Morphological correlates of swimming activity in wild largemouth bass (*Micropterus salmoides*) in their natural environment

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Abstract

Individual variation in morphology has been linked to organismal performance in numerous taxa. Recently, the relationship between functional morphology and swimming performance in teleost fishes has been studied in laboratory experiments. In this study, we evaluate the relationship between morphology and swimming activity of wild largemouth bass (*Micropterus salmoides*) during the reproductive period, providing the first data derived on free-swimming fish not exposed to forced swim trials in the laboratory. Sixteen male largemouth bass were angled from their nests, telemetered, and subsequently monitored by a whole-lake acoustic hydrophone array with sub-meter accuracy. Additionally, eleven morphological measurements were taken from digital images of each fish. A principal components analysis of the morphological measurements described 79.8% of the variance. PC1 was characterized by measures of overall body stoutness, PC2 was characterized by measures of the length and depth of the caudal region, and PC3 characterized individuals with relatively large anterior portions of the body and relatively small caudal areas. Of these variables, only PC3 showed significant relationships to swimming activity throughout the parental care period. PC3 was negatively correlated with multiple measures of swimming activity across the parental care period. Furthermore, swimming performance of individual male bass was noted to be repeatable across the parental care period indicating that this phenomenon extends beyond the laboratory.
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1. Introduction

As a behaviour, locomotion is required for survival by most animal species (Ricklefs and Miles, 1994; Domenici and Blake, 1997; Plaut, 2001; Vincent et al., 2005; Husak, 2006), and individual variation in locomotory performance is often correlated with individual variation in morphological characteristics in a variety of taxa (Garland, 1984; Brana, 2003; Fitzpatrick et al., 2005; Husak, 2006). In fish, functional morphology has been shown to relate to variation in the swimming ability of individuals (Kolok, 1992a; Pettersson and Hedenstrom, 2000; Boily and Magnan, 2002; Standen et al., 2002; Lauder and Drucker, 2004; Fisher et al., 2005; Blake et al., 2005; Ohlberger et al., 2006). It has been postulated that increased swimming ability associated with morphological differences may be advantageous in many situations such as predator prey interactions, arduous migrations, defending territories or offspring, and habitat use (Fuiman, 1994; Wintzer and Motta, 2005; Gibb et al., 2006; Ohlberger et al., 2006). Unfortunately, most assessments of the relationship between swimming performance and morphology have been confined to the laboratory partially due to the difficulty of accurately quantifying swimming ability in the wild (Hawkins and Quinn, 1996; Farrell et al., 1998; Martínez et al., 2001; Ojanguren and Brana, 2003; Lee et al., 2003; MacNutt et al., 2006).

Recent advances in biotelemetry have allowed researchers to record movements of animals in the field with fine resolution, especially in the aquatic environment (Lucas and Baras, 2000;

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Cooke et al., 2004a; Cooke et al., 2004b). The advent of three dimensional acoustic positioning systems has allowed researchers unprecedented capabilities to monitor the behaviour of wild individuals over extended time periods (Lucas and Baras, 2000; Cooke et al., 2004a; Cooke et al., 2004b; Cooke et al., 2005). Transmitters can be positioned with sub-meter accuracy every few seconds (Niezgoda et al., 2002; Cooke et al., 2005), and currently the use of these systems is limited to a handful of locations around the world (Niezgoda et al., 2002; Cooke et al., 2005). One such telemetry array has been used to monitor the behaviour of largemouth bass (*Micropterus salmoides*) year round in a Canadian lake (Cooke et al., 2005), and provides a unique opportunity to assess fish morphology and performance relationships in the wild.

