FACTORS INFLUENCING SURVIVAL, DEVELOPMENT, AND BEHAVIOR OF SHORTNOSE (*Acipenser brevirostrum*) AND ATLANTIC STURGEON (*A. oxyrhynchus*) LARVAE

by

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Abstract

Larval shortnose sturgeon *A. brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* were reared at different temperatures (13, 15, 18, & 21°C) to examine yolk utilization rate and efficiency, growth, and development. Atlantic sturgeon were consistently smaller in size, used yolk more efficiently at 13 and 15 °C and reached developmental stages sooner than shortnose. Development rate was positively correlated with rearing temperature, yet yolk utilization efficiencies and larval size at each stage were independent of rearing temperature. In a second study, I subjected larval shortnose to delayed feeding treatments of 0, 5, 10, 15, and 18 d after yolk-sac absorption, to examine effects of food deprivation on growth and survival. Starvation affected growth and survival, yet larvae showed ability to recover well. Point-of-no-return was 41 days post-fertilization, which is longer than other teleosts. Specific growth rate expressed as dry weight was highest in 15 and 18d treatments suggesting a possible compensatory growth mechanism. Strategies adopted for survival include increased search activity, swimming speed, and maintenance of high risk responsiveness.

Preface

This thesis is organized according to articles format, as specified in the UNB thesis regulations and guidelines. Chapter 1 gives a general introduction to the research performed, as well as background on species studied. Chapter 2 describes the effect of different rearing temperatures on growth, survival, timing of development, and yolk utilization efficiencies of larval shortnose sturgeon *A. brevirostrum* and Atlantic sturgeon *A. oxyrhynchus*. Chapter 3 describes the effect of delayed feeding on growth, survival, and point-of-no-return of larval shortnose sturgeon *A. brevirostrum*. Within this chapter, I also examine swimming and escape activity and relate these outcomes to possible survival strategies adopted during periods of low food availability. In Chapter 4 I discuss the results in terms of their ecological significance and also identify areas for further research.

Chapters 2, 3, and 4 include separate reference sections. The format of sections 2 and 3 are specific to the journals to which they have been submitted.

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List of Abbreviations

AGR: absolute growth rate

ANOVA: analysis of variance

BA: body area

d: day

df: degrees of freedom

dph: days post-hatch

DW: dry weight

ELH: early life history

GLM: general linear model

hrs: hours

PNR: point-of-no-return

LSM: least square means

mBA: slope of body area

|mYSA|: absolute slope of yolk-sac area

REG: regression

s: second

SE: standard error

SGR: specific growth rate

SL: standard length

SPP: species

YSA: yolk-sac area

YSH: yolk-sac height

YSL: yolk-sac length

YSV: yolk-sac volume = $(\pi/6)LH^2$

YUE: yolk utilization efficiency

YUR: yolk utilization rate

Chapter 1: Introduction

Mortality through the early life history (ELH) stages of many species of fish is high (Bailey and Houde 1989; Letcher *et al.* 1996), and has been attributed to factors such as starvation and predation (Hjort 1914; Bailey and Houde 1989). In addition, each of these factors can be directly or indirectly influenced by water temperature (Howell and Caldwell 1984; Chambers and Leggett 1987; Kamler 1992). The possible interactions between these factors may influence survival to recruitment and therefore year-class strength.

Water temperature is viewed as the most important factor influencing larval fish development (Chambers and Leggett 1987; Houde 1987; Lein *et al.* 1997). It affects larval growth, timing of development, as well as yolk utilization efficiencies (Fukuhara 1990, Kamler 1998). Variation in water temperature can have significantly different effects on larval survival. For example, larvae reared at low water temperatures exhibit slow growth, thereby lengthening stage duration and time to starvation (Haylor and Mollah 1995; Wang *et al.* 1985, 1987). This increase in time spent during vulnerable stages may also give rise to size dependent predation (Shepherd and Cushing 1980; Werner *et al.* 1983; Miller *et al.* 1988). In addition, variation in yolk utilization efficiency, caused by different rearing temperatures, has produced differences in larval size at important transition stages like yolk-sac absorption (Howell and Caldwell 1984). Smaller larvae have slower swimming and escape speeds, thereby increasing their chance of being attacked by a predator (Gamble and Fuiman 1987, Rice *et al.* 1987). Alternatively, larger larvae may be more conspicuous and more easily detected by a predator (Litvak and Leggett 1992), and with greater swimming ability may have higher

predator encounter rates (Bailey and Houde 1989; Litvak and Leggett 1992; Cowen *et al.* 1996). Although these outcomes of size-related predation have been debated to some extent (Litvak and Leggett 1992; Leggett and DeBlois 1994), the fact remains that temperature will have a significant affect on survival of developing larvae.

Starvation is viewed as a direct factor of mortality following the absorption of the yolk (Folkvord and Hunter 1986; Litvak and Leggett 1992). Such mortality has been attributed to patchy distribution of food resources during the switch to exogenous feeding (Hjort 1914; Hewitt *et al.* 1985; Letcher *et al.* 1996). With increasing degree of starvation, factors such as slow growth coupled with poor swimming and escape capability again may give rise to high levels of predation (Gamble and Fuiman 1987; Rice *et al.* 1987).

During periods of starvation, larval fish are believed to adopt certain physiological and behavioral strategies to insure survival. One school of thought, is that a larva faced with increasing degrees of starvation will reduce all metabolic expenditures (through decreasing activity levels), and maintain its escape and swimming abilities while waiting for a food patch (Wieser *et al.* 1992). Alternatively, some larvae increase activity as well as swimming and escape speeds until a food patch is located (Yin and Blaxter 1987; Mehner and Wieser 1994). However, regardless of which strategy is adopted during food deprivation, slow growth and the inability to re-establish feeding may ultimately cause increased mortality (Blaxter and Hempel 1963; Shepherd and Cushing 1980).

Many previous studies which have focused on these factors as single processes have resulted in some key concepts in larval recruitment. Concepts like the 'critical

period' theory (Hjort 1914), which identifies an important transition from endogenous to exogenous feeding; the 'match-mismatch' hypothesis (Cushing 1972), stating that larval survival is conditioned by the spatial and temporal match of prey fields; and the larval 'point-of-no-return' (Blaxter and Hempel 1963), above which a larva may not recover from starvation. Effects of temperature, starvation, and vulnerability to predation have all been researched at length as individual processes in modern teleosts (e.g. Howell 1980, Bailey and Houde 1989; Miller *et al.* 1988). However, little information on temperature and no information on the interaction of starvation and predation has been examined for larval sturgeon species.

Previous investigations on sturgeon species reported that developmental rates and overall survival are affected by temperature (Gershanovich, 1983; Wang *et al.* 1985, 1987). For example, Wang *et al.* (1987) illustrated how rates of development and dry matter loss are temperature dependent in larval white sturgeon *A. transmontanus* embryos and larvae. He also reported that at higher temperatures (>21°C) survival is significantly reduced. Similarly, Gershanovich (1983) reported daily growth rate and food requirement of larval Beluga *Huso huso* and Sheap sturgeon *A. nudiventris* increased with increasing temperatures.

Understanding how each of these factors affect sturgeon during their early life history may be very useful to fisheries managers. For example, knowledge of the timing of initial feeding may play a critical role in the success of the artificial propagation of sturgeon (Doroshov, *et al.* 1983; Gershanovich, 1983; Gisbert and Williot 1997). It has been hypothesized that all sturgeon species, being very similar in their embryonic development, may respond with similar metabolic processes when reared at different

temperatures (Wang *et al.* 1985). Therefore, gaining information on what factors affect their early life history stages may prove vital to the management of many hatchery reared sturgeon species. Artificial propagation may also afford fisheries managers a tool in the rehabilitation of exploited and naturally declining sturgeon populations. Ecologically, the information on temperature and its affects on morphology and stage development may prove to be a very useful tool for back-predicting timing of initial spawning using field collected larvae. Morphology and stage development during starvation may also be ecologically useful to fisheries managers. The collection of many larvae which have past the point-of-no-return (PNR) in a spawning area, may result in erroneous estimates of viable larval abundance (Yin and Blaxter 1986). This, combined with poor swimming and escape responses, may cause them to be more susceptible to larval sampling gear, thereby contributing to an underestimation of larval health and an overestimation of abundance of a viable year-class (Isaacs 1964). By determining the body size at the PNR, along with predicted size ranges in relation to present water temperatures, corrections can be made to more accurately determine potential survival and health of a year-class.

Two of the North American sturgeon species of great concern are the shortnose sturgeon *A. brevirostrum* and Atlantic sturgeon *A. oxyrhynchus*. In recent years, each of these species have suffered declines in the eastern United States and Canada due to anthropogenic factors such as construction of dams, water pollution, and over-fishing (Smith and Dingley 1984).

Species Status and Description

Shortnose sturgeon: The shortnose sturgeon is now protected in the United States under the Endangered Species Act (Miller 1972) and considered a species of special concern in Canada (COSEWIC 2000). Shortnose sturgeon are found in many of the large coastal waterways of eastern North America, ranging as far north as the Saint John River in New Brunswick and as far south as the St. John's River in Florida (Vladykov and Greeley 1963; Kynard 1997). The shortnose live most of their life in freshwater with a few exhibiting migrations into brackish and salt-water (Vladykov and Greeley 1963). Shortnose are considered an amphidromous species making small seasonal migrations from brackish to freshwater. Shortnose spawn in freshwater during a short period of time when specific environmental conditions are present. It has been suggested that spawning in the Saint John River, NB, Canada occurs between May 15-June 15 in the main river channels during spring freshet at water temperatures of 10-15^{0}C (Dadswell 1979). Similarly, shortnose in the Merrimack River, MA migrated to spawning grounds in April when river temperatures rose to approximately 7^{0}C and made their post-spawning migration at river temperatures around 14^{0}C (Kieffer and Kynard 1996). Hall *et al.* (1991) found shortnose in the Savannah River, SC to spawn mid-February to late-March at river temperatures of 9-12^{0}C and post spawning migrations starting mid-March to early May.

Little is known about the behavior of shortnose larvae, however, recent anecdotal laboratory observations indicate that larvae are positively rheotactic, photonegative, benthic and vigorously seek cover (Richmond and Kynard 1995). It has been hypothesized that due to this behavior, larvae may seek out and hide beneath any

available cover within spawning areas (Richmond and Kynard 1995). Shortnose sturgeon year class strength is presumably established early in life, within 1-2 months (Kynard 1997), therefore, factors affecting their survival during this period are important to long-term survival and subsequent recruitment.

Atlantic Sturgeon: A petition to place the Atlantic sturgeon on the endangered species list in the United States was considered in 1998. Although not making this federal listing, a ban was placed on the harvest and possession of Atlantic sturgeon in the United States in an effort to replenish depleted populations along the Atlantic coast (NMFS 1998). A relatively small fishery for this species still exists in eastern Canada.

The home range of the Atlantic greatly overlap that of the shortnose sturgeon (Smith and Dingley 1984). The northern subspecies *A. o. oxyrhynchus* may be found from Hamilton Inlet off the coast of Labrador (Bachus 1951) and the Gulf of St. Lawrence to the St. Johns River in eastern Florida (Smith and Dingley 1984; Vladykov and Greeley 1963). The southern subspecies *A. o. desotoi* may be found in the Gulf of Mexico and the northern coast of South America (Huff 1975; Smith and Dingley 1984). The Atlantic sturgeon, unlike the shortnose, is an anadromous species, spending about 6 years of its early life in a riverine environment and then making a migration to the open ocean for maturation (Smith and Dingley 1984). They return to freshwater only to spawn when specific environmental conditions are present. Spawning has been recorded in Delaware at 13.3-17.8 °C (Borodin 1925); South Carolina at 13-19 °C (Smith 1985); and in the Apalachicola River in Florida at 20-23 °C (Huff 1975; Wooley and Crateau 1982). Little is known about the larval stages of this species, however, juveniles are said to remain in their natal river and slowly move towards the open ocean over time. As water

temperature decreases in the winter months, Atlantic sturgeon juveniles migrate to deeper parts of the river (Smith 1985).

In order to assist fisheries managers in better managing populations of these two North American sturgeon species, information must be gathered on how direct and indirect factors such as temperature, starvation and vulnerability to predation affect survival and subsequent recruitment strategies. In chapter 2, I examined the effects of temperature on yolk-sac larvae of these two species. In chapter 3, I examine growth and starvation resistance of larval shortnose sturgeon in response to delayed feeding. In addition, I examined swimming activity and escape capabilities of shortnose larvae to determine which of the following strategies are adopted during food deprivation: i) reduction in activity levels and maintenance of high risk responsiveness while waiting for a food patch; ii) increase in activity levels to locate a food source, while maintaining high responsiveness to predators; iii) reduction in activity levels as well as responsiveness to predators to conserve energy; or iv) increase in activity levels to find a food patch, yet making a trade-off by lowering risk responsiveness. In chapter 4, I discuss the potential ecological significance of these results on the predator avoidance ability and subsequent larval survival of shortnose and Atlantic sturgeon larvae.

Chapter 2: Effects of Temperature on the Early Development, Growth, and Survival of Shortnose Sturgeon (*Acipenser brevirostrum*) and Atlantic Sturgeon (*A. oxyrhynchus*) Yolk-Sac Larvae

Introduction

Larval fish mortality is very high during early developmental stages due to their small size, poor swimming performance, and sensitivity to variations in their surrounding environment (Rice *et al.* 1987; Miller *et al.* 1988; Fuiman 1994). During these vulnerable stages, larval fish may be adversely affected by environmental factors that influence survivorship and subsequent year-class strength (Batty *et al.* 1993; Houde 1994; Claramunt and Wahl 2000).

Larvae of many fish species possess yolk which enable them to feed endogenously for various periods of time before they must search for food in the surrounding environment (Blaxter and Hempel 1966; Howell and Caldwell 1984; Kamler *et al.* 1998). Size of larvae at the time they switch from endogenous to exogenous feeding, referred to as the "critical period" in larval development, may be a very important factor affecting year-class strength of a species (Hjort 1914, Cushing 1972; Folkvord and Hunter 1986). Early developmental changes in body size (Miller *et al.* 1988; Litvak and Leggett 1992; Pepin *et al.* 1992) and sensory morphology (Fuiman 1993) may increase a larva's ability to detect and avoid predation (Blaxter and Batty 1985; Litvak and Leggett 1992; Fuiman 1994). Therefore, examination of environmental factors that affect a larva's rate of yolk utilization, body size at each key stage of development (Howell and Caldwell 1984; Houde 1987; Bailey and Houde 1989), and development of predator avoidance mechanisms are important to our understanding of

recruitment in fish.

