

# Metabolic phenotype is not associated with vulnerability to angling in bluegill sunfish (*Lepomis macrochirus*)

Michael J. Louison, J.A. Stein, and C.D. Suski

**Abstract:** Prior work has described a link between an individual's metabolic rate and a willingness to take risks. One context in which high metabolic rates and risk-prone behaviors may prove to be maladaptive is in fish that strike fishing lures only to be captured by anglers. It has been shown that metabolic phenotype may be altered by angling; however, little work has assessed metabolic rate in fish and its relationship to angling vulnerability in a realistic angling trial. To address this, we subjected a set of bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) to a series of angling sessions. Following this, a subset of 23 fish that had been captured at least once and 25 fish that had not been captured were assessed for metabolic phenotype (standard and maximum metabolic rates, postexercise oxygen consumption, and recovery time) via intermittent flow respirometry. Contrary to predictions, captured and uncaptured fish did not differ in any measurement of metabolic rate. These results suggest that metabolic phenotype is not a determinant of angling vulnerability within the studied context. It is possible, therefore, that previously described alterations in metabolic phenotype owing to angling pressure may be context-specific and may not apply to all species and angling contexts.

**Key words:** bluegill sunfish, *Lepomis macrochirus*, fisheries-induced evolution, angling vulnerability, aerobic scope, standard metabolic rate, EPOC, respirometry.

**Résumé :** Des travaux antérieurs ont décrit un lien entre le métabolisme d'un individu et une disposition à prendre des risques. Des poissons qui frappent des leurres pour ensuite être capturés par des pêcheurs à la ligne constituent un exemple de contexte où un métabolisme élevé et des comportements à risque peuvent s'avérer inadaptés. S'il a été démontré que le phénotype métabolique peut être modifié par la pêche à la ligne, peu de travaux se sont toutefois penchés sur le métabolisme chez les poissons et son lien avec la vulnérabilité à la pêche dans un essai de pêche à la ligne réaliste. Nous avons donc fait subir à un ensemble de crapets arlequins (*Lepomis macrochirus* Rafinesque, 1819), une série de séances de pêche à la ligne. Un sous-ensemble de 23 poissons qui avaient été pris au moins une fois et 25 poissons qui n'avaient pas été pris ont ensuite été évalués pour déterminer leur phénotype métabolique (métabolismes standards et maximums, consommation d'oxygène après l'exercice et période de récupération) par respirométrie à débit intermittent. Contrairement aux prédictions, nous n'avons observé aucune différence en ce qui concerne les paramètres du métabolisme mesurés entre les poissons pris et non pris. Ces résultats indiqueraient que le phénotype métabolique n'est pas un déterminant de la vulnérabilité à la pêche à la ligne dans le contexte étudié. Il est donc possible que les modifications décrites antérieurement du phénotype métabolique découlant de la pression de pêche à la ligne soient propres au contexte et ne s'appliquent pas nécessairement à toutes les espèces et tous les contextes de pêche à la ligne. [Traduit par la Rédaction]

**Mots-clés :** crapet arlequin, *Lepomis macrochirus*, évolution induite par la pêche, vulnérabilité à la pêche à la ligne, portée aérobie, métabolisme standard, COAE, respirométrie.

## Introduction

Behavioral decisions by individuals are influenced by a host of factors associated with their physiology. Energy reserves, for instance, can be a major driver of behavior, with starving individuals likely to forage in riskier situations to acquire necessary energy (Dingemanse and Wolf 2010; Sih et al. 2015; Näslund and Johnsson 2016). Alternatively, high energy reserves may lead to more aggressive and (or) bold behavior (defined as a willingness to take risks) by facilitating faster growth, resulting in larger body size that lowers vulnerability to predators or aggressive competitors (Luttbegg and Sih 2010; Wolf and Weissing 2010). The amount of energy an organism has in reserve is determined by both its foraging success and its intrinsic metabolic rate, which dictates

the pace at which acquired energy stores are used (Metcalf et al. 1995; Houston 2010). Individuals with high metabolic rates often tend to take more risks while foraging to acquire enough food to satisfy metabolic demands (Stamps 2007; Biro and Stamps 2010). This expectation has been validated in several studies that found a highly integrated relationship between metabolism and bolder behavior (Killen et al. 2012; Herrera et al. 2014; Myles-Gonzalez et al. 2015; Binder et al. 2016), though this conclusion is not unanimous (Houston 2010). What is clear, however is that an organism's metabolic phenotype (standard metabolic rate, maximum metabolic rate, and its scope for aerobic and anaerobic activity; Metcalf et al. 2016) is capable of underpinning numerous aspects of its behavior.

