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The influence of selection for vulnerability to angling on foraging ecology in largemouth bass *Micropterus salmoides*

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Several traits related to foraging behaviour were assessed in young-of-the-year produced from largemouth bass *Micropterus salmoides* that had been exposed to four generations of artificial selection for vulnerability to angling. As recreational angling may target foraging ability, this study tested the hypothesis that selection for vulnerability to angling would affect behaviours associated with foraging ecology and prey capture success. Fish selected for low vulnerability to angling captured more prey and attempted more captures than high vulnerability fish. The higher capture attempts, however, ultimately resulted in a lower capture success for low vulnerability fish. Low vulnerability fish also had higher prey rejection rates, marginally shorter reactive distance and were more efficient at converting prey consumed into growth than their high vulnerability counterparts. Selection due to recreational fishing has the potential to affect many aspects of the foraging ecology of the targeted population and highlights the importance of understanding evolutionary effects and how these need to be considered when managing populations.

Key words: capture efficiency; conversion efficiency; evolutionary effects of angling; prey rejection.

INTRODUCTION

Although the effects of selection as a result of fishing pressure have received much attention in recent years (Heino & Godo, 2002; Olsen *et al.*, 2005; Dunlop *et al.*, 2009), most of this work has focused on the effects of commercial fishing on life history characteristics of the focal species. Little work has examined the evolutionary impacts of recreational fishing and the suite of traits that make these fishes vulnerable to capture (Philipp *et al.*, 2009). Recreational fishing involves millions of people and is the dominant use of fish stocks in fresh waters in most of the industrialized societies around the world (Arlinghaus *et al.*, 2002). Recreational fishing can represent a large selective force on fish species, both through direct mortality or through other important non-lethal effects such as handling stress, increased susceptibility to infection and interruption of important reproductive behaviours (Cooke *et al.*, 2002; Lewin *et al.*, 2006; Philipp *et al.*, 2009; Redpath *et al.*, 2009).

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There are potentially important differences in the way selection acts on commercially fished species as opposed to those that are recreationally fished. In commercial fishing, selection acts primarily through the size of harvested fishes (Stokes & Law, 2000; Conover & Munch, 2002; Hutchings, 2005; Rijnsdorp *et al.*, 2005), although it can also potentially affect behaviour because size and growth are often linked (Biro & Post, 2008). Because the main objective of angling is to entice a fish to mistake a lure or bait for a natural prey item, it is reasonable to assume that selection for vulnerability to angling would affect the foraging behaviour of the selected species as well. Traits that lead to an increase in the success of capturing prey, increase the ability to discern the difference between a lure from natural prey or increase the frequency that a predator feeds may be impacted by selection due to recreational angling. It is important, therefore, to examine how selection by recreational angling might affect population foraging behaviour and energetic requirements (Cooke *et al.*, 2007; Uusi-Heikkila *et al.*, 2008; Redpath *et al.*, 2009).

Among the many aspects of predator foraging behaviour that may be affected through evolutionary change, angling-induced selection may act by targeting individuals that are less able to discern the difference between real prey and a lure or individuals that are less able to learn lure avoidance (Hackney & Linkous, 1978; Clark, 1983; Philipp *et al.*, 2009). In addition, angling-induced selection could target a range of systems that affect ability to detect or handle prey such as the sensory apparatus (sight and lateral line system) or prey handling ability (handling time, capture success and prey rejection) (Barnhisel, 1991; Breck, 1993; Mazur & Beauchamp, 2003). Selection on vulnerability may also select traits that affect the frequency of foraging including attack rates on prey, metabolic rates or handling times (Cooke *et al.*, 2007; Biro & Post, 2008; Uusi-Heikkila *et al.*, 2008). In this way, fishes that are feeding more frequently may be more vulnerable to angling than fishes that feed less frequently.

Largemouth bass *Micropterus salmoides* (Lacepède 1802) artificially selected for vulnerability to angling were used to examine foraging differences between high and low vulnerability fish. The experimental populations used for this study have undergone artificial truncation selection for vulnerability to angling across four generations (Philipp *et al.*, 2009). Work on these populations has shown that the heritability of vulnerability to angling is 0·15 (Philipp *et al.*, 2009), which is comparable to the heritability of traits such as fish size and growth rates in a range of other species. Other traits in the adults and juveniles have also been affected by this selection regimen, *i.e.* high vulnerability fish have higher metabolic rates and increases in some measures of parental care such as increased aggressiveness in defending nests and higher egg fanning rates (Cooke *et al.*, 2007; Redpath *et al.*, 2009). The effect of this selection regimen on the foraging behaviour of these fish, however, has not been tested.

