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Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish

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Abstract

In recreational fisheries, a correlation has been established between fishing-induced selection pressures and the metabolic traits of individual fish. This study used a population of largemouth bass (*Micropterus salmoides*) with lines of low vulnerability fish (LVF) and high vulnerability fish (HVF) that were previously established through artificial truncation selection experiments. The main objective was to evaluate if differential vulnerability to angling was correlated with growth, energetics and nutritional condition during the sub-adult stage. Absolute growth rate was found to be between 9% and 17% higher for LVF compared with HVF over a 6-month period in three experimental ponds. The gonadosomatic index in females was lower for LVF compared with HVF in one experimental pond. No significant differences in energy stores (measured using body constituent analysis) were observed between LVF and HVF. In addition, both groups were consuming the same prey items as evidenced by stomach content analysis. The inherent reasons behind differential vulnerability to angling are complex, and selection for these opposing phenotypes appears to select for differing growth rates, although the driving factors remain unclear. These traits are important from a life-history perspective, and alterations to their frequency as a result of fishing-induced selection could alter fish population structure. These findings further emphasize the need to incorporate evolutionary principles into fisheries management activities.

Introduction

An emerging issue in fisheries science concerns the awareness that fishing pressure is a selective force that is influencing the direction of evolutionary change (reviewed in Law 2000; Heino and Godø 2002; Jørgensen et al. 2007; Kuparinen and Merilä 2007). The specific traits that are under selection in commercial fishing are often dictated by type and size of gear, due to correlations with body size (Law 2000). Fishing-induced selection has not been as extensively studied in a recreational context, and the complexity of factors that determine the vulnerability of an individual fish to capture makes it more difficult to discern the specific traits that are under selection. Uusi-Heikkilä et al. (2008) emphasized that behavioural traits rather than life-history traits are more likely to determine an individual's vulnerability to angling. Behaviours that are likely to influence vulnerability include: wariness or boldness (Anderson and Heman 1969; Garrett 2002), aggression (Cooke et al. 2007), ability to learn (Beukema 1970; Askey et al. 2006) and spatial and temporal foraging activity (Philipp et al. 2009). If the behaviours and other

phenotypic traits that make a fish vulnerable to angling have a genetic basis, selection pressure can be exerted upon harvest (Lewin et al. 2006) and when hooking or stress-related mortality occurs in catch-and-release events (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007). Angling-induced selection is also conceivable without mortality, for example in cases of impairment during reproduction through catch-and-release angling (Cooke et al. 2002). Consequences that may become apparent as a result of these lethal and nonlethal events acting on highly vulnerable individuals could include decreased catch rates and reduced reproductive output of the population (Philipp et al. 2009). Knowledge of the specific traits under selection is crucial to understand how evolutionary changes may be manifested in terms of growth, survival and reproductive capabilities of recreational fish populations, and to develop management strategies that account for potential changes on population dynamics and viability (Ashley et al. 2003; Francis et al. 2007; Jørgensen et al. 2007).

The vast majority of research into the evolutionary consequences of fishing-induced selection has focused on the effects of commercial marine fishing from a life-history trait perspective (Jørgensen et al. 2007; Kuparinen and Merilä 2007). Changes to life-history traits have been documented in commercially exploited fish species for growth rate (e.g. grayling, *Thymallus thymallus* Haugen and Vøllestad 2001), age at maturation (e.g. Atlantic cod, *Gadus morhua* Olsen et al. 2004), size at maturation (e.g. Atlantic halibut, *Hippoglossus hippoglossus* Haug and Tjemsland 1986) and reproductive investment (e.g. North Sea plaice, *Pleuronectes platessa* Rijnsdorp et al. 2005). Similar findings have been reported in model species used in laboratory selection experiments (e.g. Atlantic silversides, *Menidia menidia* Munch et al. 2005; guppies, *Poecilia reticulata* Reznick and Ghalambor 2005). Relatively few studies on fishing-induced selection have been conducted in recreational fisheries (Lewin et al. 2006). Available research has shown that vulnerability to angling is a genetically heritable trait in an experimentally-selected population of largemouth bass (*Micropterus salmoides*), with a realized heritability of 0.15 (Philipp et al. 2009). Recent studies on fish with differential vulnerability to angling have focused on the physiological correlates of this vulnerability. This research has revealed that largemouth bass with lower levels of vulnerability have lower resting cardiac variables (Cooke et al. 2007), lower standard metabolic rates and a narrower metabolic scope for activity (T.D. Redpath, S.J. Cooke, C.D. Suski, R. Arlinghaus, P. Couture, D.H. Wahl and D.P. Philipp unpublished manuscript). While these findings have provided some insight into the traits linked to vulnerability to angling in a recreational fish species, the effects of these metabolic differences on characteristics such as growth and resource consumption have not been evaluated.

