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Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management

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Four genetically distinct stocks of age 2+ years largemouth bass *Micropterus salmoides* were produced using adults collected from two regions in the upper midwest (central Illinois, IL and south-eastern Wisconsin, WI, U.S.A.). Two pure stocks (IL × IL and WI × WI), as well as both of their reciprocal F_1 interstock hybrids (IL × WI and WI × IL) were produced in research ponds in Champaign, IL. In general, swimming performance, routine oxygen consumption and activity were highest at 18° C, intermediate at 12° C, and lowest at 6° C for all stocks. However, performance indicators varied among stocks at each of the temperatures. The pure Illinois stock (IL × IL) had the lowest activity : cost ratio at 18° C and the highest at 6° C (based upon swimming strength, routine activity rates and routine metabolic rates). The opposite pattern was observed for the other pure stock (WI × WI). Although differences were less distinct at lower temperatures, the two pure stocks (IL × IL and WI × WI) outperformed both interstock hybrids. These results indicate that not only do non-native stocks appear to have reduced performance relative to locally adapted stocks, but also that interstock hybrids exhibit performance impairments, not hybrid vigour.

Key words: adaptation; outbreeding depression; physiology; performance; conservation; *Micropterus salmoides*; stocking.

INTRODUCTION

Species of fishes that are distributed across a geographic range exist not as a panmictic group but rather as a mosaic of genetically divergent units, in some cases inter-connected by various degrees of gene flow (Soule, 1986). Environmental gradients across a species range can differentially influence the ability of organisms to survive and reproduce, depending upon their genotypes. As a result, restriction in gene flow provides the opportunity for natural selection to tailor populations genetically to their environments (Wright, 1931). Among natural populations local adaptations resulting from exposure to environmental differences are the basis for the stock concept (Berst & Simon, 1981).

Intraspecific genetic variation in fishes has been studied extensively over the past three decades (Ryman & Utter, 1987). Protein electrophoretic studies established that substantial genetic variation often exists among different

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populations of a single species (Philipp *et al.*, 1983). Such studies support the hypothesis that populations in different geographic locations have different genetic and physiological characteristics, i.e. each of these populations has evolved an adaptive suite of characters, including behaviours and physiologies, for its specific environment (Philipp, 1991).

Genetic variability has two components (Wright, 1978). The first component is the variation among individuals within populations. Such variation can be lost through selection or genetic drift (Allendorf *et al.*, 1987), particularly in populations with few reproducing individuals. The second component is the variation that exists among populations. This variation is lost when previously isolated populations are mixed, resulting in the homogenization of the two previously distinct gene pools (Campton, 1987). In addition to the homogenization of genetic variation, this mixing of populations can also result in outbreeding depression, i.e. the loss in fitness among offspring that results from the mating of too distantly related individuals. Outbreeding depression probably results from a disruption in co-adapted gene complexes that were derived through many years of natural selection during the process of local adaptation (Templeton, 1986; Thornhill, 1993).

To date, little attention has been paid to the long-term consequences of fish stocking efforts on the genetic integrity of local populations (Philipp *et al.*, 1993). Although the stock concept encourages conservation and management of fish at the level of individual stocks, and not the species as a whole, one of the most hotly debated and pressing issues in the management of wild populations is how to define the appropriate units in terms of location and numbers. A recent publication (Nielsen, 1995) has focussed on how best to define unique units for conservation in aquatic systems. However, within this publication, none of the 36 papers dealt with the physiological and energetic differences associated with different stocks identified through molecular genetic analyses. A rigorous assessment of the criteria used to define the number and location of these genetic units would be facilitated by knowing whether or not biologically meaningful differences exist among them. To date, few empirical studies have attempted to quantify physiological differences among stocks, much less to assess the fitness consequences of mixing them (Philipp & Claussen, 1995).

Understanding the genetic basis of the variation in phenotypes (e.g. behaviours, morphologies, physiologies and life histories) that are of evolutionary importance to an organism is important for the development of an effective approach to address critical issues in the conservation and management of fishes and wildlife (Allendorf, 1995). Assessing how the physiological characteristics of fish from different genetic stocks change as thermal environments vary can help understand the mechanisms involved with local adaptation (Fields *et al.*, 1987; Philipp *et al.*, 1995). Furthermore, assessing both the fitness consequences of mixing wild fish populations by measuring the impact of interbreeding on reproductive success as well as the implications of interbreeding on the physiological and energetic characteristics of the crossbred fish is a robust strategy for understanding local adaptation (Philipp & Whitt, 1991; Philipp *et al.*, 1993; Philipp & Claussen, 1995).

The focus of the present research programme is to determine how molecularly defined stock structures indicate true differential adaptation to local

environmental conditions and how that adaptation translates into biologically meaningful and measurable physiological characteristics. Specifically, a combination of approaches has been used to address the following two objectives. First, two genetically distinct stocks of largemouth bass *Micropterus salmoides* Lacépède, collected from different geographical regions in the upper midwest, were used to assess the physiological and energetic bases of adaptation to different climatic conditions. Second, these different stocks of largemouth bass, together with their two reciprocal F1 interstock hybrids, were used to quantify the resulting associated changes in a series of measurable performance characteristics. Beyond that, however, this study attempts to relate such losses in physiological or energetic performance characteristics to the potential for fitness loss (outbreeding depression) that results from the mixing of the two stocks.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

From a previous molecular genetic study (Fields *et al.*, 1997 Champaign, Illinois, U.S.A.) it was possible to propose geographic boundaries for 15 putative stocks of largemouth bass in Illinois, Minnesota, and Wisconsin, U.S.A. The stock delineation process was based on the distribution of different alleles encoded at variable protein loci based on starch gel electrophoresis combined with the distribution of different mitochondrial DNA haplotypes based on variable restriction endonuclease digestion sites.

Broodstocks were collected from two of these identified stocks (Fig. 1) in 1997. Only individuals that were fixed for different allelic genotypes at a single locus (MDH-B) were selected from each stock: (1) IL, from Central Illinois: Lake Shelbyville in the Kaskaskia River Drainage within the Mississippi River Basin; genotype = MDH $-$ B^1B^1; (2) WI, from Southeastern Wisconsin: Big Cedar Lake in the Lake Michigan Drainage within the Great Lakes Basin; genotype = MDH $-$ B^2B^2.

In 1998 adult fish (with the appropriate homozygous genotype) from each source were stocked into 0·04 ha clay-lined, earthen ponds at the Illinois Natural History Survey Aquatic Research Field Laboratory in Champaign, Illinois to produce four distinct, genetically tagged experimental stocks, each of the two pure parental stocks (IL × IL and WI × WI), as well as both reciprocal F_1 interstock hybrids (WI × IL and IL × WI). In the autumn of 1998 production ponds were drained, fingerlings from each stock were given differential fin clips for external identification and then stocked into a series of ponds in a set of ' common garden ' experiments designed to assess their relative survival and growth, as well as their relative fitness (lifetime reproductive success) after they matured. Fish fed on natural invertebrate prey as well as fathead minnows *Pimephales promelas* Rafinesque and juvenile bluegill *Lepomis macrochirus* Rafinesque produced in the ponds.