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The behavioral decisions made by individuals may have fitness consequences, particularly when applied to encounters with humans. Bolder behavior, for example, which may have provided fitness benefits in an undisturbed environment, may suddenly become maladaptive if that bold behavior leads to death at the hands of humans (Sih 2013). One context in which this possibility has been previously studied is within the realm of fisheries, where evolution (hereafter referred to as fisheries-induced evolution) can occur in exploited populations as a result of selective harvest of individuals with certain behavioral, physiological, and life-history characteristics (Uusi-Heikkilä et al. 2008; Sutter et al. 2012; Diaz Pauli and Sih 2017). In the case of recreational angling, which uses so-called “passive gears” that require a fish to make a decision to approach a lure and strike, it has often been posited that bolder individuals will be more likely to be captured (Härkönen et al. 2014; Alós et al. 2016; Arlinghaus et al. 2017). If bold individuals are more likely to be captured, then high metabolic rates should also be positively associated with capture likelihood if indeed boldness and metabolic characteristics are linked. Indeed, prior work has found that fish populations exploited by anglers undergo downward shifts in metabolic phenotype resulting from the selective capture of individuals with high metabolic rates (Redpath et al. 2010; Hessenauer et al. 2015). This evidence collectively suggests that metabolic phenotype is a physiological variable of interest in terms of driving capture by recreational anglers.

Although prior work has indicated that metabolic phenotype may be altered in exploited fish populations, work that directly quantifies whether certain phenotypes are more vulnerable to angling is lacking. Due to potential links between metabolism, behavior, and feeding or foraging, aspects of metabolic phenotype may be responsible for fish striking lures and being captured (Cooke et al. 2007; Lennox et al. 2017). Alternatively, anglers may selectively capture individuals based on an unknown variable connected to metabolic rate, which leads to metabolic phenotype being altered even though it is not the proximal driver of selection (Ketterson and Nolan 1999). In addition, whether angling-driven selection alters metabolic phenotype in multiple species targeted by recreational anglers is not known. Work demonstrating alterations in metabolic phenotype as a result of recreational harvest have largely been performed using largemouth bass (*Micropterus salmoides* (Lacépède, 1802)) (Cooke et al. 2007; Redpath et al. 2010; Hessenauer et al. 2015), and no other work has quantified the role of metabolic phenotype in driving angling vulnerability for any other species. More work is necessary to define links between metabolic phenotype and angling vulnerability in additional contexts, especially in additional species that may be subject to the effects of fisheries-induced evolution in freshwater systems.

The goal of the present study was to define whether metabolic phenotype drives capture likelihood in bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) (hereafter simply bluegill). This species is an ideal candidate for study because it is an extremely popular species targeted by recreational anglers throughout much of the eastern and central portions of the United States and Canada (Gaeta et al. 2013), and little work to this point has been done examining how individual traits may relate to capture vulnerability in this species (but see Wilson et al. 2011). In addition, positive relationships between boldness and metabolic characteristics have been previously described for this species (Binder et al. 2016), allowing us to extrapolate likely behavioral traits of bluegill based on their metabolic phenotype. We experimentally angled lake-reared bluegill held in an earthen pond to establish captured and uncaptured groups, which we then assessed for differences in metabolic phenotype. We also assessed whether metabolic phenotype was connected to the order in which fish were captured, predicting that individuals with high metabolic rates would be captured early in the angling process. Assessing capture order in addition to whether or not the fish was captured may provide insights into whether metabolic rate is connected with hook-

avoidance learning in fish. For instance, if individuals with certain metabolic phenotypes are captured in later angling sessions (after the threat of angling has been established), that may indicate that those phenotypes have a more difficult time learning to avoid striking fishing lures. We hypothesized that, in congruence with prior work on largemouth bass, individuals with high standard metabolic rates and aerobic scopes would be more vulnerable to capture. If metabolic phenotype is indeed a driver of capture likelihood in bluegill, then this finding combined with previous work would indicate that metabolic phenotype may be a key trait under selection in a larger set of contexts. This could have major impacts on not only the metabolic physiology of exploited populations, but on the ecologically relevant behaviors that are themselves linked to metabolic phenotype.

## Materials and methods

### Fish and holding conditions

A total of 160 bluegill were acquired from Jake Wolf Hatchery in Topeka, Illinois, USA, in fall 2015. The hatchery environment for these fish was in a natural lake setting, where they were able to forage for natural prey items and avoid predators (both piscine and avian), thus eliminating the possibility of fish behavior being altered as a result of rearing in typical sterile hatchery conditions (Lee and Berejikian 2008). After being acquired from the hatchery, fish were transported to the Illinois Natural History Survey's Aquatic Research Facility near Champaign, Illinois, USA. This facility consists of a wet laboratory and a series of earthen-bottom experimental ponds, all of which feature natural macrophyte cover and stocked fathead minnows (*Pimephales promelas* Rafinesque, 1820), along with natural macroinvertebrate forage. Following arrival at the facility, all fish were implanted with a passive integrated transponder (PIT) tag for individual identification and were subsequently stocked into a single 0.04 ha pond where they were held for 8 months. In spring 2016, the pond was drained and 115 bluegill (total mass =  $100.0 \pm 2.7$  g (mean  $\pm$  SE)) were recovered. These fish were then stocked into a second pond (hereafter the angling pond), which featured nearly identical conditions to the original pond, and were the subjects of the present study.