Growth is of central importance in fisheries management, and its allocation rate towards somatic and reproductive tissues influences the time to maturation, reproductive investment and harvestable biomass of a fish population (Calow 1985). Growth rate and body size are traits known to have moderate levels of heritability (reviewed for Atlantic salmon, *Salmo salar*, in Garcia de Leaniz et al. 2007), and any selection that occurs may affect the reproductive capacity and productivity of a fish population. The amount of food resources consumed will naturally influence growth rate, and any increases in standard metabolic rate will be accompanied by higher energetic costs (Priede 1985). It is therefore necessary to increase food consumption to maintain the same growth rates as individuals with lower intrinsic metabolic rates (Brett and Groves 1979; Jobling 1985). Differences in food consumption can be detected by examining the body constituents (lipid, protein, trace minerals and water content) and the energy density of protein and lipids (Breck 2008). As well, an examination of blood-based nutritional condition indicators that reflect energy reserves can provide further insight into the overall health of the fish (Congleton and Wagner 2006). An evaluation of growth rates, energetics and nutritional indicators in fish differentially selected for vulnerability to angling may provide further insight into the diversity of traits under selection as well as the consequences of selection from a fisheries management perspective.

The purpose of this study was to evaluate growth, energetics and nutritional status in two experimental lines of largemouth bass (*M. salmoides* Lacépède) with differential vulnerability to angling (Philipp et al. 2009). We tested the null hypothesis of no differences in growth rate, body condition, energetic status, feeding and nutritional condition between low vulnerability fish (LVF) and high vulnerability fish (HVF). Fish were held in experimental ponds in central Illinois to provide a semi-natural environment complete with variation in food abundance, abiotic conditions and predation. Although pond experiments lack the level of control that can be achieved in a laboratory environment, pond studies yield data that are ecologically relevant.

Materials and methods

Study animals

The model species chosen for these experiments was the largemouth bass, because it is subjected to high levels of angling pressure in North America (Pullis and Laughland 1999). This study takes advantage of a unique artificial truncation selection experiment that began several

decades ago at the Illinois Natural History Survey (Philipp et al. 2009). Beginning in 1977, largemouth bass in Ridge Lake (39.40°N, 88.16°W; 7.1 ha surface area) were subjected to four consecutive seasons of angling, and catch histories of tagged individuals were recorded as part of a project evaluating the impact of catch-and-release angling (Burkett et al. 1984). Following these four seasons of angling, the lake was drained and the largemouth bass were collected. Based on an assessment of individual catch histories, two divergent experimental lines, each with two replicate lines, were selected for low and high vulnerability to angling (Philipp et al. 2009). Low vulnerability brood fish (LVF) were never captured across all four seasons, and HVF were captured more than four times in a single season (Philipp et al. 2009). Five pairs in each parental (P1) generation of each line were bred in separate experimental ponds to produce first (F1) generation offspring, which were then differentiated by pelvic fin clips (Philipp et al. 2009). The offspring from each replicated line ($n = 200$) were raised together in a common pond for 3 years until the individuals were large enough to be angled (Philipp et al. 2009). A selection procedure using experimental angling over one season was repeated on the F1 fish, and LVF and HVF were again separated into different experimental ponds for breeding (Philipp et al. 2009). The F2 generation offspring were raised in a manner similar to the F1 generation, and the same selection procedure was repeated until the F4 generation. The response to selection was found to increase with each generation, and LVF displayed a heightened response as compared with HVF (Philipp et al. 2009). The fish used in this research were bred naturally in ponds in the spring of 2006 as part of an F4 generation, and they had not experienced any further artificial selection.

Growth assessment

In April 2007, age 1 largemouth bass [LVF, $n = 161$, TL = 66 ± 0.5 mm (mean ± SE), WT = 3.6 ± 0.01 g; HVF, $n = 161$, TL = 71 ± 0.5 mm, WT = 4.7 ± 0.1 g; where $P < 0.001$ for TL and WT] were removed from a common garden experimental pond (0.1 ha with a maximum depth of 2.5 m) at the University of Illinois in Champaign-Urbana. The fish were then re-stocked into four smaller experimental ponds (0.04 ha with a maximum depth of 2 m), with each pond containing 40 LVF and 40 HVF to provide ample space for growth across the summer season. Although the density of stocked fish may appear high when compared against densities found in wild bass populations, previous studies that utilized similar ponds as mesocosms have not documented any impairment to growth (Baur et al. 1979; Buck and Hooe 1986; Isely et al. 1987). Any concerns related to the artificially high density would be mainly for food resource competition. As this type of competition occurs regularly for wild largemouth bass, this was not an issue in this study. Each pond contained a standing stock of naturally reproducing fathead minnows (*Pimephales promelas* Rafinesque) providing forage for the largemouth bass. The presence of the fathead minnow populations was confirmed in October 2006, and the populations of fathead minnows were also enhanced through stocking at that time. Naturalized populations of benthic invertebrates, zooplankton and occasionally terrestrial invertebrates provided additional food sources. Our initial experimental design utilized four ponds as replicates (to be able to control for a pond effect) to assess absolute growth over a 6-month period. We intended to remove a sub-sample of fish from each pond in July and again in October. However, due to unforeseen mortalities over the course of the spring and early summer, one pond (Pond C) was entirely lost and the remaining three ponds saw declines in overall numbers. The mortality data was expressed in terms of percentages. These experimental ponds are considered mesocosms of natural systems, and therefore mortality can occur due to disease outbreaks, predation by birds and rapid fluctuations in temperature or dissolved oxygen. To ensure that we would have sufficient sample sizes at both sampling periods, we abandoned the original strategy to use each pond as a replicate. Rather, fish sampled in July (by seine net) were taken randomly from Pond B, and fish sampled in October (by draining down the ponds) were taken randomly from Pond A and Pond D. Comparisons between LVF and HVF were conducted for individual ponds, because it was not possible to separate potential seasonal changes from potential pond effects. Change in length (mm) since removal from the common pond was calculated by subtracting the initial mean length (based on $n = 40$) for either LVF or HVF (from each pond) from the total length of each individual sampled from either Pond B, Pond A, or Pond D because it was not possible to uniquely mark individual fish. Absolute growth rate was determined by dividing the change in length by the number of days, expressed as mm day^{-1} (Jobling 1985; Leitner et al. 2002).