Water temperature is considered to be the most important environmental factor influencing larval fish development (Chambers and Leggett 1987; Houde, 1987; Kamler 1992). Influences on morphological, physiological, and behavioral aspects such as yolk-sac utilization rate and efficiency, growth, predator avoidance, and survival can all be affected by water temperature (Bailey and Houde 1989; Kamler *et al.* 1998; Shepherd *et al.* 2000). Although many studies have illustrated these effects on larval fish development of more modern teleosts (May 1974; Howell 1980; Johns *et al.* 1981; Haylor and Mollah 1995; Kamler *et al.* 1998), there is limited information on how water temperature affects the early development of larval sturgeon. The two studies that we are aware of, have found that temperature does affect development and survival rates of larval sturgeon (Wang *et al.* 1985, 1987 [white *A. transmontanus* and lake sturgeon *A. fulvescens*]; Gershanovich and Taufik 1992 [beluga *Huso huso* and sterlet sturgeon *A. ruthenus*]). However, these studies, as well as most others, begin at the egg stage resulting in larvae of different sizes at the start of the experiment. Since eggs of many sturgeon species are spawned within a narrow range of temperatures and have a relatively short incubation period (< 10 days for many species), they may experience little variation in temperature. However, after hatching larval sturgeon (with a stage duration of 40-60d in some species; Richmond and Kynard 1995) will undoubtedly experience a wider range of temperature variation than during the incubation period. Therefore, it is of interest to determine the effect of temperature on developing post-hatch sturgeon larvae. It is also of interest to determine if other species of sturgeon react similarly to a wide range of

temperatures, particularly since many of the 26 known sturgeon species are currently threatened or endangered throughout their range of distribution (Moyle and Cech 1996).

Two of the North American species, the shortnose *A. brevirostrum* and Atlantic *A. oxyrhynchus* sturgeon, have suffered recent declines in the eastern United States and Canada primarily due to anthropogenic factors such as construction of dams, water pollution, and over-fishing (Smith and Dingley 1984). Shortnose were placed on the Endangered Species List in 1973 (Kynard 1997) and are now considered a species of special concern in Canada (COSEWIC 2000). Although Atlantic sturgeon have not been placed on a federal listing, a ban was placed on harvest and possession in the United States (a small fishery still exists in Canada) in an effort to replenish depleted populations along the Atlantic coast (NMFS 1998). Presently, no data are available on how environmental factors influence mortality during the early life history stages of these two species (Kynard 1997; Smith and Dingley 1984). A large body size, tough leathery skin and bony scutes allow sturgeon to be relatively well equipped, at the juvenile and adult stage, to withstand starvation and attacks from predators. In addition, since they primarily feed by olfactory and tactile stimulation, sturgeon are able to feed at night or in extremely turbid environments, thereby reducing attacks from visual predators (including avian attacks). Since starvation and predation may be insignificant in the late juvenile through adult stages, it is likely that survival through the ELH stages of larval sturgeon is more important in determining year-class strength. The objective of this paper was to determine the effects of temperature of development, growth, and development during the yolk-sac stage of these two species. We discuss how these effects may influence potential predation avoidance ability and subsequent larval survival.

Materials and Methods

Egg collection and incubation.- Between May 1 and May 15, 1998, mature shortnose sturgeon were collected with short-set (< 6 hrs.) gill nets in the Kennebecasis River, NB, Canada (N45°30' W66°55'; water temp: 13-16 °C). Mature Atlantic sturgeon were collected in a similar fashion between July 1 and July 7, 1998 in the Saint John River, NB, Canada (N45°33' W66°02'; water temp: 16-18 °C). On May 18, 1998, eggs and sperm were collected from one female and two male shortnose, and fertilization was performed using procedures specified by Doroshov *et al.* (1983). This spawning procedure was repeated on July 8, 1998, for Atlantic sturgeon. Approximately 500 ml of fertilized eggs were placed into each of three MacDonald incubation jars in a partial recirculation system. Flows to the jars were set at 3 L/min to allow adequate oxygenation of the eggs. Eggs were incubated at a mean temperature of 17 °C, which is similar to natural spawning temperatures for both species (Huff 1975; Wooley and Crateau 1985; for additional reviews see Kynard 1997).

Experimental design.- Four treatment tanks were set-up and maintained at 13, 15, 18, and 21°C. Temperature treatments were chosen based on literature (Huff 1975; Wooley and Crateau 1985; for additional review see Kynard 1997) and field data. A fluorescent light was placed in each tank creating a light intensity of ≈700 lux at the water surface (Lutron LX-101 lux meter; intensity was chosen based on Richmond and Kynard 1995). An opaque black plastic sheet was placed over the treatment tanks to block any additional light. Photoperiod for the experimental tanks was set at 15L:9D. Each treatment tank contained three or four replicate trays (1000 ml pyrex trays filled with 700 ml of de-chlorinated water). Upon hatch, (shortnose: 192 hrs; Atlantic: 120 hrs),

40 larvae were placed into each tray. Water in each of the replicate trays (600 ml) was replaced twice daily.

Data collection and analysis.- Larvae (3-4) were sampled from each treatment group every other day, starting at hatch. Each larva was anesthetized in a 25 mg/L solution of tricaine methanesulfonate (MS-222), placed under a microscope (Olympus SZ6045), and videotaped live with a video camera (Sony DXC-1821) attached to a super-VHS video-cassette-recorder (Panasonic AG-5700) for later analysis with an image analysis system (Optimas v5.2 BioScan Inc., Edmonds, Washington). After morphological data were collected, larvae were then preserved in 10% phosphate-buffered formalin. The data obtained from each larva, at each temperature, included: yolk-sac length (YSL), height (YSH), and area (YSA), body area (BA), and standard length (SL). Elliptical yolk-sac volume (mm^3) was calculated using the formula of a spheroid: $YSV = (\pi/6)LH^2$ where L is the length of the yolk-sac and H is height (Blaxter and Hempel 1963). Note, yolk-sac volume also included lipid volume due to difficulties in distinguishing between the yolk and lipid globule with image analysis. Standard length (mm) was measured from the anterior-most point of the developing rostrum to the posterior-most point of the notochord. Body area (mm^2) was measured excluding the yolk-sac and finfold areas.

In addition to morphological analysis, I examined development of escape response, as well as, percent mortality over time for each temperature treatment. Sturgeon, like many other fish species, exhibit a C-type startle response (a rapid movement of the body trunk in the shape of a 'C' [Blaxter and Batty 1985]) to escape predation. Each treatment tank was tapped daily to stimulate this response through

mechanical vibration; and the date of the first occurrence of this response was recorded. The time to 100% mortality was determined for each treatment replicate over time (excluding loss through sampling).

In cases of missing data points, due to poor video quality (20 out of 450), preserved larvae were re-videotaped at a later date (12 months post-fixation). To account for any changes in size that may have occurred in that time interval, multiple larvae (8-25) from each temperature treatment had YSA, SL, and BA re-measured. Regressions were run on measurements of live versus preserved specimens (Proc. Reg. SAS Institute Inc., 1992). All regressions were found to be significant ($P < 0.0001$; mean $r^2 > 0.9904$). I then tested if the slopes were different than 1 and intercepts different than 0 using the formula t = (parameter est. - parameter val. hypoth.) / stnd. err of parameter est. (Zar 1996). The resulting slopes (means: ysa = 1.033 ± 0.007; ba = 0.980 ± 0.011; and sl = 1.006 ± 0.008) and intercepts (means: ysa = 0.012 ± 0.008; ba = 0.056 ± 0.255; and sl = 0.008 ± 0.142) were not significantly different ($P > 0.05$) than 1 and 0 (respectively), indicating no significant shrinkage occurred during the time of post-fixation. Therefore, parameters from preserved larvae were substituted where needed.

Yolk utilization rate (YUR) for both species were determined by calculating slopes from a regression analysis (Proc REG. SAS Institute Inc. 1992) of YSV for each temperature treatment over the duration of the experiment. Yolk utilization efficiency (YUE) for each species was determined by comparing the rate of body area growth (slope of body area against age regression: mBA) to the rate of yolk utilized (absolute value of slope of yolk-sac area against age regression: |mYSA|) until the complete absorption of the yolk (YUE = mBA/ |mYSA|). Growth rates to a maximum SL on yolk reserves were

determined by calculating slopes from a regression analysis (Proc REG. SAS Institute Inc. 1992) for each temperature treatment to the point where maximum SL was attained. Analysis of data between temperature treatments and species on time to yolk-sac absorption, YUR, YUE, larval growth, size at escape response, size at yolk-sac absorption, and larval survival, were all compared using 2-way ANOVAs (Proc GLM, general linear models; SAS Institute 1992). When an interaction ($P < 0.2$; see Winer 1971 [page 379] for justification of a conservative type II error rate of 0.2) between species and temperature was present, the model was separated into one-way ANOVAs to reveal significance. If the model showed no interaction, the term was dropped and the model re-run. Least–square means (LSMs) were used for *a posteriori* comparisons, and probabilities were adjusted for multiple comparisons using Tukey's correction (SAS Institute Inc. 1992). Level of significance for main effects and *a posteriori* comparisons were set at an α of 0.05.

All data were tested for normality (Proc Univariate; SAS Institute 1992) and homogeneity of variance (F_{max} -test; Sokal and Rohlf 1981). Analysis were run on $\log_{10}$ or arcsine-square-root transformed data in cases of non-normality or heterogeneity of variance. The time to first escape response, due to lack of variance within treatments, was compared using a non-parametric Wilcoxon rank test. Lastly, measurements (YSV, YSA, SL, and BA) of the larvae at hatch were also compared between temperatures with 1-way ANOVAs to confirm no significant differences within each species at the start of the experiment.

Results

Morphological Comparisons at Hatch

Diameter of shortnose eggs (3.5 mm ± 0.088 SE) after fertilization and hydration were significantly larger than Atlantic sturgeon (2.2 mm ± 0.115 SE) (df = 1, 4; $P = 0.0010$). At the start of the experiment (0 days post hatch [dph]), the yolk-sac area and volume for each species were not significantly different between temperature treatments. Shortnose larvae, however, possessed significantly larger (all temperatures = df = 1, 5; $P < 0.0053$) yolk-sac area (mean 5.13 mm^2 ± 0.159 standard error [SE]) and volume (mean 5.20 mm^3 ± 0.279 SE) than Atlantic sturgeon larvae (mean 4.06 mm^2 ± 0.076 SE; mean 4.17 mm^3 ± 0.141 SE respectively). Similarly, the standard length and body area for each species at hatch were not significantly different between temperature treatments. Shortnose larvae were significantly greater (all $P < 0.0021$) in standard length (mean 10.73 mm ± 0.287 SE) and body area (mean 15.76 mm^2 ± 0.191 SE) than Atlantic sturgeon larvae (mean 9.81 mm ± 0.086 SE; mean 10.41 mm^2 ± 0.206 SE respectively). Since the measurements BA and SL were affected in the same way throughout the results of the experiment, only SL was used as growth parameter and BA was only used in calculation of YUE.

Time to Yolk-Sac Absorption

The resulting 2-way ANOVA on the time to complete yolk-sac absorption for both shortnose and Atlantic sturgeon was significant (df = 7, 19; $P = 0.0001$) and exhibited an interaction between species and rearing temperature (df = 3, 19; $P = 0.0061$). With increasing temperature (13 to 21°C), resulting 1-way ANOVAs for both species showed a

significant reduction in the time to yolk-sac absorption (Atlantic: df = 3, 8; shortnose: df = 3, 11 ; $P = 0.0001$; Figure 2.1). Shortnose sturgeon took longer (df = 1, 5; all $P > 0.05$) to absorb the yolk-sac than Atlantic at 13, 15, and 18 °C. However, at 21°C there was no significant difference between species.

Standard Length at Yolk Absorption

No effect of temperature was detected on the standard length at the time of yolk-sac absorption for each species. However, resulting 1-way ANOVAs between species revealed that shortnose did have a significantly greater standard length than Atlantic sturgeon larvae at each rearing temperature tested (Table 2.1).

Yolk Utilization Rate

The resulting 2-way ANOVA on the yolk-sac utilization rate (YUR) (slopes of YSV) for both shortnose and Atlantic sturgeon was significant (df = 7, 19; $P = 0.0001$) and showed an interaction between species and rearing temperature (df = 3, 19; $P = 0.0010$). Resulting 1-way ANOVAs revealed that a reduction in temperature significantly decreased the rate of yolk volume utilized over the experimental period for both species (Table 2.2). Shortnose larvae utilized yolk volume at a faster rate than Atlantic larvae at lower rearing temperatures (13 and 15 °C; Table 2.2).

Yolk Utilization Efficiency

The 2-way ANOVA on the yolk utilization efficiency (YUE) for both shortnose and Atlantic sturgeon was significant (df = 7, 19; $P = 0.0020$) and exhibited an interaction

between species and rearing temperature (df = 3, 19; P = 0.1841). Subsequent 1-way ANOVAs showed that within each species YUE was not significantly different between temperature treatments. However, Atlantic sturgeon larvae were more efficient than shortnose at 13 °C (df = 1, 5; P = 0.0029) and 15 °C (df = 1, 5; P = 0.0068) (close at 18 °C: P = 0.0770) in the amount of body tissue incorporated for the amount of yolk-sac area utilized (Figure 2.2).

Escape Response

Time to initial escape response, for both species (df = 7, 19; P = 0.0001), was significantly delayed at the lowest rearing temperatures (13 and 15 °C; Figure 2.3). Atlantic larvae exhibited the initiation of the c-type escape response significantly earlier than shortnose, at all temperature treatments (df = 1, 5; P = 0.0001). Standard length of both species at initiation of escape response was not significantly different between rearing temperatures. Shortnose had a significantly greater standard length at the initiation of escape response than Atlantic sturgeon larvae at each rearing temperature tested (Table 2.1).

Maximum Standard Length on Yolk Reserves

The 2-way ANOVAs on the time to reach a maximum standard length on yolk reserves, in both species, were significant (df = 7, 19; P = 0.0001) and showed an interaction between species and rearing temperature (df = 3, 19; P = 0.1979). Subsequent 1-way ANOVAs revealed that for both species, time to reach a maximum length was significantly delayed with a reduction in temperature (Atlantic: df = 3, 8; shortnose: df =

3, 11; P = 0.0001; Figure 2.4). A species comparison revealed that Atlantic larvae reached a maximum standard length sooner than shortnose sturgeon larvae (df = 1,4; all P < 0.0457).

