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Anti-predator behavior of larval walleyes and saugeyes

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This study was conducted to investigate differences in the anti-predator behavior of larval walleyes (*Sander vitreus*) and saugeyes (walleye × sauger [*Sander canadensis*]). Larval fish (5-7 and 12-14 days old) were exposed to a simulated predator to determine the number of attacks required to elicit a response and to determine differences in movement rates and orientation (e.g. time spent in the upper water column) between species related to predator attack. Five to seven day old saugeyes exhibited a response to the model predator on the first or second approach, while walleyes required one to seven approaches. In addition, 5-7 day old saugeyes responded to a simulated attack by rapidly swimming; whereas, walleyes showed little response in swimming action. When larvae were 12-14 days old, both walleyes and saugeyes responded to the simulated predator attack on the first or second approach by rapidly swimming. Regardless of age, neither walleyes nor saugeyes showed a response in orientation to predator attack. This study suggests that anti-predator behavior is one possible mechanism for high survival and recruitment of saugeyes relative to walleyes and that older walleyes (i.e. > 12 days old) should be stocked during years when predator densities are high.

Keywords: walleye, saugeye, anti-predator, larvae.

Introduction

Survival of larval fishes is generally considered to be one of the most important factors regulating recruitment of fishes. Although a variety of factors influence survival, starvation and predation are the two primary mechanisms affecting mortality of larval fishes (Cushing 1972; Blaxter 1986; Bailey and Houde 1989). Starvation generally occurs over short time periods and at small sizes, while predation occurs throughout ontogeny (Cushing 1972; Bailey and Houde 1989). Thus, predation has the potential to be a critical component influencing survival and recruitment of fishes over long time periods. Predation on juveniles and adults can have important implications for fish population dynamics, but predation on fish eggs and larvae is often a dominant factor influencing recruitment in marine (Bailey and Houde 1989) and freshwater systems (Brandt et al. 1987).

Walleye (*Sander vitreus*; formerly *Stizostedion vitreum*; Nelson et al. 2003) is one of the most popular sport fish in the midwestern U.S. (Colby, McNicol and Ryder 1979; Carlander 1997). In Kansas, walleye was first introduced in the late 1940s and is now one of the most preferred sport fish in the state (Burlingame 1998). Although some natural reproduction occurs in Kansas reservoirs, larval walleyes are frequently stocked to supplement natural reproduction. Inconsistent recruitment and year-class failure of walleyes in reservoir systems across their distribution has lead to the widespread stocking of saugeyes (walleye × sauger [*Sander canadensis*; formerly *Stizostedion canadense*; Nelson et al. 2003]), which often exhibit faster growth and higher stocking success than walleyes in reservoirs (Lynch, Johnson and Schell 1982; Humphreys, Wilson and Peterson 1984; Johnson, Smith and Carline 1988). Recent research suggests that although abiotic factors (e.g. thermal characteristics, water levels) influence walleye recruitment during most years, predation by juvenile white crappies (*Pomoxis annularis*) can have an overriding influence on larval walleye survival and recruitment in Kansas reservoirs (Quist, Guy and Stephen 2003). The reason for high stocking success of saugeyes versus walleyes is largely unknown, but because predation can limit survival and recruitment of larval walleyes, one potential mechanism is a difference in the behavioral response of larval walleyes and saugeyes to predators.

The purpose of this study was to investigate differences in the anti-predator behavior of larval walleyes and saugeyes using a controlled experiment. Specifically, larval fish were exposed to a simulated predator to determine behavioral differences between species that might help explain high survival of saugeyes in reservoir systems. In addition, the experiment was conducted using two age classes of larval fish (i.e. 5-7 and 12-14 days old) to provide insight as to the age when larval fish should be stocked into systems with high piscivore densities.

Methods

Larval walleyes and saugeyes (i.e. 3-4 days old) were obtained from Milford Fish Hatchery (Kansas Department of Wildlife and Parks; Junction City, Kansas) during 2002 and transported approximately 45 km to laboratory facilities at Kansas State University (Manhattan, Kansas). Fish were housed in aquaria and fed zooplankton (*ad libitum*) three times per day. Dead zooplankton and dead or cannibalistic fish were removed prior to each feeding. Mean water temperature (mean ± SE; 13.7 ± 0.9°C) and dissolved oxygen concentrations (8.1 ± 0.4 mg/L) in aquaria were similar to those observed in Kansas reservoirs during the spring.