Dissections and blood sampling

All largemouth bass sampled from each pond had their lengths recorded to the nearest mm, and their weights recorded to the nearest 0.1 g. Fulton's condition factor was calculated according to the following equation:

$$K_{TL} = (100\,000)(W)/L^3$$

where W = weight in g, and L = total length in mm (Lagler 1956).

A sub-sample of fish collected from the common pond (in April) was euthanized by cerebral percussion (LVF, $n = 15$; HVF, $n = 17$). The liver was removed and weighed, and the carcass was homogenized in a food chopper and frozen in airtight bags at −20°C for future energetic analyses. Sub-samples of fish were collected from Pond B (in July) (LVF, $n = 13$; HVF, $n = 13$) and Pond A (in October) (LVF, $n = 10$; HVF, $n = 4$), and they were euthanized using concentrated anesthetic (250 mg L^{-1} of tricaine methanesulfonate buffered by 500 mg L^{-1} of sodium bicarbonate) (Summerfelt and Smith 1990). Sampling proceeded once the fish had lost equilibrium and ceased ventilation (~2 min). Blood samples (1 mL) were taken from the caudal vein with a 1.9 cm, 26-gauge needle and a syringe previously rinsed with a solution of heparinized saline to prevent coagulation (Houston 1990; Russell 1990). The blood was immediately transferred to a 1.5 mL microcentrifuge tube and centrifuged at 10 000 g for 2 min. The plasma (supernatant) was separated from the blood cells, stored in liquid nitrogen and transferred to a −80°C freezer in the laboratory.

Dissections were undertaken on the fish collected from ponds B and A to separate the liver, gonads, stomach and intestines. The weight of all organs was recorded to the nearest 0.01 g. Liver weight and gonad weight (females only) were expressed as a percentage of the total body weight to yield the hepatosomatic index (HSI) and the gonadosomatic index (GSI) (Coelho and Erzini 2006). Estimates were made in terms of the percentage of material found in the stomach and the gut, and the stomach and gut were weighed together. The contents of the stomach were examined, and the basic types of forage were identified (i.e. invertebrate, minnow). The presence or absence of prey types within each stomach enabled a comparison between LVF and HVF in terms of preferred forage over approximately the previous 24 h (Franssen and Gido 2006). The remainder of the carcass was coarsely homogenized in a food processor and frozen at −20°C for future energetic analyses.

Energetic analyses

To ensure an accurate assessment of the whole body lipid stores, a portion (6–8 g) of each homogenized carcass was ground into a powder under liquid nitrogen using a mortar and pestle (Booth et al. 1995). Samples (2 g) of the powdered carcasses were dried overnight (18 h) to a constant mass at 80°C. The dried samples were then crushed using a glass pestle, and a portion (0.2 g) was used in the lipid extraction procedure. The lipid content of the whole body (fish from all ponds) and the livers and gonads (Pond A) was determined using the Smedes and Askland (1999) modification of the chloroform-methanol extraction technique developed by Bligh and Dyer (1959). Briefly, the samples were combined with chloroform, methanol and water in a 1:2:0.8 mL ratio and placed in an ultrasonic bath (Fisher Scientific FS20, Pittsburg, PA) for 15 min. Additional amounts of chloroform and water were added, and the samples were centrifuged at 2500 g for 10 min (VWR Clinical 50 Centrifuge, West Chester, PA). The solvent layer of chloroform (containing the lipids) was removed using a pipette and filtered through sodium sulfate and quartz wool, and the extraction procedure was repeated on the supernatant. The extracted lipids were left overnight (to allow the chloroform to evaporate), dried for 1 h at 60°C and weighed to calculate the percent of lipids by dry mass. These values for the dried samples were then expressed in terms of percent of lipid by wet mass. Each individual fish was analyzed in duplicate, and the variation between the percentages for the sub-samples was never >2%.