In both species, no effect of temperature was detected on the maximum standard length attained over the experimental period. However, resulting 1-way ANOVAs revealed that shortnose did attain a significantly greater standard length than Atlantic sturgeon larvae at each rearing temperature tested (Table 2.1). The 2-way ANOVA on the growth rate to maximum standard length (slopes of SL) for both shortnose and Atlantic sturgeon was significant (df = 7, 19; P = 0.0001) and showed an interaction between species and rearing temperature (df = 3, 19; P = 0.0929). Resulting 1-way ANOVAs revealed that a reduction in temperature significantly decreased the rate of growth to maximum SL on yolk reserves over the experimental period for both species (Shortnose were only significant at 21 °C; Table 2.3). Atlantic larvae grew at a faster rate than shortnose at 18 °C.

Survival

The 2-way ANOVA comparing the time to 100% mortality between species was significant (df = 7, 19; P = 0.0001) and showed an interaction between species and temperature (df = 3, 19; P = 0.0128). Subsequent 1-Way ANOVAs revealed that both species of sturgeon survived longer at lower rearing temperatures, with mortality increasing rapidly after yolk-sac absorption (Atlantic: df = 3, 8; shortnose: df = 3, 11; P = 0.0001; Figure 2.5A and B; Table 2.4).

Discussion

Interspecific Comparison

It has previously been reported that eggs of larger diameter produce larger larvae (Blaxter and Hempel 1963; Hunter 1981; Chambers *et al.* 1989). Since shortnose eggs were larger in diameter than those collected from Atlantic sturgeon, it follows that morphological measures (SL, BA, and YSA) of shortnose at hatch were also significantly larger. A bigger size at hatch may have advantages such as increased range of prey sizes (Hunter 1981), as well as, better predator avoidance capabilities (Bailey 1984; Miller *et al.* 1988). However, larger larvae may have greater chances of encountering or being detected by predators (Bailey and Houde 1989; Litvak and Leggett 1992; Pepin *et al.* 1992). Shortnose sturgeon also developed more slowly than Atlantic sturgeon larvae reared at the same temperatures. Shortnose spawn earlier (April-June) and at lower temperatures (7-15 °C) (Dadswell 1979; Hall *et al.* 1991; Kynard 1997) than Atlantic sturgeon (June-August; 13-23 °C) (Huff 1975; Wooley and Crateau 1985; Smith 1985). The prolonged developmental stages and larger size of larval shortnose at hatch may be an evolved mechanism necessary to survive through periods in the spring which are relatively poor in primary and secondary productivity caused by low temperatures (Seip and Reynolds 1990) and poor water clarity (Scholtz *et al.* 1988). In contrast, Atlantic sturgeon spawn during mid-summer months when food production is most abundant.

Yolk-Sac Stage

Yolk-sac utilization rates and time (post-hatch) to complete yolk-sac absorption exhibited a significant inverse relationship with temperature for both shortnose and

Atlantic sturgeon larvae. This has also been reported for sturgeon (Wang *et al.* 1985, 1987; Gershanovich and Taufik 1992) and other, more modern, teleost species (May 1974; Howell 1980; Fukuhara 1990). In contrast, the yolk-sac utilization efficiencies within each species were not directly affected by rearing temperature. Yolk utilization efficiency is directly dependent on the relationship of the rate at which the yolk is utilized in metabolic processes with the rate at which it is incorporated into body tissue (Blaxter and Hempel 1966). The similar efficiencies within these species, along with a similar size at absorption, indicates their ability to balance the rise in metabolic requirement at higher temperatures with a reduction in the developmental time. A study of white sturgeon *A. transmontanus* found that the conversion of yolk proteins to tissues was not affected between 11-17 °C yet was lower at 20 °C (lipid and ash content varied between temperatures). Similar physiological balances have been reported in summer flounder *Paralichthys dentatus* (Johns *et al.* 1981; Johns and Howell 1980) and yellowtail flounder *Limanda ferruginea* (Howell 1980). Shortnose larvae absorbed their yolk at a faster rate than Atlantic sturgeon at 13 and 15 °C (close at 18 °C), and were not as efficient in utilizing it for body tissue at these temperatures. Due to their higher metabolic demands, larger larvae tend to experience a decline in efficiency with development (for reviews see Kamler 1992). In this case, shortnose (larger at all developmental stages) would be expected to have lower efficiencies than Atlantic sturgeon reared at the same temperatures. The differences in efficiencies may also reflect a difference in yolk quality between the two species. Since marine species retain more protein for growth than freshwater species (Kamler 1992), and mature Atlantic sturgeon spend most of their time in a marine environment (Smith 1985), the maternal influence on the egg yolk quality

may result in higher caloric value than that of shortnose. This may result in more body tissue incorporated in Atlantic sturgeon larvae as the yolk is utilized.

Similar to yolk utilization efficiency, size of shortnose and Atlantic sturgeon larvae at yolk-sac absorption, as well as the maximum SL attained from yolk reserves, was independent of temperature for both species. Comparable body size, regardless of rearing temperature has been reported by a number of studies (Howell 1980; Johns and Howell 1980; Quants 1985; Kamler *et al.* 1998). In contrast, some studies have shown that larval size at the time of yolk-sac absorption is dependent on temperature (May 1974; Hamor and Garside 1977; Haylor and Mollah 1995; Lein *et al.* 1997) resulting in larger larvae at higher rearing temperatures. The findings of this study continue to suggest that a mechanism may be present which mediates the amount of yolk utilized for metabolic processes, with that which is used in the formation of body tissues (Blaxter and Hempel 1966; Howell 1980).

Escape Initiation

The development of escape response is essential in allowing larvae to avoid and survive predatory attacks (Eaton and Didomenico 1986; Fuiman 1989). Studies on more modern teleosts have reported escape response is directly linked to rearing temperature (Shepherd *et al.* 2000). For example, the development escape response in larval herring *Clupea harengus* is affected by temperature, attributed to temperature mediated variations in larval growth (Batty *et al.* 1993). Some studies have indicated that overall developmental rates in several sturgeon species such as beluga *Huso huso*, sterlet *A. ruthenus*, white *A. transmontanus*, and lake *A. fulvescens* sturgeon are affected by rearing temperature

(Gershanovich and Taufik 1992; Wang *et al.* 1985, 1987). However, few studies have looked at how temperature affects the development or mechanisms responsible for escape response in sturgeon. Sevryuga sturgeon *A. stellatus* larvae develop their lateral line canals at some point after hatching, yet at hatch possess many free neuromasts around the body, with aggregations along the lateral portion of the body wall (Disler 1971). With the use of scanning electron mircrographs, Richmond and Kynard (1995) found that shortnose sturgeon larvae incubated at 13-15 °C began forming a lateral-line system by the 9th dph in conjunction with the development of an active swimming ability. However, the actual initiation of a C-type escape was not tested. The present study revealed that the development of escape response in larval shortnose and Atlantic sturgeon was prolonged in lower rearing temperatures. This suggests that the systems responsible for anti-predator defenses are delayed in their morphological development with a reduction in temperature.

Survival

Starting at hatch, both shortnose and Atlantic sturgeon survived considerably longer at lower rearing temperatures (13 and 15 °C), with mortality increasing rapidly following the full absorption of the yolk. The acceleration of mortality in yolk-sac larvae in higher temperatures is often attributed to higher metabolic rates, which result in faster absorption of endogenous energy sources (Kamler 1992). Similar direct affects of temperature on the timing of mass mortality has also been reported for white sturgeon *A. transmontanus* and lake sturgeon *A. fulvescens* (Wang *et al.* 1985) and more modern teleost fish like stone flounder *Kareius bicoloratus* (Oozeki *et al.* 1989) and Nile tilapia

Oreochromis niloticus (Rana 1990). Other species of sturgeon, such as white sturgeon *A. transmontanus* and lake sturgeon *A. fulvescens*, possess a broad range of temperature tolerance (≈ 11-26 °C) (no lower identified; Wang *et al.* 1985). Although not the focus of this study, the apparent range of temperatures tolerated by these two species is wide. Clearly, to determine the tolerance of these species during their early life history stages, a broader range of temperatures would be required.

Ecological Significance

Experiencing variations in river temperatures within their range of tolerance, wild larval shortnose and Atlantic sturgeon may experience both beneficial and deleterious effects on survival. With a faster yolk-utilization and growth rate, larvae reared at high temperatures may switch to exogenous feeding much sooner than those reared at lower temperatures; (Wang *et al.* 1987), thereby avoiding additional risks of predation (Howell 1980; Miller *et al.* 1988; Kamler *et al.* 1998). In contrast, the accelerated larval development may result in a lack of synchronization with food availability (Bagenal 1971; Cushing 1972; Kamler *et al.* 1998). This has been referred to as the "match-mismatch" hypothesis, which suggests that larval survival and recruitment are conditioned by the match of larvae with prey fields in time and space (Cushing 1972).

In addition to timing of stage development (yolk absorption, escape initiation, max. size), the size of shortnose and Atlantic larvae at the start of these stages may determine their ability to effectively swim and feed. At a larger size, a larva's ability to survive, avoid predation, and effectively capture prey may increase (Blaxter 1969; Hunter 1972; Howell and Caldwell 1984; Miller *et al.* 1988). Present findings indicate that at the

critical yolk-sac absorption stage, similar foraging and escape opportunity may be afforded for both species of sturgeon larvae developing in a wide range of temperatures. Since predation is considered to be a major factor of mortality during the yolk-sac stage (Batty 1989; Blaxter and Fuiman 1990), the timing of development of anti-predator defense mechanisms is very important, if not the most important factor in determining a newly hatched larva's potential for survival (Eaton and Didomenico 1986; Fuiman 1989). The chances of survival for larval fish increase once they complete their developmental functions needed to effectively escape from predation and adequately feed in the surrounding environment (Gisbert 1999). Intraspecific comparisons revealed that both shortnose and Atlantic sturgeon larvae exhibited similar sizes at first escape response when raised at different temperatures. This may allow relatively similar ability to avoid predation when these mechanisms are fully developed. It must be considered, however, that escape speeds may vary at different temperatures (Shepherd *et al.* 2000), and that a delay in development of the systems needed to react to attacking predators may inevitably affect survival.

Shortnose and Atlantic sturgeon are representatives of a group of fish considered by many as "living fossils" (Edson 1956; Gardiner 1984), persisting as one of the few remaining forms of prehistoric armored fishes from the Mesozoic age (150-250 million years ago) (Edson 1956). The ability of these sturgeon species to survive for so long, through possibly overwhelming conditions, attests to their unique ability to adapt to broad variations in their surrounding environment. It is possible that many sturgeon species may be "grossly" similar in their metabolic processes in fluctuating temperatures since there exists similarities in spawning temperatures and egg embryogenesis of all

species, despite geographic location (Detlaff *et al.* 1981; Wang *et al.* 1985). It seems that their ability to survive and adapt to a wide range of temperatures may afford a competitive advantage over more stenothermic species, which may be more dependent on water temperatures to condition survival.

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Table 2.1 *Developmental Sizes.* Standard length (SL) at yolk absorption and initial escape response, and maximum SL attained for larval shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* at each temperature (13, 15, 18, and 21°C). ANOVAs were run first as saturated models (non-significant interactions were dropped and the model re-run). Significance ($P < 0.05$) between temperatures (within each species) is indicated by different superscript letters. Significance between species is indicated by an (*) and *P* value. SE = ± 1 standard error.

Stage Measured	Species	Temp (°C)	Mean SL (mm)	± 1 SE	Significance Between Spp.
At Yolk Absorption	Shortnose	21	17.7508 ^{A}	0.6898	* (0.0477)
		18	17.8289 ^{A}	0.4507	* (0.0208)
		15	17.4665 ^{A}	0.2926	* (0.0005)
		13	18.5583 ^{A}	0.2683	* (0.0002)
	Atlantic	21	15.4027 ^{a}	0.4535	
		18	15.1536 ^{a}	0.7185	
		15	14.4498 ^{a}	0.1708	
		13	14.4671 ^{a}	0.1185	
At First Escape Resp.	Shortnose	21	16.9040 ^{A}	0.1300	* (0.0001)
		18	16.5274 ^{A}	0.1383	* (0.0001)
		15	16.0247 ^{A}	0.3011	* (0.0014)
		13	16.0085 ^{A}	0.5284	* (0.0108)
	Atlantic	21	13.5464 ^{a}	0.2727	
		18	13.2303 ^{a}	0.2973	
		15	13.6088 ^{a}	0.1594	
		13	13.4041 ^{a}	0.2339	
Max Size Attained	Shortnose	21	18.5668 ^{A}	0.2789	* (0.0007)
		18	18.3500 ^{A}	0.0361	* (0.0007)
		15	18.7199 ^{A}	0.4235	* (0.0007)
		13	18.5583 ^{A}	0.2688	* (0.0021)
	Atlantic	21	15.5862 ^{a}	0.2624	
		18	15.6383 ^{a}	0.4314	
		15	15.0151 ^{a}	0.0188	
		13	14.9926 ^{a}	0.4263	

Table 2.2 *Yolk Utilization Rate (YUR).* Results from regression analysis on the effect of temperature (13, 15, 18, and 21°C) and species (shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus*) on yolk-sac volume absorption rate over the experimental period. 2-way ANOVAs were run on $\log_{10}$ transformed slopes (to meet assumption of homogeneity of variance) first as saturated models. (Since a significant interaction was detected [$P = 0.0010$] the model was decomposed into 1-way ANOVAs). Mean values represent replicate trays within each treatment (n = 3-4). Significance between temperatures (within each species) is indicated by different superscript letters. The species, reared at the same temperature, which is significantly greater in value is indicated by an (*) and *P* value Significance was set at an α of 0.05. SE = ± 1 standard error.

Species	Temp (°C)	Mean Slope ($mm^3 \cdot day^{-1}$)	± 1 SE	Mean r^2	Model *P*'s	Significance Between Spp.
shortnose	21	-0.51180 ^{A}	0.02577	0.91443	< 0.0191	0.0659
	18	-0.31974 ^{B}	0.03429	0.81145	< 0.0011	0.1685
	15	-0.27766 ^{C}	0.01376	0.83760	= 0.0001	* 0.0003
	13	-0.18114 ^{C}	0.00616	0.77423	= 0.0001	* 0.0077
Atlantic	21	-0.68710 ^{a}	0.04417	0.91980	< 0.0475	
	18	-0.41665 ^{b}	0.13903	0.84530	< 0.0159	
	15	-0.13449 ^{bc}	0.00986	0.60963	< 0.0033	
	13	-0.11723 ^{c}	0.02596	0.59590	< 0.0031	

Table 2.3 *Growth.* Results from regression analysis on the effect of temperature on growth rate to maximum standard length for both shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* over the experimental period. 2-way ANOVAs were run on the $\log_{10}$ transformed (to meet assumption of homogeneity of variance) slopes first as saturated models. (Since a significant interaction was detected [$P = 0.09290$] the model was decomposed into 1-way ANOVAs). Mean values represent replicate trays within each treatment (n = 3-4). Significance between temperatures (within each species) is indicated by different superscript letters. The species, reared at the same temperature, which is significantly greater in value is indicated by an (*) and *P* value. Significance was set at an α of 0.05. SE = ± 1 standard error.