The purpose of this study was to examine the foraging ecology under laboratory conditions of *M. salmoides* selected for high and low vulnerability to angling. Although the precise behavioural mechanics of what makes a *M. salmoides* or any fishes vulnerable to angling are not well understood, the main objective of angling is to entice a fish to mistake a lure or bait for natural prey and strike. Therefore, this study tested the hypothesis that vulnerability to angling is at least in part related to foraging ecology and observable differences between fish selected for high and low vulnerability to angling should be detected in their ability to detect and process prey, frequency of foraging and in predatory aggression.

METHODS

ORIGIN OF HIGH AND LOW VULNERABILITY STOCKS

Micropterus salmoides used in this experiment are the F5 generation of a selection regime that was initiated in 1977 on fish from Ridge Lake, Coles County, IL, U.S.A. For a detailed description of the selection process, see Cooke *et al*. (2007) and Philipp *et al*. (2009). Briefly, beginning in 1977, *M. salmoides* were subjected to four consecutive seasons of angling in which the catch histories of all angled fish were recorded. On the basis of individual catch histories, *M. salmoides* that had been captured four or more times were used to establish a high vulnerability line, whereas *M. salmoides* that had never been captured were used to establish a low vulnerability line. High and low vulnerability lines were then separated and bred in 0·08 ha experimental ponds. After successful reproduction, the offspring (F1) were reared together in a set of three ponds until they matured (3 years). These F1 fish were experimentally angled over one season, and high and low vulnerability fish were again separated for breeding to establish an F2 generation. This same selection regime was repeated through to the F4 generation. All *M. salmoides* used in these experiments were young-of-the-year (YOY) individuals spawned in the spring of 2007 in 0·4 ha drainable ponds from adults of the F4 generation. The *M. salmoides* were reared in separate ponds until they were collected in the late summer and early autumn of 2007 and then used in the experiments described below.

FOOD CONSUMPTION, GROWTH AND CONVERSION EFFICIENCY

Food consumption was examined in a flow-through system consisting of 22 1100 l tanks and a 1000 l filtering tank (temperature range 20·5 to 24·0° C during the experiment, mean $\pm$ S.E. $= 22{\cdot}2 \pm 0{\cdot}3°$ C). Individual *M. salmoides* ($n = 11$ for both high and low vulnerability lines) were measured in total length (L_T to nearest mm) and weighed (to the nearest 0·1 g) prior to placing individual fish into a separate tank. Each day for 14 days, small fusiform fish prey (*Pimephales promelas* Rafinesque 1820; 0·4–1·4 g each) were weighed and fed *ad libitum* (five to eight fish depending on size) such that the *M. salmoides* could not consume all prey in 24 h. Prey remaining at the end of the 24 h period were removed and weighed before adding new prey each day. Food consumption (g $\text{g}^{-1}\text{day}^{-1}$) was determined by summing biomass of prey consumed over the 2 week period and dividing by initial mass per day. At the end of the 2 week period, each individual *M. salmoides* was again measured and weighed to determine relative growth as change in L_T and mass divided by initial L_T (mm mm^{-1} $\text{day}^{-1)}$ or mass (g $\text{g}^{-1}\text{day}^{-1}$) per day. Conversion efficiency (g g^{-1}) was calculated for each fish by dividing the total mass of prey consumed by the total growth (g) of the individual *M. salmoides*. Food consumption, growth and conversion efficiency were then compared between treatments using an ANCOVA in SAS (Proc GLM; www.sas.com), using *M. salmoides* size as a covariate. There were no interactions between size and treatment for any of the three metrics ($P > 0{\cdot}05$ in all cases) and the interaction was deleted from the model.

FORAGING BEHAVIOUR

Foraging behaviours were studied in a 260 l tank (140 cm × 55 cm × 35 cm) with a glass front and white background on all other sides. Temperature during the experiment ranged from 20 to 23° C (mean $\pm$ S.E. $= 21{\cdot}7 \pm 0{\cdot}4°$ C). A 40 l cylindrical chamber that could be raised completely out of the water was used to hold the *M. salmoides* separate from prey for a 24 h acclimation period before the start of the experiment. Five individual bluegill *Lepomis macrochirus* Rafinesque 1819 prey of optimal sizes (25–30% of the L_T of the *M. salmoides*; Einfalt & Wahl, 1997) were used in each trial. Foraging behaviours of high ($n = 41$) and low ($n = 42$) *M. salmoides* on *L. macrochirus* were recorded on video for 30 min and later analysed. During analysis, measurements were made on predator activity, including the time spent searching, motionless and following a prey item. The time spent in each category could be calculated as the difference between the time the behaviour started and the time the behaviour changed to another, summed for the duration of the trial. In addition, for each attempt to capture a prey item, the reaction distance (estimated from 1 cm grids along all dimensions of the tank), capture success, handling time and any rejections (prey released after being captured) were recorded.