The remaining whole body constituents (water, protein and trace mineral) were analyzed following the methods outlined in Crossin and Hinch (2005). A representative sample (2 g) of each homogenized carcass was selected (avoiding large pieces of bone and skin), and they were weighed and dried overnight (18 h) to a constant mass at 80°C. Once dry, the samples were re-weighed to determine the percent of water by wet mass. The dried samples were then combusted for 2 h in a muffle furnace at 500–600°C, and the remaining ash was weighed to determine the percentage of trace minerals by wet mass. Each individual fish was analyzed in duplicate, and the variation between the percentages of the sub-samples was never >2%. The percent of body protein was determined by the relationship $C_P = 100-(C_W + C_A + C_L)$, where C_W, C_A, and C_L = percent water, ash, and lipid respectively (Berg et al. 1998; Hendry et al. 2000).

Fish energy density was calculated according to the following equation:

$$d = fD_f + pD_p,$$

where d = energy density in MJ kg^{-1}, f and P = fraction of lipids and proteins from the samples, expressed in g kg^{-1}, D_f and D_p = energy density of lipids and protein in fish, expressed in MJ g^{-1} (Breck 2008). The energy density values for lipids and proteins were derived from the values presented for fish in Brett and Groves (1979), where lipids in fish contain 0.0362 MJ g^{-1} and proteins in fish contain 0.0201 MJ g^{-1}.

Nutritional indicator analyses

Plasma from LVF and HVF sampled from Pond B were analyzed for concentrations of biochemical components

that form an index of nutritional condition in fish (total protein, cholesterol, triglycerides, calcium, and magnesium) (Wagner and Congleton 2004; Congleton and Wagner 2006). These analyses were conducted on a Roche Hitachi 917 analyzer (Basal, Switzerland) and based upon the International Federation of Clinical Chemistry and Laboratory Medicine (IFCC) standard reference model. To ensure proper quality control, all assays followed procedural guidelines for standardization and quality assurance established by the Veterinary Laboratory Association Quality Assurance Program, College of American Pathologists, and the Canadian Food Inspection Agency External Proficiency Panel.

Statistical analysis

For all data, normality was assessed using a one-sample Kolmogorov–Smirnov test and homogeneity of variance was assessed using the Levene's test. The comparisons of growth rates, whole body constituents, energetic indices, stomach and gut content percentages and weights, and nutritional indicators between LVF and HVF in each individual pond were conducted using *t*-tests. The type of prey items in the stomach contents between LVF and HVF were compared using a chi-square test. Arcsine square-root transformations were carried out on all proportional data (whole body constituents). All analyses were carried out using JMP 7.0 (SAS Institute). Values are reported as means (±SE) and tests are interpreted at a significance level (α) of 0.05. Due to multiple comparisons between similar parameters, sequential Bonferroni corrections were applied to the level of significance used to test each null hypothesis (Rice 1989). Bonferroni corrections assume independent comparisons, however our comparisons are not fully independent and thus the correction is likely too conservative. Bonferroni corrections are used in this study as benchmarks, and any results deemed nonsignificant based on this conservative criterion may in fact still be important (Cabin and Mitchell 2000; Moran 2003).

Results

Many of the results highlighted below demonstrate changes between the ponds, which were each sampled at different periods throughout the growing season. Due to the inherent uncertainty over whether these changes are due to individual pond effects or seasonal differences, the results will be presented on a pond-by-pond basis. LVF exhibited consistently higher absolute growth rates than HVF in all three ponds, with growth rates that were between 8.7% and 17.3% greater (Table 1). While growth rate in Pond B was significantly different between LVF and HVF without the Bonferroni correction ($P = 0.037$; $\alpha = 0.05$), it merely approached significance when assessed under the more conservative Bonferroni criterion ($\alpha = 0.017$). The total length and weight for LVF was 8% and 23% less than for HVF when the experiments were initiated from the common pond. LVF and HVF demonstrated similar measurements when Pond B was seined, but the total length for LVF was 6–7.5% greater than for HVF when Pond A and Pond D were drained. These total lengths were significantly different when assessed against $\alpha = 0.05$ (Pond A: $P = 0.022$; Pond D: $P = 0.039$) but not when assessed against the Bonferroni criterion ($\alpha = 0.017$).

Fulton's condition factor was not significantly different between LVF and HVF in any of the three ponds

Table 1. Comparison of growth for low vulnerability (LVF) and high vulnerability (HVF) largemouth bass in three separate ponds.