Species	Temp (°C)	Mean Slope ($mm \cdot day^{-1}$)	± 1 SE	Mean r^2	Model *P*'s	Significance Between Spp.
Shortnose	21	0.57249 ^{A}	0.06082	0.89908	< 0.0017	0.1940
	18	0.33640 ^{B}	0.02193	0.85925	< 0.0002	* 0.0365
	15	0.23171 ^{C}	0.00405	0.84555	0.0001	0.2028
	13	0.19778 ^{C}	0.01624	0.87147	0.0001	0.7276
Atlantic	21	0.68600 ^{a}	0.02805	0.97147	< 0.0031	
	18	0.44193 ^{b}	0.03195	0.93163	< 0.0006	
	15	0.20376 ^{c}	0.02207	0.88130	0.0001	
	13	0.20283 ^{c}	0.00187	0.90450	0.0001	

Table 2.4 *Survival.* Results from 2-way ANOVAs on the time to 100% mortality for each rearing temperature (13, 15, 18, and 21°C) between species (shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus*). ANOVAs on $\log_{10}$ transformed data (to meet assumption of homogeneity of variance) were run first as saturated models. (Since a significant interaction was detected [P = 0.0322] the model was decomposed into 1-way ANOVAs). Mean values represent replicate trays within each treatment (n=3-4). Significance between temperatures (within each species) is indicated by different superscript letters. The species, reared at the same temperature, which is significantly greater in value is indicated by an (*) and P value Significance was set at an α of 0.05. SE = ± 1 standard error.

Variable	Species	Temp (°C)	Mean Days	± 1 SE	Significance Between Spp.
Time to 100% Mortality (d)	shortnose	21	26.5 ^{A}	0.95743	* 0.0009
		18	34.5 ^{B}	1.25831	* 0.0005
		15	41.0 ^{C}	2.00000	* 0.0381
		13	40.7 ^{C}	5.70088	0.0890
	Atlantic	21	18.3 ^{a}	0.94648	
		18	22.0 ^{b}	3.02765	
		15	34.3 ^{c}	0.94648	
		13	37.3 ^{c}	1.04083	

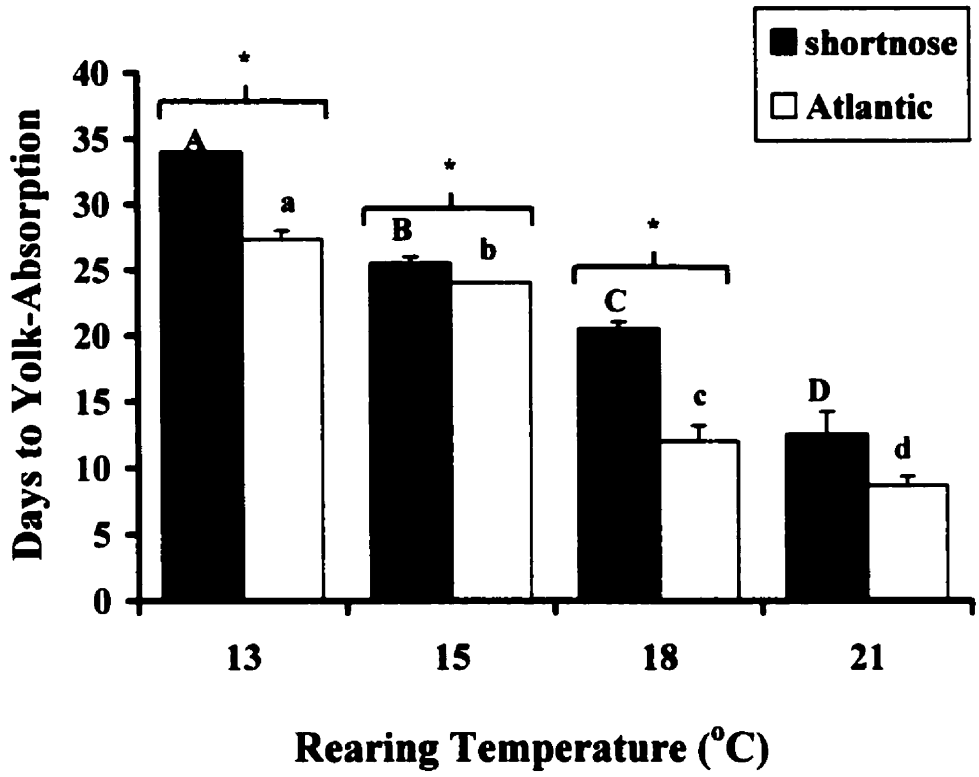

Figure 2.1 *Yolk-Sac Absorption.* Mean time (days) to yolk-sac absorption for larval shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* at each rearing temperature. Values with different letters are significantly different (lowercase = Atlantic). Significance was set at an α of 0.05. Horizontal bars with (*) over treatments indicate significant difference between species. Error bars represent ± 1 standard error.

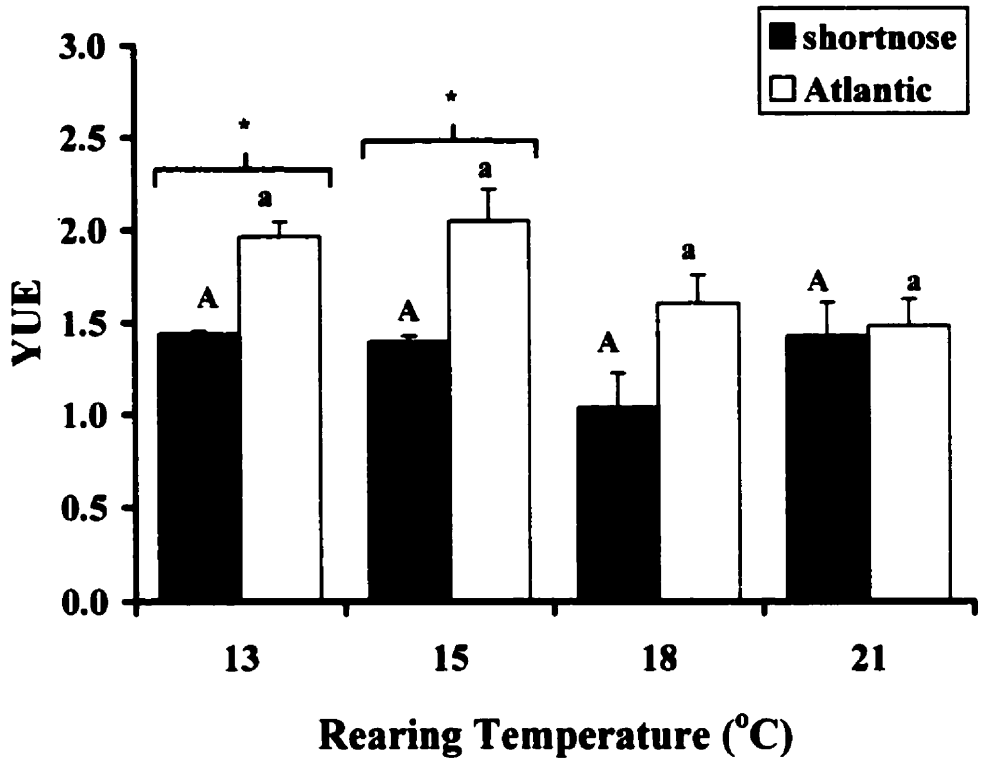

Figure 2.2 *Yolk utilization efficiency (YUE).* Mean YUE for larval shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* at each rearing temperature. Values with different letters are significantly different (lowercase = Atlantic). Significance was set at an α of 0.05. Horizontal bars with (*) over treatments indicate significant difference between species. Error bars represent ± 1 standard error.

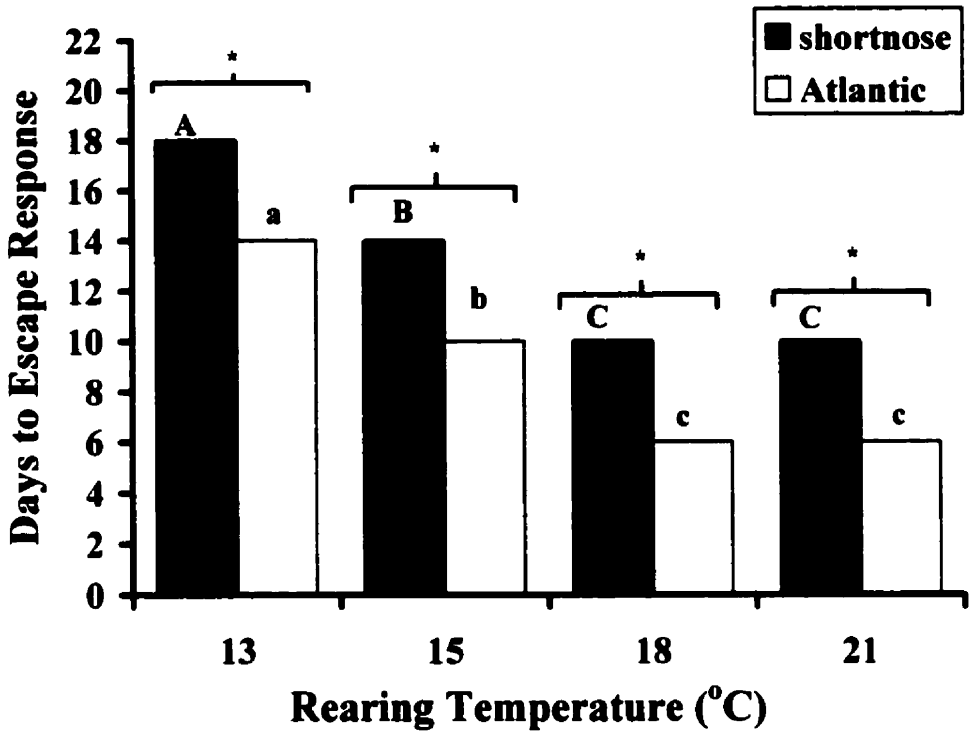

Figure 2.3 *Escape Response.* Mean time (days) to initiate first escape response for larval shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* at each rearing temperature. Values with different letters are significantly different (lowercase = Atlantic). Significance was set at an α of 0.05. Horizontal bars with (*) over treatments indicate significant difference between species.

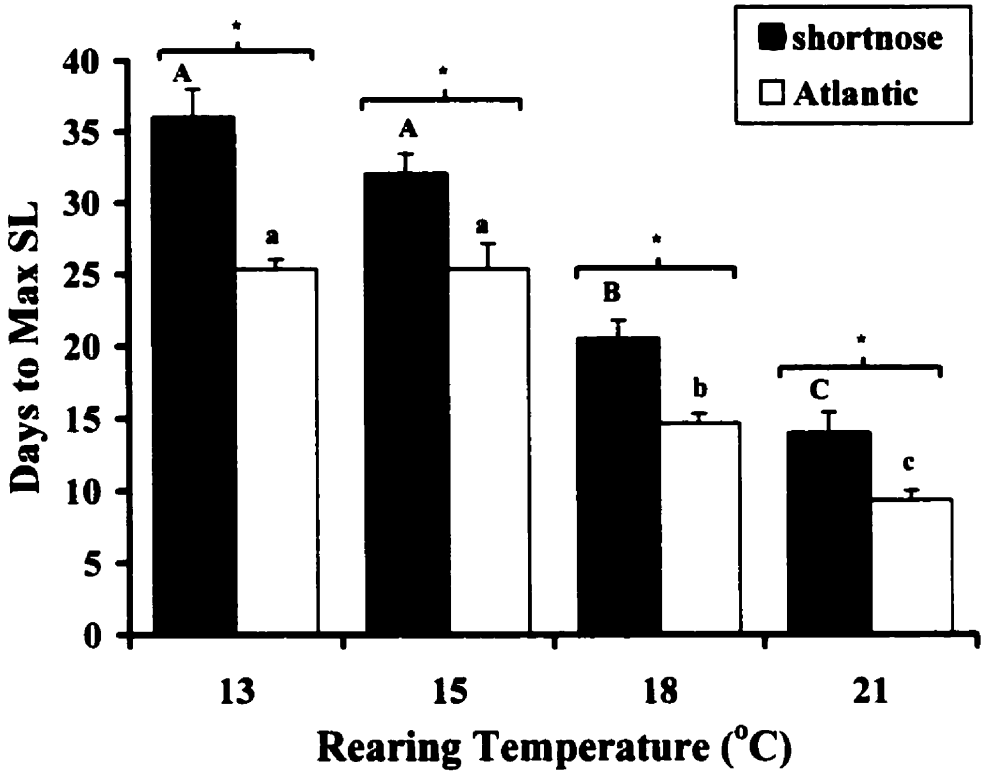

Figure 2.4 *Maximum Standard Length (SL).* Mean time (days) to reach a maximum standard length for larval shortnose sturgeon *Acipenser brevirostrum* and Atlantic sturgeon *A. oxyrhynchus* at each rearing temperature. Values with different letters are significantly different (lowercase = Atlantic). Significance was set at an α of 0.05. Horizontal bars with (*) over treatments indicate significant difference between species. Error bars represent ± 1 standard error.

Figure 2.5 *Survival.* Survival curves for shortnose sturgeon *Acipenser brevirostrum* (A) and Atlantic sturgeon *A. oxyrhynchus* (B) reared at each temperature. The point of yolk-sac absorption (A-temp) and escape initiation (E-temp) are represented by arrows on the graph.

