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Effects of hatchery rearing on Florida largemouth bass *Micropterus floridanus* resource allocation and performance under semi-natural conditions

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This study examined the growth, activity, metabolism and post-release survival of three groups of Florida largemouth bass *Micropterus floridanus*: wild-caught fish, hatchery fish reared according to standard practice (hatchery standard) and hatchery fish reared under reduced and unpredictable food provisioning (hatchery manipulated). Hatchery-standard fish differed from wild-caught fish in all measured variables, including survival in semi-natural ponds. Hatchery-standard and hatchery-manipulated fish showed higher activity levels, faster growth and lower standard metabolic rates than wild-caught fish in the hatchery. Fish reared under the manipulated feeding regime showed increased metabolic rates and increased post-release growth, similar to wild-caught fish. Their activity levels and post-release survival, however, remained similar to those of hatchery-standard fish. Activity was negatively correlated with post-release survival and failure of the feed manipulation to reduce activity may have contributed to its failure to improve post-release survival. Activity and post-release survival may be influenced by characteristics of the rearing environment other than the feeding regime, such as stock density or water flow rates.

Key words: behaviour; domestication; fisheries enhancement; life history; standard metabolic rate.

INTRODUCTION

Cultured fishes are stocked into natural ecosystems for the purposes of fisheries enhancement and restoration (Cowx, 1994; Lorenzen *et al.*, 2010). In culturing fishes for stocking, culturists are being faced with the issue of inadvertent domestication that leads to fishes that differ from wild conspecifics in biological traits and often survive poorly in natural environments. Culture conditions tend to differ from the environmental conditions fishes experience in the wild in ways designed to maximize

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growth and survival. This can give rise to changes in the organisms' biology due to developmental (phenotypic) plasticity as well as the action of natural selection (Price, 2002; Huntingford, 2004). Domestication effects can result in a broad array of altered behavioural, morphological, physiological, ecological and genetic traits (Olla *et al.*, 1998; Brown & Laland, 2001; Huntingford, 2004; Thorpe, 2004), ultimately producing organisms that perform better under culture conditions than wild conspecifics (Reisenbichler & McIntyre, 1977; Reisenbichler *et al.*, 2004). As a result, domesticated fishes may be less fit when released in complex, unpredictable environments (Ford, 2002; Saikkonen *et al.*, 2011; Huntingford *et al.*, 2012) which may limit the effectiveness of stocking programmes (Brown & Day, 2002; Huntingford, 2004).

To address the issues of domestication, research has focused on studies examining the developmental and behavioural deficits of cultured fishes relative to their wild counterparts. The predominant domestication effects include accelerated growth, early maturity, high activity and aggression, and reduced foraging efficiency and anti-predatory skills (Álvarez & Nicieza, 2003; Brown *et al.*, 2003; Metcalfe *et al.*, 2003; Thorpe, 2004). The life-history patterns emerging from most of these domestication effects are analogous to those predicted in low risk, high resource environments in that, they reflect changes in resource allocation to growth and reproduction and away from resource conservation, foraging and predator avoidance skills (Thorpe, 2004; Saikkonen *et al.*, 2011; Lorenzen *et al.*, 2012). This has led to hypothesize that these domestication effects are derived from fundamental changes in life history (Beilharz *et al.*, 1993; Thorpe, 2004; Lorenzen *et al.*, 2012). Life history, or an organism's developmental schedule, is often plastic and characterized by allocation to competing interests (*i.e.* survival, growth and reproduction) in ways that maximize fitness. As a consequence, cultured organisms may reallocate resources in ways that maximize fitness in artificial environments ultimately causing behavioural and developmental changes that are not favourable after release. Food availability has been suggested to play a large role in determining the future direction of development (*i.e.* life-history trajectory) (Thorpe, 1989; Mangel, 2008; Monaghan, 2008) and act as a mechanism by which domestication selection could operate (Glover *et al.*, 2004). Relatively few studies, however, have analysed domestication processes through a life-history framework to investigate the effects of resource availability in culture settings. Elucidating how life history and resource allocation are influenced by feed availability will shed light on domestication processes and ultimately help inform husbandry decisions that can produce fish better suited for stocking.