		Vulnerability				Test	
	Parameter	LVF	*n*	HVF	*n*	statistic (*T*)	*P*-value
Common pond (April)	Total length (mm)	66 ± 0.5	161	71 ± 0.5	161	7.660	**<0.001**
	Weight (g)	3.6 ± 0.01	161	4.7 ± 0.1	161	7.468	**<0.001**
Pond A (October)	Total length (mm)	262 ± 2.9	10	247 ± 4.9	4	−2.631	0.022*
	Weight (g)	265 ± 13.7	10	229 ± 17.4	4	−1.472	0.167
	Absolute growth (mm day^{-1})	1.02 ± 0.02	10	0.92 ± 0.03	4	−3.398	**0.005**
Pond B (July)	Total length (mm)	168 ± 3.3	13	163 ± 2.3	13	−1.194	0.244
	Weight (g)	60 ± 5.7	13	56 ± 2.3	13	−0.640	0.528
	Absolute growth (mm day^{-1})	0.85 ± 0.03	13	0.78 ± 0.02	13	−2.208	0.037*
Pond D (October)	Total length (mm)	200 ± 4.0	8	185 ± 5.3	8	−2.284	0.039*
	Weight (g)	95 ± 6.7	8	79 ± 8.3	8	−1.528	0.149
	Absolute growth (mm day^{-1})	0.69 ± 0.02	8	0.57 ± 0.03	8	−3.564	**0.003**

Data are presented as mean ± SE.

As multiple comparisons were conducted, Bonferroni corrections were applied. Significant values based on the criterion $\alpha = 0.017$ are in boldface type. Significant values prior to Bonferroni corrections $\alpha = 0.05$ are indicated by an asterisk.

(Table 2). The HSI demonstrated no differences between LVF and HVF, although HSI was higher for fish sampled from the common pond as compared with Pond A and Pond B. Female LVF demonstrated a lower GSI compared with HVF in Pond B.

The stomach and gut content percentages, as well as the gut weight, were not significantly different between LVF and HVF in either Pond A or Pond B (Table 3). An assessment of the stomach contents revealed that the majority of individuals (85%) were consuming aquatic invertebrates in both Pond A and Pond B. The chi-square test demonstrated no differences between the prey items in the stomach contents of the LVF and the HVF for either pond (Pond A: calculated $\chi^2 = 2.0$, critical $\chi^2 = 3.84$; Pond B: calculated $\chi^2 = 0.62$, critical $\chi^2 = 3.84$).

No differences were observed between LVF and HVF for energy stores, as assessed by whole body constituent analysis (in terms of percent lipid, protein, trace minerals, and water), or for the calculated energy density values (Table 4). There were no differences between the percentage of lipids within the livers and the gonads of the LVF and HVF collected from Pond A. Energy stores and the calculated energy density values varied across the ponds. Although percent lipid values and energy densities were higher and water content was lower for fish in Pond B compared with the common pond, these values were stable between Pond A and Pond B. Although percent protein and trace mineral values were similar between fish in the common pond and Pond B, these values varied between Pond A and Pond B.

From the suite of plasma biochemical indicators that were assessed as an indication of nutritional condition (total protein, cholesterol, triglycerides, calcium, and magnesium), only magnesium approached a significant difference between LVF and HVF (Table 5). This difference was significant when assessed under the criterion of $\alpha = 0.05$, although under the Bonferroni correction this difference was not significant. The levels of magnesium were 17% lower for LVF as compared with HVF.

Survival of LVF and HVF was highly variable across ponds and was the highest in Pond B (Table 6). There was a clear trend of higher survival of LVF compared with HVF across all ponds.

Table 2. Comparison of body condition for low vulnerability (LVF) and high vulnerability (HVF) largemouth bass in three separate ponds.

		Vulnerability				Test	
	Parameter	LVF	*n*	HVF	*n*	statistic (*T*)	*P*-value
Common pond (April)	Fulton's condition factor	1.19 ± 0.02	15	1.24 ± 0.02	17	1.920	0.064
	Hepatosomatic index (%)	2.30 ± 0.25	15	2.26 ± 0.13	17	−0.159	0.875
Pond A (October)	Fulton's condition factor	1.46 ± 0.03	10	1.51 ± 0.05	4	0.785	0.448
	Hepatosomatic index (%)	0.93 ± 0.04	10	1.03 ± 0.12	4	1.035	0.321
	Gonadosomatic index (%)	1.32 ± 0.11	6	1.58 ± 0.01	3	2.309	0.069
Pond B (July)	Fulton's condition factor	1.24 ± 0.04	13	1.29 ± 0.01	13	1.375	0.182
	Hepatosomatic index (%)	1.05 ± 0.09	13	0.96 ± 0.05	13	−0.888	0.383
	Gonadosomatic index (%)	0.49 ± 0.02	8	0.65 ± 0.03	7	4.141	**0.001**

Data are presented as mean ± SE.
As multiple comparisons were conducted, Bonferroni corrections were applied. Significant values based on the criterion $\alpha = 0.017$ are in boldface type.

Table 3. Comparison of stomach and gut analyses between low vulnerability (LVF) and high vulnerability (HVF) largemouth bass presented as mean ± SE.

		Vulnerability				Test	
	Parameter	HVF	*n*	LVF	*n*	statistic (*T*)	*P*-value
Pond A (October)	Stomach contents (%)	5 ± 2.0	4	35 ± 11.1	10	−2.224	0.051
	Gut contents (%)	6 ± 4.7	4	23 ± 8.6	10	−1.720	0.111
	Stomach and gut weight (g)	11.43 ± 0.96	4	16.16 ± 1.94	10	−1.484	0.164
Pond B (July)	Stomach contents (%)	26 ± 6.3	13	42 ± 7.0	13	−1.673	0.107
	Gut contents (%)	32 ± 5.3	13	22 ± 3.3	13	1.601	0.125
	Stomach and gut weight (g)	2.65 ± 0.10	13	3.59 ± 0.71	13	−1.320	0.199

As multiple comparisons were conducted, Bonferroni corrections were applied. The significance of values was based on the criterion $\alpha = 0.017$.