To initiate the experiment, a single larval fish was transferred from the holding tank to a small, circular (254 mm diameter × 127 mm deep) experimental chamber. The experimental chamber was located in an enclosed area that prevented fish from observing outside movements that could have potentially altered their behavior. Fish were allowed to acclimate in the experimental chamber for 5 minutes prior to beginning the experiment. Behavior of larval walleyes and saugeyes was observed and recorded every 5 seconds for 10 minutes prior to the simulated attack of a predator. Recorded behaviors included whether the larvae was in the upper or lower half of the water column and whether the fish was rapidly swimming (> 1 body length/second), slowly swimming (< 1 body length/second), or still. The bottom of the experimental chamber contained a grid system (30 × 30 mm grids) that allowed us to estimate distance moved by each larval fish. Total distance traveled was estimated by counting and summing the number of grids crossed during the 10-minute period. After the initial 10 minutes, a model predator was used to simulate an attack by a piscivorous fish. The model predator was a fishing lure (Zara Spook®, Heddon Lures; 102 mm long × 25 mm diameter) with all hardware removed. A 0.5-m piece of wire was attached to the posterior end of the model, which prevented the larvae from observing the experimenter when the model predator was introduced to the experimental chamber. The simulated predator was placed in the water at the end opposite to the fish and slowly (approximately 50 mm/second) advanced towards the larval walleye or saugeye. Higgs and Fuiman (1996) reported that responsiveness was unaffected by variation in the speed of attack by a model predator. If the larvae did not respond on the initial approach or contact with the model predator, we repeated the procedure up to nine more times. Similar methods have been used to examine anti-predator behavior of other larval fish species (e.g. Higgs and Fuiman 1996; Chick and Van Den Avyle 2000). We recorded the number of attacks required to elicit a response from each fish, and the same behaviors that were recorded prior to the simulated attack were also recorded post-attack at 5 second intervals for 10 minutes. The experiment was replicated for 25 individual fish of each species during two time periods. First, we examined behavior two days after larvae were transported from the hatchery (hereafter termed week 1) to represent the size and age when larval walleyes are stocked into Kansas reservoirs. We also examined behaviors nine days following removal from the hatchery (hereafter termed week 2).

Statistical analyses

Orientation (i.e. upper or lower water column) and movement (i.e. still, slowly swimming, or rapidly swimming) of larvae were expressed as the percentages of observations that a particular behavior was observed. For example, over the 10-minute period (pre- or post-predator), 120 observations were recorded for each fish. The percentage of time that a behavior was observed was the number of observations (i.e. number of 5-second intervals) divided by 120. Because percentage data often exhibit a skewed distribution, all percentage data were arc-sine square-root transformed prior to analysis (Sokal and Rohlf 1995).

A statistical concern with the type of experimental design used in this study is that pre- and post-treatment behaviors are not independent because each fish is treated as a replicate. The most suitable analytical method that accounts for non-independence is to conduct the statistical analysis on differences (e.g. paired *t*-test; Sokal and Rohlf 1995). Therefore, differences (pre-treatment minus post-treatment) in orientation, movement, and total distance traveled, and the number of attacks required to elicit a response were used as dependent variables in the analysis. With regard to orientation, only the proportion of time rapidly swimming was included in the analysis because it was highly correlated (i.e. not independent) with the amount of time a fish was slowly swimming or still. The amount of time spent in the upper water column was included in the analysis and the proportion of time spent in the lower water column was excluded for similar reasons. Multivariate analysis of variance (MANOVA) was first used to determine if the dependent variable differed between species and time periods (Johnson 1998). Two-way analysis of variance (ANOVA) and linear contrasts (Milliken and Johnson 1992) were performed on each variable because the MANOVA indicated differences for one or more of the variables ($P = 0.0001$).

Results

Prior to the simulated attack, larval walleyes exhibited little movement and spent most of their time in the upper portion of the water column during week 1 (Table 1). Larval saugeyes also spent most of their time in the upper water column during the first time period, but were usually observed slowly swimming. Because walleyes were primarily still, total distance traveled was much lower for larval walleyes compared to saugeyes. During week 2, both walleyes and saugeyes were most frequently observed in the lower portion of the water column where they were

Table 1. Mean percent of observations when larval walleyes or saugeyes were in the upper or lower half of the water column. Distance represents the mean total distance traveled and movement represents the mean percentage of time still, slowly swimming (slow), and rapidly swimming (rapid). All values represent behavior prior to attack by a simulated predator during week 1 (5-7 day old larvae) and week 2 (12-14 day old larvae). Standard errors are provided in parentheses.