This study aimed to relate fish morphology to swimming activity of largemouth bass. For several reasons that will become apparent, we focused on the reproductive period. When water temperatures reach 14 °C in spring, male largemouth bass move to the littoral zone and construct nests (saucer shaped depressions in the substrate) in which egg deposition and fertilization occur (Kramer and Smith, 1962). After spawning, the male largemouth bass becomes sole parental care giver by actively guarding the nest from possible brood predators as well as fanning the brood to provide proper oxygenation and prevent sedimentation (Kramer and Smith, 1962). To successfully raise the brood, these male largemouth bass will continue to provide parental care until the brood becomes independent, which can often require one month (Kramer and Smith, 1962; Ridgway, 1988). The parental care period is recognized as one of the most stressful and energetically costly times of a male bass's life due to the fact that the male is extremely active making movements in a localized area above and adjacent to the nest (Cooke et al., 2002) and cannot forage normally to replenish energy lost in said movements (Hinch and Collins, 1991; Mackereth et al., 1999; Cooke et al., 2002). As such, we believed that individual variation in morphology as it related to locomotory performance as well as overall body condition would affect the swimming ability of a male largemouth bass during the reproductive period. Individuals characterized by morphometric measures that correlated with improved hydrodynamics and increased propulsion were expected to exhibit higher swimming speeds than other fish. Also, due to the energetic constraints during the parental care period, it was expected that individuals that were characterized by morphology that indicated increased body condition and pre-spawn energy stores would be more active than others. Also, we predicted that largemouth bass swimming behaviour in the wild would be repeatable throughout the parental care period as has been noted in laboratory studies on this species (Kolok, 1992b).

2. Methods

2.1. Study site

This study was carried out from May 1st to June 5th, 2005 on Warner Lake, eastern Ontario (44°31′N, 76°20′W). Warner Lake is an 8.3 ha research lake wholly enclosed on Queen's University Biological Station (QUBS) property and is the site of

a telemetric ecological observatory. The lake shoreline is characterized by extensive littoral zone featuring fallen timber and some submergent and emergent macrophyte growth. Further details on the lake structure and community can be found in Suski (2000) and Hanson et al. (2007). The backbone of the ecological observatory is a fixed underwater acoustic telemetry array, and system details can be found in Niezgoda et al. (2002) and Hanson et al. (2007). Briefly, 13 permanently moored hydrophones configured in optimal geometry monitor telemetered fish movements throughout the lake. Hydrophones are connected to two on shore, multi-port MAP_600 (Lotek Wireless Inc.) receivers through fixed cabling. The system relies upon code division multiple access (CDMA) technology that encodes data transmitted from tags and allows for sub-meter positioning due to the elimination of signal collision events and subsequent data loss. Sub-meter positioning of transmission events results from previous differential GPS surveys (±0.2 m) of hydrophone locations (Niezgoda et al., 2002). Positions calculated with as few as four hydrophones show sub-meter accuracy within the footprint of the array and accuracy of greater than 1 m outside of the footprint. As more hydrophones are added to each position solution, error significantly decreases (Niezgoda et al., 2002). Received data are stored on flash cards on site and later transferred to a personal computer for processing.