Florida largemouth bass *Micropterus floridanus* (LeSueur 1822) were used as a study species to examine the role of resource availability and resource allocation in the developmental plasticity contributing to domestication effects. Previous studies have documented domestication effects in *M. floridanus* including poor foraging skills (Porak *et al.*, 2002; Wintzer & Motta, 2005; Pouder *et al.*, 2010), reduced anti-predatory behaviour (Buckmeier *et al.*, 2005) and increased movement after release (B. Thompson, pers. comm., 2014).

The aim of this study was to assess how hatchery rearing affects physiological traits related to resource allocation (activity, growth and metabolism) and post-release survival, and whether changes in resource provisioning in culture can be used to manipulate these traits to become more wild-like.

MATERIALS AND METHODS

REARING CONDITIONS

Juvenile cultured *M. floridanus* were reared at the Florida Bass Conservation Center (FBCC) in Webster, Florida, U.S.A. A total of 25 male–female pairs of wild-caught, pure strain *M. floridanus* were spawned under temperature and photoperiod manipulations. After several days of hatching, fry were transferred to a 0·4 ha pond. After 30 days, *c.* 5000 25–35 mm total length (L_T) fingerlings were collected from the outdoor pond and transferred to indoor flow-through 378 l tanks. This intensive, flow-through culture system has striking differences compared with the natural environment experienced by wild *M. floridanus*. The major discrepancies between environments are shown in Table I. In this study, two of these attributes, food predictability and feeding rate, were manipulated in culture. After 30 days of feed-training to pellet food, fingerlings ($47{\cdot}2 \pm 5{\cdot}8$ mm L_T, mean ± S.D.) were divided among two treatments with different feeding regimes: normal, predictable rations (hatchery-standard treatment) or reduced, unpredictable rations (hatchery-manipulated treatment). The hatchery-standard fish were fed 10% body mass daily partitioned among five feeding events evenly distributed between 0800 and 1800 hours. The hatchery-manipulated fish were fed at 4% body mass divided between two random feeding events between 0800 and 1800 hours imitating a more wild-like feeding pattern. These feeding treatments lasted 64 days after which a sub-sample of fish was taken from each group. Hatchery-standard and hatchery-manipulated fish were $89{\cdot}0 \pm 7{\cdot}1$ and $87{\cdot}9 \pm 7{\cdot}3$ mm L_T (mean ± S.D.), respectively. These individuals were anaesthetized with 25 g l^{-1} tricaine methanesulphonate (MS-222) (Western Chemical; www.wchemical.com) and tagged in the body cavity with 8 mm full duplex, passive integrated transponder (PIT) tags (Oregon RFID; www.oregonrfid.com). After tagging, the respective feeding treatments were maintained for three more weeks until the mean size reached the desired stocking L_T of >100 mm.

COLLECTION AND MAINTENANCE OF WILD JUVENILES

Wild *M. floridanus* of similar size ($n = 180$, $132{\cdot}6 \pm 12{\cdot}7$ mm L_T, mean ± S.D.) were collected in south-west Florida from the Hardee Lakes Fisheries Management Area, FL, *via* electrofishing. The collection site of the hatchery brood fish was in the same genetic management zone as these wild-caught juveniles (Barthel *et al.*, 2010); therefore, genetic differences between wild and hatchery treatments should be minimized. Wild-caught *M. floridanus*, 75–180 mm L_T and suspected to be in the age 1 year class, were transported to the hatchery and maintained in a 4900 l tank with plastic plants to reduce stress and imitate a wild-like environment. The wild juveniles were fed juvenile domesticated koi carp *Cyprinus carpio* L. 1758 fingerlings twice a week. They would not inherently consume pelleted feeds or dead fish. Wild-caught fish were held in hatchery tanks for 10 days before they were injected with PIT tags using the same protocols described above and then held in hatchery tanks for five more days until experimental measurements were performed.