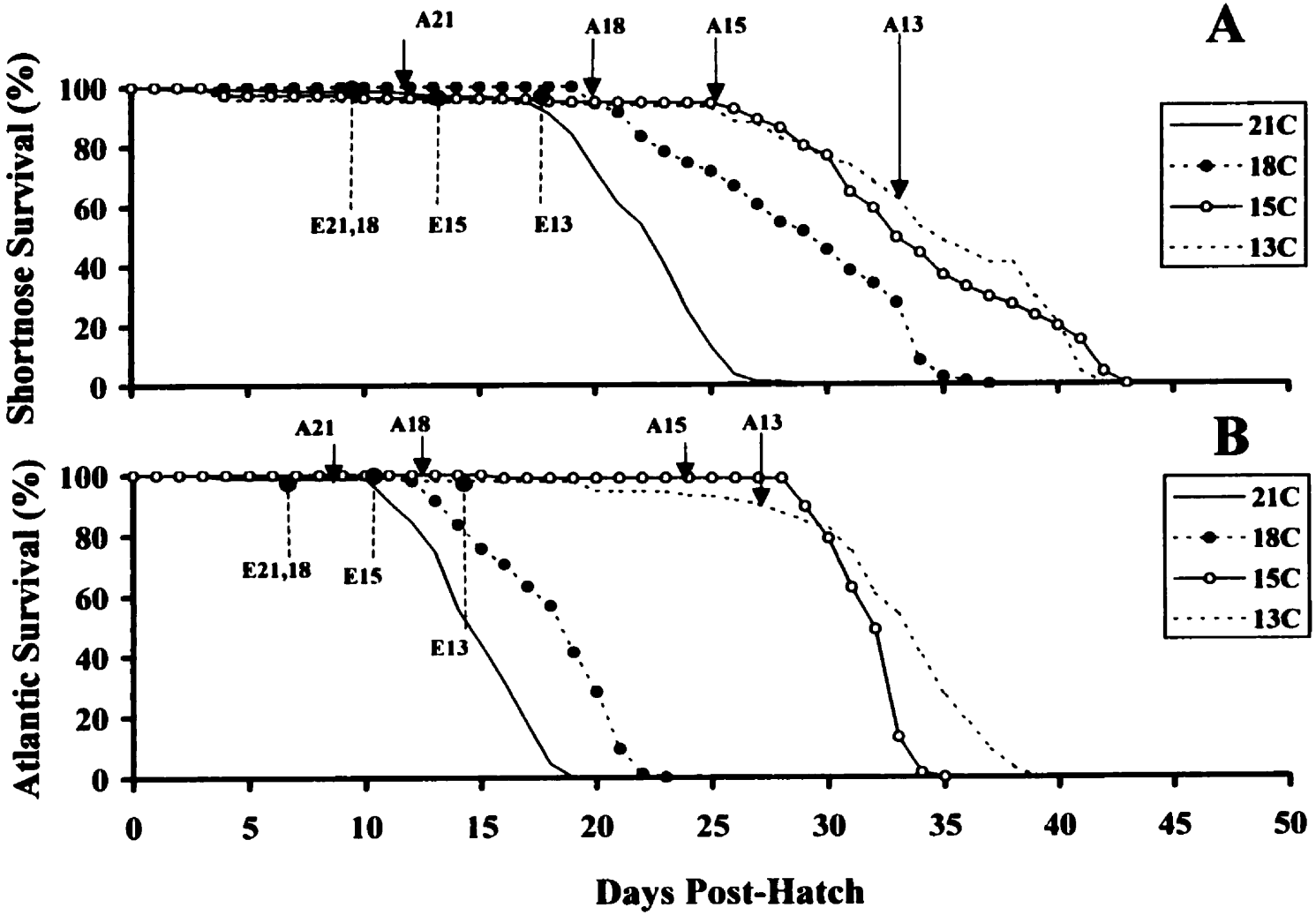
A
B
A21
A18
A15
A13
E21,18
E15
E13
21C
18C
15C
13C
Shortnose Survival (%)
Atlantic Survival (%)
0
20
40
60
80
100
0
5
10
15
20
25
30
35
40
45
50
Days Post-Hatch

Figure 2.5

Chapter 3: Growth, Survivorship, and Predator Avoidance Capability of Larval Shortnose Sturgeon (*Acipenser brevirostrum*) in Response to Delayed Feeding.

Introduction

The ability of fish larvae to grow and survive through their early life history (ELH) stages ultimately plays a role in recruitment and year-class formation (Houde 1987). Starvation (Hjort 1914; May 1974) and predation (Bailey and Houde 1989; Batty 1989; Blaxter and Fuiman 1990) during these ELH stages have been hypothesized as being the primary factors involved in regulating survival. Larval susceptibility to predation, linked to such factors as frequency of encounter and ability to avoid and escape an attacking predator, is affected by degree of starvation (Gamble and Fuiman 1987; Purcell et al. 1987; Bailey and Houde 1989). Examining the interaction of starvation and predation and how it affects larval survival is important to our understanding of recruitment.

Predation is considered to be the main factor of mortality during the egg and yolk-sac stage, (Batty 1989; Paradise et al. 1996), while direct mortality due to starvation seems to only be a factor following the transition to exogenous feeding (Folkvord and Hunter 1986; Litvak and Leggett 1992). Linked to patchy or inadequate distribution of food resources prior to the initiation of feeding, this "critical" switch to exogenous food sources has been suggested to be a period of increased mortality (Hjort 1914; Hewitt et al. 1985; Taggart and Leggett 1987; Letcher et al. 1996). It has been hypothesized that larval survival and recruitment is conditioned by the match of larvae with prey fields in time and space; referred to as the "match-mismatch" hypothesis (Cushing 1972). Therefore, larvae must locate food patches during this critical period before a time of

irreversible starvation or "point-of-no-return" is reached (PNR: point during starvation where 50% of the larvae are still alive yet are unable to feed even when food becomes available; Blaxter and Hempel 1963; reviewed in McGurk 1984; Miller et al. 1988). Once a larva has successfully initiated feeding, starvation resistance dramatically increases (Blaxter 1969; Hunter 1981).

Some species of larval fish found in "mismatch" conditions are able to resist and recover from the effects of relatively long periods (days or weeks) of starvation (Gotceitas et al. 1996). However, during this time, starvation can result in increased vulnerability to predation. For example, starving larvae may be less able to avoid and escape attacking predators than fed larvae (Gamble and Fuiman 1987; Rice et al. 1987). Alternatively, smaller size and reduced activity during starvation may reduce the likelihood of being located by such predators (Gamble and Fuiman 1987; Litvak and Leggett 1992; Pepin et al. 1992). It has been suggested that temporal variations in risks to predation may be a crucial element dictating animal behavior (Lima and Bednekoff 1999). Therefore, a starving larva may use different behaviors to increase chances of locating food, while remaining vigilant to predators. Two schools of thought debate the most probable response or "risk allocation" (Lima and Bednekoff 1999) to starvation for a developing larva: 1) a larva will reduce metabolic expenditures to conserve energy for predator alertness and foraging once a food patch is encountered (Wieser et al. 1992); 2) in spite of the energetic costs, a larva maintains risk responsiveness and increases activity levels to increase the probability of encountering a food patch (Blaxter and Ehrlich 1974; Yin and Blaxter 1987, Mehner and Wieser 1994). Regardless of the strategy used, increased vulnerability of larvae during mismatch conditions, compounded with slow

growth and development (Shepherd and Cushing 1980; Werner et al. 1983), may ultimately result in increased mortality during this larval stage.

Information is somewhat limited on the effects of starvation in relation to susceptibility of larvae to predation, and virtually no information exists on the interaction of these two factors in any of the 26 species of sturgeon. Early-life mortality is particularly important in determining year-class strength in sturgeon, since their large body size, tough leathery skin, and bony scutes translates to less mortality risks during the juvenile and adult stages (Cech et al. 1984). The importance of examining such ELH mortality is even greater since many of these species are threatened or endangered throughout their range of distribution. One such North American species, commercially harvested in past years, is the shortnose sturgeon (*A. brevirostrum*). Shortnose sturgeon are now protected in the United States under the Endangered Species Act (Miller 1972) and considered a species of special concern in Canada (COSEWIC 2000).

The first objective of this paper was to examine growth and starvation resistance of larval shortnose sturgeon in response to delayed feeding. Although two strategies for combining risk-responsiveness and activity level have been suggested, there are actually 4 possible combinations of these couplets. Therefore, the second objective was to examine swimming activity and escape capabilities to determine which of the following responses or combination of responses are utilized during starvation: 1) reduction in activity levels and maintenance of high risk responsiveness while waiting for a food patch; 2) increase in activity levels to locate a food source, while maintaining high responsiveness to predators; 3) reduction in activity levels as well as responsiveness to

predators to conserve energy; or 4) increase in activity levels to find a food patch, yet making a trade-off by lowering risk responsiveness.

Materials and Methods

Egg Collection and Incubation - Short-set gill nets were used to collect reproductively mature shortnose sturgeon in the Saint John River, New Brunswick, Canada between April 20 and May 1, 1999 (N45°33' W66°02'; water temp: 15-16 °C). On May 5, 1999 fertilization procedures (as specified by Doroshov et al. 1983) were performed using eggs collected from one female and sperm from two mature shortnose sturgeon males. Fertilized eggs were incubated in MacDonald incubation jars (approximately 500 ml in each) in a partial re-circulation system (3 L/min). All eggs were incubated at a constant temperature of 17 °C until hatching on May 13, 1999 (approximately 200 hrs post-fertilization).

Larval Rearing and Experimental Design - Directly following hatch (0 days post hatch [dph]), larvae were separated into six delayed feeding treatments, each of which contained three replicate trays (1000 ml Pyrex trays [15 x 25 cm] filled with 700 ml of de-chlorinated water) stocked with 30 larvae. In the first treatment, food was offered to the larvae directly following yolk absorption (15 dph). Larvae in the second through fifth treatments were starved for 5, 10, 15, and 18 days after complete yolk absorption (respectively). Larvae in the sixth treatment were denied food for the duration of the experiment. Larvae in feeding treatments were offered live brine shrimp nauplii *Artemia* spp. *ad libitum* twice daily. Prior to feeding, all trays were cleaned of all uneaten nauplii and waste and replaced with 600 ml of de-chlorinated water (7.0-8.0 mg/l of dissolved

oxygen). Starved replicates were also cleaned and water replaced in order to maintain similar methods of handling of each treatment. All trays were kept at a constant 17 °C by being placed into a (75 x 150 cm lined table) water bath filled with 5 cm of de-chlorinated water. A fluorescent light (photoperiod set at 15L:9D) placed above the lined experimental table provided a light intensity of ≈ 700 lux at the water surface (Lurtron LX-101 lux meter; intensity chosen based on Richmond and Kynard 1995).

Survival and PNR

The point-of-no-return (PNR) for larval shortnose was defined as the time when 50% of larvae offered *Artemia* nauplii failed to initiate feeding (Blaxter and Hempel 1963). Incidence of feeding was determined by examining the gut color after approximately 1 hr of darkness (shortnose larvae experience a loss of body coloration, and their gut becomes semi-transparent following darkness). The cumulative number of dead larvae for each treatment replicate was calculated each day (excluding loss through sampling).

Growth

Growth measurements were obtained by sampling larvae (n = 2) at random from each of the 3 replicate trays at the start of each feeding trial. Each larva was then anaesthetized with 25 mg/L solution of tricaine methanesulfonate (MS-222), placed under a microscope (Olympus SZ6045) and videotaped live with a video camera (Sony DXC-1821) attached to a super-VHS video-cassette-recorder (Panasonic AG-5700) for

later analysis. Standard length (SL) (mm) from the anterior most point of the developing rostrum to the posterior most point of the notochord was measured with an image analysis system (Optimas v5.2 BioScan Inc., Edmonds, Washington). Larvae were then preserved in 10% phosphate-buffered formalin for later dry weight (DW) analysis. Dry weight of each larva was obtained by placing preserved larvae into pre-weighed aluminum foil containers and then into a drying oven for 24 hrs at 60 °C. Dried larvae were then weighed to the nearest 0.0001 g on an electronic micro-balance (Mettler AE 240). For each delayed feeding treatment, absolute (AGR) and specific growth rates (SGR) at first feeding period (first feeding to next sample day) and experiment termination (day 19 to day 23) were determined with the following equations (Ricker 1979; Kamler 1992):

$$\text{AGR: } G_a = (w_2 - w_1)/(t_2 - t_1)$$

$$\text{SGR: } G_s = 100 \times (\log_e w_2 - \log_e w_1)/(t_2 - t_1)$$

where w_i is DW or SL at time t_i.

Swimming Activity and Speeds

Larval swimming behavior and activity levels were recorded with a video camera (Panasonic WVDB 400) placed over the top of each individual rearing tray. The video signal was passed through a time date generator (Panasonic WJ-810) before being recorded on a super-VHS video-cassette-recorder (Panasonic AG-5700) so that each frame would be timed to the nearest $1 \cdot 100^{-1}$ of a second. The camera, attached to a sliding apparatus, was moved into place over each individual rearing tank with minimal disturbance from vibrations. Larval activity was recorded for 20s per replicate at a speed

of 30 frames·s^{-1}, at a shutter speed of 1·500s^{-1}. Recordings were performed at the start of each feeding trial, prior to food being offered in each tank, and after all dead larval were removed. From these recordings, the proportion of larvae actively swimming or not swimming (body movements with no forward motion or not moving at all) was calculated. In addition to activity levels, swimming performance was also analyzed using the image analysis system. Swimming data were obtained only from larvae that were actively swimming within the 20s observation period. These larvae were assigned numbers and 3 were randomly chosen for analysis of swimming performance. The data collected included average time spent swimming, the average distance traveled during a swimming bout, and the average speed of each swimming bout. Coordinate points on swimming performance were obtained for each larvae every second of the recorded swimming bout.

Escape Response and Speeds

Two types of predatory attack simulations, tactile and mechanical vibration, were used to examine escape behavior and responsiveness of shortnose larvae. These two types of stimulations, may be received by very different sensory pathways (e.g. free neuromasts on the body, a gas filled swimbladder, or otic bulla; Blaxter and Batty 1985). Each replicate tray was placed in a 3 walled experimental chamber (to reduce visual stimulation) with the top open for video recording and one side open to perform the experiment.

Tactile stimulation: After a 5 min acclimation period, the first escape response was induced by tactile stimuli by touching the posterior trunk of the larvae with a blunt

probe and recording the subsequent reaction. Three fish from each replicate were "attacked" with the blunt probe. Care was taken to avoid repeated stimulation of the same individual larvae in order not to have confounding affects from habituation. The subsequent reaction was recorded at a speed of 30 frames·s^{-1} (shutter speed of 1·500s^{-1}) with a video camera over the experimental chamber, equipped again with a time date generator (Panasonic WJ-810). Coordinate points on escape responses were obtained for each larva at every other frame (1·15s^{-1}) of recorded response. Mean and maximum ("burst") escape speeds, which allows larvae to escape attacks by lunging predators (Webb and Corolla 1981), were determined using these data.

Mechanical Vibration: The second predatory attack, simulating vibration disturbances from attacking predators, was achieved by releasing a rubber ball (8.80 g) attached to a 24 cm long string which swung from a pre-measured height of 26 cm. After the ball was released, it struck the side of the rearing tray sending a vibration through the water column. Again, the reaction was recorded with video. Data analyzed were the proportion of larvae responding to the vibrations caused by the rubber ball, indicated by "C-type" body movement (a rapid escape movement of the body trunk in the shape of a 'C'; Blaxter and Batty 1985).