### Experimental angling

Experimental angling to quantify angling vulnerability in bluegill occurred between 8 and 10 July 2016 and consisted of five 90 min angling sessions. On all 3 days, a morning angling session was conducted beginning at 0700; on 8 and 9 July, an afternoon session was conducted beginning at 1730. For each angling session, the perimeter of the pond was divided in half and one of two experienced anglers fished each half. Every 30 min during the 90 min session (30 min subunits are hereafter referred to as periods), the anglers switched sides of the pond. Both anglers used identical gear commonly used by anglers targeting bluegill. This gear consisted of light-action spinning rods spooled with 1.8 kg Berkley® Trilene monofilament fishing line, tied to a single 12 Eagle Claw® J-Hook suspended from a slip-bobber. Hooks were baited with Berkley® Crappie Nibbles that were colored chartreuse, pink, or white. During each 30 min period, each angler used a different colored bait as determined by random selection and casted to all areas within the pond to maximize catch rates. Fish captured via angling were identified by PIT tag before being released back into the pond within 1 min of capture, and the color of lure and section of the pond where capture occurred were noted. All fish, except for one, were hooked in the mouth with minimal tissue damage; the fish that was deep-hooked in the gullet failed to recover in a separate tank and was subsequently euthanized. Although released fish were available to be potentially captured a second time, only two recapture events occurred over the five angling sessions. All fish that were captured at least once over the five angling sessions were considered vulnerable to

angling for the study. Following the angling sessions, a total of 34 bluegill were captured (2 of which had been captured twice) and 81 bluegill were not captured. In addition to these captures, anglers also noted when a strike was detected, evidenced by the bobber being pulled below the surface of the water, but a fish was not successfully landed (e.g., situations where bluegill “nibbled” the lure and likely never fully ingested the hook into its mouth). These situations were considered “misses”, in line with previous angling research on bluegill (Cooke et al. 2005).

Five days following the conclusion of angling, the pond was drained and 54 bluegill (24 captured, 30 uncaptured) were randomly selected and transferred to a series of 1175 L circular holding tanks connected to a recirculating flow-through system that brought water in continuously from an adjacent pond. The remaining fish that were not used in the study were subsequently stocked into a separate on-site pond. Tanks were stocked at a density of nine fish per tank (four captured, five uncaptured). Water temperatures in the tanks matched ambient conditions in the ponds (daily temperature =  $25.98 \pm 0.2$  °C (mean  $\pm$  SE)). During holding, fish were fed daily with frozen bloodworms (Chironomidae). A total of 48 fish ( $n = 23$  captured fish,  $n = 25$  uncaptured) out of this group of 54 were then assessed for metabolic rate, beginning on 20 July. We chose not to assess all 115 fish for metabolic phenotype because we were concerned that the photoperiod and ambient temperature would change over extended period required to conduct respirometry assessments on all fish, thus biasing assessments of metabolic rates (Biswas and Takeuchi 2002).

### Metabolic phenotype assessment

The 48 bluegill randomly selected following angling trials were assessed for metabolic phenotype via intermittent flow respirometry (Metcalfe et al. 1995; Redpath et al. 2010; Nelson and Chabot 2011). Four fish were analyzed each day over the course of 12 days, beginning on 21 July 2016. During these 12 days, fish that had not yet been assessed for metabolic phenotype continued to be held in holding tanks described above. On the day before analyses, each bluegill was loaded into an individual 27 L black Perspex box fed by a flow-through recirculation system that maintained dissolved oxygen above  $10 \text{ mg}\cdot\text{L}^{-1}$  and temperature at  $24$  °C using an air stone and a heater–chiller (Teco®, Ravenna, Italy) in the reservoir tank that fed the system. This was done to ensure that all fish were fasted for 24 h before conducting respirometry trials (Nelson and Chabot 2011) and to allow fish an opportunity to acclimate to the water temperatures employed in the respirometry setup. On the day of the trial, each bluegill was removed from its individual container and placed into a 190 L tank and immediately exercised to exhaustion via “tail pinching” (Norin and Clark 2016), where an observer attempted to grab the tail of the fish forcing it to burst to escape. All fish were considered exhausted when they no longer made attempts to escape and could be easily grabbed by the observer without successive bursts. Immediately following exercise, fish were loaded into one of four 5.26 L individual respirometry cylinders immersed in a 585 L tank. Water temperatures in the tank were maintained at  $24$  °C using heater–chillers and dissolved oxygen in the tank was maintained near 100% saturation with a series of air stones. Dissolved oxygen levels in the cylinders were monitored continuously using fiber optic oxygen probes (Loligo Systems®, Tjele, Denmark). The measurement cycle was determined following a series of pilot trials and went as follows: 10 min flush, 5 min wait, and 12 min measurement; thus, the measurement cycle provided an individual measurement of metabolic rate ( $\dot{M}_{\text{O}_2}$  given in  $\text{mg O}_2 \text{ consumed}\cdot(\text{kg fish mass})^{-1}\cdot\text{h}^{-1}$ ) every 27 min. All fish were held in respirometry chambers overnight before being removed the following morning (17–18 h later). Following removal, a measurement of background metabolic rate was taken by measuring oxygen consumption in the cylinders without the fish. Background respiration as a result of microbial activity was then cor-

rected for each measurement based on a linear increase in  $\dot{M}_{\text{O}_2}$  from the outset of the trial (when pilot trials previously showed background  $\dot{M}_{\text{O}_2}$  values to be at zero) to the background  $\dot{M}_{\text{O}_2}$  value obtained after removing the fish (Rodgers et al. 2016). To keep background respiration at a minimum, the entire setup (all tubing and chambers) was cleaned in a 10% bleach solution before each trial.