During autumn, 2000 some of each stock were seined from the ponds and held in raceways at various times 1 week prior to experimentation, when ambient water temperatures were 6, 12 and 18° C. Water temperatures were relatively stable for a period of *c.* 2 weeks prior to experimentation but varied up to 3° C on a diel basis. During the actual physiological experiments, water temperatures were controlled so that they varied by no more than 1° C. All experiments were conducted between 1000 and 1600 hours. Fish were exposed to natural photoperiods of Champaign, Illinois, during residency in pond and raceway environments, as well as during experimentation. Experiments were conducted between 18 September and 4 December 2000.

SWIMMING PERFORMANCE

Swimming challenges were conducted in a 56 l modified Blazka-type swim chamber (Smith & Newcomb, 1970). The swim chamber was continuously supplied with aerated

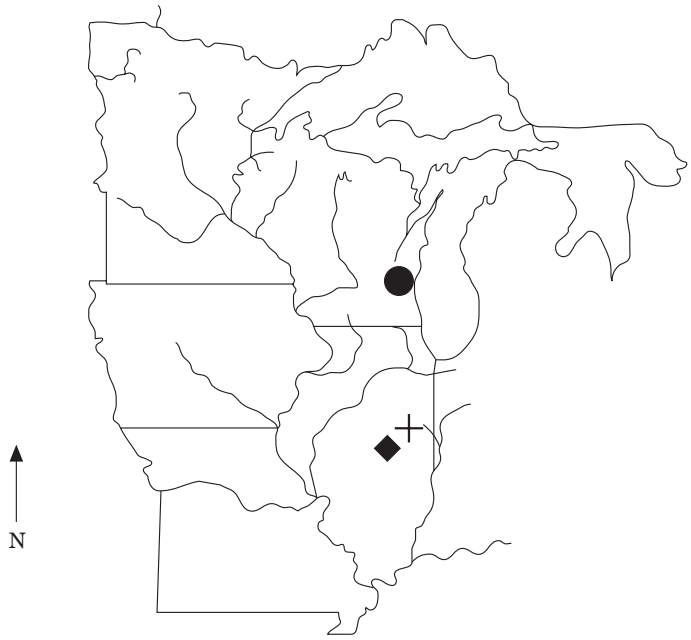

FIG. 1. Map of midwest U.S.A. including Illinois and Wisconsin, where the two stocks originated. The Illinois stock (IL × IL) (◆) was from the Kaskaskia River drainage and the Wisconsin stock (WI × WI) (●) was from Big Cedar Lake in the western Lake Michigan drainage. The location of fish holding and experimentation (INHS) (+) is also indicated on the map and is within the Kaskaskia River Drainage.

water at the appropriate temperature and was operated on a flow-through basis during the swimming challenge. Individual fish were removed from holding tanks where they had been fasted for 4 days prior to experimentation to ensure they were in a post-absorptive state (Beamish, 1964) and then placed into the chamber. Fish were acclimated at a water flow rate of 0·1 m s^{-1} (*c.* 0·5 body-lengths s^{-1}) for 30 min (Peake *et al.*, 1997). A light gradient was used to encourage fish to swim. Following acclimation, fish were exposed to a series of stepwise velocity increments to determine their maximum aerobic swimming capacity (critical swimming velocity, U_{crit}; Beamish, 1978). The velocity was increased by 0·1 m s^{-1} increments every 15 min, until the test fish were fatigued (Farlinger & Beamish, 1977). Fatigue was defined as the point at which the fish became impinged on the rear blocking screen twice and refused to swim, despite temporary changes in flow or tapping on the side of the chamber (Peake *et al.*, 1997).

Once fatigue had been reached, the post-exercise ventilation rate (opercular movement) was recorded over a 30 s period. Fish were then removed from the chamber, measured (total length, L_T), weighed (g), and then a fish was given a temporary clip to ensure that individuals were not used more than once. Fish were then released back into the 0·04 ha holding pond. Critical swimming speeds were calculated using the formula outlined in Beamish (1978) and expressed both in absolute (m s^{-1}) terms and in body-lengths per s to account for variation in L_T (Hammer, 1995).

STATIC RESPIROMETRY

Respirometers consisted of acrylic boxes with lids (volume, 4·1 l). Three sides of the respirometers were covered with white tape to minimize external disturbance and to improve the ability to record fish activity with videography. Respirometers were placed on top of stir plates and magnetic stir bars were placed inside the respirometer (Chipps *et al.*, 2000). The stirring bar was used for mixing the water and maintaining a

homogenous oxygen concentration within the respirometer during an experiment (Steffensen, 1989). A plastic grid was placed above the stir bar to ensure that it did not contact or disturb the fish, while still permitting water circulation. Oxygen saturation inside the respirometer ranged from 75 to 90% and never fell below 6 mg l^{-1} (Dahlberg *et al.*, 1968). Water temperature never varied $> \pm 0{\cdot}1^{\circ}$ C during the experiments.

Prior to experimentation, fish were held in tanks where they had been starved for 4 days to avoid the confounding effects of respiration associated with digestive processes (Glass, 1968). Individual fish were introduced to the respirometer without exposing fish to air and were provided continually with aerated water for 30 min. Although this acclimation period is seemingly brief, the fish were not handled by net or exposed to air, thus minimizing stress responses. An initial dissolved oxygen value was recorded using a self-stirring oxygen probe (YSI 5903, Yellow Springs Instruments Inc.), and the respirometers were sealed. The respirometers were left undisturbed during a 30 min period, after which, a final dissolved oxygen reading was collected. Biological oxygen demand was undetectable over the 30 min respirometry period at all three water temperatures. The fish were removed from the respirometer and enumerated and marked the same way as those removed from the swimming chamber. Routine oxygen consumption (M_{O_2}) in mg of oxygen per kg of mass per h was calculated from:

$$(M_{O_2} = (V_r\, \Delta D_O)\, (\Delta T W)^{-1}$$

where V_r is the volume of water in the respirometer (l), W is the mass of the fish (kg), ΔD_O is the change in dissolved oxygen (mg), and ΔT is the duration of the respirometry trial.

To examine the temperature dependence of stock-specific routine oxygen consumption, Q_{10} rates were calculated (Schmidt-Nielsen, 1997) from:

$$Q_{10} = 10(R_2 R_1^{-1})\, (T_2 - T_1)^{-1}$$

where R_1 and R_2 are the rates of oxygen consumption at temperature T_1 and T_2. Q_{10} values were calculated for mean routine oxygen consumption values for temperature shifts of 6–12, 12–18 and 6–18° C.