Table 4. Comparison of energetics for low vulnerability (LVF) and high vulnerability (HVF) largemouth bass in three separate ponds.

		Vulnerability				Test	
	Parameter	LVF	*n*	HVF	*n*	statistic (*T*)	*P*-value
Common pond (April)	Lipid (%)	2.24 ± 0.08	15	2.22 ± 0.11	17	−0.164	0.871
	Protein (%)	17.2 ± 0.13	15	17.1 ± 0.17	17	−0.580	0.566
	Trace minerals (%)	4.29 ± 0.12	15	4.47 ± 0.18	17	0.777	0.443
	Water (%)	76.3 ± 0.24	15	76.2 ± 0.27	17	−0.116	0.909
	Energy density (MJ kg^{-1})	4.27 ± 0.04	15	4.24 ± 0.04	17	−0.557	0.582
Pond A (October)	Lipid (%)	3.52 ± 0.25	10	3.79 ± 0.32	4	0.613	0.551
	Protein (%)	18.4 ± 0.28	10	18.4 ± 0.97	4	−0.059	0.954
	Trace minerals (%)	3.62 ± 0.28	10	3.19 ± 0.35	4	−0.821	0.428
	Water (%)	74.5 ± 0.49	10	74.7 ± 1.26	4	0.193	0.851
	Energy density (MJ kg^{-1})	4.97 ± 0.11	10	5.06 ± 0.26	4	0.391	0.703
Pond B (July)	Lipid (%)	3.80 ± 0.18	13	3.48 ± 0.11	13	1.505	0.145
	Lipid – liver (%)	5.49 ± 0.19	10	5.07 ± 0.32	4	−1.160	0.270
	Lipid – gonad (%)	4.60 ± 0.23	6	4.25 ± 0.74	3	−0.060	0.570
	Protein (%)	17.6 ± 0.18	13	17.6 ± 0.11	13	−0.131	0.897
	Trace minerals (%)	4.56 ± 0.21	13	4.55 ± 0.14	13	0.033	0.974
	Water (%)	74.0 ± 0.39	13	74.4 ± 0.22	13	0.811	0.426
	Energy density (MJ kg^{-1})	4.92 ± 0.07	13	4.80 ± 0.04	13	−1.597	0.123

Data are presented as mean ± SE.
As multiple comparisons were conducted, Bonferroni corrections were applied. The significance of values was based on the criterion $\alpha = 0.01$.

Table 5. Comparison of nutritional indicators between low vulnerability (LVF) and high vulnerability (HVF) largemouth bass presented as mean ± SE.

	Vulnerability					
Parameter	HVF	*n*	LVF	*n*	Test statistic	*P*-value
Total protein (g L^{-1})	31 ± 0.8	12	30 ± 0.8	11	$T = 0.72$	0.48
Cholesterol (mmol L^{-1})	8.7 ± 0.3	12	8.4 ± 0.3	11	$T = 0.77$	0.45
Triglycerides (mmol L^{-1})	3.55 ± 0.33	12	3.15 ± 0.38	11	$T = 0.80$	0.44
Calcium (mmol L^{-1})	3.51 ± 0.18	12	3.33 ± 0.04	11	$U = -0.37$	0.71
Magnesium (mmol L^{-1})	1.83 ± 0.11	12	1.52 ± 0.05	11	$U = -2.34$	0.02*

Data were analyzed using a *t*-test (*T*) or a Mann-Whitney *U* test (*U*). As multiple comparisons were conducted, Bonferroni corrections were applied. The significance of values was based on the criterion $\alpha = 0.01$. Significant values prior to Bonferroni corrections ($\alpha = 0.05$) are indicated by an asterisk.

Table 6. Survival rates for low vulnerability (LVF) and high vulnerability (HVF) largemouth bass stocked in four experimental ponds.

Pond and stock	No stocked	Date sampled	No of fish recovered	% survival
Pond A				
LVF	41	11-Oct-07	20	49
HVF	41		4	10
Pond B				
LVF	40	30-Jul-07	25	63
HVF	40		22	55
Pond D				
LVF	40	16-Oct-07	12	30
HVF	40		8	20

Discussion

This study revealed that life-history traits are correlated with vulnerability to angling in largemouth bass in a manner that conflicts with the findings in commercial marine fisheries, where selection has mainly been size-based (Kuparinen and Merilä 2007; Law 2007). Specifically, differences in growth rates and GSI were observed between the two experimental lines of largemouth bass leading us to reject our null hypothesis. When initially sampled in the common pond, LVF displayed a lower length and weight than HVF. However, for Pond B (sampled in July) these differences were no longer evident, and for Pond A (sampled in October) the initial trend had reversed, with LVF displaying a greater length than

HVF. When assessed against the baseline values, LVF achieved higher absolute growth rates (mm day $^{-1}$) than HVF across all three experimental ponds.