Due to video problems, the swimming and escape activity of only one replicate tray was properly videotaped at the start of the experiment (SL and DW were all obtained for each treatment). To obtain this missing swimming and escape activity, larval shortnose from an additional cross (May 4, 2000) of two males and one female shortnose were incubated in the same fashion as in 1999, and the experiment was repeated at yolk absorption for all treatments. To account for possible differences in larvae, due to year

and parentage, SL and DW of the 2000 cohort larvae were compared with the previous year. The comparison of experimental day 1 measures showed no significant difference in SL and DW at the start of the experiment (df = 1, 40; both $P > 0.1405$). In addition, mean swimming and escape activity of the one replicate videotaped in 1999 were all found to be within the range of the new experimental day 1 replicates. Therefore, swimming and escape data of shortnose from May 4, 2000 were substituted at the start of the experiment.

Data Analysis

All data were analyzed using a two-way nested analysis of variance (ANOVA) with repeated measures (Proc ANOVA; SAS Institute 1992) which compared main affects between treatment groups over the duration of the experiment. When an interaction ($P < 0.2$; see Winer, 1971 [page 379] for justification of a conservative type II error rate) between main effects was present the model was separated into one-way ANOVAs to reveal significance within treatments (within-treatment comparisons were nested one-way ANOVAs with repeated measures). If the model showed no interaction, the term was dropped and the model re-run. Least–square means (LSMs) were used for *a posteriori* comparisons, and probabilities were adjusted for multiple comparisons using Tukey's correction (SAS Institute Inc., 1992). Level of significance for main effects was set at an α of 0.05. All data were tested for normality and homogeneity of variance (Proc Univariate: Sas Institute 1992; F_{max} –test: Sokal and Rohlf, 1981). Analysis were run on $\log_{10}$ transformed data in cases of non-normality or heterogeneity of variance. Percentage data was arcsine-square-root transformed to also meet the assumptions of

ANOVAs. In addition, measurements (SL and DW) of the larvae at yolk-absorption were also compared with 1-way ANOVAs between treatments to confirm no significant differences at the start of the experiment.

Results

Growth

Morphological comparisons at the start of the experiment were not significantly different in mean SL and DW between treatment groups. Resulting 2-way repeated measures ANOVAs on mean SL and DW between treatment groups over the experimental period showed interactions between delayed feeding treatments and sample time (df = 20, 50; P = 0.0001). The 1-way repeated measure ANOVAs on SL and DW for each treatment were all significant (df range 4-5, 10-20; all $P < 0.0195$) and showed that growth in SL and DW were delayed with increasing starvation (Figure 3.1 & 3.2). Resulting 1-way ANOVAs at each sample day revealed significance between treatment groups only after the initiation of first feeding for each treatment.

ANOVAs for mean absolute and specific growth rates of SL and DW (with the exception of SGRs of DW) at the period of initial feeding for each treatment (day of first feeding to next sample day) showed no significant differences between feeding treatments (Table 3.1). ANOVAs for mean SGRs of DW were significantly higher (df = 4, 10; $P < 0.05$) for treatments starved 15 and 18 d respectively (Table 3.1). However, mean growth rates of SL and DW for the period at the end of the experiment (day 19 to 23) were all highest in treatments fed for longer periods of time. Mean SGRs during this interval were highest for DW in the treatments denied food for 5 and 10 days respectively

(Table 3.1).

Survival and PNR

Treatments denied food for 0 and 5 days exhibited 100% survival up to the time food was offered. The delay in feeding for treatments starved for 10, 15, and 18 d significantly lowered survival (df = 4, 10; $P < 0.05$) to first feeding to 90.5% ± 1.19 SE, 66.7% ± 2.56 SE, and 41.7% ± 1.83 SE respectively (significance: 10 > 15 > 18 d starved; $P = 0.001$; Figure 3.3). ANOVAs on survival to the end of the experiment showed no significant difference between the 0 and 5 d starved groups, however, survival to the end of the experiment in groups starved 10, 15, and 18 d was again significantly reduced (df = 4, 10; $P < 0.05$) to 71.2% ± 3.03 SE, 45.4% ± 2.62 SE, and 28.8% ± 3.03 SE respectively (significance: 10 > 15 > 18 d starved; $P = 0.001$; Figure 3.3). Since there was no variance in 0 and 5 d starved treatments, homogeneity of variance could not be met. However, Zar (1996) indicates that ANOVAs are robust enough to detect differences as long as one assumption is met. Replicate tanks from the treatment never fed showed 100% mortality by day 21 (36 dph).

Shortnose had a point-of-no-return (55.7% initiated feeding) at approximately 18 d following the full absorption of the yolk (33 d post-hatch; 41 d post-fertilization) at 17 °C. The ANOVA on the % first feeding revealed no significant difference in 0 and 5 d starved treatments, however, feeding in treatments starved 10, 15, and 18 d was significant reduced (Table 3.2).

Swimming Activity

There was an interaction between delayed feeding treatments and sample time (df = 20, 49; $P = 0.0001$) in the 2-way repeated measures ANOVA on mean % swimming between treatment groups over the experimental period. One-way repeated measure ANOVAs for each treatment were all significant (df range 4-5, 10-19; all $P < 0.0252$) and showed that % swimming activity significantly increased with level of starvation, while activity was reduced once food was offered (Figure 3.4). There was no significant difference in % swimming between treatment groups for 1-way ANOVAs at day 1, 6, and 23 (Figure 3.4).

Swimming Speeds

Mean swimming speeds over the experimental period (2-way repeated measures ANOVA) showed an interaction between delayed feeding treatments and sample time (df = 20; 49 $P = 0.1087$). One-way repeated measure ANOVAs for each treatment were all significant (df range 4-5, 10-19; all $P < 0.0015$) with swimming speed decreasing significantly from day 1 to day 6 for all treatments (Figure 3.5). Swimming speed was higher in starved than fed treatments. Treatments starved for 15 and 18 d significantly increased swimming speed once food was offered. This increase in swimming speeds in the 15 d group was then followed by a significant decrease in speeds similar to those of other fed treatments. Resulting 1-way ANOVAs at each sample day showed no significant difference in swimming speeds between treatments on day 1 and 6 of the experiment. ANOVAs for remaining sampling days showed that groups starved for 0 and 5 d had significantly slower (df = 5, 15; all $P < 0.05$) swimming speeds on days 11, 16,

and 19 than starved treatments (10 d treatment also significantly different than 15 d treatment on day 19) (Figure 3.5). On day 23, the 18 d starved group was significantly higher than all other fed treatments (df = 4, 9; $P = 0.001$).

Escape Response to Probe

There was an interaction between delayed feeding treatments and sample time (df = 20, 48; $P = 0.0001$; Figure 3.6 & 3.7) for escape speeds (maximum and mean) over the experimental period (2-way repeated measures ANOVA). One-way repeated measure ANOVAs for each treatment were all significant (df range 4-5, 9-20; all $P < 0.0038$) and revealed decreases in escape speeds from day 1 to day 6 for all treatments (Figure 3.6). This reduction was not as significant in maximum escape speeds (Figure 3.7). All treatments experienced significant increases in escape speeds after feeding was initiated. The 0, 5, and 10 d starved groups had lower (although not significantly) mean escape speeds after first feeding followed by increasing responses to the end of the experiment. However, treatments starved for 15 and 18 d demonstrated better escape initiation to stimulation by the probe than fed treatments directly following the initiation of feeding. Resulting 1-way ANOVAs at each sample day revealed no significant difference in escape speeds between treatments on day 1, 6, and 11 of the experiment. ANOVAs for remaining sampling days indicated that treatments which were starved less had overall faster escape speeds than treatments denied food for longer periods (Figure 3.6 & 3.7).

Escape Response to Mechanical Vibration

The 2-way repeated measures ANOVA on the mean percent of shortnose larvae

exhibiting escape response (to ball striking the side of the tank) over the experimental period showed an interaction between delayed feeding treatments and sample time (df = 20, 48; $P = 0.0091$). Except for the completely starved group, 1-way repeated measure ANOVAs for all other treatment were significant (df = 4-5, 9-19; all $P < 0.0273$) and showed that % responding increased with level of feeding. Those denied food stayed at the same level of response until food was provided (Figure 3.8). All treatments exhibited an increase in response from day 1 to 6. Resulting 1-way ANOVAs at each sample day showed no significant difference in % response on day 1, 6, or 23. ANOVAs for remaining sampling days revealed that groups only starved 0 and 5 d had significantly higher (df = 5, 15; all $P < 0.05$) percent response on days 11, 16, and 19 than starved treatments (Figure 3.8). The 18 d starved group had the highest % increase in response (29%) following food being offered.

Discussion

Growth

Growth rates of shortnose larvae were directly affected by the degree of starvation. Since starvation causes the arrest of normal tissue synthesis (Theilacker 1978), a delay in growth with increasing degrees of starvation is to be expected. In larval shortnose, the resumption of normal growth, despite the degree of starvation, may allow a rapid recovery and restoration of damaged tissues that may have occurred during this period. This type of recovery growth has been reported in delayed feeding studies of Siberian sturgeon *A. baeri* (Gisbert and Williot 1997), as well as larvae of more modern teleost species like bloater *Coregonus hoyi* (Rice et al. 1987), summer flounder

Paralichthys dentatus (Bisbal and Bengtson 1995), and Atlantic cod *Gadus morhua* (Gotceitas et al. 1996). Growth rates, except SGRs of dry weight, after first feeding (first feeding to next sampling date) were not significantly different across feeding treatments. The SGRs of dry weight during this period, however, were the highest in treatments starved for the longest periods (15 and 18 d). This type of growth "spurt" may reflect a type of compensatory mechanism used by these larvae when food is limited or patchily distributed. Alternatively, it may simply be an artifact of feeding rate, where those denied food for the longest term experience a short period of hyperphagia (Jobling and Koskela 1996; hyperphagia: excessive ingestion of food beyond that needed for basic energy requirements). At the termination of the experiment, however, growth rates, including SGRs of dry weight, were highest in treatments starved for the shortest time. Similar short durations of compensatory growth have been reported for juvenile cyprinids (Wieser et al. 1992).

The ability of larval shortnose to resist starvation for long periods until PNR, with rapid growth after initiation of feeding, may assist survival during spring when food production is relatively low. Starvation may, however, be an important factor in determining survivorship since losses from starvation and predation are often size dependent (Miller et at. 1988; Booman et al. 1991; Pepin et al. 1991). Therefore, the delay in growth of larval shortnose, caused by a period of food deprivation, may result in a large reduction in survival and subsequent recruitment (Folkvord and Hunter 1986; Rice et al. 1987; Bailey and Houde 1989).

Survival and PNR

Survivorship of shortnose sturgeon larvae to both first feeding stage and at termination of the experiment were equally high in treatments denied food for 0 and 5 days. Mortality, however, became much more dependent on the degree of starvation past the 11^{th} day of the experiment (> 10 d starved treatments). Similar studies have shown that starvation is a direct source of mortality in young fish (McGurk 1984; Theilacker 1986; Margulies 1993). Conversely, studies of other fish species, such as freshwater bloater *Coregonus hoyi*, suggest that starvation may be a more important indirect source of mortality, affecting larval foraging success and predation risk. This may be the case with larval shortnose sturgeon, since they exhibited high resistance to starvation, along with the resumption of normal growth after feeding.

Little information exists as to when larval sturgeon should begin feeding following the absorption of endogenous energy reserves (Gisbert and Williot 1997). The present study indicates that shortnose sturgeon larvae can survive for a "remarkable" 41 days post-fertilization (18 d starvation) at 17 °C to the point of irreversible starvation. Comparing shortnose larvae to the PNR of 25 marine species summarized by McGurk (1984), shows that shortnose take considerably longer to reach PNR from fertilization than most species with similar ELH stages. The observed PNR of 41 days post-fertilization was significantly longer ($P < 0.001$) than the predicted PNR of 30.7 d post-fertilization ± 0.43 SE by McGurk's original regression equation ($t_s = 0.5 + 1.3*t_y$; where t_s is the time from fertilization to PNR and t_y to yolk absorption). Like shortnose, larval bloch *Channa striatus* (another freshwater spp.) also had a PNR well above that predicted by McGurk's regression equation (Arul 1991). Such deviates were suggested by McGurk

(1984) and Arul (1991) to be related to the presence of a large oil globule which is absorbed much slower (relative to yolk) during food deprivation (Arul 1991; Quants 1985). The oil globule, reported to have a higher energy content than the yolk proteins (Eldridge et al. 1981), may aid in prolonging or even avoiding PNR altogether (McGurk 1984; Chambers et al. 1989; Eldridge et al. 1981; Rogers and Westin 1981). The oil globule of larval shortnose was 45% ± 0.032 SE of the total calculated yolk volume at hatch. It may, however, also reflect differences in the quality of yolk constituents between freshwater and marine larvae. Freshwater species have been reported to produce larger eggs, with larger amounts of yolk and lipid for endogenous energy (Bagarinao 1986). As a result, they produce larger larvae at hatch (Chambers et. al 1989; Miller et al. 1988). Some marine species, however, like striped bass *Morone saxatilis* (Rogers and Westin 1981; Eldridge et al. 1981) and California grunion *Leuresthes tenuis* (May 1971) also have relatively large amounts of lipid at hatch and exhibit high resistance to starvation.

Much of the existing ELH literature places more emphasis on the larval-stage dynamics of marine fishes, with little emphasis on the ELH dynamics of freshwater species (Houde 1994). Starvation mortality has been suggested to be more probable for marine larvae because of their small body size, high energetic demands and ingestion rates (Houde 1994). However, there is little evidence to support their claim and I feel that more study of ELH in freshwater species is needed.