EXPERIMENTAL MEASUREMENTS

Experimental measurements began two and a half weeks prior to pond stocking and lasted *c.* 1 week. The allocation patterns of hatchery-standard, hatchery-manipulated and wild-caught fish were characterized by measuring investments into growth, activity and maintenance. Activity and maintenance metabolism were measured in 46 juvenile fish. Activity was measured using a behavioural assay prior to metabolic studies. Fish were individually released into a 1000 l circular tank (183 cm in diameter) and filmed using GoPro Hero HD video cameras (www.gopro.com) above the tank. A 200 mm × 200 mm grid was applied to the bottom of the tank for the quantification of activity. Activity was quantified in terms of gridlines crossed in a 5 min observation period. During video analysis, data collection began at the fish's first movement, in order to eliminate individual differences in acclimation time. Because the experimental tank was circular, the rate at which a fish crossed the gridlines at the perimeter differed from the rate within the middle of the tank. Because fish frequently swam along the perimeter of the tank, a correction factor was applied to the gridlines crossed at the perimeter to standardize the measure of movement. The rate of gridlines crossed per second was calculated.

TABLE I. Major environment differences between the standard hatchery environment, the manipulated hatchery environment and a natural *Micropterus floridanus* environment

	Hatchery standard	Hatchery manipulated	Natural environment
Feed type	Pellet feeds	Pellet feeds	*Dorosoma* spp., *Lepomis macrochirus*, invertebrates (Miranda & Pugh, 1997)
Feed predictability	Highly predictable	Less predictable	Unpredictable
Feeding rate	10% body mass	4% body mass	0–2% body mass (Adams *et al.*, 1982)
Predation	Juvenile *M. floridanus* (*i.e.* cannibalism)	Juvenile *M. floridanus* (*i.e.* cannibalism)	Adult and juvenile *M. floridanus*, other predatory fishes, birds (Post *et al.*, 1998)
Habitat complexity	None	None	Mean ± S.E. per cent area covered: 41 ± 5% (Hoyer & Canfield, 1996)
Density of conspecifics	8–16 fingerlings l^{-1} (Sloane & Lovshin, 1995)	8–16 fingerlings l^{-1} (Sloane & Lovshin, 1995)	1·54e-5–3·67e-3 fingerlings l^{-1} (Parkos & Wahl, 2010)
Water flow	0·6–1·0 cm s^{-1}	0·6–1·0 cm s^{-1}	Very little to none

Oxygen consumption rate (VO_2) is commonly used as an indirect measure of aerobic metabolism and was measured in this study. A Brett-style respirometer was composed of a single, closed-loop circuit connected to a water pump (Brett, 1964). A 355·6 mm long, 101·6 mm diameter plastic tube served as the swim tunnel and was attached to a water pump *via* a polyvinyl chloride (PVC) pipe and plastic tubing. A YSI professional optical dissolved oxygen instrument and probe (Yellow Springs Instrument Company; www.ysi.com) were used to measure dissolved oxygen in the respirometer and the probe was calibrated using the water saturated air method. The probe was positioned in the apparatus and fixed into place with epoxy. Plastic grids were mounted on the front and back of the swimming tunnel to promote laminar flow (Bell & Terhune, 1970) and prevent the fish from leaving the swim tunnel. The apparatus was submerged in a larger water bath and temperature was maintained at $26{\cdot}10 \pm 0{\cdot}95^{\circ}$ C (mean ± S.D.). Prior to respirometry tests, fish were held in flow-through holding tanks where the temperature was $25{\cdot}83 \pm 0{\cdot}40^{\circ}$ C (mean ± S.D.). Fish were starved 24–95 h prior to the swim tests to eliminate the effects of digestive metabolism. Oxygen consumption was measured at three water velocities (5·9, 8·0 and 14·0 cm s^{-1}) for 46 juvenile fish and the water velocities were corrected for the solid blocking effect according to Bell & Terhune (1970). At each velocity, fish were given 2 min to acclimate in the metabolic chamber and then an additional minute to acclimate to the flow until data collection began. Dissolved oxygen was measured over a 15 min period and biological oxygen demand (BOD) was accounted for when determining the oxygen consumption rate of the fish. The standard metabolic rate (R_S) was estimated according to Brett (1964) by extrapolating the relationship of oxygen consumption as a function of swimming speed to a swimming speed of 0 cm s^{-1}. Prior to analysis, values of metabolic rates and body mass were ln transformed. Mass-independent values of R_S were calculated from a least-squares linear regression of ln-scaled absolute R_S on ln-scaled body mass and expressed as residual R_S (rR_S). Thus, fish with higher than expected R_S have positive residuals and fish with lower than expected R_S have negative residuals.