Calculation of metabolic phenotype metrics was performed following methods described in Killen et al. (2015). Standard metabolic rate (SMR) was calculated as the mean of the lowest tenth percentile of  $\dot{M}_{\text{O}_2}$  values collected during overnight holding. Maximum metabolic rate (MMR) was determined as the single largest individual  $\dot{M}_{\text{O}_2}$  obtained following exercise. Aerobic scope (AS) was calculated as the difference between MMR and SMR for each fish and routine metabolic rate (RMR) was defined as the mean of all  $\dot{M}_{\text{O}_2}$  measurements, excluding the first 2 h after loading. The determination of RMR was then used to calculate excess post-exercise oxygen consumption (EPOC). For this, a sixth-order polynomial recovery function was constructed that ran through all collected  $\dot{M}_{\text{O}_2}$  values obtained following exercise and overnight. EPOC was then defined as the area under this curve and above RMR between the onset of the trial and the point where the recovery curve intersected with RMR (Killen et al. 2015). Recovery time ( $T_r$ ) was defined as the time needed before the fish had recovered 50% of its AS, as taken from  $\dot{M}_{\text{O}_2}$  values. Although we are conscious of prior studies that have shown that stressors can influence measures of metabolic phenotype, we found it unlikely that the process of being captured would have impacted measurements of metabolic phenotype because prior work has shown that fish can recover normal metabolic cardiovascular function within 12 h of the angling stressor (Milligan et al. 2000; Cooke et al. 2003).

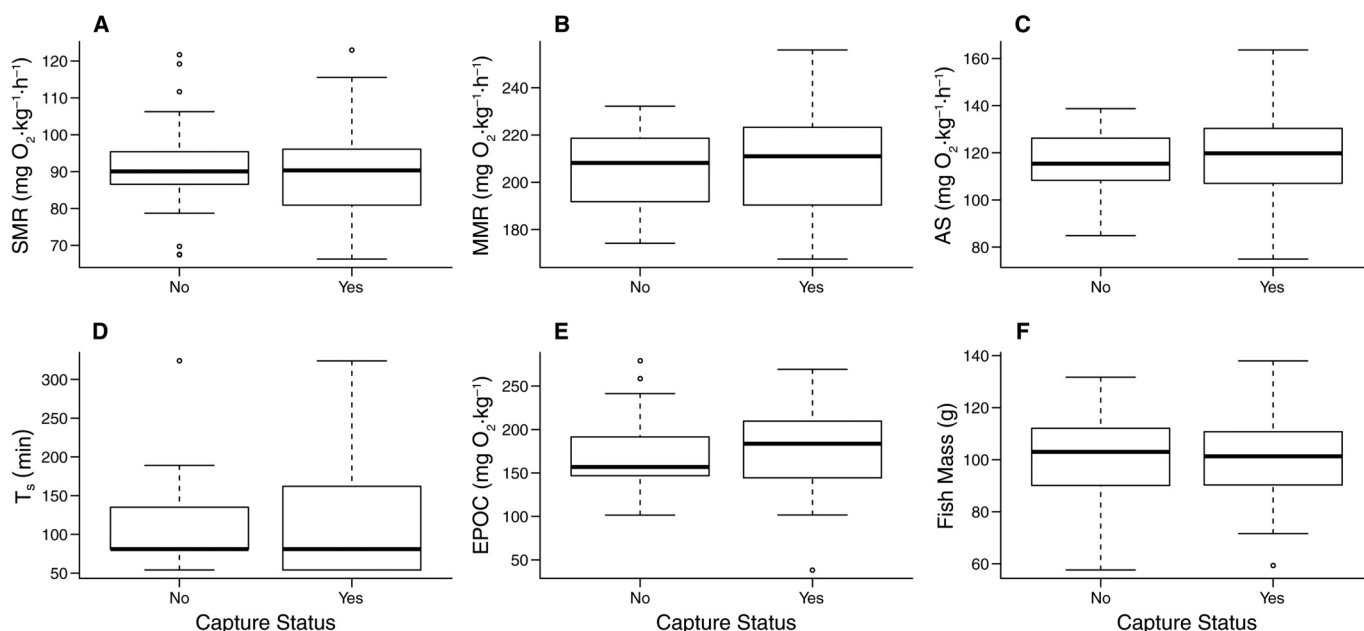
### Statistical analysis

To reduce the number of variables assessed and to account for correlations among metabolic metrics (SMR, MMR, AS,  $T_r$ , and EPOC), principal components analysis (PCA) based on the correlation matrix was performed. Component scores for each fish were varimax rotated based on the maximum-likelihood solution, components with an eigenvalue over 1 were retained, and factor loadings with an absolute value  $\geq 0.4$  were considered significant contributors to each factor (Kaiser 1960; King et al. 2016). Once components were extracted, Pearson’s correlation tests were run to determine if any components were associated with fish mass.