Multivariate analysis of covariance (MANCOVA) with fish size as a covariate was conducted to determine if any behaviours were significantly different between high and low lines. Once a significant MANCOVA was found, each variable was analysed using an ANCOVA, again using size as a covariate. There were no interactions between size and treatment for any behaviour ($P > 0{\cdot}05$ in all cases) and these interactions were deleted from the model.

ETHICAL NOTE

Micropterus salmoides are piscivorous predators and to understand how selection based on vulnerability to angling has affected the foraging ecology of this species it was necessary to observe these fish foraging on natural prey. Prey fishes were only exposed to a predator for one trial and all remaining prey fishes were returned to their source populations. All procedures conformed to the University of Illinois Institutional Animal Care and Use Committee.

RESULTS

FOOD CONSUMPTION, GROWTH AND CONVERSION EFFICIENCY

High and low vulnerability *M. salmoides* did not differ in mean ± S.E. size at the beginning (high vulnerability $156{\cdot}5 \pm 3{\cdot}5$ mm L_T, $53{\cdot}9 \pm 4{\cdot}0$ g; low vulnerability $159{\cdot}7 \pm 3{\cdot}5$ mm L_T, $56{\cdot}4 \pm 4{\cdot}0$ g; $P > 0{\cdot}05$) nor the end (high vulnerability $173{\cdot}0 \pm 3{\cdot}4$ mm L_T, $73{\cdot}4 \pm 5{\cdot}2$ g; low vulnerability $176{\cdot}3 \pm 3{\cdot}4$ mm L_T, $77{\cdot}8 \pm 5{\cdot}2$ g; $P > 0{\cdot}05$) of the feeding experiment. Food consumption (mean ± S.E.) did not differ between high and low vulnerability fish ($0{\cdot}081 \pm 0{\cdot}004$ g g^{-1} day^{-1} low vulnerability, $0{\cdot}082 \pm 0{\cdot}004$ g g^{-1} day^{-1} high vulnerability, $F_{1,19} = 0{\cdot}1$, $P > 0{\cdot}05$) and size was not a significant covariate ($F_{1,19} = 0{\cdot}03$, $P > 0{\cdot}05$). No significant differences in relative growth were observed between the two selected lines when fed *ad libitum*. Both mean ± S.E. relative growth in length ($0{\cdot}0075 \pm 0{\cdot}0004$ mm mm^{-1} day^{-1} L_T low vulnerability, $0{\cdot}0075 \pm 0{\cdot}0004$ mm mm^{-1} day^{-1} L_T high vulnerability, $F_{1,19} = 0{\cdot}00$, $P > 0{\cdot}05$) and mass ($0{\cdot}028 \pm 0{\cdot}002$ g g^{-1} day^{-1} low vulnerability, $0{\cdot}026 \pm 0{\cdot}002$ g g^{-1} day^{-1} high vulnerability, $F_{1,19} = 0{\cdot}63$, $P > 0{\cdot}05$) did not differ significantly between the two populations. Size was a significant covariate for the relative growth in L_T ($F_{1,19} = 4{\cdot}5$, $P < 0{\cdot}05$) with fish having a smaller relative growth in L_T with increasing size for both selected lines. When consumption and growth were combined to calculate conversion efficiency, high and low vulnerability fish did show a significant difference ($F_{1,19} = 6{\cdot}58$, $P < 0{\cdot}05$) with low vulnerability *M. salmoides* being more efficient at converting prey biomass into growth than high vulnerability *M. salmoides* (Fig. 1). Size was again a significant covariate ($F_{1,19} = 6{\cdot}63$, $P < 0{\cdot}05$) with conversion efficiency decreasing similarly with size for both the selected lines (*i.e.* no significant interactions between selected line and size).

FORAGING BEHAVIOUR

Mean ± S.E. size did not differ between high ($134{\cdot}9 \pm 3{\cdot}0$ mm L_T) and low ($137{\cdot}5 \pm 2{\cdot}8$ mm L_T) vulnerability *M. salmoides* ($F_{1,72} = 0{\cdot}38$, $P > 0{\cdot}05$) used in