2.2. Study animals

Starting on May 9th, 2004, snorkel surveys of the littoral zone were conducted daily to locate largemouth bass (*M. salmoides*) that were actively guarding nests. Upon locating an active bass nest (one that contained a guarding male and eggs), the snorkeler placed a numbered PVC tile near the nest and recorded nest location, nest depth, and number of eggs within the nest (visual, categorical assessment ranging from low of 1 to high of 5; Suski and Philipp 2004). A total of 16 males, each located guarding 1-day-old eggs, were used in this study. These fish were collected by angling the day after original location of the nest. Each fish was briefly angled (<10 s) from the nest and placed in a cooler of fresh lake water. Individuals were then removed from the cooler and held flat on a spatially referenced tray and digitally photographed (Sony DSC-P1, 3.3 megapixel) from 1 m directly above. Fish were also measured for total length (mean±SD, 415.7±33.0 mm, range, 320–447 mm) and gape (to the nearest mm measured by opening the mouth with calipers) before being returned to the cooler. Subsequently, fish were placed in a foam lined surgery trough that was filled with fresh lake water for transmitter attachment. Acoustic transmitters (Model CTP-M11-25, 11 mm × 25 mm, mass 23.9 g, signal transmission rate 2.5 s, Lotek Wireless Inc.) were externally attached to the nesting largemouth bass by a wire passed through the dorsal musculature (approximately 2 mm below the dorsal fin) using two hypodermic needles (21 gauge, 1.5″) (Cooke, 2003). Applied transmitters weighed less than 2–3% of the body weight so as to avoid an effect of the tag on individual behaviour (Winter, 1983; Brown et al., 1999). A rubber backing plate was positioned on the opposite side of the fish to prevent injury from the wire. Fish were then released within 5 m of the nest. The total amount of
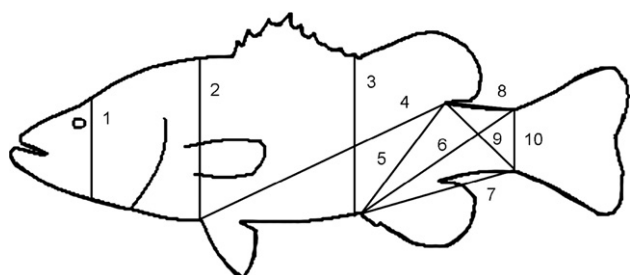
Fig. 1. Morphological traits measured for use in principal components analysis of the swimming performance of wild largemouth bass in Warner Lake, Ontario. 1. Head depth 1 (HD1), 2. head depth 2 (HD2), 3. body depth at the insertion of the spiny dorsal fin (PELVDF), 4. insertion of the pelvic fin to the posterior aspect of the soft dorsal fin (PELVSD), 5. insertion of the anal fin to the posterior aspect of the soft dorsal fin (ANSD), 6. insertion of the anal fin to the top caudal flexure (ANC1), 7. insertion of the anal fin to the bottom caudal flexure (ANC2), 8. posterior aspect of the soft dorsal fin to the top caudal flexure (SDC1), 9. posterior aspect of the soft dorsal fin to the bottom caudal flexure (SDC2), and 10. caudal flexure depth.

time required for both surgery and the capture of a digital image was less than 2 min. After release, fish movements were remotely monitored by the abovementioned acoustic telemetry array, and daily snorkeling surveys determined if the fish was present on the nest. Data recording was terminated when an individual left the nest area as a result of successfully raising a brood or abandoning the nest.

2.3. Data processing and analysis

Data processing details may be found in Niezgoda et al. (2002) and Hanson et al. (2007). Briefly, raw positional data were loaded into the program BioMAP (v. 2.1.12.1; Lotek Inc.) and then subjected to an internal two dimensional positioning engine. Fish position estimates computed by the telemetry equipment will have a precision level dictated by hydrophone geometry, fish tag location and the underlying temporal resolution of the receiver (Niezgoda et al., 2002). Invariably, estimate records will also contain spurious outliers that are artifacts of signal measurement, propagation anomalies and the mechanics of position estimation. To prepare data for further analysis two treatments are applied to position estimate records. The first treatment identifies and removes outliers based on a statistical outlier removal technique that separates samples on the basis of significance with respect to the underlying trend (Coifman and Wickerhauser, 1995). The second treatment smoothes the trajectory of position estimates by means of an adaptive trend filter (Wakeling et al., 2002). Information on the movements of each individual across the parental care period was determined by querying the fully filtered data set for each day the individual was present guarding the nest on a daily basis. Measures of daily maximum swim speed and daily distance traveled were calculated for each day the individual was on the nest (day defined as starting with the point to 00:00 h and ending with the closest signal to 23:59:59 h). Two dimensional distances between successive XY positions were calculated (with the assumption that the fish maintained constant depth) and summed across the day to determine the daily distance traveled. Subsequently, the mean daily distance traveled (a metric de-

Table 1
Results of simple linear regressions of total length by mean maximum swimming speed, mean daily distance traveled, median swimming speed and median daily distance traveled