To determine if the two anglers were systematically capturing fish with different metabolic phenotypes, Student’s *t* tests were run comparing all extracted principal components between anglers. A Fisher’s exact test was then used to determine if one angler captured a disproportionate number of fish relative to the other angler. A one-way analysis of variance (ANOVA) was used to determine if any extracted components for captured fish differed depending on the color of the lure on which they were captured.

To determine if angling selected for particular metabolic characteristics, a binary logistic regression was run to determine if any extracted components or fish mass were associated with capture status. In addition, an ordinal regression was performed to determine if metabolic metrics influenced the order in which fish were captured. For this analysis, only captured fish were assessed and fish capture was binned by angling session. This approach was taken, rather than running the analysis based on the actual order of capture (for instance, the first, second, third fish captured, and so on), to account for the fact that the likelihood of capture may depend on both intrinsic characteristics (e.g., metabolic phenotype) and chance encounter with the lure. By grouping all captured fish by session of capture, this issue is eliminated because, within each angling session, the entire pond was angled and every fish likely was presented with a lure, especially given the relatively small size (0.04 ha) of the angling pond.

**Fig. 1.** Box plots describing (A) standard metabolic rate (SMR), (B) maximum metabolic rate (MMR), (C) aerobic scope (AS), (D) recovery time ( $T_s$ ), (E) excess postexercise oxygen consumption (EPOC), and (F) fish mass for bluegill sunfish (*Lepomis macrochirus*) by capture status ( $n = 23$  yes (captured),  $n = 25$  no (uncaptured)). No measure of metabolic phenotype differed between captured and uncaptured fish. Box limits indicate the 25th (lower) and 75th (upper) percentiles, whiskers indicate 1.5 times the interquartile range above and below the 75th and 25th percentiles, respectively, open circles are outliers, and the solid horizontal line indicates the median.



**Table 1.** Factor loadings of metabolic metrics across all bluegill sunfish (*Lepomis macrochirus*) derived from principal components analysis (PCA).

Factor	Loading		
	PC1	PC2	PC3
SMR (mg O <sub>2</sub> ·kg <sup>-1</sup> ·h <sup>-1</sup> )			0.989
MMR (mg O <sub>2</sub> ·kg <sup>-1</sup> ·h <sup>-1</sup> )	0.815		0.575
AS (mg O <sub>2</sub> ·kg <sup>-1</sup> ·h <sup>-1</sup> )	0.974		
EPOC (mg O <sub>2</sub> ·kg <sup>-1</sup> )	0.490	0.747	
$T_s$ (h)		0.956	
Eigenvalue	1.96	1.77	1.03
% Variance explained	39.22	35.41	21.46

**Note:** SMR, standard metabolic rate; MMR, maximum metabolic rate; AS, aerobic scope; EPOC, excess postexercise oxygen consumption;  $T_s$ , recovery time.

For all tests, homogeneity of variances on raw data were confirmed using Levene’s tests and normality was assessed following visual inspection of residual q–q plots. All analyses were conducted in R version 3.3.1 (R Foundation of Statistical Computing, Vienna, Austria; available from <https://www.r-project.org/>) and the level of significance ( $\alpha$ ) used for all tests was 0.05.

**Results**

Summaries of all metabolic metrics and fish mass by capture status are given in Figs. 1A–1F. Three principal components of metabolic phenotype with eigenvalues over 1 were extracted from these metabolic metrics (PC1–PC3). MMR and AS loaded positively on PC1,  $T_s$  and EPOC loaded positively on PC2, and SMR and MMR loaded positively on PC3 (Table 1). Cumulatively, the three extracted components explained over 96% of the total variance in the data (Table 1). No relationship was present between fish mass and PC1; however, mass was significantly and negatively associated with both PC2 (Student’s  $t$  test,  $t = -2.39$ ,  $p = 0.02$ ) and PC3 (Student’s  $t$  test,  $t = -3.95$ ,  $p < 0.001$ ). This indicates that larger fish