During the 30 min respirometry trial, fish movements in the respirometer (during a 10 min period in the middle of the respirometry trial) were recorded using an 8 mm video camera on a tripod. A digital timer placed beside the respirometer was used to document the time of recording to the nearest s. Images recorded were played at 0·2 speed using an editing suite (Mitubishi Inc.). For the entire 10 min period two measures were transcribed. First, the time spent both swimming and resting was classified. The resting mode was assigned to fish that maintained position. The second measure was the number of turns performed in the 10 min period. Turns were classified as every change of lateral position by 45° and were expressed as turns h^{-1}.

To examine the role of activity in influencing routine oxygen consumption, indices were derived by dividing oxygen consumption independently by the two activity metrics (Watt, 1986). These indices were created using mean values for all temperature-specific data series for each of the stocks. These indices provided a specifc routine cost of activity for both turns h^{-1} and the proportion of time spent swimming.

DATA ANALYSIS

Data were visually assessed for normality using quantile plots and homogeneity of variance using residual plots (SYSTAT, V8.0, SAS Institute). When appropriate, transformations were conducted consistent with the degree of departure from normality or homogeneity of variance and the type of data (e.g. proportional). The premise of all analyses was to test two null hypotheses: (1) that there were no differences among the stocks at each of the three temperatures and (2) there were no differences within each of the stocks across the three different temperatures (JMP, V3.2.2, SAS Institute). All tests were conducted using two-way analysis of variance with stock being the main effect and water temperature the secondary effect. Planned contrasts were used to examine where

specific differences of interest occurred. All values reported are means ± S.E.. Tests were considered significant at $\alpha = 0{\cdot}05$.

RESULTS

SWIMMING PERFORMANCE CHALLENGE

Although fish used in the swimming experiments were all 2+ years in age and were generally of similar size (Table I), some specific differences in both L_T (Table II) and mass (Table II) varied with temperature and stock. The critical swimming speeds did not vary among stocks but did vary within each stock across water temperatures (Tables I and II). In general, critical swimming speeds increased with water temperature (Fig. 2); i.e. at 6 and 18° C they were significantly different, but at 12° C, values were generally intermediate and not significantly different (Table I).

Because the size of fish varied somewhat within stocks at different temperatures, and among stocks at the same temperature, we also examined swimming performance in bodylengths s^{-1} was also examined. Size adjusted swimming speeds varied with both temperature and stock (Tables I and II). The same trend of increasing swimming performance with increasing water temperatures was observed. In general, stock specific swimming performance was lowest at 6° C, and highest at 18° C, and usually significantly different (Table I; Fig. 2). At 12° C swimming performance was generally intermediate and not significantly different from the 6 or 18° C fish. At the lowest temperature (6° C) swimming performance was similar among stocks. However, at 12° C, IL × WI had lower swimming performance than IL × IL. At the highest temperature (18° C), more differences were apparent, with IL × IL fish achieving higher swimming speeds than both IL × WI and WI × WI stocks (Table I).

At 12 and 18° C, all fish swam during the swimming trials. However, at the lowest temperature (6° C), some fish refused to swim during the acclimation period or the trial. These individuals were excluded, and the proportion of each stock that did not swim at the lowest temperature was calculated. More IL × IL (33 %) and WI × IL (33%) fish failed to swim than the other two stocks. WI × WI fish (11%) failed to swim fewer times than the IL × WI fish (17%).

The post exercise ventilation rates varied by water temperature but not by stock (Table II). For all stocks, ventilation rates were lowest at 6° C, intermediate at 12° C, and highest at 18° C. All comparisons resulted in significant differences (Table I).

STATIC RESPIROMETRY

As for the fish used in the swimming performance challenges, fish used for the activity and MO_2 assessments were all 2+ years in age and generally of similar size (Table III). Some significant differences in L_T (Table IV) and masses (Table IV), however, were observed to vary with both water temperature and stock.

Routine oxygen consumption rates varied with both stock and temperature (Table IV). No significant differences in oxygen consumption were noted at the lowest temperature among stocks, but several significant differences did exist at intermediate and high temperatures (Table III; Fig. 3). In general, routine oxygen consumption was lowest at 6° C, intermediate at 12° C, and highest at

TABLE I. Meristics and swimming challenge results for stocks of largemouth bass at three water temperatures. All values are means (± 1 S.E.M.). Dissimilar letters indicate significantly different ($P<0{\cdot}05$) values within a stock at the three different temperatures. Dissimilar numbers indicate significantly different ($P<0{\cdot}05$) values between stocks at each temperature. Although 108 fish were used, at low water temperatures, 11 fish refused to swim. The masses and lengths are based on all fish, whereas the swimming speeds and ventilation rates are based only upon those that swam. (Sample sizes are in parentheses.)

Temperature (° C)	Stock	n	L_T (mm)	Mass (g)	Critical swimming speed (cm sec^{-1})	Critical swimming speed (body length s^{-1})	Post-exercise ventilation rate (ventilations min^{-1})
6	IL × IL	12 (8)	$159 \pm 1^{a,1}$	$45 \pm 1^{a,1}$	$30{\cdot}1 \pm 2{\cdot}2^{a,1}$	$1{\cdot}90 \pm 0{\cdot}14^{a,1}$	$27{\cdot}5 \pm 1{\cdot}6^{a,1}$
6	IL × WI	11 (9)	$186 \pm 2^{a,b,2}$	$73 \pm 3^{a,2}$	$31{\cdot}8 \pm 3{\cdot}0^{a,1}$	$1{\cdot}70 \pm 0{\cdot}15^{a,1}$	$29{\cdot}0 \pm 1{\cdot}3^{a,1}$
6	WI × IL	12 (8)	$176 \pm 3^{a,3}$	$65 \pm 4^{a,2,3}$	$32{\cdot}3 \pm 3{\cdot}3^{a,1}$	$1{\cdot}88 \pm 0{\cdot}21^{a,1}$	$29{\cdot}6 \pm 1{\cdot}7^{a,1}$
6	WI × WI	9 (8)	$175 \pm 3^{a,3}$	$59 \pm 3^{a,3}$	$30{\cdot}6 \pm 2{\cdot}4^{a,1}$	$1{\cdot}74 \pm 0{\cdot}14^{a,1}$	$31{\cdot}5 \pm 2{\cdot}6^{a,1}$
12	IL × IL	13	$170 \pm 5^{b,1}$	$59 \pm 6^{b,1}$	$34{\cdot}6 \pm 2{\cdot}8^{a,1}$	$2{\cdot}06 \pm 0{\cdot}19^{a,1}$	$45{\cdot}7 \pm 1{\cdot}7^{b,1}$
12	IL × WI	8	$182 \pm 1^{a,2}$	$69 \pm 2^{a,2}$	$29{\cdot}4 \pm 2{\cdot}3^{a,1}$	$1{\cdot}61 \pm 0{\cdot}11^{a,2}$	$44{\cdot}6 \pm 3{\cdot}3^{b,1}$
12	WI × IL	8	$180 \pm 2^{a,2}$	$67 \pm 4^{a,2}$	$35{\cdot}6 \pm 1{\cdot}5^{a,1}$	$1{\cdot}98 \pm 0{\cdot}09^{a,1,2}$	$46{\cdot}0 \pm 2{\cdot}2^{b,1}$
12	WI × WI	7	$177 \pm 4^{a,1,2}$	$63 \pm 4^{a,1,2}$	$35{\cdot}2 \pm 3{\cdot}5^{a,b,1}$	$2{\cdot}01 \pm 0{\cdot}25^{a,b,1,2}$	$48{\cdot}7 \pm 2{\cdot}5^{b,1}$
18	IL × IL	7	$166 \pm 4^{a,b,1}$	$51 \pm 5^{a,b,1}$	$47{\cdot}4 \pm 2{\cdot}7^{b,1}$	$2{\cdot}86 \pm 0{\cdot}18^{b,1}$	$86{\cdot}9 \pm 8{\cdot}3^{c,1}$
18	IL × WI	7	$193 \pm 4^{b,2}$	$84 \pm 7^{b,2}$	$43{\cdot}6 \pm 2{\cdot}0^{b,1}$	$2{\cdot}25 \pm 0{\cdot}07^{b,2}$	$87{\cdot}1 \pm 4{\cdot}5^{c,1}$
18	WI × IL	7	$183 \pm 2^{a,3}$	$66 \pm 2^{a,3}$	$46{\cdot}7 \pm 1{\cdot}3^{b,1}$	$2{\cdot}55 \pm 0{\cdot}08^{b,1,2}$	$87{\cdot}7 \pm 5{\cdot}8^{c,1}$
18	WI × WI	7	$187 \pm 2^{b,2,3}$	$71 \pm 3^{a,3}$	$40{\cdot}9 \pm 1{\cdot}6^{b,1}$	$2{\cdot}19 \pm 0{\cdot}10^{b,2}$	$85{\cdot}1 \pm 6{\cdot}0^{c,1}$