Response variable	R^2	Parameter estimate	d.f.	F-ratio	P	Observed power	Least significant number
Mean maximum swimming speed (m/s)	0.0002	0.001	1, 14	0.002	0.964	0.050	28946
Mean daily distance traveled (m)	0.024	4.07	1, 14	0.339	0.570	0.085	184

scribing the amount of voluntary activity per day) was determined for each individual across the parental care period and used in analysis. Also, the maximum daily swim speed (defined as the fastest rate of travel between two successive XY positions) was calculated for each individual as a metric describing burst swimming behaviour associated with chasing off potential brood predators. Again, the mean swim speed was calculated by individual for further analysis as a measurement of voluntary swimming speed. Unfortunately, no field derived metric analogous to critical swimming speed could be constructed from the available data.

Additionally, to analyze data on a finer scale, analyses were carried out on positional data gathered on the fourth day of parental care for each fish. At this time period, broods have developed from eggs to egg sac fry and this transition has been noted as a time where largemouth bass are highly active (Cooke et al., 2002). Also, we standardized the behaviour of males with respect to parental investment by testing a specific day during the nest guarding period that is related to brood development. These analyses were also performed due to the fact that individual fish guarded their broods for various time periods ranging from 4 to 25 days. For this day, maximum swimming speed and distance traveled were calculated by the methods stated above for each individual. Also, mean swimming speed was determined as the average of all instantaneous swimming speeds calculated across the day for each fish.

Table 2
Loading of the morphological measurements into three principal factors by principal components analysis (PC1, PC2, and PC3)

	PC1	PC2	PC3
Eigenvalue	5.622	2.045	1.108
HD1	0.289	0.022	**0.569**
HD2	**0.371**	−0.012	**0.302**
PELDVF	**0.350**	−0.210	0.022
PELVSD	**0.383**	−0.237	−0.163
ANSD	**0.367**	−0.259	−0.192
ANC1	**0.312**	−0.014	−0.078
ANC2	**0.302**	0.262	**−0.358**
SDC1	0.053	**0.592**	0.289
SDC2	0.180	**0.558**	−0.002
CFD	**0.338**	0.257	**−0.346**
Gape	0.194	−0.189	**0.428**
% Variance explained	51.1	18.6	10.1

Variables that contribute maximally to each factor are in bold.

Table 3
Results of simple linear regressions of principal components vs. swimming performance factors

Factor	Response variable	R^2	Parameter estimate	*d.f.*	*F*-ratio	*P*	Observed power	Least significant number
Mean maximum swimming speed (m/s)	PC1	0.010	−0.116	1, 14	0.143	0.711	0.064	434
	PC2	0.157	−0.759	1, 14	2.602	0.129	0.324	26
	PC3	0.172	−1.079	1, 14	2.899	0.111	0.355	24
Mean daily distance traveled (m)	PC1	0.089	104.921	1, 14	1.373	0.261	0.194	47
	PC2	0.010	−56.964	1, 14	0.135	0.718	0.064	457
	PC3	0.330	−454.163	1, 14	6.883	***0.020***	0.685	12

Significant values ($\alpha = 0.05$) are presented in boldface and italicized type.

Digital images of individuals were measured for a suite of morphological characteristics (Fig. 1) using the program ImageJ (Abramoff et al., 2004). The following dimensions, modified from Hawkins and Quinn (1996), were measured: head depth 1 (HD1); head depth 2 (HD2); body depth at posterior aspect of the dorsal fin (PELVDF); origin of the pelvic fin to posterior aspect of the soft dorsal fin (PELVSD); origin of the anal fin to posterior aspect of the soft dorsal fin (ANSD); origin of the anal fin to the top of caudal flexure (ANC1); insertion of the anal fin to bottom of the caudal flexure (ANC2); posterior aspect of the soft dorsal fin to top of the caudal flexure (SDC1); posterior aspect of the soft dorsal fin to bottom of the caudal flexure (SDC2); and the caudal flexure depth (CFD). Morphological measures were resolved to the nearest millimeter. Additionally, gape and total length (measured at the time of capture) were used in subsequent analysis.