The total amount of energy ingested by a fish is partitioned towards growth (somatic and reproductive), metabolism (standard, feeding and active), and excretion (which remains constant) (Brett and Groves 1979; Calow 1985). LVF have a lower standard metabolic rate (SMR) (Cooke et al. 2007; Redpath et al. unpublished manuscript), affording them the opportunity to decrease their energy intake yet maintain a stable growth rate (Brett 1979; Brett and Groves 1979). The faster growth rate found in LVF may indicate that they are more than capable of consuming sufficient food resources [estimated to be 30% less than those of HVF (Cooke et al. 2007)] to support their reduced metabolism. Indeed, if feeding rates were equal, we would expect LVF to have higher growth rates. If the assumption that both groups of fish display the same metabolic scope is made, then the increased foraging required by HVF to support their higher SMR would necessarily encompass a greater portion of their active metabolism (Priede 1985). Locomotion in fish requires considerable amounts of energy (Brett and Groves 1979), and any increases in activity by HVF could result in less available scope for feeding metabolism and digestion processes, resulting in decreased growth (Priede 1985). HVF have indeed displayed a greater metabolic scope for activity (Redpath et al. unpublished manuscript). The finding of a slower growth rate in HVF may be evidence that their metabolic scope is still not broad enough to account for the increased energy requirements of a higher standard metabolic rate and related foraging activity. In juvenile sand sharks (*Carcharhinus plumbeus*), it has been shown that 34–100% of the metabolic scope is required to sustain routine metabolic rates, a factor that is thought to result in slower growth rates (Dowd et al. 2006). We assumed that food resources were not a limiting factor in our study, given the presence of naturally reproducing fathead minnows and aquatic invertebrates in each pond. Without a measurement of actual food consumption, it is difficult to determine ingestion rates and relative allocation towards metabolic requirements. Regardless of the metabolic constraints, LVF and HVF have demonstrated different growth rates, and any change in allocation of energy may affect a variety of life-history traits (Calow 1985).

The metabolic demands placed on the energy budget are maintained in balance with the requirements for growth, but trade-offs can occur in the synthesis of tissues for somatic and reproductive purposes (Calow 1985). There is some evidence in the literature of trade-offs between somatic growth and gonadal investment being linked to vulnerability to angling. In a heavily exploited stream where the fish had become less vulnerable to angling pressure over time, mature female brook trout (*Salvelinus fontinalis*) exhibited slower growth rates and allocated more energy to gonadal tissue than fish from a stream with less angling pressure (Nuhfer and Alexander 1994). Although these results are contrary to those in the current study, the brook trout were exploited based on size and faster-growing individuals were removed at a higher rate (Nuhfer and Alexander 1994). Similarly, a life-history model on pike (*Esox lucius*) exploited by recreational fishing suggests that selection would favour individuals with increased reproductive investment, which would in turn reduce the energy available for somatic growth (Arlinghaus et al. In Press).

It has been hypothesized that for recreational fisheries, selection operates on behavioural traits rather than directly on body size-related traits (Uusi-Heikkilä et al. 2008). This corresponds to the selection procedure in this study, whereby the largemouth bass were selected based on vulnerability to angling which is largely a function of behavioural-driven susceptibility to passive angling gear (Philipp et al. 2009). Therefore, the predicted evolutionary changes in life-history traits for size-selective commercial fisheries may not correspond to changes in a recreational fishery. A slight, but significant, difference was detected between the GSI of LVF and HVF. LVF had a lower GSI along with a higher growth rate when compared with HVF. The fact that these fish were sub-adults limits any conclusions regarding reproductive investment and its effects on size at age. The differences in GSI between the two groups were not sufficiently large, from a biological point of view, to explain the observed differences in growth rate. The data suggest that there is the potential for a trade-off to occur between somatic and reproductive growth, and this relationship is one that merits further investigation. A thorough examination of mature LVF and HVF in terms of age at maturation, fecundity and growth rate (in relation to metabolism) is necessary to fully understand the effects of fishing-induced selection from a life-history standpoint.

The amount of energy available to a fish has implications for growth, survival, and reproduction (Calow 1985), and the stored energy is reflected by the whole body constituents (lipid, protein, trace minerals and water) and the energy density (an index of energy contained in the lipid and protein) (Breck 2008). Recent feeding history and nutritional condition have typically been determined by analysis of body constituents and energy density (Elliott 1976), and they are now known to be correlated with certain biochemical factors circulating in the blood (Wagner and Congleton 2004; Congleton and Wagner 2006). The changes in body composition and energy density determined from the whole body

constituent analysis for LVF and HVF across ponds over the 6-month period were similar to expected trends during periods of growth. The percent of lipid and protein in brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdneri*) has been shown to increase along with the size of the fish and the amount of food resources consumed, while the water content is proportionally reduced (Elliott 1976; Weatherley and Gill 1983). Although all body constituents and energy densities fluctuated across the ponds, no significant differences were observed between LVF and HVF in any of the ponds. Based on these similarities, LVF and HVF appear to be consuming a similar amount of food resources and deriving equivalent energy units.