TABLE II. Analysis of variance model parameters for largemouth bass used for swimming performance challenges. ANOVA summaries provided for total length of fish (mm), mass of fish (g), absolute critical swimming speeds (U-crit cm sec^{-1}), length adjusted critical swimming speeds (body lengths s^{-1}), and post-exercise ventilation rates. For all parameters the main effect was stock and the secondary effect was water temperature

Parameter	Source	*SS*	d.f.	*F*	*P*
L_T	Stock	7117·52	3	25·3094	<0·001
	Temperature	1194·19	2	6·3697	0·003
	Stock × temperature	841·89	6	1·4968	0·187
	Error	8999·04	96		
Mass	Stock	8002·32	3	19·1475	<0·001
	Temperature	985·42	2	3·5368	0·033
	Stock × temperature	1592·81	6	1·9056	0·088
	Error	13373·76	96		
Absolute U_{Crit}	Stock	164·97	3	1·0117	0·392
	Temperature	3030·17	2	27·8733	<0·001
	Stock × temperature	263·71	6	0·8086	0·566
	Error	8063·93	85		
Length adjusted U_{Crit}	Stock	2·44	3	3·8797	0·012
	Temperature	7·34	2	17·4901	<0·001
	Stock × temperature	1·04	6	0·8272	0·552
	Error	17·83	85		
Ventilation rates	Stock	47·02	3	0·1539	0·927
	Temperature	54747·78	2	268·8211	<0·001
	Stock × temperature	110·10	6	0·1802	0·982
	Error	8960·99	85		

18° C. Significant differences existed for all comparisons except between the 12 and 18° C for WI × WI fish (Table III). At 12° C, IL × IL fish consumed significantly more oxygen than those from the IL × WI stock and at the highest temperature, IL × IL fish consumed significantly more oxygen than all other stocks.

Q_{10} values for the temperature dependence of routine oxygen consumption were generally high (>2) (Fig. 4). For the IL × IL, WI × IL, and WI × WI, values were highest for 6–12° C, lowest for 12–18° C, and thus intermediate for 6–18° C. The Q_{10} pattern for IL × WI fish differed in that values were lowest for 6–12° C, highest for 12–18° C, and thus intermediate for 6–18° C.

The activity levels of fish indicated by the proportion of time spent swimming in the respirometers varied with both temperature and stock (Table IV). At the lowest temperature, fish swimming activity was similar among stocks (Fig. 5; Table III). At the intermediate temperature IL × IL fish were significantly more active than WI × IL fish. At the highest temperature, IL × IL fish were more active than all but the WI × IL fish. WI × WI fish had the lowest activity levels at 18° C, different from all but the IL × WI stock. There was substantial variation in the activity levels of individual stocks at different temperatures. Only IL × IL fish activity increased significantly with water temperature, being lowest at 6° C, intermediate at 12° C, and highest at 18° C. Activity levels of fish from the WI × IL stock were equally low at 6 and 12° C, and significantly higher

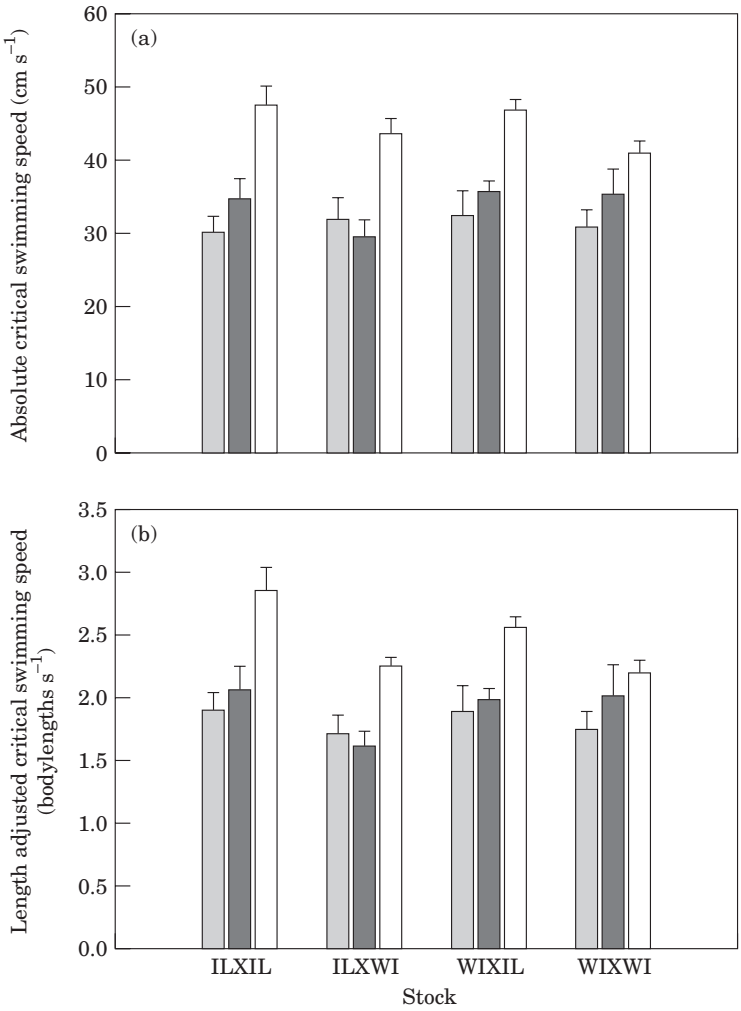

FIG. 2. Effects of water temperature and stock on the swimming performance of largemouth bass; (a) critical swimming speed and (b) length corrected critical swimming speed. ▨ is 6° C; ■, 12° C; □, 18° C. Data are means ± S.E.

at 18° C. Conversely, activity levels of fish from the WI × WI and IL × WI stocks did not vary with water temperature (Table III).