Swimming and Escape Activity

Larval shortnose had a significant reduction in swimming and escape speeds from day 0 to 5 of the experiment. This may have been caused in part by a physiological or behavioral development, such as a switch from cutanious to gill respiration occurring near the yolk absorption stage. The switch to gill respiration may result in better oxygen supply to tissues and ultimately a change in swimming behavior and activity patterns (Gisbert et al. 1999). Swimming and escape velocity is very important in determining the outcome of a predatory attack (Browman et al. 1989; Fuiman 1989). It has been suggested that sturgeon are relatively slow swimmers, and possess poor acceleration ability (Gershanovich and Taufik 1992). This assumption does not seem to be the case for larval shortnose. Shortnose sturgeon larvae in the non-delayed feeding group exhibited swimming speeds comparable to that of other fish. For example, larval shortnose exhibited mean swimming speeds of 1.4 $BL \cdot s^{-1}$, which is similar to speeds of 0.9-1.2 $BL \cdot s^{-1}$ reported for larval striped bass *Morone saxatalis* (Chick and Van Den Avyle 2000) and swimming speed of 1.5 $BL \cdot s^{-1}$ for larval bloater *Coregonus hoyi* (Rice et al. 1993). Shortnose also exhibited similar escape speeds when compared to other species. For example, in non-delayed feeding treatments, larval shortnose had mean and maximum escape speeds as high as 11.4 $BL \cdot s^{-1}$ and 19.4 $BL \cdot s^{-1}$, respectively. Other studies have reported similar ranges of mean and maximum escape speeds such as 5.7-8.6 $BL \cdot s^{-1}$ and 12.1-16.1 $BL \cdot s^{-1}$, respectively, for several marine fish species (Yin and Blaxter 1987); 5.9–15.0 $BL \cdot s^{-1}$ for American plaice *Hippoglossiodes platessoides* (Shepherd et al. 2000); and 8–9 $BL \cdot s^{-1}$ and 15–17 $BL \cdot s^{-1}$ for larval herring *Clupea harengus* (Batty et al. 1993) (all in response to pipette or tactile stimulation). As shown in this study, larval

shortnose possess swimming and escape abilities similar to that of other modern teleost larvae. Since sturgeon live most of their lives in swift current environments, the ability to successfully swim, accelerate, and maintain position in swift river environment may require the use of such locomotor abilities.

Survival Strategies During Starvation

Larval shortnose completely denied food during this experiment, responded by markedly increasing their swimming activity with increasing levels of starvation. At the same time, these larvae also maintained high levels of risk responsiveness (through swimming, escape speeds, and responsiveness to mechanical vibrations) until the PNR. This is similar to the first hypothesized behavioral response identified in my objectives. My results contrast findings that some larval fish reduce their activity levels during starvation (Ehrlich and Muszynski 1982; Wieser et al. 1992; Jonas and Wahl 1998; Chick and Van Den Avyle 2000) to conserve energy. Other studies, however, have reported very similar larval behaviors, showing an increase in swimming or "search" activity during progressive starvation until PNR is reached (Wyatt 1972; Blaxter and Ehrlich 1974; Rice et al. 1987; Yin and Blaxter 1987). A larva's increased activity level combined with maintaining high risk responsiveness may be an adaptive strategy to guard against predation attacks while increasing the means by which it locates a food patch. This, however, may additionally increase predator encounter rates (Cowan et al. 1996; Letcher et al. 1996). Since larval swimming and escape capabilities increase with size (Folkvord and Hunter 1986; Bailey and Houde 1989; Miller et al. 1988), the vulnerability to predation may certainly be affected by the degree of starvation (Purcell et al. 1987;

Gamble and Hay 1989). However, it is also possible that smaller and relatively slower larvae, as a result of food limitation, may be less conspicuous to predators than those exposed to higher food densities (Folkvord and Hunter 1986; Litvak and Leggett 1992).

Following feeding, behavioral responses observed by larval shortnose during varying degrees of starvation were somewhat different in relation to those originally hypothesized in my objectives. With the exception of 18 d starved treatments, most fed larvae, past the first feeding stage, reduced their activity levels and swimming speeds, while greatly increasing escape speeds to the end of the experiment. During the short period directly after food was offered, however, larvae showed quite different tendencies in behavior, depending on the degree of starvation. For example, direclty after feeding, those larvae starved only short periods (0 and 5 d) exhibited low activity levels, as well as low risk responsiveness. Those starved 10 d maintained high activity levels, and low risk responsiveness; while those starved 15 d maintained high activity levels and increased risk responsiveness. Those starved until PNR (18 d), demonstrated a reduction in activity levels (possibly since they had past PNR), yet significantly increased their risk responsiveness after food was provided. The apparent trend of lower escape speeds following feeding in larvae starved shorter periods is unexpected, since it has been reported that many larval fish show an increase escape response directly after feeding (Folkvord and Hunter 1986; Miller et al. 1988; Bailey and Houde 1989). It has been suggested, however, that during the interval from starvation to satiation, metabolic rates may not "re-adapt" immediately to high levels of food availability (Wilson and Osbourn 1960). In addition, newly fed larvae (starved for only short periods) may be so

"preoccupied" in becoming satiated that they may not respond as well to a tactile stimulation.

Shortnose larvae hatch in riverine systems, which are much different than that of open lakes or ocean environments. Increasing activity levels during periods of starvation, especially vertically in such an environment, may allow a "re-location" downstream to potentially more productive areas. It would make sense that when a larva locates a suitable food patch, their swimming activity level should decrease, as was seen in the 0, 5, and 10 d starved treatments. The relatively good swimming and escape responses from 15 and 18 d starved treatments following feeding may be strategies adopted to maximize feeding efficiency (evident by higher SGRs) and risk responsiveness once prey items are located.

Since shortnose spawn in the spring during periods of low, growth may be slower and risk of starvation higher than larvae hatched during summer months. The ability of larval shortnose sturgeon to withstand relatively long periods of food deprivation past yolk absorption may be an ecological adaptation to survive periods of low food availability and patchy distribution. It is important to consider that the effects from starvation may be magnified in wild populations due to high energetic costs of negotiating large swift river systems, avoiding predation, and securing suitable nursery and foraging habitats (Bestgen 1996). These strategies utilized by shortnose during periods of starvation may be an evolutionary adaptation for their survival during their vulnerable ELH stages.

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Table 3.1 *Growth Rates.* Mean absolute and specific growth rates for larval shortnose sturgeon *Acipenser brevirostrum* during the interval at first feeding (first feeding to next sample day) and experiment end (interval from day 19 to 23). Significance between treatment means is indicated by different superscript letters ($P < 0.05$; LSMs; SAS Institute 1992). SE = ± 1 standard error.

Interval	Treatment (d starved)	Mean SL AGR ($mm \cdot day^{-1}$)	± 1 SE	Mean DW AGR ($mg \cdot day^{-1}$)	± 1 SE	Mean SL SGR ($\% \cdot day^{-1}$)	± 1 SE	Mean DW SGR ($\% \cdot day^{-1}$)	± 1 SE
Beginning Feeding	0	0.32242 ^{A}	0.03183	0.16000 ^{A}	0.02000	1.84056 ^{A}	0.18756	4.55769 ^{A}	0.60148
	5	0.26362 ^{A}	0.01638	0.21369 ^{A}	0.01378	1.46156 ^{A}	0.10101	6.24156 ^{A}	0.64330
	10	0.27319 ^{A}	0.03138	0.21333 ^{A}	0.01764	1.51626 ^{A}	0.17725	6.46103 ^{A}	0.75356
	15	0.22552 ^{A}	0.00988	0.26667 ^{A}	0.01925	1.27001 ^{A}	0.05408	13.60750 ^{B}	1.67171
	18	0.23101 ^{A}	0.02399	0.23333 ^{A}	0.05069	1.28352 ^{A}	0.12847	10.19696 ^{AB}	2.56385
End Feeding	0	1.12501 ^{A}	0.10875	2.54122 ^{A}	0.15074	4.06048 ^{A}	0.42713	15.57379 ^{AB}	1.06469
	5	1.11659 ^{A}	0.08116	2.78148 ^{A}	0.12189	4.32420 ^{A}	0.33540	20.80274 ^{A}	0.54838
	10	0.63849 ^{B}	0.02824	1.20833 ^{B}	0.11024	3.00509 ^{AB}	0.12570	19.42892 ^{A}	0.74856
	15	0.44782 ^{BC}	0.06243	0.62500 ^{C}	0.08036	2.35560 ^{BC}	0.31545	17.88249 ^{AB}	2.75828
	18	0.23101 ^{C}	0.02399	0.23333 ^{C}	0.05069	1.28352 ^{C}	0.12847	10.19696 ^{B}	2.56385

Table 3.2 *Point-of-No-Return (PNR).* Results from ANOVA on the effect of delayed feeding on the mean percent of larvae feeding after 1 hour of feed exposure. Analysis was run on arcsine square root transformed data to meet assumptions of normality. Mean values represent replicate trays within each treatment (n = 3). Significance between treatment means is indicated by different superscript letters. SE = ± 1 standard error.

Treatment (d starved)	Sample Day	Age (d post-fertilization)	% Feeding (un-transformed data)	± 1 SE
0	1	23	100.00 ^{A}	0.00000
5	6	28	100.00 ^{A}	0.00000
10	11	33	90.26 ^{B}	1.17403
15	16	38	71.46 ^{C}	2.48709
18	19	41	55.71 ^{D}	2.97381

Figure 3.1 *Standard Length.* Mean SL for larval shortnose sturgeon *Acipenser brevirostrum* in each delayed feeding treatment over the experimental period. Error bars represent ± 1 standard error.

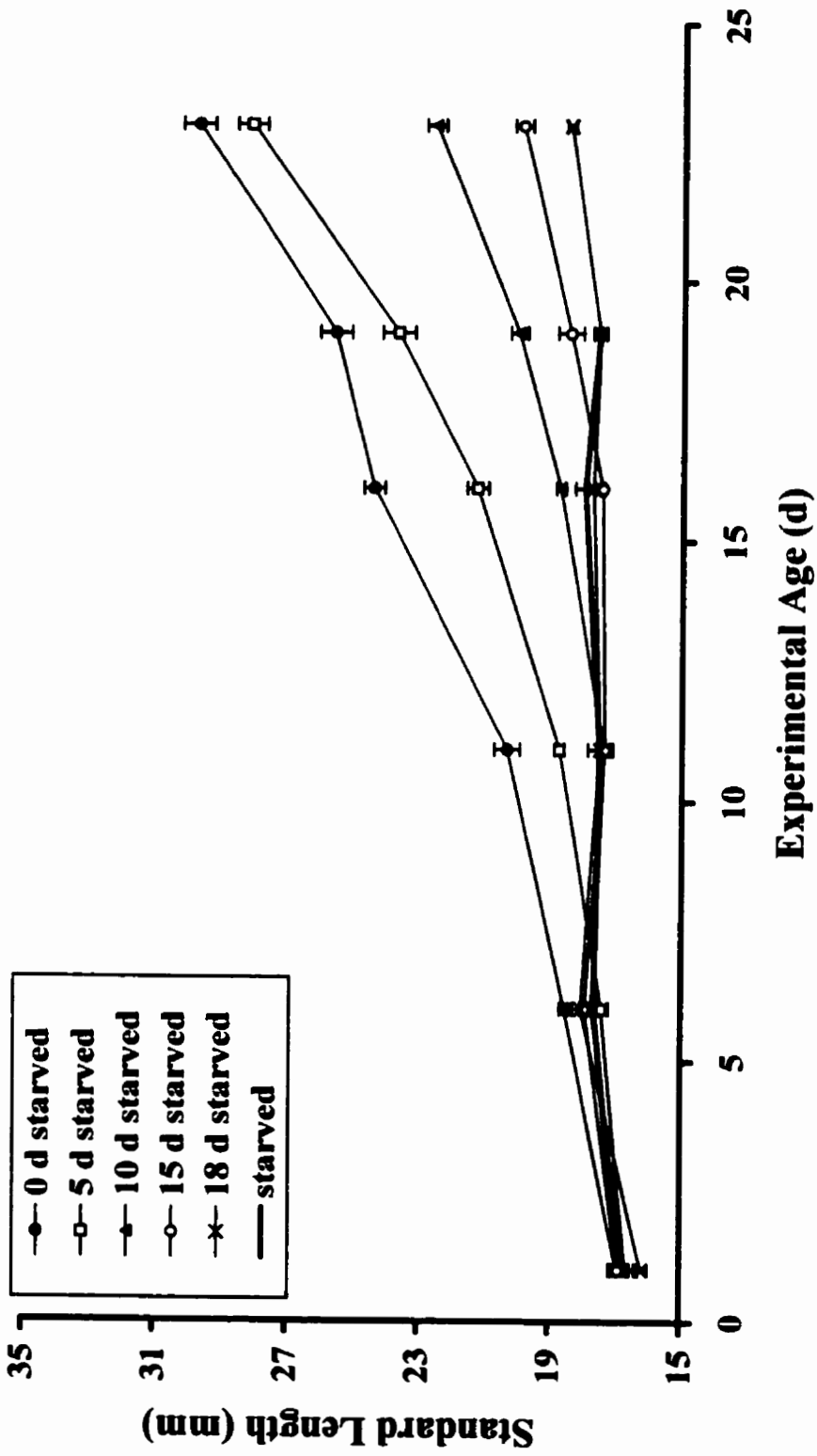
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved
Standard Length (mm)
35
31
27
23
19
15
0
5
10
15
20
25
Experimental Age (d)

Figure 3.1

Figure 3.2 *Dry Weight.* Mean DW for larval shortnose sturgeon *Acipenser brevirostrum* in each delayed feeding treatment over the experimental period. Error bars represent ± 1 standard error.

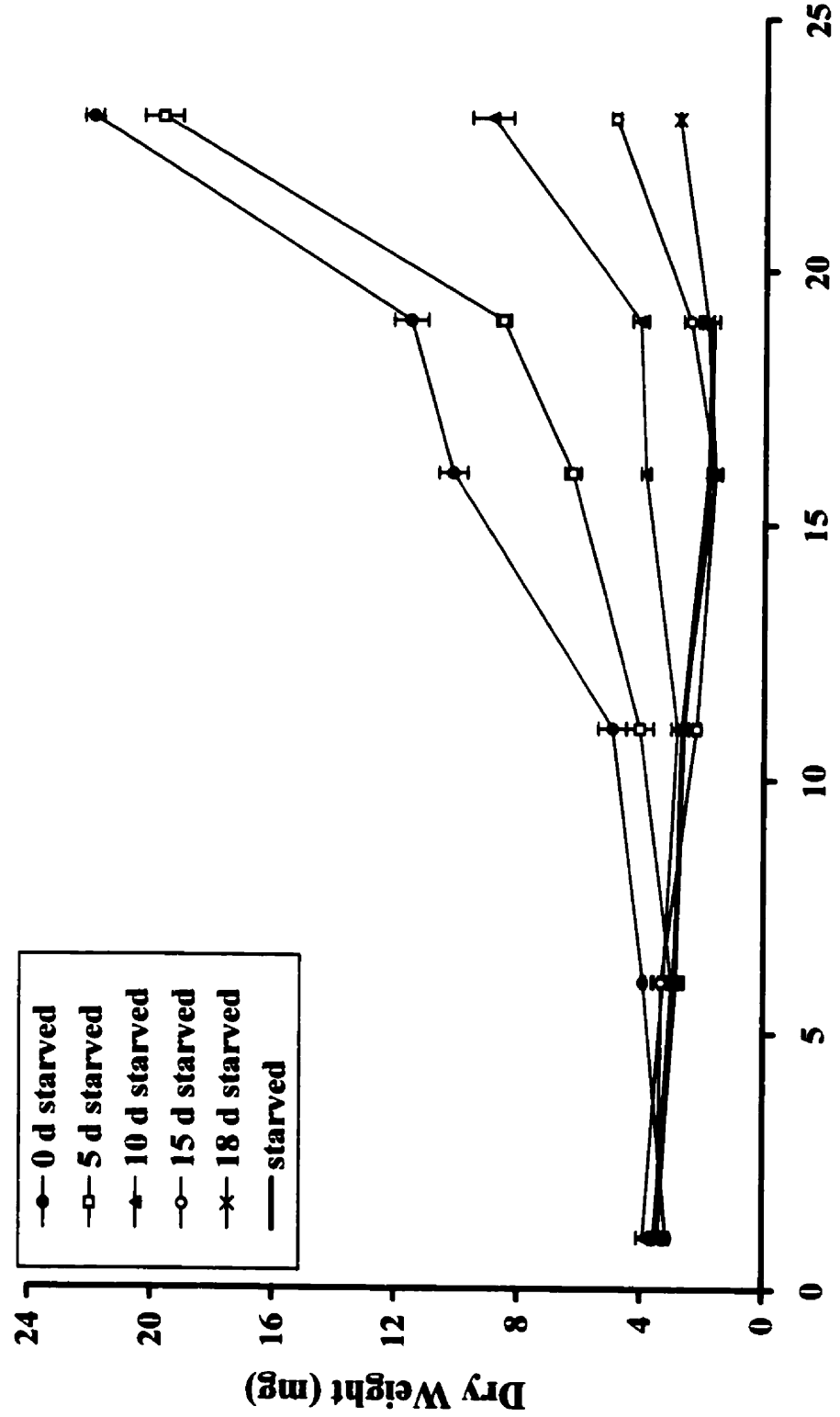
Dry Weight (mg)
24
20
16
12
8
4
0
0
5
10
15
20
25
Experimental Age (d)
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved

Figure 3.2

Figure 3.3 *Survival.* Mean survival for shortnose sturgeon *Acipenser brevirostrum* in delayed feeding treatments over the experimental period. Time to PNR is indicated by an arrow with the amount that fed when food was available. Error bars represent ± 1 standard error.