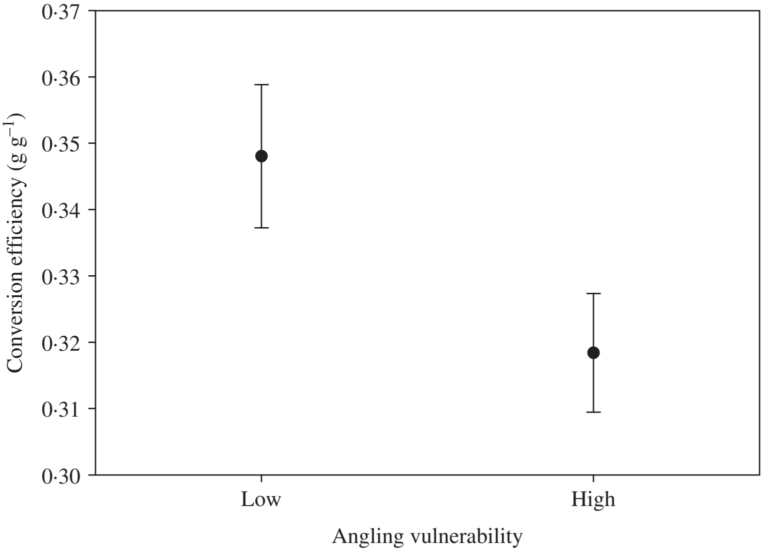

FIG. 1. Conversion efficiency (mean ± S.E.) feeding on fish prey for *Micropterus salmoides* selected for high and low vulnerability to angling. Values were obtained from *M. salmoides* fed *ad libitum* over a 2 week period.

the behavioural trials. In addition, size was not a significant covariate for most behavioural measurements (all $P > 0·05$), except as indicated below. Examining all behaviours simultaneously to account for multiple dependant variables, foraging differed between high and low vulnerability *M. salmoides* ($\lambda_{1,4,17} = 0·43$, $F_{10,36} = 4·95$, $P < 0·001$). Some behaviours were more important than others in contributing to these differences. Time spent motionless, searching and following prey did not differ between high and low vulnerability *M. salmoides* ($P > 0·05$ in all cases; Fig. 2). In addition, activity (time spent searching and following combined) did not differ between high and low lines ($F_{1,71} = 0·46$, $P > 0·05$). In contrast, behaviours involved with capturing and consuming prey did differ between high and low vulnerability *M. salmoides*. Time to the first strike at a prey item was shorter for low vulnerability *M. salmoides* than for high vulnerability *M. salmoides* [Fig. 3(a); $F_{1,65} = 22·23$, $P < 0·001$]. In addition, the number of strikes was greater for the low (8·5 per fish) than high vulnerability (3·6 per fish) *M. salmoides* [$F_{1,67} = 31·56$, $P < 0·001$; Fig. 3(b)]. The higher number of strikes resulted in a greater number of prey consumed for the low (2·7 prey) than high vulnerability *M. salmoides* [1·2 prey; $F_{1,66} = 38·77$, $P < 0·001$; Fig. 3(c)]. Size was a signifiant covariate with the number of prey consumed decreasing as expected similarly with size for both the selected lines ($F_{1,66} = 8·89$, $P < 0·01$). Low vulnerability *M. salmoides*, however, had a decreased capture efficiency (40 *v*. 50%) than high vulnerability fish [$F_{1,61} = 4·85$, $P < 0·05$; Fig. 3(d)]. Low vulnerability fish also had a greater rejection rate than did their high vulnerability counterparts [$F_{1,50} = 9·18$, $P < 0·01$; Fig. 3(e)]. Few high vulnerability fish released their prey after a capture ($n = 2$) compared to low vulnerability fish ($n = 17$). The mean ± S.E. reaction distance was marginally longer for high vulnerability *M. salmoides* (7·6 ± 0·6 cm) than for low vulnerability *M. salmoides* [6·2 ± 0·6 cm,