Similar patterns to those observed for the proportion of time swimming were observed for turning rates. Turning rates varied with both stock and water temperature (Table IV). At the lowest temperature (6° C), turning rates did not differ among stocks (Table III; Fig. 5). At 12° C, IL × IL fish turned more than did WI × IL fish and at 18° C, IL × IL fish turned more than both the WI × IL and the WI × WI fish. There were no consistent trends in the stock specific turning rates with water temperature. Only IL × IL fish increased significantly with water temperature, being lowest at 6° C, intermediate at 12° C, and highest at 18° C. There were no temperature-specific differences in turning rate for IL × WI, WI × IL, or WI × WI fish (Table III).

TABLE III. Meristics, routine oxygen consumption and activity results for stocks of largemouth bass at three water temperatures. All values means (± 1 S.E.M.). Dissimilar letters indicate significantly different ($P<0{\cdot}05$) values within a stock at the three different temperatures. Dissimilar numbers indicate significantly different ($P<0{\cdot}05$) values between stocks at each temperature

Temperature (° C)	Stock	n	L_T (mm)	Mass (g)	Routine oxygen consumption (mg kg^{-1} h^{-1})	Turning rate (turns h^{-1})	Swimming activity (proportion of time swimming)
6	IL × IL	9	$160 \pm 2^{a,1}$	$45 \pm 2^{a,1}$	$46{\cdot}9 \pm 7{\cdot}8^{a,1}$	$4{\cdot}6 \pm 3{\cdot}6^{a,1}$	$1{\cdot}1 \pm 0{\cdot}9^{a,1}$
6	IL × WI	10	$188 \pm 2^{a,2}$	$75 \pm 3^{a,2}$	$45{\cdot}1 \pm 4{\cdot}8^{a,1}$	$16{\cdot}7 \pm 13{\cdot}7^{a,1}$	$5{\cdot}0 \pm 3{\cdot}5^{a,1}$
6	WI × IL	9	$175 \pm 4^{a,3}$	$63 \pm 4^{a,3}$	$40{\cdot}3 \pm 4{\cdot}0^{a,1}$	$20{\cdot}8 \pm 13{\cdot}6^{a,1}$	$11{\cdot}8 \pm 4{\cdot}7^{a,1}$
6	WI × WI	8	$173 \pm 3^{a,3}$	$57 \pm 3^{a,3}$	$39{\cdot}6 \pm 8{\cdot}9^{a,1}$	$32{\cdot}6 \pm 31{\cdot}6^{a,1}$	$13{\cdot}8 \pm 12{\cdot}9^{a,1}$
12	IL × IL	13	$170 \pm 5^{b,1}$	$58 \pm 6^{b,1}$	$123{\cdot}2 \pm 10{\cdot}9^{b,1}$	$64{\cdot}1 \pm 16{\cdot}7^{b,1}$	$28{\cdot}5 \pm 8{\cdot}4^{b,1}$
12	IL × WI	8	$181 \pm 1^{b,2}$	$67 \pm 2^{b,1}$	$75{\cdot}5 \pm 15{\cdot}9^{b,2}$	$44{\cdot}6 \pm 25{\cdot}9^{a,1,2}$	$14{\cdot}9 \pm 7{\cdot}7^{a,2,1}$
12	WI × IL	7	$177 \pm 3^{a,1,2}$	$61 \pm 2^{a,1}$	$91{\cdot}6 \pm 20{\cdot}0^{b,1,2}$	$15{\cdot}3 \pm 9{\cdot}2^{a,2}$	$11{\cdot}3 \pm 5{\cdot}0^{a,2}$
12	WI × WI	7	$178 \pm 4^{a,1,2}$	$63 \pm 4^{a,1}$	$101{\cdot}9 \pm 17{\cdot}6^{b,1,2}$	$52{\cdot}0 \pm 25{\cdot}7^{a,1,2}$	$30{\cdot}5 \pm 13{\cdot}4^{a,1,2}$
18	IL × IL	7	$167 \pm 4^{a,1}$	$51 \pm 5^{a,1}$	$192{\cdot}5 \pm 25{\cdot}1^{c,1}$	$144{\cdot}9 \pm 42{\cdot}5^{c,1}$	$65{\cdot}9 \pm 14{\cdot}2^{c,1}$
18	IL × WI	7	$193 \pm 5^{c,2}$	$87 \pm 6^{c,2}$	$144{\cdot}2 \pm 14{\cdot}6^{c,2}$	$8{\cdot}4 \pm 6{\cdot}6^{a,2}$	$12{\cdot}4 \pm 5{\cdot}9^{a,2,3}$
18	WI × IL	8	$183 \pm 2^{a,3}$	$65 \pm 2^{a,3}$	$149{\cdot}9 \pm 19{\cdot}1^{c,2}$	$53{\cdot}8 \pm 26{\cdot}6^{a,1,2}$	$40{\cdot}6 \pm 14{\cdot}2^{b,1,2}$
18	WI × WI	6	$186 \pm 3^{b,2,3}$	$71 \pm 3^{b,3}$	$138{\cdot}8 \pm 12{\cdot}1^{b,2}$	$7{\cdot}8 \pm 6{\cdot}8^{a,2}$	$11{\cdot}6 \pm 5{\cdot}7^{a,3}$

TABLE IV. Analysis of variance model parameters for largemouth bass used for static respirometry trials and spontaneous activity determination. ANOVA summaries for L_T (mm), mass of fish (g), routine oxygen consumption, swimming activity as measured by the percentage of time swimming and turning rate. For all parameters the main effect was stock and the secondary effect was water temperature

Parameter	Source	*SS*	d.f.	*F*	*P*
L_T	Stock	6143·30	3	20·8819	<0·001
	Temperature	1056·12	2	5·3848	0·006
	Stock × temperature	942·58	6	1·6020	0·156
	Error	8531·59	78		
Mass	Stock	47·02	3	0·1539	0·927
	Temperature	54747·78	2	268·8211	<0·001
	Stock × temperature	110·10	6	0·1802	0·982
	Error	8960·99	85		
Routine oxygen consumption	Stock	14174·24	3	2·9838	0·036
	Temperature	188227·57	2	59·4362	<0·001
	Stock × temperature	9664·40	6	1·0172	0·420
	Error	123508·42	78		
Swimming activity*	Stock	1·43	3	4·8684	0·004
	Temperature	1·89	2	9·6695	<0·001
	Stock × temperature	2·99	6	5·0997	<0·001
	Error	7·62	78		
Turning rate**	Stock	258·17	3	5·3646	0·002
	Temperature	171·14	2	5·3344	0·007
	Stock × temperature	356·61	6	3·6428	0·003
	Error	1251·22	78		

*Swimming activity data were arcsine transformed prior to analysis.
**The homogeneity of variance assumption was violated for turning rate thus data were log transformed and analyses were completed on these values.