After experimentation but prior to stocking, all fish were treated for an outbreak of *Flavobacterium columnare*, a common warm-water disease, for 10 days with 50 ppm oxytetracycline hydrochloride and 0·5% salt solution to eliminate the bacteria. One week prior to stocking, hatchery-standard and hatchery-manipulated fish were weaned onto *C. carpio* fingerlings according to standard hatchery practices.

POND STUDY

A total of 235 juveniles, consisting of 90 hatchery-standard, 86 hatchery-manipulated and 56 wild-caught fish, were stocked in semi-natural outdoor ponds to determine if survival differences existed among treatments. Twenty-nine of these fish were characterized with metabolism and activity measurements. Three replicate, 0·1 ha, 1·5 m deep ponds were tilled and supplemented with six piles of dead branches to serve as refuge. Ponds were filled and stocked with predators and forage 2 months prior to stocking experimental fish, to imitate a natural environment. Specifically, the ponds were stocked with 10–12 pairs of adult bluegill *Lepomis macrochirus* Rafinesque 1819 ($179{\cdot}3 \pm 26{\cdot}9$ mm L_T, mean ± S.D.) providing eggs and fry as forage for the juvenile *M. floridanus*. The ponds were also stocked with eastern mosquitofish *Gambusia holbrooki* Girard 1859 as additional forage. Each pond was stocked with one large *M. floridanus* (350–450 mm L_T), one medium *M. floridanus* (300–340 mm L_T), two small *M. floridanus* (170–270 mm L_T) and a bowfin *Amia calva* L. 1766 (380–450 mm L_T). Juveniles were gently released into ponds using dip nets and each pond received 24–33 hatchery-standard fish, 24–31 hatchery-manipulated fish and 19–21 wild-caught fish. After a five-week period, the ponds were drained to a depth of 0·25 m and surviving individuals were collected *via* seining and identified. This experimental protocol was approved following ethics reviewed by the University of Florida's Institute for Food and Agricultural Sciences, Committee for Non-Regulatory Animal Research (Approval No. 004-12FAS).

DATA ANALYSIS

To determine whether the food provisioning influenced R_S, activity and growth, one-factor analysis of variance (ANOVA) followed by Tukey HSD *post hoc* analysis were performed assuming a significance level of $\alpha \leq 0{\cdot}05$. A logistic regression was used to predict the outcome

TABLE II. Mean ± S.D. *Micropterus floridanus* total length (L_T), wet mass (M), oxygen consumption rate (VO_2RS) and sample size (n) for the pond experiment

	Treatment		
	Hatchery standard	Hatchery manipulated	Wild caught
Oxygen consumption rate			
n	14	20	12
L_T (mm)	97 ± 9	93 ± 21	116 ± 16
M (kg)	0·0095 ± 0·0020	0·0104 ± 0·0027	0·0181 ± 0·0064
VO_2RS ($mgO_2\ kg^{-1}\ h^{-1}$)	64·93 (39·57)	101·82 (49·89)	158·95 (85·03)
Pond stocking			
n	90	86	59
L_T (mm)	105 ± 12	101 ± 10	132 ± 19
M (kg)	0·0139 ± 0·0060	0·0127 ± 0·0043	0·0251 ± 0·0095

of the binary-dependent variable (*i.e.* survival) based on multiple predictor variables including L_T, R_S and activity. A forward stepwise search algorithm was used to find the most parsimonious model according to the Akaike's information criterion (AIC). Models with AIC < 2 from the best model were considered to have equivalent explanatory power. Residual growth after stocking was calculated by regressing the ln-scaled change in L_T on the ln-scaled initial L_T. All analyses were carried out using R 2.14.1 (www.r-project.org).