2.4. Statistical analysis

All analyses were performed in the statistical package JMP IN v 4.0 and the level of significance for all tests (α) was assessed at 0.05 (Zar, 1999). All values presented represent means±S.D. unless otherwise noted. To determine if size played a role in swimming performance during the spawning period, least squares linear regressions of total length by mean maximum swimming speed and mean daily distance traveled were performed (Ojanguren and Brana, 2003). To remove the possible effects of allometric growth on morphological measurements, the residuals of the least squares linear regressi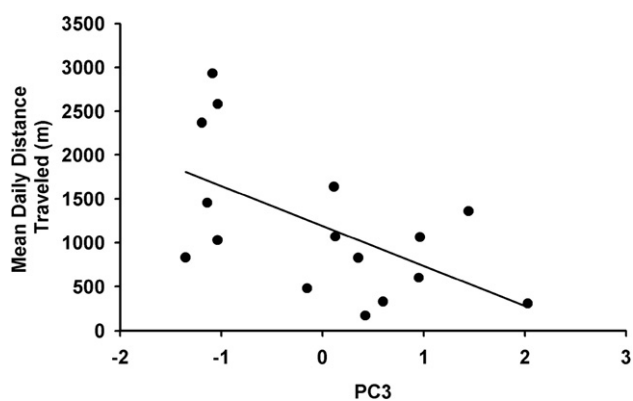on of log transformed traits on log transformed fish lengths were used in subsequent principal components analysis (Tabachnick and Fidell, 1989; Hawkins and Quinn, 1996; Ojanguren and Brana, 2003). The Kaiser–Guttman criteria (or latent root criteria) was used to determine which principal factors would be retained for later analysis (Kaiser, 1960). Principal factors with eigenvalue scores of greater than 1 were subsequently used to determine the relationship between morphology and swimming behaviour (Kaiser, 1960). Least squares linear regression between principal factors and both mean maximum swimming speed and mean daily distance traveled was then performed (Hawkins and Quinn, 1996; Ojanguren and Brana, 2003). *Post-hoc* power analyses were conducted using the observed effect size and variance to determine the power of each regression as well as the least number of samples required to determine significant differences given these effect sizes, and are presented with *P*-values to aid in data interpretation (Thomas, 1997).

The repeatability of swimming performance (both maximum swimming speed and daily distance traveled) of individuals across the parental care period was tested by conducting Spearman's coefficient of rank correlation tests on measures of swimming behaviour from the first full day of monitoring and the last full day of monitoring (Kolok, 1992b; Zar, 1999). If there was significant correlation between the rank order of individual swimming behaviours across the parental care period, this performance was repeatable. To aid in data interpretation, *post-hoc* power analyses were conducted using observed effect size
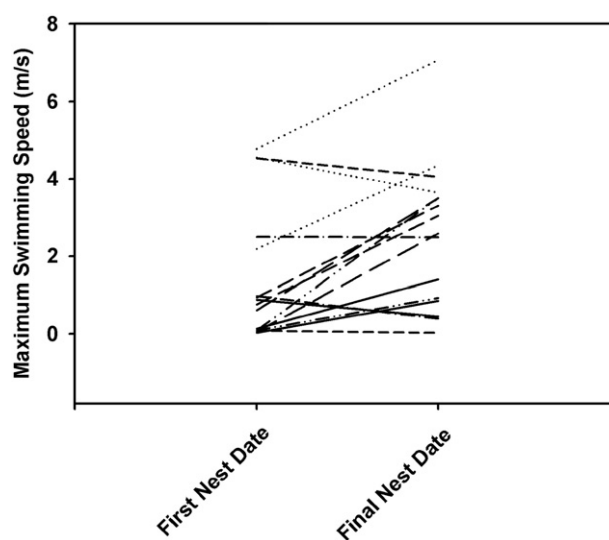

Fig. 2. Linear regressions of PC3 by mean daily distance traveled of nest guarding male largemouth bass across the parental care period ($R^2 = 0.330$, $F_{1,14}$ ratio = 6.883, $P = 0.020$).