	Week 1		**Week 2**	
	Walleye	**Saugeye**	**Walleye**	**Saugeye**
Orientation				
Upper (%)	79.2 (1.6)	71.7 (7.1)	16.7 (5.0)	33.3 (10.4)
Lower (%)	20.8 (1.6)	28.3 (7.1)	83.3 (5.0)	66.7 (10.4)
Movement				
Still (%)	78.3 (4.7)	27.2 (6.9)	43.3 (11.2)	20.0 (8.3)
Slow (%)	13.9 (3.9)	65.0 (6.5)	50.8 (10.6)	76.7 (8.5)
Rapid (%)	7.8 (2.2)	7.8 (1.5)	4.2 (1.9)	3.3 (2.5)
Distance (mm)	308.0 (81.3)	948.0 (163.9)	445.5 (105.7)	747.0 (104.0)

swimming slowly. Little time was spent rapidly swimming in the experimental chamber for either species prior to the simulated predator attack (Table 1).

Response to the model predator varied between species and time period. During week 1, saugeyes exhibited a response to the model predator on the first or second approach (Fig. 1). The number of approaches required to elicit a response by larval walleyes varied from 1 to 7 and was significantly higher than for saugeyes. Walleyes showed little response with regard to rapid swimming action or total distance traveled. Conversely, larval saugeye responded to the model predator by swimming rapidly, as reflected by the percentage of time spent rapidly swimming and total distance traveled during week 1 (Fig. 1). During the second week, larval walleyes and saugeyes were similar with regard to their behavior, where both species responded to the simulated attack by rapidly swimming large distances.

Discussion

The greatest difference between species was the amount of time rapidly swimming and the number of attacks required to elicit a response. Little response in the orientation of larvae in the water column was observed in our study. One explanation for this result is that individuals are simply attempting to maximize their distance from predators, regardless of the orientation. Alternatively, the shallow depth of the experimental chamber may have prevented fish from moving to deeper water. Because individuals should seek to maximize their distance from a predator, one of the most common anti-predator behaviors is a panic response where fish exhibit rapid burst of swimming (Weihs and Webb 1984; Eaton and DiDomenico 1986; Williams et al. 1996). For example, Giles (1984) examined the behavior of larval three-spined sticklebacks (*Gasterosteus aculeatus*) to a simulated predator attack and found that most fish exhibited a panic