RESULTS

At the end of hatchery rearing, the mean L_T of hatchery-standard and hatchery-manipulated fish were similar, but both were significantly lower than the mean L_T of

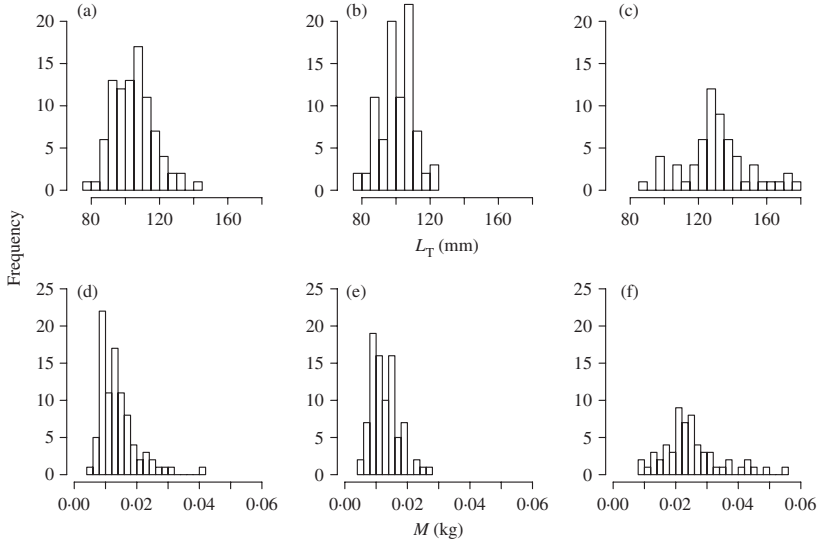

FIG. 1. (a–c) Total length (L_T) and (d–f) wet mass (M) for each group of *Micropterus floridanus* after hatchery treatment and prior to the pond experiment: (a, d) hatchery standard, (b, e) hatchery manipulated and (c, f) wild caught.

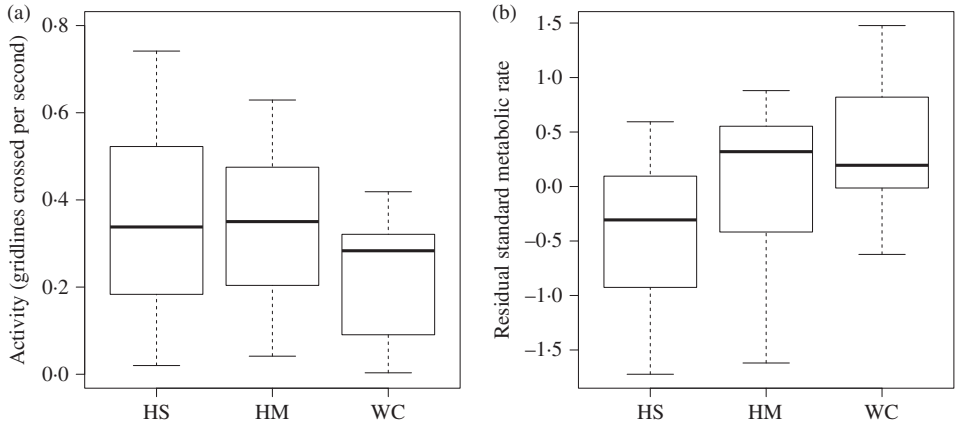

FIG. 2. (a) Activity (proportion of crossed gridlines per second) and (b) residual standard metabolic rate of hatchery-standard (HS), hatchery-manipulated (HM) and wild-caught (WC) treatments of *Micropterus floridanus*. Bold bars represent the median, the boxes represent the interquartile range and the whiskers represent 1·5 times the interquartile range.