Fig. 3. Repeatability of maximum daily swim speed across the parental care period by 16 largemouth bass in Warner Lake (Spearman's rho = 0.570, $P = 0.0213$).

Table 4
Results of simple linear regressions of principal components vs. maximum swimming speed on the fourth day of nest guarding

Factor	Response variable	R^2	Parameter estimate	d.f.	F-ratio	P	Observed power	Least significant number
Maximum swimming speed (m/s)	PC1	0.119	0.223	1, 14	1.883	0.192	0.249	35
	PC2	0.138	−0.398	1, 14	2.233	0.157	0.286	30
	PC3	0.026	−0.237	1, 14	0.380	0.547	0.088	164
Mean swimming speed (m/s)	PC1	0.012	0.002	1, 14	0.177	0.681	0.068	350
	PC2	0.015	0.003	1, 14	0.212	0.653	0.071	293
	PC3	0.410	−0.023	1, 14	9.738	*0.008*	0.827	9
Distance traveled (m)	PC1	0.095	198.602	1, 14	1.476	0.245	0.205	44
	PC2	0.010	105.621	1, 14	0.139	0.715	0.064	446
	PC3	0.329	−831.580	1, 14	6.876	*0.020*	0.684	12

Significant values ($\alpha = 0.05$) are presented in boldface and italicized type.

and variance and using predetermined effect size (5%) and the observed variance (Thomas, 1997).

3. Results

3.1. Entire reproductive period

There was no relationship between size and swimming activity metrics including mean (mean maximum swimming speed $R^2 = 0.0002$, $F_{1,14} = 0.002$, $P = 0.9639$) across the parental care period in nest guarding male bass, as revealed by linear regression (Table 1). However, principal components analysis produced three factors describing 79.8% of the variance in the morphological variables surveyed in this study (Table 2). Principal component 1 (PC1) was characterized by high positive factor loadings for HSD2, PELVDF, PELVSD, ANSD, ANC1, ANC2 and CFD (Table 2), representing overall body stoutness and accounting for 51.1% of the variance. SDC1 and SDC2 had high positive factor loadings for principal component 2 (PC2) (Table 2). This factor accounted for 18.6% of the variance and mainly described the length and depth of the caudal region and potential for propulsion ability. Lastly, principal component three accounted for 10.1% of the variance and described stoutness of the anterior portion of the fish (high positive factor loadings for HD1, HD2, and gape) and skinniness in the posterior portion of the fish (high negative factor loadings for ANC2 and CFD) (Table 2). Of the principal components formulated, only PC3 explained significant proportions of the variation in swimming performance of largemouth bass across the parental care period (Table 3). PC3 was negatively correlated with mean daily distance traveled ($R^2 = 0.330$, $F_{1,14}$ ratio $= 6.883$, $P = 0.020$; Table 3, Fig. 2). The other two principal components did not statistically correlate with swimming performance during the parental care period, though statistical power was generally low ($1 - \beta < 0.70$), suggesting that larger sample sizes would be needed to find significant differences (Table 3). Across the parental care period, maximum daily swimming speed was found to be repeatable by individual bass (Spearman's rho $= 0.570$, $P = 0.0213$; Fig. 3), but daily distance traveled was not (Spearman's rho $= 0.131$, $P = 0.6287$).