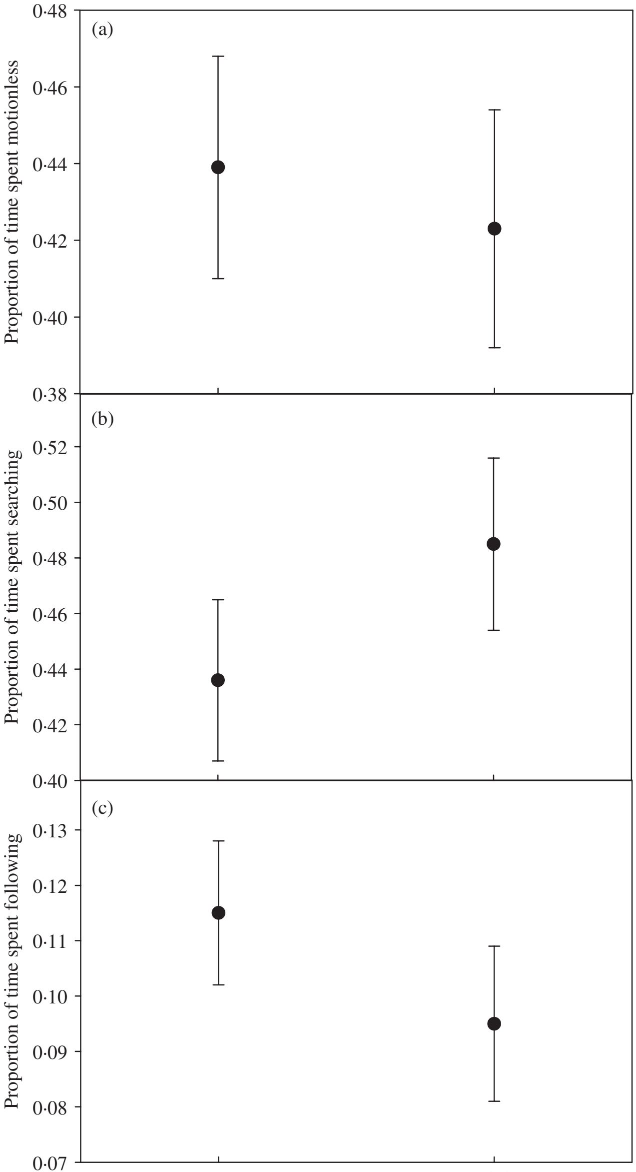

Fig. 2. Behavioural differences (mean ± s.e.) between high and low vulnerability *Micropterus salmoides* for proportion of time spent (a) motionless, (b) searching and (c) following prey. Behaviours were recorded during a 30 min period during which observations were made continuously.

$F_{1,66} = 2{\cdot}98$, $P > 0{\cdot}05$; Fig. 3(f)]. Mean ± s.e. handling time did not differ between high (50·9 ± 8·3 s) and low (53·8 ± 7·0 s) vulnerability *M. salmoides* ($F_{1,57} = 0{\cdot}07$, $P > 0{\cdot}5$), but was influenced by size ($F_{1,57} = 5{\cdot}58$, $P < 0{\cdot}05$). Handling time was higher in larger *M. salmoides* but was similar for both the selected lines.

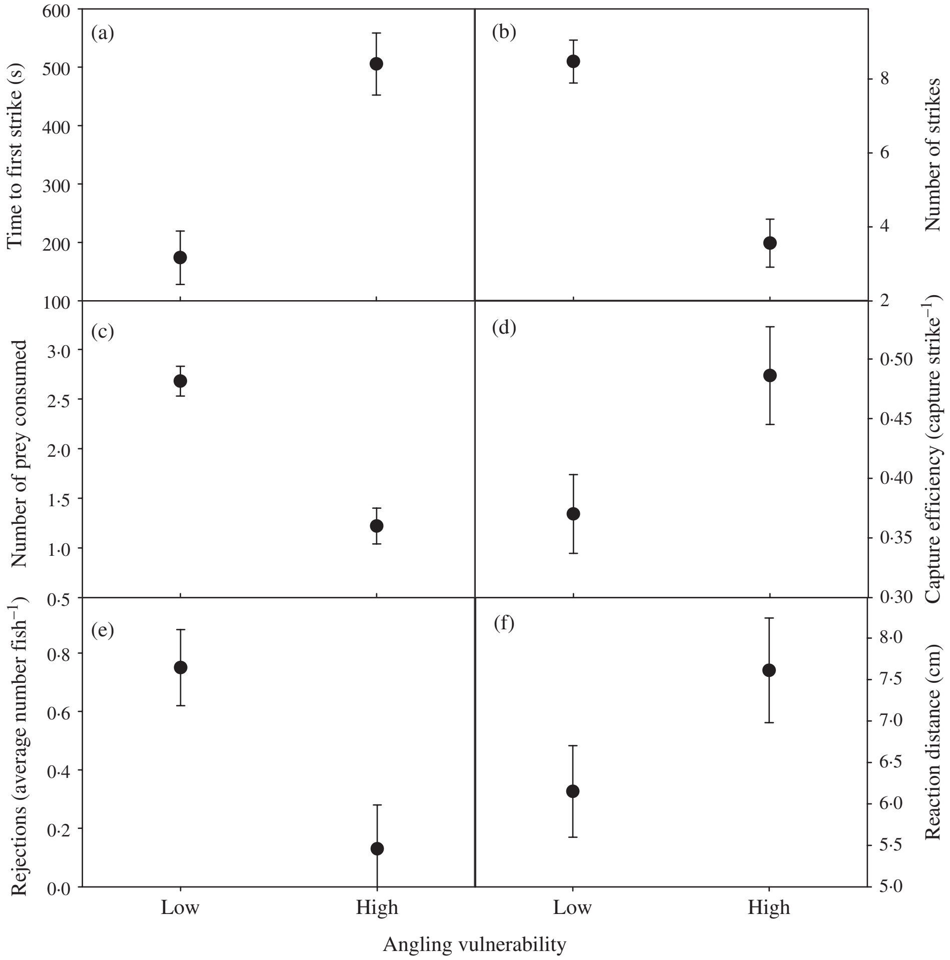

FIG. 3. Behavioural differences (mean ± S.E.) between high and low vulnerability *Micropterus salmoides* for (a) time to first strike on a prey, (b) number of strikes on prey, (c) number of prey consumed, (d) capture success, (e) rejections and (f) reaction distance.