The pattern of relative efficiency (activity : cost ratio) of swimming activity for the IL × IL fish indicated that they were least efficient at 6° C, and most efficient at 18° C (Fig. 6). The WI × WI stock followed the opposite pattern of efficiency, being least efficient at 18° C and most efficient at 6° C. The F1 hybrid stocks exhibited inconsistent and variable efficiency patterns, but were generally intermediate to the two pure stocks (Fig. 6). The efficiency patterns for turning rates were similar to those observed for swimming activity (Fig. 6).

DISCUSSION

SWIMMING PERFORMANCE CHALLENGE

Swimming requires the integration of numerous physiological processes, which, if quantified, can provide information on the general health and stress levels of fishes (Schreck, 1990). Stocks that have existed under different environmental conditions, such as photoperiod and temperature, have probably developed adaptations to those local conditions. Because swimming performance has been shown to differ with photoperiod (Kolok, 1991) in addition to temperature, the use of swimming performance challenges is an appropriate strategy for examining stock specific differences in local adaptation. Higher

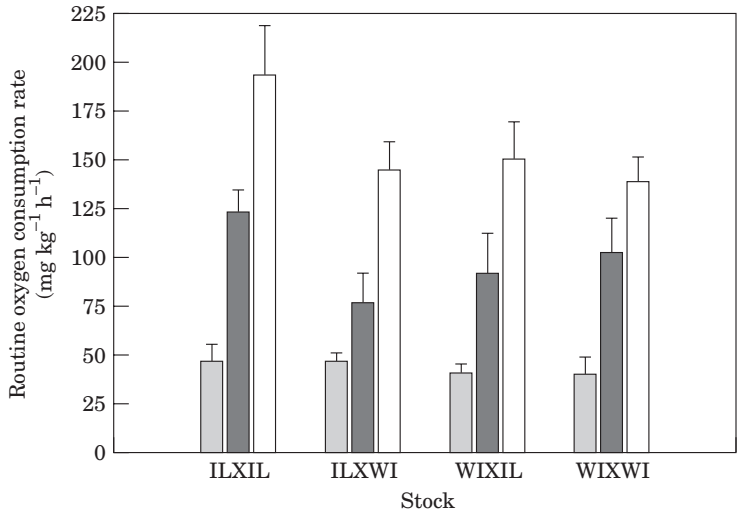

FIG. 3. Effects of water temperature and stock on the routine oxygen consumption rates of largemouth bass. □, 6° C; ▩, 12° C; □, 18° C. Data are means ± S.E.

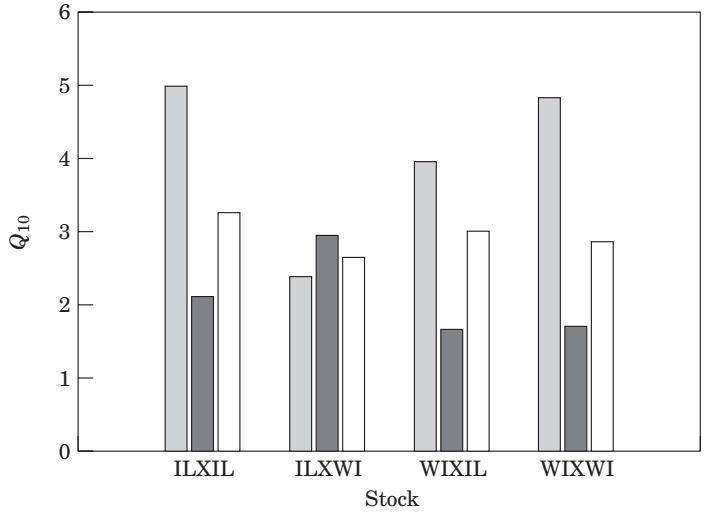

FIG. 4. Q_{10} values for routine oxygen consumption of different stocks of largemouth bass between different temperatures. □, 6–12° C, ▩, 12–18° C, □, 6–18° C. Calculated from mean routine oxygen consumption values.

critical swimming speeds may be related to enhanced biochemical pathway efficiencies that have evolved over many generations in response to these differences in local conditions. There are several examples of intraspecific variation in critical swimming speed. Some of these focus on interindividual variation in performance among fish from the same population (Kolok, 1999). However, most have focussed on variation among different populations. Some of these studies compared variation among natural populations, usually occupying different environments (Nelson *et al.*, 1994), while others have compared

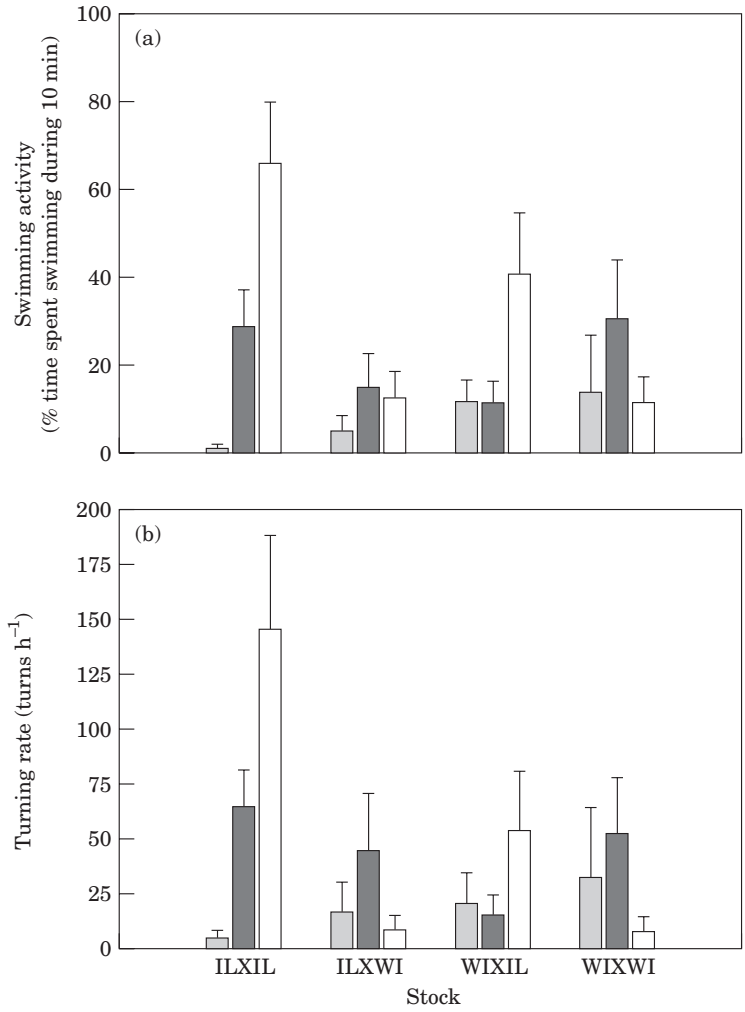

FIG. 5. Effects of water temperature and stock on largemouth bass activity during static respirometry trials. (a) Swimming activity measured using videography; (b) turning rate. ▫, 6° C; ▩, 12° C; □, 18° C. Data are means ± 1 S.E.

different hatchery strains (Thomas & Donahoo, 1977), or different natural (DiMichele & Powers, 1982) or artificially selected (Tsuyuki & Williscroft, 1977) genotypes. The general conclusion of these studies is that swimming performance varies among populations in response to selection.