3.2. Egg sac fry stage

To determine the proportion of variation associated with differences in morphology, the three principal components were

regressed against maximum swimming speed, mean swimming speed, and distance traveled of each individual on the fourth day of nesting (when broods had developed from eggs to the egg sac fry) (Table 4). PC3 was negatively correlated with mean swimming speed at this stage of brood development ($R^2 = 0.410$, $F_{1,14}$ ratio $= 9.738$, $P = 0.0075$) (Table 4, Fig. 4A). Also, PC3 was negatively correlated with distance traveled on this day ($R^2 = 0.329$, $F_{1,14}$ ratio $= 6.826$, $P = 0.0201$) (Table 4, Fig. 4B). Again, no statistically significant correlations between the other two principal components and swimming performance on the fourth day of nest guarding, though it should be noted that statistical power was generally low ($1 - \beta < 0.70$), suggesting
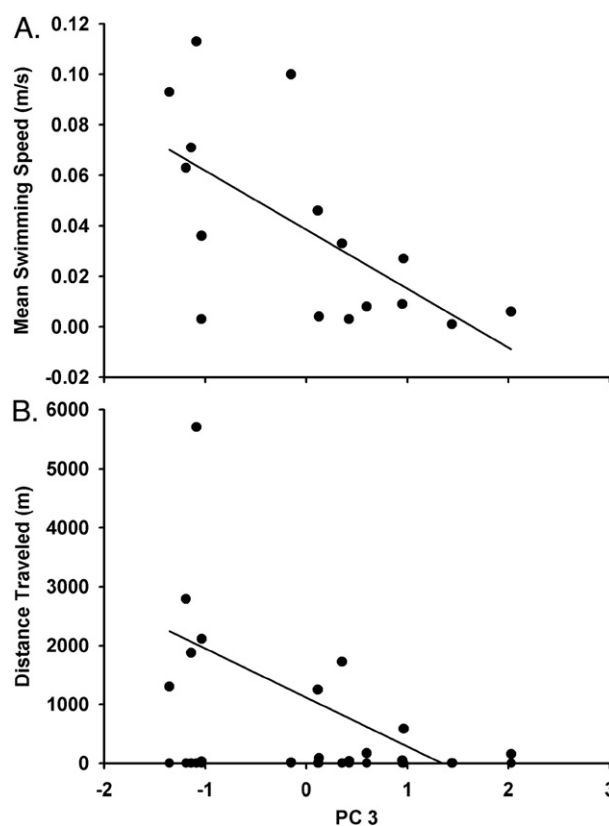

Fig. 4. Linear regression of principal component three by measurements of swimming performance on the fourth day of parental care by nest guarding male largemouth bass (A. mean swimming speed [$R^2 = 0.410$, $F_{1,14}$ ratio $= 9.738$, $P = 0.0075$], and B. distance traveled [$R^2 = 0.329$, $F_{1,14}$ ratio $= 6.826$, $P = 0.0201$]).

that larger sample sizes would be needed to find significant differences (Tables 4).

4. Discussion

Though there is an abundance of literature relating to the relationships between morphology and swimming performance (generally defined as sprint performance or endurance), to date, there is a lack of information regarding the similar relationships between voluntary activity (similar to the measures of this study) and functional morphology. Unfortunately, it is currently impossible to construct a metric of field based activity that is analogous to laboratory based sprint or critical swimming speeds. However, recent research has noted that individual variation in sprint performance is positively correlated with variation in voluntary activity in fish (McDonald et al., 2007). Due to the possible existence of correlation between sprint and voluntary swimming activities, the remainder of this discussion will draw upon literature concerning the relationships between morphology and sprint performance to guide interpretation of the data on voluntary activity generated through this study.

Of all the morphological measurements evaluated in this study, those summarized by PC3 were negatively correlated with swimming activity of largemouth bass during the reproductive period. PC3 was strongly correlated with measures of the larger size of the head and smaller size of the caudal region (Table 2). There are several biomechanical interpretations of why this particular suite of morphological characteristics would influence swimming behaviour. First, the negative relationship may be due to simple hydrodynamic inefficiency. A large head would increase the drag experienced by an individual while swimming, thereby slowing the fish (Weihs and Webb, 1983). Similarly, Boily and Magnan (2002) showed that swimming costs were higher for individual yellow perch characterized by stout body shapes most likely as a result of hydrodynamic drag. Additionally, largemouth bass swim by undulating the body and caudal fin (the subcarangiform swimming mode), ultimately achieving propulsion via lateral movements of the caudal region of the body (Webb, 1993; Johnson et al., 1994). The negative relationship between an undersized caudal region and swimming performance has been shown in multiple teleost fish species (Hawkins and Quinn, 1996; Ojanguren and Brana, 2003).