DISCUSSION

Differences in foraging ability and energy conversion were observed among juvenile *M. salmoides* that had undergone artificial selection for vulnerability to angling. Fish from the line that had been selected for high vulnerability to angling showed greater foraging effectiveness but less efficient energy conversion than fish that had been selected for low vulnerability to angling. These differences are probably related to differences in either the sensory ability or post-capture handling of prey between these two selected lines. Differences in foraging efficiency and energy conversion may also be related to differences in observed metabolic rates which may lead to differences in hunger levels and feeding urgency.

Previous research with these fish found that high vulnerability fish had a higher resting metabolic rate than low vulnerability fish (Cooke *et al.*, 2007; Redpath *et al.*, 2009). The differences in conversion efficiency observed are consistent with these differences in metabolic rate providing further evidence for energetic differences between the high and low vulnerability fish. Although neither consumption nor growth was significantly different, a combination of slightly lower consumption and slightly higher growth of low vulnerability fish resulted in higher conversion efficiency. As a result, high vulnerability fish had a lower efficiency at converting prey resources into growth than low vulnerability fish. It was expected that low vulnerability fish would grow more quickly than high vulnerability fish. While these laboratory assessments of growth showed no such difference between the two lines, the short duration and low replication may have made it difficult to detect differences in growth. A longer-term assessment of growth in ponds for these fish did find that low vulnerability fish grew more quickly than high vulnerability fish (Redpath *et al.*, 2009). Higher growth by low vulnerability fish in the field may be attributed to a higher conversion efficiency and suggests that low vulnerability fish do not need to feed as often as high vulnerability fish. Other differences from the field such as high water clarity, high prey availability and lack of refuges may have also contributed to the ability to detect growth differences between the two selected lines in the laboratory by making it easier to capture and consume prey (Miner & Stein, 1996; Robertis *et al.*, 2003).

Differences in energetic requirements between high and low vulnerability *M. salmoides* may have influenced other differences in foraging behaviour observed in this study. All else being equal, individuals with a higher metabolic rate should have higher energy requirements and consume more than individuals with lower metabolic rates (Vezina *et al.*, 2006; Finstad *et al.*, 2007). Higher metabolic rates have also been linked to higher gastric evacuation rates (Koshiishi, 1986) suggesting that individuals with a higher metabolic rate may be hungry more often than individuals with a lower metabolic rate. Hunger level has been shown to affect many aspects of foraging behaviour in other fish species (Biro *et al.*, 1996; Stoner, 2003). Increases in hunger level can lead to lower rejection rates (Bryan, 1973), a decrease in the number of foraging attempts, an increase in capture efficiency and an increase in reactive distance (Croy & Hughes, 1991). These relationships are similar to what was observed for these selected lines, where high vulnerability fish had lower rejection rates, fewer strikes, increased capture efficiency and marginally higher reactive distances compared to low vulnerability fish. Foraging behaviour may ultimately be mediated through differences in hunger level that are the result of differences in energy utilization.

Some of these same differences in foraging behaviour observed in this study might be explained by differences in the ability of these two groups to detect and process prey. *Micropterus salmoides* are visually feeding predators (Shoup & Wahl, 2009) and as such, it seems likely that one or more sensory systems could be affected by selection for vulnerability to angling. The ability of a fish to strike at a prey item is dependent on detecting the prey, accurately assessing position, being motivated and making a strike based on that information (Stoner, 2003; Donatti *et al.*, 2008; Rapo *et al.*, 2009). If selection for vulnerability to angling affected any of the systems used to make these assessments, differences in foraging would be expected as well. Previous work with *M. salmoides* and other species of fishes often find that as ability to detect prey decreases, the reactive distance decreases as well (Sweka & Hartman, 2001; Mazur & Beauchamp, 2003; Richmond *et al*., 2004). Reactive distance was marginally different, with high vulnerability fish initiating strikes when prey were further away. One possible mechanism for differences in capture success may be that high vulnerability fish are better able to detect prey.

In addition to detection, fishes can also access the suitability of prey through post-capture handling (Ferno & Huse, 1983; Sibbing, 1988) through taste or tactile stimuli (Sibbing, 1988; Aihara *et al*., 2008; Finger, 2008). Behavioural observations of Atlantic cod *Gadus morhua* L. 1758 interacting with baits with and without hooks showed that fish reacted to the hook while manipulating the bait, which often resulted in incomplete mouth closure (Ferno & Huse, 1983). Thus, a fish's reaction to spiny structures may influence the vulnerability of fish to hooking and capture. Similar behaviour may occur when interacting with prey with morphological defences to predators (Hoogland *et al*., 1956–1957; Barnhisel, 1991; Kolar & Wahl, 1998) such as spiny dorsal and anal fin rays of *L. macrochirus* (Wahl & Stein, 1988; Einfalt & Wahl, 1997). Low vulnerability fish may have had a harder time coping with the spines on these prey than high vulnerability fish, contributing to the higher prey rejection rates and low capture success observed for these fish.