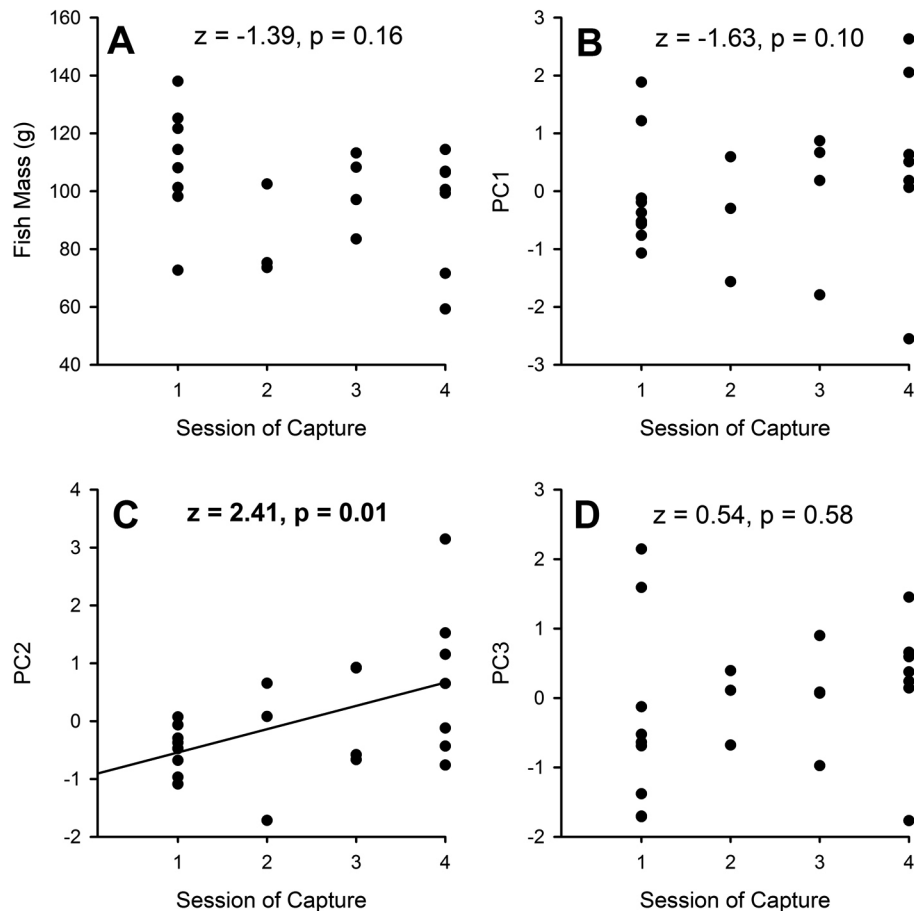
**Table 2.** Output of binary logistic regression analysis examining relationships between principal components (PC) of metabolic phenotype and angling vulnerability in bluegill sunfish (*Lepomis macrochirus*) ( $n = 23$  captured,  $n = 25$  uncaptured).

Factor	Estimate	SE	$z$	$p$
Intercept	1.06	2.05	0.52	0.60
Fish mass	-0.01	0.02	-0.56	0.57
PC1	0.18	0.30	0.61	0.54
PC2	-0.03	0.32	-0.11	0.91
PC3	-0.23	0.35	-0.66	0.50

had a shorter recovery time and smaller EPOC, as well as a lower SMR, than smaller fish.

Angling resulted in the capture of 34 of the available 115 fish (36 total capture events, including 2 recaptures). Twelve of the capture events occurred in session one, 6 in session two, 7 in session three, and 11 in session four. No fish were captured during session five. The subsample of fish used for respirometry paralleled the proportion of fish caught in each session overall, with nine fish captured in session one, three captured in session two, four captured in session three, and seven captured in session four. When a strike was detected, as evidenced by the bobber being pulled beneath the surface of the water, the landing success rate across both anglers was 51.4%. Although this potentially leaves several fish that struck the bait classified as “uncaptured”, this landing rate is comparable with previously reported landing rates for bluegill anglers (Cooke et al. 2005), making the angling regime used presently a realistic representation of angling selection on bluegill in the wild. Furthermore, the majority of misses were nibbles, where fish likely did not completely ingest the hook. In our case, fish that fully struck the hook were classified as vulnerable, whereas nibbles were not considered indicative of a vulnerable fish. Of the total captures, 23 (64%) fish were captured by one angler and 13 fish were captured by the second angler. Although this difference in the proportion of captures by each angler was

**Fig. 2.** (A, B, C, D) Relationships between extracted principal components (PC) of metabolic phenotype and session in which bluegill sunfish (*Lepomis macrochirus*) ( $n = 23$ ) were captured. Statistical outputs provided are derived from an ordinal regression analysis that included fish mass as the independent variable and the session in which the fish was captured as the dependent variable. The regression line in panel C indicates a significant relationship between PC2 and angling session, with higher scores associated with capture in later sessions.



statistically significant (Fisher's exact test,  $p = 0.03$ ), no components of metabolic phenotype nor fish mass differed across anglers (Student's  $t$  tests, all  $p > 0.3$  for all extracted metabolic components and fish mass) or lure color (ANOVA,  $p > 0.17$  for all components and fish mass). Therefore, all captures were pooled regardless of angler or lure color for the metabolic phenotype comparison between captured and uncaptured fish.

Neither extracted metabolic components nor fish mass were a significant predictor of capture (Table 2). However, among the captured fish, PC2 was significantly associated with the session in which fish were captured, with those fish that were captured later tending to have a higher PC2 score (Figs. 2A–2D).