Second, the morphological relationships evidenced by PC3 may relate to the nutritional status of the bass during the spawning period. Studies of the morphology of fish subjected to starvation have repeatedly noted that as an individual fish starves and consumes internal energy stores, overall body shape changes (Gwak et al., 1999; Smith et al., 2005). The resultant body shape is characterized by a large head relative to the posterior end of the individual (Gwak et al., 1999; Smith et al., 2005). As such, it is possible that PC3 is related to the nutritional status of male largemouth bass at the beginning of the spawn. In northern latitudes (where this study was carried out), immediately prior to spawning, bass have spent the winter under ice presumably not feeding and relying on energy stores (Crawshaw, 1984; Mackereth et al., 1999). Immediately following winter, bass enter another time

of energy depletion, the reproductive period (Mackereth et al., 1999).

During the parental care period, male largemouth bass are highly active while defending and maintaining their brood, and only forage opportunistically, which can lead to an energy deficit at this time period of an individual's life (Kramer and Smith, 1962; Ridgway, 1988; Hinch and Collins, 1991; Mackereth et al., 1999; Cooke et al., 2002). As such, males are thought to primarily live off internal energy stores while partaking in parental care activities (Hinch and Collins, 1991; Ridgway and Shuter, 1994; Mackereth et al., 1999). Individuals that start the parental care period that have already experienced starvation (as indicated by the body morphology summarized by PC3) would have less energy to expend on care activities and may curtail swimming movements, both in distance traveled as well as in rate of movement, to conserve energy stores for later use. In multiple fish species, starvation disturbs the physiological status of an individual due to the breakdown of muscle tissue and disruption of proteins associated with locomotor performance (Loughna and Goldspink, 1984; Beardall and Johnston, 1983; van Dijk et al., 2002; Simpkins et al., 2003; Lapointe et al., 2006). In a number of fish species, starvation has been positively correlated with reductions in swimming activity and reduction in activity levels similar to what was seen in this study (Wieser et al., 1992; van Dijk et al., 2002). Additionally, Kolok (1992b) noted that there was a positive correlation between condition index and swimming performance in winter acclimated largemouth bass.

Lastly, studies have provided evidence that there is a genetic basis to swimming performance in fishes that would be unrelated to morphology. In multiple studies, it has been noted that the hierarchies of swimming performance between individuals is generally conserved even in the face of various biotic and abiotic stressors. Swimming performance has been noted to be a heritable trait in fish (Nicoletto, 1995; Garenc et al., 1998) and that performance is imbedded within individual phenotypic variation that can be acted upon by selective pressure (Ghalambor et al., 2003). Kolok (1992a) found that largemouth bass swimming performance was repeatable over a range of temperatures, indicating that the best swimmers maintained their performance regardless of ambient temperature. Martínez et al. (2001) found that cod (*Gadus morhua*) maintained individual hierarchies of sprint speed even through periods of starvation. Similarly, across this study, the hierarchy of individual swimming behaviour, measured as maximum daily swim speed at the start and end of parental care, was conserved. All of these facts lend credence to the genetic basis of swimming performance in fish.

In summary, we provide some of the first evidence from the wild that morphology is correlated with swimming activity. Also, although well documented in the laboratory, until now little information of the repeatability of swimming behaviour has shown for wild fish. As transmitter technology becomes more advanced, extremely rapid transmission rates (on the order of sub-second) with increased longevity will allow researchers to focus on seasonal variation of swimming behaviour.

Coupling this technology with non-lethal physiological sampling will also allow researchers to couple field based estimates of swimming behaviour with individual differences in physiological and energetic status.

Acknowledgements

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