Several measurements of predatory aggression seem to have been affected by selection for vulnerability to angling. Although the time spent following prey was not different between *M. salmoides* lines, fish that were selected for low vulnerability to angling were quicker to attack prey, had a higher attack rate and had higher consumption than high vulnerability fish. These results are somewhat counterintuitive, although the link between foraging and vulnerability to angling is poorly understood. One possible explanation for more aggressive predatory behaviour is that it could be linked through behavioural syndromes (Sih *et al*., 2004) to factors influenced by selection for vulnerability to angling. If vulnerability to angling is influenced by other behaviours such as boldness, intraspecific interactions or nesting behaviour, then the foraging differences observed could be accounted for more by the way these fish respond in these other behavioural contexts than when foraging. As the factors that make fishes vulnerable to angling are poorly understood, more research is clearly needed to fully understand how selection by recreational angling might influence the overall ecology and physiology of affected populations.

This study provides support for the idea that selection induced by recreational fishing has the potential to influence foraging behaviour in targeted populations. It also highlights the importance of understanding evolutionary effects of fishing on populations and how this needs to be considered when managing these populations. Differences in foraging behaviours of predators could also impact population dynamics and antipredator traits of their prey (Preisser *et al*., 2007; Lazzaro *et al*., 2009). In addition, different foraging strategies are often linked to other behaviours such as aggression, boldness, life history characteristics and the amount of risk an individual is willing to accept while foraging (Sih *et al*., 2004; Uusi-Heikkila *et al*., 2008). Changes in these characteristics within a fished population could have impacts not only on the rest of the ecosystem, but also on the potential quality of the fishery (Conover & Munch, 2002; Olsen *et al*. 2005; Biro & Post, 2008). These questions as well as management techniques that could help ameliorate the impacts of a population evolving in response to recreational fishing need to be addressed.

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References

Aihara, Y., Yasuoka, A., Iwamoto, S., Yoshida, Y., Misaka, T. & Abe, K. (2008). Construction of a taste-blind medaka fish and quantitative assay of its preference-aversion behavior. *Genes, Brain and Behavior* **7,** 924–932.

Arlinghaus, R., Mehner, T. & Cowx, I. G. (2002). Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries* **3,** 261–316.

Barnhisel, D. R. (1991). The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defense against young fish. *Journal of Plankton Research* **13,** 529–537.

Biro, P. A. & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America* **105,** 2919–2922.

Biro, P. A., Ridgeway, M. S. & McLaughlin, R. L. (1996). Does the rate of foraging attempts predict ingestion rate for young-of-the-year brook trout (*Salvelinus fontinalis*) in the field? *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 1814–1820.

Breck, J. E. (1993). Foraging theory and piscivorous fish: are forage fish just big zooplankton? *Transactions of the American Fisheries Society* **122,** 902–911.

Bryan, J. E. (1973). Feeding history, parental stock, and food selection in rainbow trout. *Behaviour* **45,** 123–153.

Clark, R. D. Jr. (1983). Potential effects of voluntary catch and release of fish on recreational fisheries. *North American Journal of Fisheries Management* **3,** 306–314.

Conover, D. O. & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science* **297,** 94–96.

Cooke, S. J., Schreer, J. F., Wahl, D. H. & Philipp, D. P. (2002). Physiological impacts of catch-and-release angling practices on largemouth and smallmouth bass. *American Fisheries Society Symposium* **31,** 489–512.

Cooke, S. J., Suski, C. D., Ostrand, K. G., Wahl, D. H. & Philipp, D. P. (2007). Physiological and behavioural consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* **80,** 480–490.

Croy, M. I. & Hughes, R. N. (1991). The influence of hunger on feeding behaviour and on the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal Behaviour* **41,** 161–170.

Donatti, L., Zaleski, T., Calil, P. & Fanta, E. (2008). Photoperiod and feeding behavior of the Antarctic fish *Notothenia rossii* (Perciformes: Nototheniidae) and functional morphology of chemical and visual sensory structures used in foraging. *Revista Brasileira de Zoologia* **25,** 254–262.

Dunlop, E. S., Enberg, K., Jorgensen, C. & Heino, M. (2009). Toward Darwinian fisheries management. *Evolutionary Applications* **2,** 245–259.

Einfalt, L. M. & Wahl, D. H. (1997). Prey selection by juvenile walleye as influenced by prey morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 2618–2626.

