**(2): R253–R258. PMID:2201218.
- Blake, R.W. 2004. Fish functional design and swimming performance. *J. Fish Biol.* **65**(5): 1193–1222. doi:10.1111/j.0022-1112.2004.00568.x.
- Blazka, P., Volf, M., and Ceplea, M. 1960. A new type of respirometer for determination of the metabolism of fish in an active state. *Physiol. Bohemoslov.* **9**: 553–560.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183–1226.
- Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* **11**: 99–113.
- Cooke, S.J., Bunt, C.M., Schreer, J.F., and Wahl, D.H. 2001. Comparison of several techniques for mobility and activity estimates of smallmouth bass in lentic environments. *J. Fish Biol.* **58**(2): 573–587. doi:10.1111/j.1095-8649.2001.tb02273.x.
- Cooke, S.J., Graeb, B.D.S., Suski, C.D., and Ostrand, K.G. 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. *J. Fish Biol.* **62**(6): 1366–1380. doi:10.1046/j.1095-8649.2003.00119.x.
- Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., and Butler, P.J. 2004a. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* **19**(6): 334–343. doi:10.1016/j.tree.2004.04.003. PMID:16701280.
- Cooke, S.J., Thorstad, E.B., and Hinch, S.G. 2004b. Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish Fish.* **5**: 21–52.
- Cooke, S.J., Niezgodka, G., Hanson, K.C., Suski, C.D., Tinline, R., and Philipp, D.P. 2005. Use of CDMA acoustic telemetry to document 3-D positions of fish: relevance to the design and monitoring of aquatic protected areas. *Mar. Technol. Soc. J.* **39**: 17–27.
- Egginton, S., and Sidell, B.D. 1989. Thermal acclimation induces adaptive changes in subcellular structure of fish skeletal muscle. *Am. J. Physiol.* **256**(1): R1–R9. PMID:2912202.
- Farrell, A.P., Gamperl, A.K., and Birtwell, I.K. 1998. Prolonged swimming, recovery and repeat swimming performance of mature sockeye salmon *Oncorhynchus nerka* exposed to moderate hypoxia and pentachlorophenol. *J. Exp. Biol.* **201**(14): 2183–2193. PMID:9639592.
- Gregory, T.R., and Wood, C.M. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **55**(7): 1583–1590. doi:10.1139/cjfas-55-7-1583.
- Guderley, H. 1990. Functional significance of metabolic responses to thermal acclimation in fish muscle. *Am. J. Physiol.* **259**(2): R245–R252. PMID:2201217.
- Guderley, H., and Blier, P. 1988. Thermal acclimation in fish: conservative and labile properties of swimming muscle. *Can. J. Zool.* **66**(5): 1105–1115. doi:10.1139/z88-162.
- Hammer, C. 1995. Fatigue and exercise tests with fish. *Comp. Biochem. Physiol. A Physiol.* **112**(1): 1–20. doi:10.1016/0300-9629(95)00060-K.
- Hanson, K.C., Cooke, S.J., Suski, C.D., Neizogda, G., Phelan, F.J.S., Tinline, R., and Philipp, D.P. 2007. Assessment of largemouth bass (*Micropterus salmoides*) behaviour and activity at multiple spatial and temporal scales utilizing a whole-lake ecological telemetry array. *Hydrobiologia*, **582**: 243–256. doi:10.1007/s10750-006-0549-6.
- Hanson, K.C., Cooke, S.J., Hinch, S.G., Crossin, G.T., Patterson, D.A., English, K.K., Donaldson, M.R., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Individual variation in migration speed of upriver-migrating sockeye salmon in the Fraser River in relation to their physiological and energetic status at marine approach. *Physiol. Biochem. Zool.* **81**(3): 255–268. doi:10.1086/529460. PMID:18419519.
- Hertz, P.E., Huey, R.B., and Garland, T., Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or boy scouts? *Am. Zool.* **28**: 927–938.
- Hess-Nielsen, N., and Wickerhauser, M.V. 1996. Wavelets and time-frequency analysis. *Proc. IEEE*, **84**(4): 523–540. doi:10.1109/5.488698.