## Discussion

Metabolic phenotype did not influence whether or not an individual bluegill was captured during experimental angling. Metabolic rate describes the rate of energy consumption in organisms; individuals that have high metabolic rates will need to have high rates of food consumption to meet their energetic demands (Biro and Stamps 2010). Metabolic phenotype is a heritable characteristic in organisms that has been found to correlate positively with several ecologically relevant behavioral characteristics including boldness, aggression, performance, and activity level (Biro and Stamps 2008, 2010; Reale et al. 2010; Metcalfe et al. 2016). This positive relationship has also been found in bluegill, with bold individuals having higher aerobic scopes for activity (Binder et al. 2016). In turn, these behaviors can be drivers of fitness; a frequent finding has been that bolder, more active, and (or) aggressive

individuals achieve higher fitness (Biro and Stamps 2008). This relationship, however, has not been universally demonstrated and may be dependent on life stage (Ballew et al. 2017) or selective pressures that may lead to the decoupling of behavioral and metabolic characteristics (Houston 2010; Hille and Cooper 2015). Although this is possible, we have no reason to suspect that the relationship between metabolic phenotype and boldness in bluegill, demonstrated by Binder et al. (2016), is any different for fish in the current study. The bluegill used in this study are the products of natural reproduction in a lake featuring a full suite of native predators, as well as typical forage and cover items. Therefore, the selective pressures on these bluegill were likely similar to those in any other natural environment, including the lake the bluegill described in Binder et al. (2016) were taken from. If we are to assume, therefore, the same link between metabolic phenotype and behavior is common for bluegill, then angling-driven selection based on metabolic phenotype could drive evolutionary changes in the behavior of exploited populations (Arlinghaus et al. 2017). However, because the current study showed that metabolic phenotype did not impact whether or not an individual was captured, we would not expect anglers to impart selection on metabolic phenotypes for bluegill.

Previous work has examined the role of behavior (particularly boldness) in driving vulnerability to capture independent of metabolic phenotype, with some studies suggesting that bold individuals are more vulnerable and thus would be selected against in an environment exploited by anglers (Härkönen et al. 2014; Alós et al. 2016). Additionally, studies using lines of largemouth bass

artificially selected for differing vulnerability to angling found not only that the “high vulnerability” line exhibited higher metabolic rates relative to less vulnerable fish (Cooke et al. 2007; Redpath et al. 2010), but also that more aggressive nest defense behavior in highly vulnerable fish led to higher reproductive success (Sutter et al. 2012). Furthermore, Hessenauer et al. (2015) showed that largemouth bass from unfished reservoirs had higher SMR relative to fish from reservoirs exploited by anglers, providing further evidence that angling-induced selection can influence metabolic rates. Although it is tempting to then generalize these findings to all species, some evidence exists indicating that relationships among metabolic phenotype, behavior, and angling vulnerability may differ in bluegill compared with other species. Although a prior study of bluegill showed that a positive relationship between metabolic rate and boldness is indeed present (Binder et al. 2016), another study that assessed the relationship between boldness and angling vulnerability found that individuals captured via angling were shyer than those captured via seining (Wilson et al. 2011). Under this combined framework where shyer individuals are more vulnerable to angling, it might therefore be expected that individuals with lower metabolic rates would actually be more likely to be caught; however, the data in our study do not support this prediction. Perhaps the angling context (lure type, size of the pond, etc.) used in this study prevented the selective capture of certain metabolic phenotypes or did not provide enough angling time to detect a significant effect of metabolism on angling vulnerability. Future work will be needed to determine if metabolic phenotype may indeed be under selection in bluegill, focusing on the role of metabolism in various contexts.

Among captured fish, individuals with longer recovery times and lower EPOC were more likely to be captured in later angling sessions. However, given the relatively low number of captured fish and the lack of relationship between session of capture and other aspects of metabolic phenotype, this finding is difficult to interpret. Prior to the outset of the study, we posited that capture order might be either positively or negatively associated with metabolic phenotype (particularly SMR and aerobic scope) even if overall mean metabolic rate was similar between captured and uncaptured fish, through several possible mechanisms. First, high metabolic rates are driven by relatively high allocation costs, with a greater amount of energy being routed towards active behavior, sexual development, digestion, and other needs (Enberg et al. 2012). This would lead fish to have to feed more frequently to satisfy those demands, in turn leading to a greater probability of striking a fishing bait. In a second connected mechanism, higher activity levels as a result of high metabolic rates could have led bluegill to be more likely to randomly encounter fishing gear (Stamps 2007). Finally, at least two studies (Metcalf et al. 1995; Killen et al. 2014) have found a positive relationship between metabolic rate and aggression, which may facilitate dominance over the food resource (in this case, the bait), leading to more captures. Alternatively, if feeding motivation and behavior are not driving lure striking, then the phenotype of individuals captured early or late in the angling process could be driven by relative learning ability. It is well established that fish are able to learn to avoid lures following a period of angling pressure (Young and Hayes 2004; Lennox et al. 2016). The process of learning has been previously described as a type of behavioral flexibility (Stamps 2016), and high metabolic rates, while positively associated with boldness, have been negatively associated with behavioral flexibility (Koolhaas et al. 1999). With regards to capture order, it would then be possible that fish caught later in the angling process would have higher metabolic rates, as behaviorally flexible individuals with lower metabolic rates would have altered their behaviors to avoid striking the bait more successfully. However, neither of these possible mechanisms were supported by our data, which found no relationship between capture order and aerobic components (SMR, MMR, AS) of metabolic phenotype. This finding

presents another piece of evidence that, for bluegill, metabolic phenotype is not associated with angling vulnerability.