wild-caught fish (Table II; ANOVA, $F_{2,232} = 101{\cdot}1$, $P < 0{\cdot}001$; Tukey HSD: hatchery standard and hatchery manipulated, $P > 0{\cdot}05$; hatchery standard and wild caught, $P < 0{\cdot}001$; wild caught and hatchery manipulated, $P < 0{\cdot}001$). Hatchery-standard fish had slightly greater variation in L_T than hatchery-manipulated fish but the variation of both was smaller than that observed in wild-caught fish (Fig. 1). Fish mass was not significantly different between hatchery-standard and hatchery-manipulated fish (ANOVA, $F_{2,232} = 72{\cdot}06$, $P < 0{\cdot}001$; Tukey HSD: hatchery standard and hatchery manipulated, $P > 0{\cdot}05$; hatchery standard and wild caught, $P < 0{\cdot}001$; wild caught and hatchery manipulated, $P < 0{\cdot}001$).

Activity did not differ significantly between hatchery-standard and hatchery-manipulated fish, but both were significantly more active than wild-caught fish (ANOVA, $F_{2,75} = 3{\cdot}127$, $P < 0{\cdot}05$; Tukey HSD: hatchery standard and hatchery manipulated, $P > 0{\cdot}05$; hatchery standard and wild caught, $P < 0{\cdot}05$; wild caught and hatchery manipulated, $P > 0{\cdot}05$) (Fig. 2). The average number of gridlines crossed per second for hatchery-standard, hatchery-manipulated and wild-caught fish were 0·35 ($n = 32$), 0·34 ($n = 31$) and 0·22 ($n = 15$).

Oxygen consumption (VO_2) ranged from 13·3 to 320·0 $mgO_2\ kg^{-1}\ h^{-1}$. For all groups combined, the relationship between VO_2 and swimming speed (S; cm s^{-1}) was the following: $\ln VO_2 = 0{\cdot}109\,S + 3{\cdot}682$ ($r^2 = 0{\cdot}411$). The average standard metabolic rates (VO_2RS) by treatment are presented in Table II. Hatchery-standard and hatchery-manipulated fish had a significantly lower rR_S than wild-caught fish, but feed manipulation resulted in fish with a slightly higher rR_S similar to that of wild-caught fish (ANOVA, $F_{2,43} = 4{\cdot}187$, $P < 0{\cdot}05$; Tukey HSD: hatchery standard and hatchery manipulated, $P > 0{\cdot}05$; hatchery standard and wild caught, $P < 0{\cdot}05$; wild caught and hatchery manipulated, $P > 0{\cdot}05$) (Fig. 1).

Growth of hatchery-reared fish under semi-natural conditions was significantly improved by the feed manipulation (Fig. 3). Hatchery-manipulated fish showed a residual growth rate (*i.e.* accounting for body size) similar to wild-caught fish and

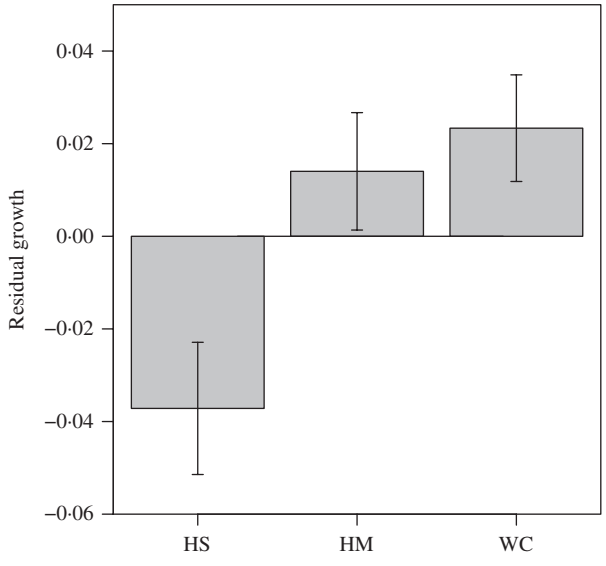

FIG. 3. Residual growth rate over five-week period in semi-natural environments of hatchery-standard (HS), hatchery-manipulated (HM) and wild-caught (WC) treatments of *Micropterus floridanus*.