- Hochachka, P.W., and Somero, G.N. 1984. Biochemical adaptations. Oxford University Press, New York.
- Irschick, D.J. 2003. Measuring performance in nature: implications for studies of fitness within populations. *Integr. Comp. Biol.* **43**(3): 396–407. doi:10.1093/icb/43.3.396.
- Irschick, D.J., and Garland, T., Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**(1): 367–396. doi:10.1146/annurev.ecolsys.32.081501.114048.
- Johnston, I.A., and Dunn, J. 1987. Temperature acclimation and metabolism in ectotherms with particular reference to teleost fish. *Symp. Soc. Exp. Biol.* **41**: 67–93. PMID:3332497.
- Kolok, A.S. 1991. Temperature compensation in two centrarchid fishes: do winter-quiescent fish undergo cellular temperature compensation? *Trans. Am. Fish. Soc.* **120**(1): 52–57. doi:10.1577/1548-8659(1991)120<0052:TCITCF>2.3.CO;2.
- Kolok, A.S. 1992. Morphological and physiological correlates with swimming performance in juvenile largemouth bass. *Am. J. Physiol.* **263**(5): R1042–R1048. PMID:1443221.
- Lucas, M.C., and Baras, E. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish Fish.* **1**: 283–316.
- McDonald, D.G., Keeler, R.A., and McFarlane, W.J. 2007. The relationships among sprint performance, voluntary swimming activity, and social dominance in juvenile rainbow trout. *Physiol. Biochem. Zool.* **80**(6): 619–634. doi:10.1086/521089. PMID:17909998.
- Nelson, J.A., Gotwalt, P.S., Reidy, S.P., and Webber, D.M. 2002. Beyond U_{crit} : matching swimming performance tests to the physiological ecology of the animal, including a new fish ‘drag stip’. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **133**(2): 289–302. doi:10.1016/S1095-6433(02)00161-7.
- Niezgodka, G., Benfield, M., Sisak, M., and Anson, P. 2002. Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. *Hydrobiologia*, **483**(1/3): 275–286. doi:10.1023/A:1021368720967.
- Peake, S.J., and Farrell, A.P. 2004. Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass

- (*Micropterus dolomieu*). J. Exp. Biol. **207**(9): 1563–1575. doi:10.1242/jeb.00927. PMID:15037650.
- Plaut, I. 2001. Critical swimming speed: its ecological relevance. Comp. Biochem. Physiol. A Mol. Integr. Physiol. **131**(1): 41–50. doi:10.1016/S1095-6433(01)00462-7.
- Pough, F.B. 1989. Organismal performance and Darwinian fitness: approaches and interpretations. Physiol. Zool. **62**: 199–236.
- Randall, D., and Brauner, C. 1991. Effects of environmental factors on exercise in fish. J. Exp. Biol. **160**: 113–126.
- Rome, L.C., Loughna, P.T., and Goldspink, G. 1985. Temperature acclimation: improved sustained swimming performance in carp at low temperatures. Science (Washington, D.C.), **228**(4696): 194–196. doi:10.1126/science.228.4696.194. PMID:17779642.
- Swanson, C., Young, P.S., and Cech, J.J., Jr. 2004. Swimming in two-vector flows: performance and behaviour of juvenile Chinook salmon near a simulated screened water diversion. Trans. Am. Fish. Soc. **133**(2): 265–278. doi:10.1577/03-068.
- Swanson, C., Young, P.S., and Cech, J.J., Jr. 2005. Close encounters with a fish screen: integrating physiological and behavioural results to protect endangered species in exploited ecosystems. Trans. Am. Fish. Soc. **134**(5): 1111–1123. doi:10.1577/T04-121.1.
- Swingland, I.R., and Greenwood, P.J. 1983. The ecology of animal movement. Clarendon Press, Oxford, UK.
- Tschantz, D.R., Crockett, E.L., Niewiarowski, P.H., and Londraville, R.L. 2002. Cold acclimation strategy is highly variable among the sunfishes (Centrarchidae). Physiol. Biochem. Zool. **75**(6): 544–556. doi:10.1086/344492. PMID:12601611.