The lack of significant differences in absolute critical swimming speeds is not surprising based upon the small but significant differences in L_T among stocks. Other studies for which variation in the size of fish existed have had to incorporate a length correction either by generation of a mass or length index or through the use of regression residuals (Kolok, 1999). Initially both corrections were attempted, but the choice was made to express the critical swimming speed in terms of body-lengths s^{-1} for several reasons. First, the ANOVAs yielded similar results, with *F*-values being sufficiently low in the index correction to

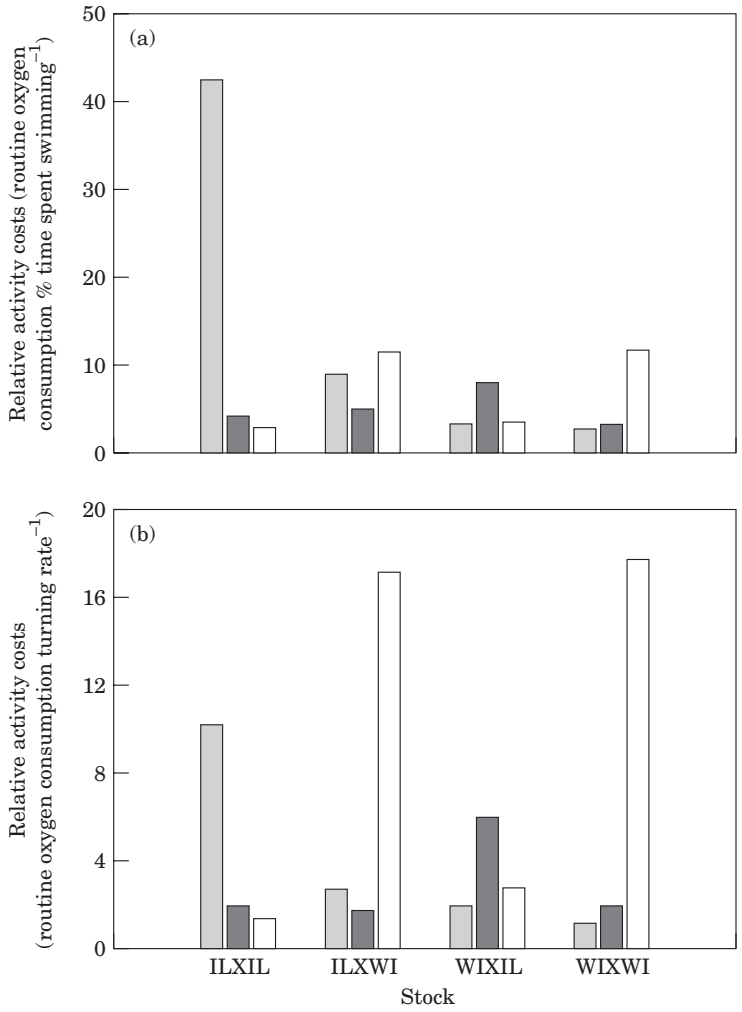

FIG. 6. Effects of water temperature and stock on the relative activity costs (activity : cost ratio) during static respirometry trials of largemouth bass, based on: (a) the proportion of time swimming; (b) turning rates. All efficiency calculations were based upon mean values. □, 6°C; ▩, 12°C; □, 18°C.

permit detection of differences (Packard & Boardman, 1988). Furthermore, for reporting purposes, it is more logical to express swimming performance as a length index using the metric bodylengths s^{-1} to facilitate ecologically meaningful comparisons.

The observed relationship of swimming performance with water temperature was as expected. The trend of decreasing swimming performance with decreasing water temperatures has been documented for sub-adult largemouth bass (Beamish, 1970; Kolok, 1991, 1992). Indeed, as water temperatures approach 5° C, largemouth bass generally become quiescent (Lemons & Crawshaw, 1985; Kolok, 1992). At 6° C, some instances were observed where fish did not swim in a similar way to those observed by Beamish (1970). However, those that did swim had values that were comparable to other published values at

similar temperatures (absolute U_{crit}, *c.* 30 cm s^{-1}, length corrected U_{crit}, *c.* 1·6–1·9 bodylength s^{-1}). Across their historical geographic range largemouth bass are exposed to temperatures ranging from 0 to >35° C. The temperatures chosen to compare performances were at the lower end of the available temperatures for this species. If swimming trials were conducted at 24 or 30° C, the trend of increasing performance with water temperature would probably continue.

Stock specific differences, although not overly apparent in terms of absolute critical swimming speed, were present after length correction particularly at higher temperatures. At the lowest temperature, no significant differences were noted, but at 12° C the IL × WI fish were the poorest performers, and at 18° C, both the IL × WI and the WI × WI stocks were poor performers. The WI × IL fish were similar to the IL × IL in swimming performance. The fact that the IL × WI stock had a performance impairment, but that the WI × IL did not suggests that swimming performance may follow a paternal lineage. Indeed, this highlights the need for examining swimming performance in the F_2 generation.

The post-exercise ventilation rates varied across temperatures but not among stocks. This measure, although not overly interesting, is important in that it suggests that although different stocks varied in their critical swimming speed, when fatigued, they were equally exhausted. As critical swimming speed is analogous to the maximum aerobic capacity of fishes, the lack of stock-specific variance in the temperature-specific post exercise ventilation rates in the present study, indicated that all fish were indeed exercised to capacity. However, from an efficiency perspective those fish that had higher swimming performance levels would be expected to have higher post-exercise ventilation rates. The fact that the ventilation rates were similar probably indicates improved efficiency of the Illinois stock and the WI × IL relative to the pure Wisconsin stock or the reciprocal interstock hybrid (IL × WI). However, to speculate on efficiency, future assessments should focus on measures such as cardiac output.

STATIC RESPIROMETRY

Oxygen consumption and activity of largemouth bass generally both increase with water temperature. In this study the routine oxygen consumption of fish was measured. Routine oxygen consumption differs from standard oxygen consumption in that it assumes that some level of spontaneous activity will occur (Fry, 1957, 1971). A general trend was observed of increasing routine oxygen consumption with increasing water temperature in all stocks. This trend of increased oxygen consumption with temperature is consistent with previously published studies. Although at low and intermediate temperatures only one significant difference was observed, upon graphical inspection, routine oxygen consumption rates of fish from the IL × IL stock were consistently the highest. The magnitude of this difference increased at the highest water temperature, where IL × IL fish had significantly higher routine oxygen consumption rates than the Wisconsin stock and the interstock hybrids. The present study was not the first to examine intraspecific variation in oxygen consumption. For example Giles (1991) examined stock specific patterns in oxygen consumption among three strains of Arctic charr *Salvelinus alpinus* (L.) and concluded that

population or strain is a more appropriate unit for physiological definition and management than the commonly used species approach.