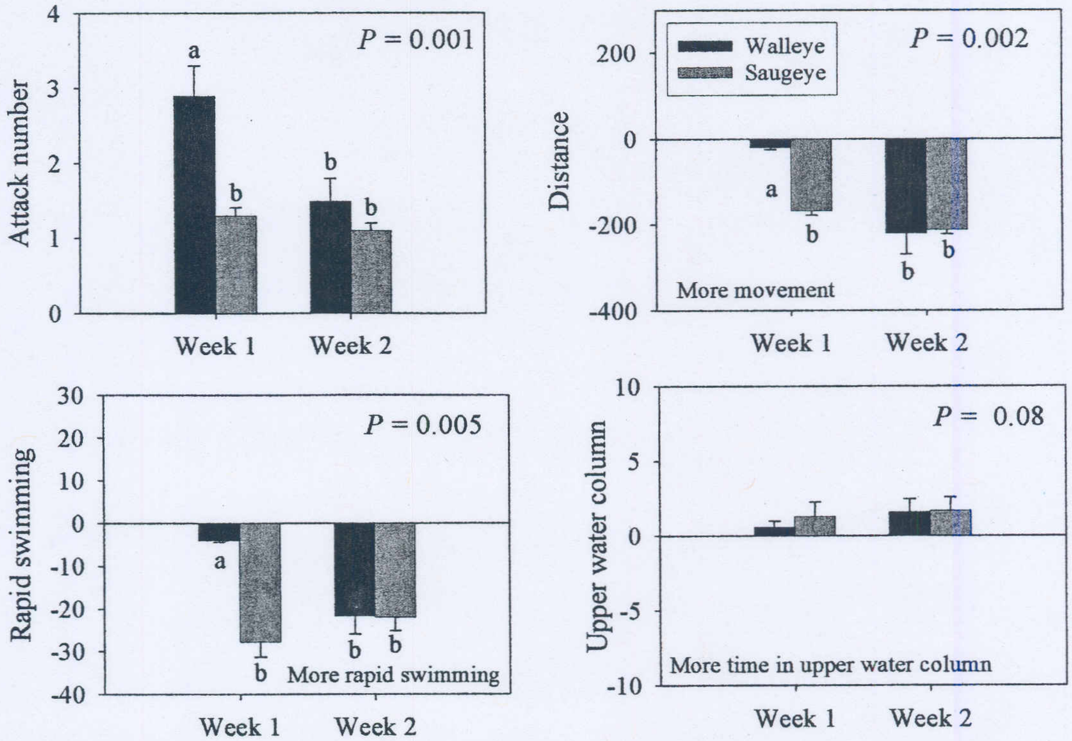

Figure 1. Differences (i.e. pre- minus post-attack by a simulated predator) between total distance traveled (distance, mm), percentage of time spent rapidly swimming (rapid swimming, %), and percentage of time spent in the upper half of the water column (upper column, %) of individual larvae during week 1 (5-7 day old fish) and week 2 (12-14 day old fish). Number of attacks (attack number) required to elicit a response is also presented. Bars represent one standard error and bars with different letters indicate a significant difference ($P \leq 0.05$). For all panels except attack number, negative values indicate that a higher proportion of observations were observed for a behavior after the attack by the simulated predator.

response after being exposed to the model predator. The experiment also illustrated that older sticklebacks had a stronger predator response than younger fish. We found a similar result where larval saugeyes exhibited a panic response during both time periods. Conversely, walleyes did not exhibit a rapid swimming response until week 2 when they were at least 12 days old. Reactive distance is also a common measure of anti-predator behavior (e.g. Chick and Van Den Avyle 2000). Although we did not measure reactive distance of each fish, larval saugeyes displayed a response as soon as the model predator was introduced to the experimental chamber and most fish responded when the model was over four body lengths away. Conversely, larval walleyes did not respond until the model predator was within one body length during week 1. Larval walleyes required another week to respond to the simulated predator in the same manner as saugeye, suggesting that saugeyes exhibited a stronger response than larval walleyes, at least at the age when they are commonly stocked.

Predators can be an important factor influencing survival of fishes, especially when species have little or no history of co-occurrence with predators (Gophen et al. 1993). For example, Seghers (1973) found that guppy (*Poecillia reticulata*) populations exhibited variation in their tendency to school, distance at which they reacted to a predator, and motor response (e.g. rapid swimming, jumping out of the water) upon encountering a predator. Guppies from areas that contained predators schooled more tightly, had higher reactive distances, and reacted with stronger motor patterns than guppies from populations lacking predators. Magurran (1990) studied two populations of European minnows (*Phoxinus phoxinus*) that had either a long history of sympatry with northern pike (*Esox lucius*) or no experience of northern pike predation. Similar to Seghers (1973), experienced fish behaved more cautiously towards northern pike than fish from inexperienced populations which were quickly consumed. Walleyes evolved in the northern portions of the U.S. and Canada where fish assemblages are relatively simple (Colby, McNicol and Ryder 1979). The historic southern distribution of walleyes is generally thought to have been limited by interactions with centrarchids (Collette et al. 1977). Conversely, saugers are native to the Great Plains and southern regions of the U.S. where fish assemblages are complex (Lee et al. 1980). Thus, saugers may have historically had to contend with multiple predators during all stages of ontogeny and evolved strong anti-predator behaviors relative to walleyes. These differences in evolutionary history may partially explain the differences between walleyes and saugeyes observed in our study and the success of saugeyes in reservoir systems that often contain abundant predators. Although inclusion of sauger in the experiment would have provided additional insight, no sauger were available for our study.

Stocking success of larval saugeyes is often much higher than for walleyes in reservoirs characteristic of the southern Great Plains (Lynch, Johnson and Schell 1982; Johnson, Smith and Carline 1988). Because predation can have a significant effect on recruitment of percids in reservoirs (Quist, Guy and Stephen 2003), the results of this study suggest that anti-predator behavior may partially explain why larval saugeyes survive and recruit in these systems. The current status of sauger in the Great Plains has resulted in concerns (i.e. back-crossing) related to continued stocking of saugeye (e.g. Billington, Brooks and Heidinger 1997). In the future, walleyes will continue to be stocked into reservoirs not only because of concerns regarding sauger conservation, but because anglers prefer walleyes (e.g. Burlingame 1998). If walleyes are to be stocked into reservoir systems with abundant predators, one approach would be to stock fingerlings which likely have anti-predator behaviors and are beyond the gape-limitations of many predators. However, larval walleyes will continue to be stocked because they are less expensive than fingerlings to produce. Currently, the Kansas Department of Wildlife and Parks stocks 3-5 day old larval walleyes, which showed little or no response to predators in our study. Therefore, the results of this experiment suggest that older walleyes (> 12 days old) should be stocked during years when reservoir predator densities are high.

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