While most of the nutritional indicators assessed in the plasma did not differ, plasma magnesium levels were 17% lower for LVF compared with HVF. Magnesium is essential in many enzymatic reactions for intermediary metabolism, and it is acquired mainly through dietary sources in freshwater fish (Lall 2002). In a recent study on smallmouth bass (*Micropterus dolomieu*) that fasted across the parental care period, increases in plasma magnesium levels were observed towards the end of the period (Hanson and Cooke In Press), when the opportunities for foraging became more frequent (Hinch and Collins 1991). While neither LVF nor HVF are suspected of having fasted (due to evidence in the stomach and gut contents to indicate recent feeding), it is possible that HVF derived their higher magnesium concentrations simply by consuming higher numbers of prey items. However, the lack of differences between the stomach and gut contents between the two groups challenges this supposition. Several studies in the literature have examined the effects of a diet deficient in magnesium on fish. Milkfish (*Chanos chanos*) that were fed a diet free of magnesium were actually found to have the same growth rates as control fish (Miñoso et al. 1999). In a contrasting study using freshwater tilapia, (*Oreochromis mossambicus*), the individuals fed diets low in magnesium were found to have significantly lower body weights than the control fish (van der Velden et al. 1991). These two examples serve to highlight some of the conflicting evidence that exists regarding the effects of magnesium on growth rates in fish. Although there is no reason to suspect that LVF and HVF suffer from a magnesium deficiency, the influence that their differing magnesium concentrations may have had on their growth rates remains unclear.

Although this study did not set out to evaluate mortality rates between the two lines of largemouth bass, some general patterns were observed throughout the research period. A trend towards higher survival amongst LVF was noted, as compared with HVF. Mortalities in a naturalized pond environment tend to occur for a variety of reasons, including disease outbreaks, predation by birds, and rapid fluctuations in temperature and/or dissolved oxygen. The cause(s) of the mortality observed in this study is (are) unclear, and it is also unknown why a greater percentage of HVF were susceptible. It is possible that insufficient amounts of dissolved oxygen or high temperatures within the ponds were contributing factors, and these variables are intrinsically linked with metabolic functions (Brett and Groves 1979). As it has been shown that LVF and HVF have differing metabolic rates, the relationship between the disparate mortality rates and the abiotic conditions of the ponds is certainly one that merits future investigation.

To conclude, we found that sub-adult growth rates differ between the two experimental lines of largemouth bass selected for high and low vulnerability to angling, but the body constituent and energy density analyses indicate that LVF and HVF are both consuming sufficient food resources. However, it appeared that in LVF, a greater portion of the available energy may be directed towards somatic growth rather than metabolic processes. Additional research is needed that focuses on adult fish and that combines laboratory and field studies to better understand all aspects of the bioenergetics (e.g. food conversion efficiency, specific dynamic action, and field activity levels) of LVF and HVF. Although it is not entirely clear mechanistically why the growth rate of HVF is lower than the growth capacity of LVF, the implications for fish populations selected for low vulnerability to angling are interesting. For example, if individuals with HVF traits (higher standard metabolic rate and slower sub-adult growth rate) are removed from a population at a faster rate, the traits of the remaining fish could begin to shift towards those more characteristic of LVF (lower standard metabolic rate and faster sub-adult growth rate). Concomitant with faster sub-adult growth rate might be changes in timing of maturation, which may affect recruitment dynamics and productivity of the fish stocks. The remaining fish will also become more difficult to catch, thus diminishing the quality of the fishery (Cooke et al. 2007; Uusi-Heikkilä et al. 2008). It is currently unclear what impacts such changes may have on the biology of the species, yet their implications for the fishery quality are obvious when fish become harder to catch despite faster growth. Management strategies need to account for this issue prior to the onset of evolutionary changes that may be difficult to reverse (Law 2000; Stockwell et al. 2003). One obvious route of action might be to reduce fishing mortality through the implementation of mandatory catch-and-release policies (Arlinghaus et al. 2007). Other methods would be to proactively manage angling effort by the implementation of aquatic protected areas (Berkeley et al. 2004). This would allow a refuge area where angling pressure is removed and fish with

differing behavioural patterns and associated traits can flourish. A final option is to close the fishery entirely during the reproductive period (Schramm et al. 1995) and to establish minimum-harvest limits that give all individuals an opportunity to reproduce multiple times, thus minimizing potential losses from the gene pool. As most recreational fishing regulations involve catch-and-release, the potential for unintentional mortalities that result from hooking injuries and the associated physiological stress of an angling event should be minimized (Cooke and Suski 2005). Long-term monitoring programs are still a necessary aspect of any prudent management strategies (Philipp et al. 2009). Without monitoring, it is difficult to determine if declining catch rates are due to a tangible reduction in numbers or to an increased presence of fish with low vulnerability to angling.

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