The Q_{10} values that are reported are high, indicating that the fish are generally conforming to changes in water temperature. Values around 1 indicate thermal compensation, whereas values of *c.* $\geqslant 2$ indicate temperature conformity. Indeed, almost all of the values were $\geqslant 2$. These unusually high Q_{10} values, especially for 6–12° C are probably attributable to high levels of spontaneous locomotory activity. Indeed, one of the largest determinants of the trends in routine oxygen consumption that was observed was the spontaneous activity of fish while the respirometry trials were being conducted. The trends in both turning rate and the proportion of time spent swimming followed that of routine oxygen consumption for IL × IL fish, but not for the other three stocks.

There is some evidence that selection for physiological efficiency is important in long lived-multiple brood organisms (Priede, 1977) such as largemouth bass. Energy savings are generally related to reductions in standard metabolic rate (Fry, 1957; Alexander, 1967; Priede, 1977). Because routine metabolic rates were measured, it is not possible to establish if interstock differences in standard metabolic rate were also present. However, because spontaneous activity was monitored, it was possible to calculate efficiency indices (activity : cost ratios) based upon the cost of activity. Interestingly, a direct relationship was observed between efficiency (activity : cost ratio) and water temperature for IL × IL fish, and in general, the opposite trend for all other stocks. The activity costs for IL × IL were highest at 6° C and lowest at 18° C. The pattern was most striking for fish from the more northern stock (WI × WI), and somewhat more variable and intermediate for the interstock hybrids. Because natural selection should favour the maximization of physiological efficiencies (Lotka, 1922), the hypothesis is raised that the IL × IL fish are better adapted to the 12 and 18° C temperatures, whereas the WI × WI stock is more efficient at the cooler temperature (6° C). Realistically, both of these stocks experience peaks in efficiency, and performance, at different optimum levels with reduced efficiency both at lower than optimum and higher then optimum temperatures. In this study, it is entirely possible that largemouth bass from the IL × IL stock have better efficiency at a higher (optimum) temperature not tested in this study (i.e. >18° C). Individuals with the lowest basal metabolic costs can partition more energetic resources to somatic growth and reproduction (Alexander, 1967). Energetic efficiency is adaptive because energy saved in locomotion or standard metabolic rates can be diverted into reproduction so that more efficient genotypes are selected (Priede, 1977). With lower metabolic rates, there is greater scope for activity available (Priede, 1985) that could also enhance the ability of IL × IL to complete costly but essential activities such as predator avoidance. Indeed, behaviour and physiology are probably linked through co-adapted gene complexes.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Much of the current thinking in conservation biology is focussed on the need to protect the genetic resources of species, i.e. the genetic variation both within and among populations. Often, the greatest threats to genetic resources of a wild population arise from the culture and stocking activities of fisheries management

agencies. Recent molecular population genetic studies have been used to promote the use of the stock concept in fisheries management by defining multiple stocks for a number of species (Neilsen, 1995). Those stock proposals are, in reality, only a set of hypotheses waiting to be tested: it is unclear if stocks defined using molecular markers actually contain biologically meaningful differences. There has been substantial concern regarding the effects of stocking and translocation programmes on the genetic resources of naturally reproducing populations of fish species because of the potential for the introgression of native stocks with introduced non-native stocks following their translocation (Philipp *et al.*, 1983; Hindar *et al.*, 1991; Philipp, 1991; Fleming, 1994; Hindar & Jonsson, 1994).

The project undertaken here was an extension of an earlier population genetic study (Fields *et al.*, 1997) that was intended to permit the development of regional management strategies based on genetic conservation principles. The project focussed on the upper midwest portion of the U.S.A., where largemouth bass are one of the most widely dispersed (MacCrimmon & Robbins, 1975) and intensively managed species. Owing to the diversity of habitats in which they occur, these fish have been subjected to a variety of differential selection pressures. Although the extent of these differences are magnified by a broad geographic distribution, local adaptation of largemouth bass populations has also been identified at smaller scales (Philipp & Claussen, 1995). It is suggested that the population genetic structure of largemouth bass in the upper midwest has been most heavily influenced by their reinvasion patterns following glacial retreat during the Wisconsin Glaciation (Fields *et al.*, 1997). Even though this disturbance has been fairly recent in evolutionary time (*c.* 10 000 years), meaningful genetic differences exist among populations in this region.

Fish from the local Illinois population consistently had the highest performance and were more efficient, particularly at higher temperatures. Fish from the more northern Wisconsin stock and the two F_1 hybrid stocks performed worse in Illinois than the Illinois fish and were less efficient. At the lower temperatures these differences were less apparent, with fish from the WI × WI stock or either F_1 hybrid stock in some cases performing as well as, or better than the Illinois fish. The magnitude of stock specific differences could increase if examinations were conducted at even higher temperatures.

Advances in fish culture techniques have resulted in increased production capacity (Stroud, 1986), which has provided unparalleled potential for genetic manipulation relative to any other groups of vertebrate organisms (Ryman *et al.*, 1994). Although there is little direct evidence for outbreeding depression among unmanipulated populations of vertebrates (Templeton, 1986), cases of anthropogenically induced outbreeding depression are more common (Shields, 1993). The results presented here provide additional evidence for the role of local adaptation and interstock hybridization in affecting physiological performance and efficiencies, which probably also affects fitness.

The stocking, transfer and introduction of fish are practices that occur around the world with little assessment of the effects on endemic populations (Cowx, 1994). These activities are particularly pervasive in developing countries where priority is given to economic growth, the need for food security, and income generation (Welcomme & Bartley, 1998). Cowx (1999) provides a globally

applicable framework for dealing with stocking and transfers. These conclusions of his strategy are supported here, and in particular, emphasize the importance of maintaining genetic integrity. It is also clear that the recognition of local adaptation and concern over the potential for outbreeding depression require incorporation into aquaculture operations (Cross, 2000) and fisheries management.

The stocks established by the authors in an outdoor aquatic research complex permit controlled experiments and comparative evaluations. In the wild, once transfers and introductions take place, it will be difficult to assess the effects of these practices. Although the focus of most stocking programmes is to supplement natural stocks in an attempt to increase abundance, it is most likely that the introduction of non-native stocks from other regions will be counter-productive. Indeed, if locally adapted fish breed with introduced fish, that outbreeding may lead to impaired performance of their progeny. This result would probably be magnified in future generations as F_X individuals are established. There is clearly a need for additional assessments focussing on the physiological and fitness impacts resulting from such irresponsible stocking strategies.

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