significantly higher than hatchery-standard fish ($F_{2,133} = 6{\cdot}531$, $P < 0{\cdot}01$; Tukey HSD: hatchery standard and hatchery manipulated, $P < 0{\cdot}05$; hatchery standard and wild caught, $P < 0{\cdot}01$; wild caught and hatchery manipulated, $P > 0{\cdot}05$). Conversely, survival of hatchery-reared fish under semi-natural conditions was not influenced by the feed manipulation. Hatchery-standard and hatchery-manipulated fish showed similar survival, considerably lower than that of wild-caught fish ($\chi^2 = 17{\cdot}913$, d.f. $= 2$, $P < 0{\cdot}001$; Fig. 4).

Micropterus floridanus survival under semi-natural conditions (Table III) was best predicted by a model with a single variable, L_T ($\beta_1 = 0{\cdot}061$). The $L_T + A$ (where A is activity, $\beta_1 = 0{\cdot}054$, $\beta_2 = -0{\cdot}011$), $L_T + M$ (where M is mass, $\beta_1 = 0{\cdot}057$, $\beta_2 = 0{\cdot}015$) and $L_T + rR_S$ ($\beta_1 = 0{\cdot}061$, $\beta_2 = 0{\cdot}024$) models were not statistically distinguishable and, hence, were also good predictors of survival.

DISCUSSION

Hatchery-standard and hatchery-manipulated fish were different from wild-caught fish in all measured variables. The feeding manipulation affected residual R_S and post-release growth, but not activity or post-release survival.

The results of this study show that hatchery-standard and hatchery-manipulated fish were considerably more active than wild-caught fish. Such behaviour may be promoted in the hatchery due to high flow rates that force *M. floridanus* (naturally a sedentary species of standing waters) to swim constantly, as well as by high rearing densities that elevate social interactions. A field study found that released hatchery-reared *M. floridanus* had higher movement rates and utilized more open water habitat than wild *M. floridanus* (B. Thompson, pers. comm., 2014), indicating that elevated activity in

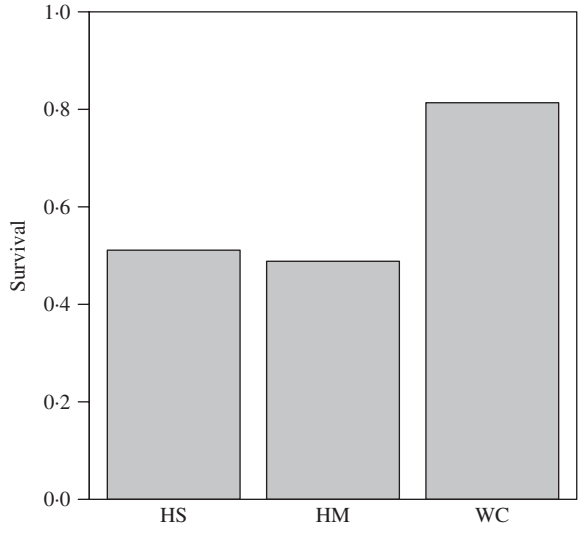

FIG. 4. Five-week post-release survival rates in semi-natural environments of hatchery-standard (HS), hatchery-manipulated (HM) and wild-caught (WC) treatments of *Micropterus floridanus*.

hatchery-reared *M. floridanus* persists after release. While being active may be beneficial in culture environments, it can be detrimental in the wild by increasing vulnerability to predation and energy expenditure (Olla *et al.*, 1998; Brown & Laland, 2001; Careau *et al.*, 2008). In fact, this study showed a negative correlation between activity and survival in semi-natural environments.