Ferno, A. & Huse, I. (1983). The effect of experience on the behavior of cod (*Gadus morhua* L.) towards a baited hook. *Fisheries Research* **2,** 19–28.

Finger, T. E. (2008). Sorting food from stones: the vagal taste system in goldfish, *Carassius auratus*. *Journal of Comparative Physiology A* **194,** 135–143.

Finstad, A. G., Forseth, T., Ugedal, O. & Naesje, T. F. (2007). Metabolic rate, behaviour and winter performance in juvenile Atlantic salmon. *Functional Ecology* **21,** 905–912.

Hackney, P. A. & Linkous, T. I. (1978). Striking behavior of the largemouth bass and use of the binomial distribution for its analyses. *Transactions of the American Fisheries Society* **107,** 682–688.

Heino, M. & Godo, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science* **70,** 639–656.

Hoogland, R., Morris, D. & Tinbergen, N. (1956–1957). The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defense against predators (*Perca* and *Esox*). *Behaviour* **10,** 205–236.

Hutchings, J. A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 824–832.

Kolar, C. S. & Wahl, D. H. (1998). Daphnid morphology deters fish predators. *Oecologia* **116,** 556–564.

Koshiishi, Y. (1986). Effect of feeding level and dietary composition on growth and feed efficiency of chum salmon, *Oncorhynchus keta* (Walbaum), fed in seawater and freshwater. *Bulletin of the Japan Sea and Regional Fisheries Research Laboratory* **36,** 15–27.

Lazzaro, X., Lacroix, G., Gauzens, B., Gignoux, J. & Lengendre, S. (2009). Predator foraging behaviour drives food-web topological structure. *Journal of Animal Ecology* **78,** 1307–1317.

Lewin, W., Arlinghaus, R. & Mehner, T. (2006). Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science* **14,** 305–367.

Mazur, M. M. & Beauchamp, D. A. (2003). A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environmental Biology of Fishes* **67,** 397–405.

Miner, J. G. & Stein, R. A. (1996). Detection of predators and habitat choice by small bluegills: effect of turbidity and alternative prey. *Transactions of the American Fisheries Society* **125,** 97–103.

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J. & Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 811–823.

Philipp, D. P., Cooke, S. J., Claussen, J. E., Koppelman, J. B., Suski, C. D. & Burkett, D. P. (2009). Selection for vulnerability to angling in largemouth bass. *Transactions of the American Fisheries Society* **138,** 189–199.

Preisser, E. L., Orrock, J. L. & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology* **88,** 2744–2751.

Rapo, M. A., Jiang, H., Grosenbaugh, M. A. & Coombs, S. (2009). Using computational fluid dynamics to calculate the stimulus to the lateral line of a fish in still water. *The Journal of Experimental Biology* **212,** 1494–1505.

Redpath, T. D., Cooke, S. J., Arlinghaus, R., Wahl, D. H. & Philipp, D. P. (2009). Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. *Evolutionary Applications* **2,** 312–323.

Richmond, H. E., Hrabik, T. R. & Mensinger, A. F. (2004). Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. *Journal of Fish Biology* **35,** 195–205.

Rijnsdorp, A. D., Grift, R. E. & Kraak, S. B. M. (2005). Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 833–843.

Robertis, A. D., Ryer, C. H., Veloza, A. & Brodeur, R. D. (2003). Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences* **60,** 1517–1526.

Shoup, D. E. & Wahl, D. H. (2009). The effects of turbidity on prey selection by piscivorous largemouth bass. *Transactions of the American Fisheries Society* **138,** 1018–1027.

Sibbing, F. A. (1988). Specializations and limitations in the utilization of food resources by the carp, *Cyprinus carpio*: a study of oral food processing. *Environmental Biology of Fishes* **22,** 161–178.

Sih, A, Bell, A. M., Johnson, J. C. & Ziemba, R. (2004). Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* **79,** 241–277.

Stokes, K. & Law, R. (2000). Fishing as an evolutionary force. *Marine Ecology Progress Series* **208,** 299–313.

Stoner, A. W. (2003). Hunger and light level alter response to bait by Pacific halibut: laboratory analysis of detection, location and attack. *Journal of Fish Biology* **62,** 1176–1193.

Sweka, J. A. & Hartman, K. J. (2001). Influence of turbidity on brook trout reactive distance and foraging success. *Transactions of the American Fisheries Society* **130,** 138–146.

Uusi-Heikkila, S., Wolter, C., Klefoth, T. & Arlinghaus, R. (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology and Evolution* **23,** 419–421.

Vezina, F., Speakman, J. R. & Williams, T. D. (2006). Individually variable energy management strategies in relation to energetic costs of egg production. *Ecology* **87,** 2447–2458.

Wahl, D. H. & Stein, R. A. (1988). Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* **117,** 142–151.