Vulnerability to angling for a fish is likely driven by a host of behavioral and state-driven factors (Lennox et al. 2017). Although prior work has found metabolic phenotype to be altered in heavily angled populations (Redpath et al. 2010; Hessenauer et al. 2015), we propose four potential explanations for why metabolic phenotype did not predict capture for bluegill that could be explored in future work. First, metabolic phenotype may not be a major driver of capture in fish, at least over short periods of angling, but still may be altered over a longer period of time due to its covariance with other physiological or behavioral characteristics that are actually proximal drivers (Ketterson and Nolan 1999). For example, a recent study found that, over a week of angling, individual largemouth bass that showed lower increases in cortisol concentration in plasma following a stressor were more likely to be captured (Louison et al. 2017). Although cortisol levels and metabolic rate were not correlated in that study, the fact that these physiological traits have been shown to be linked previously (Careau et al. 2008) could provide a route through which metabolic phenotype could evolve under the selective pressure of angling even if metabolic rate is not the proximal driver of vulnerability. A second alternative explanation could be that conditions present in the pond altered the selectivity of capture based on metabolic phenotype. The pond where angling took place featured a high density of forage between the stocked juvenile fathead minnows and natural aquatic invertebrates. Under these conditions, it is possible that all fish, regardless of their metabolic rate, were fed to satiation. As a result, the angled population may not have differed in feeding motivation, which could eliminate the role of metabolic rate in driving the response to fishing baits. A third potential explanation applies to the species used in the present study. Although many studies have quantified the relationship between boldness or activity and angling vulnerability, a notable exception to the general finding that boldness is positively correlated with vulnerability (Alós et al. 2012, 2016; Härkönen et al. 2014; Villegas-Ríos et al. 2014) was found in bluegill, where individuals that were caught via angling were shyer than those captured from the same area via seining (Wilson et al. 2011). These results indicate that there is perhaps something specific and unknown about this species and its behavior that leads to individuals with the high boldness or high metabolic rate phenotype (Binder et al. 2016) to not be more vulnerable to angling as in other species. However, it should be noted that, in the study by Wilson et al. (2011), when seined fish were subjected to angling in an artificial environment, it was the bolder fish that were found to be more vulnerable. This could indicate that vulnerability to angling is driven both by the fish's phenotype and by the angling environment, which would lead to particular phenotypes being more vulnerable in some situations but not in others. Alternatively, the lack of a relationship between metabolic phenotype and capture likelihood may be related to the methodology of the study, specifically angling over a relatively short period of time (single captures over three angling sessions). This short period may not have allowed for angling in a wide variety of environmental contexts (different water temperatures, forage availability, photoperiod, etc.) that change seasonally, and metabolic phenotype may prove to be a driver of capture likelihood under alternative environmental conditions. Indeed, previous work that demonstrated an impact of angling on metabolic rate in largemouth bass occurred over several generations (Redpath et al. 2010; Hessenauer et al. 2015). Further work will therefore be necessary to determine if the findings seen in this study apply to all environmental contexts in bluegill, and also to examine how environmental context may change patterns of angling-induced selection in other targeted species.

The selective capture of individuals with particular traits has the potential to evolutionarily alter exploited fish populations.

This process of fisheries-induced evolution has previously been quantified in commercially exploited marine fisheries, with studies demonstrating alterations in life-history traits such as age at maturity and mean growth rate (Devine et al. 2012; Kuparinen and Hutchings 2012; Eikeset et al. 2013). The potential for fisheries-induced evolution to occur in recreationally-targeted fisheries has been demonstrated as well (Edeline et al. 2007; Philipp et al. 2009). For recreational stocks, this necessitates the determination of characteristics that may be drivers of angling vulnerability, and thus under selective pressure. Metabolic phenotype emerges as a primary variable of interest, due to its cascading impacts on the behavior and ecology of individuals (Metcalf et al. 1995; Killen et al. 2012; Myles-Gonzalez et al. 2015) and the fact that prior studies have indicated that it may be under selective pressure in recreationally fished populations (Redpath et al. 2010; Hessenauer et al. 2015). We found no evidence that any measurement of metabolic phenotype is a determinant of angling vulnerability in bluegill in the context of acute, short-term fishing pressure. This finding is a further demonstration of the fact that the drivers of angling vulnerability may not be simple, and that within different contexts (different times of year, gear types, targeted species), angling-induced selection may or may not cause evolution in particular traits. Because metabolic phenotype has been shown to be linked to boldness, and prior work has shown that bolder bluegill are not more vulnerable to capture (Wilson et al. 2011), a behavioral cascade leading to shyer average behavior and lowered metabolic rates in exploited populations (Arlinghaus et al. 2017) may therefore be unlikely to occur for this species. The lack of a metabolic influence on capture likelihood, however, does not preclude the possibility that bluegill populations have indeed been evolutionarily changed due to angling, with alternative characteristics driving angling vulnerability. Going forward, it will be incumbent on managers and researchers to continue to investigate these possible factors, with an eye towards accurate predictions of how various targeted species may evolutionarily respond to angling pressure.

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