This study also showed that hatchery-standard fish had a lower rR_S than wild-caught fish. This may suggest fundamental differences in the behaviour and personality of hatchery-standard and wild-caught fish, such as lower responsiveness and exploration in novel environments by hatchery fish (Careau *et al.*, 2008). Feed manipulation resulted in fish with a slightly higher rR_S similar to that of wild-caught fish and also improved post-release growth, but not survival. The higher rR_S of hatchery-manipulated and wild-caught fish may also indicate intrinsic morphological

TABLE III. Comparison of models predicting *Micropterus floridanus* survival under semi-natural conditions ($n = 29$). The four most parsimonious models and the null model are presented here. The best model is highlighted in dark grey and models with equivalent explanatory power are highlighted in light grey

Model	Number of parameters	Parameter estimates	AIC	ΔAIC
L_T	1	0·061	33·97	0
$L_T + A$	2	0·054, −0·011	34·69	0·72
$L_T + rR_S$	2	0·061, 0·024	35·97	2·00
M	1	0·142	36·15	2·18
Null	1	−0·7985	37·92	3·95

L_T, total length; A, activity; rR_S, residual standard metabolic rate; M, mass; AIC, Akaike's information criterion.

differences (*i.e.* size of metabolic organs) and, consequently, improved resource assimilation (Brett & Groves, 1979; McNab, 1980; Priede, 1985).

Hatchery-standard fish had lower growth rates after release in semi-natural environments than wild-caught fish. The lower growth rates of hatchery standard fish may be the result of poor foraging abilities. Studies by Sosiak *et al.* (1979) and Olla *et al.* (1998) have found that released hatchery-reared fish had deficits in foraging behaviour 2 months after release. By limiting growth rates of released fish, foraging deficits may expose hatchery fish to prolonged periods of high predation ultimately reducing the success of stock enhancements. Feed manipulation resulted in fish that grew more quickly after release similar to wild-caught fish. The faster growth of hatchery-manipulated fish may suggest improved foraging skills as well as improved resource assimilation characterized by elevated R_S. Similarly, a laboratory study by Braithwaite & Salvanes (2005) found that hatchery fish reared under increased environmental variability (*i.e.* food availability) were able to consume a greater proportion of prey than fish reared under constant food availability. Based on the results of their study and this study, it appears fish can develop more flexible behaviour that may improve post-release growth by experiencing environmental variability by means of a simple cost-effective feed manipulation.

Survival of hatchery-standard and hatchery-manipulated fish in semi-natural environments was significantly lower than wild-caught fish, similar to the results of Jonsson *et al.* (2003) and Lorenzen (2006). Poor survival of hatchery-reared fish may be associated with the large differences in energy expenditure, behaviour and life histories found in this study and others (Fleming & Gross, 1993; Gross, 1998; Huntingford, 2004; Thorpe, 2004). The model results of this study showed a negative correlation between activity and survival, suggesting that greater activity may expose fish to greater predation risk. Activity level of hatchery-standard and hatchery-manipulated fish was not influenced by the feed manipulation, and this may explain why survival was also not influenced by the manipulation. Future work should investigate methods of producing less active hatchery fish as well as assess the effects of feed manipulation on long-term performance recognizing that the objectives of many fisheries enhancement programmes rely on survival of hatchery fish to recruitment to the fishery.

Based on the results of this study and others (Metcalfe *et al.*, 1989, 1995; Thorpe, 1991, 2004; Metcalfe & Monaghan, 2003), hatchery-rearing imparts considerable modifications to life-history strategies. Shifts in life-history strategies are likely to result in atypical behavioural strategies and survival. To this end, substantial improvements are needed in the methods and husbandry practices used to rear fishes for stocking programmes. The aim of hatcheries should focus on developing fishes that are behaviourally, physiologically and genetically similar to wild fishes (Brown & Laland, 2001). This may require modifications to the rearing environment in ways that present cultured fishes with conditions similar to natural environments. In this study, food predictability and feeding rate were manipulated showing that a simple feed manipulation in culture settings could produce hatchery-reared fish with more similar allocation patterns to wild fish but failed to improve survival. Furthermore, these fish required only two fifths of the feed required under standard hatchery practices with no loss in body size or growth rate. Future work should investigate implementing additional manipulations to the hatchery environment (*e.g.* addition of predators, reduction in water flow rates and reduction of rearing densities) with the aim to improve lifelong survival and fitness. Improvements in fish culture methods should remain a priority

for stocking programmes given improvements in post-release survival will ultimately increase the effectiveness of stock enhancement practices.

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