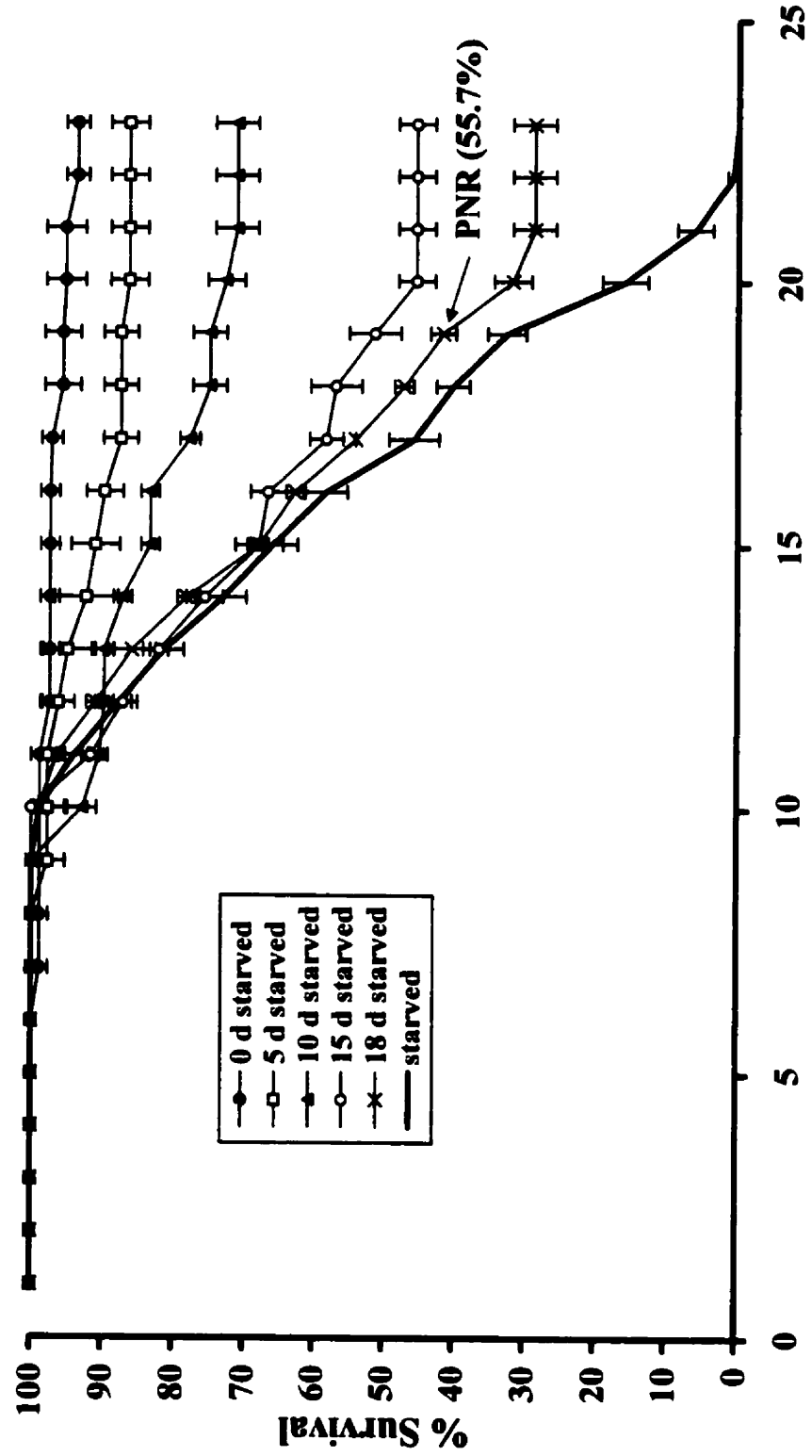
% Survival
Experimental Age (d)
PNR (55.7%)
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25

Figure 3.3

Figure 3.4 *Swimming Activity.* Mean % of larval shortnose sturgeon *Acipenser brevirostrum* in each feeding treatment actively swimming over the experimental period. Horizontal bars with an asterisks (*) indicates those treatments which are significantly different ($P < 0.05$) from unmarked treatment groups at that sample period. Error bars represent ± 1 standard error.

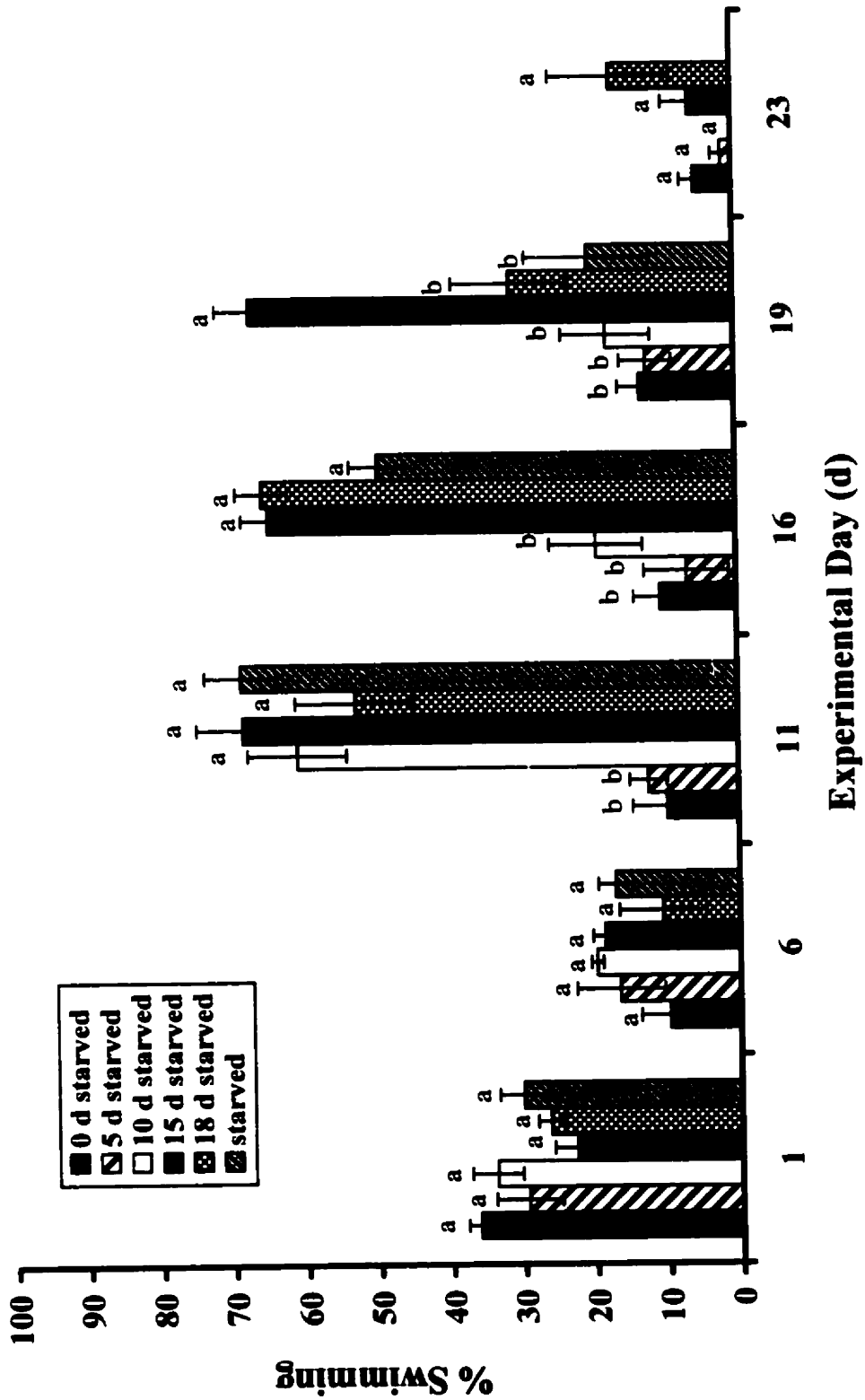
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved
% Swimming
Experimental Day (d)
0
10
20
30
40
50
60
70
80
90
100
1
6
11
16
19
23

Figure 3.4

Figure 3.5 *Swimming Speed.* Mean swimming speeds for larval shortnose sturgeon *Acipenser brevirostrum* in each delayed feeding treatment over the experimental period. Groups with different letters are significantly different ($P < 0.05$) at that sample period. Error bars represent ± 1 standard error.

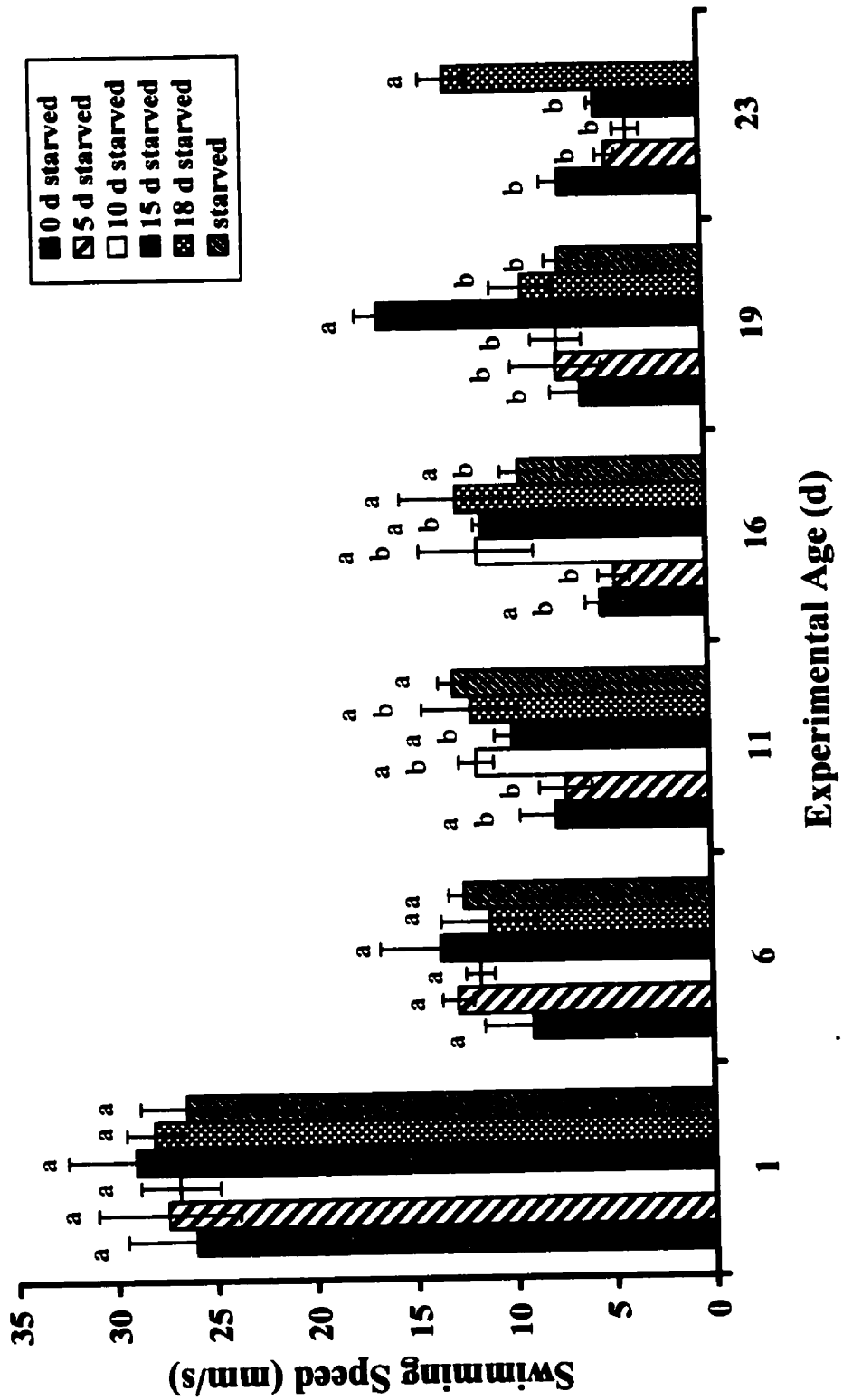
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved
Swimming Speed (mm/s)
Experimental Age (d)
0
5
10
15
20
25
30
35
1
6
11
16
19
23

Figure 3.5

Figure 3.6 *Escape Speed to Tactile Stimulation.* Mean escape speeds for larval shortnose sturgeon *Acipenser brevirostrum* in each delayed feeding treatment over the experimental period. Groups with different letters are significantly different ($P < 0.05$) at that sample period. Error bars represent ± 1 standard error.

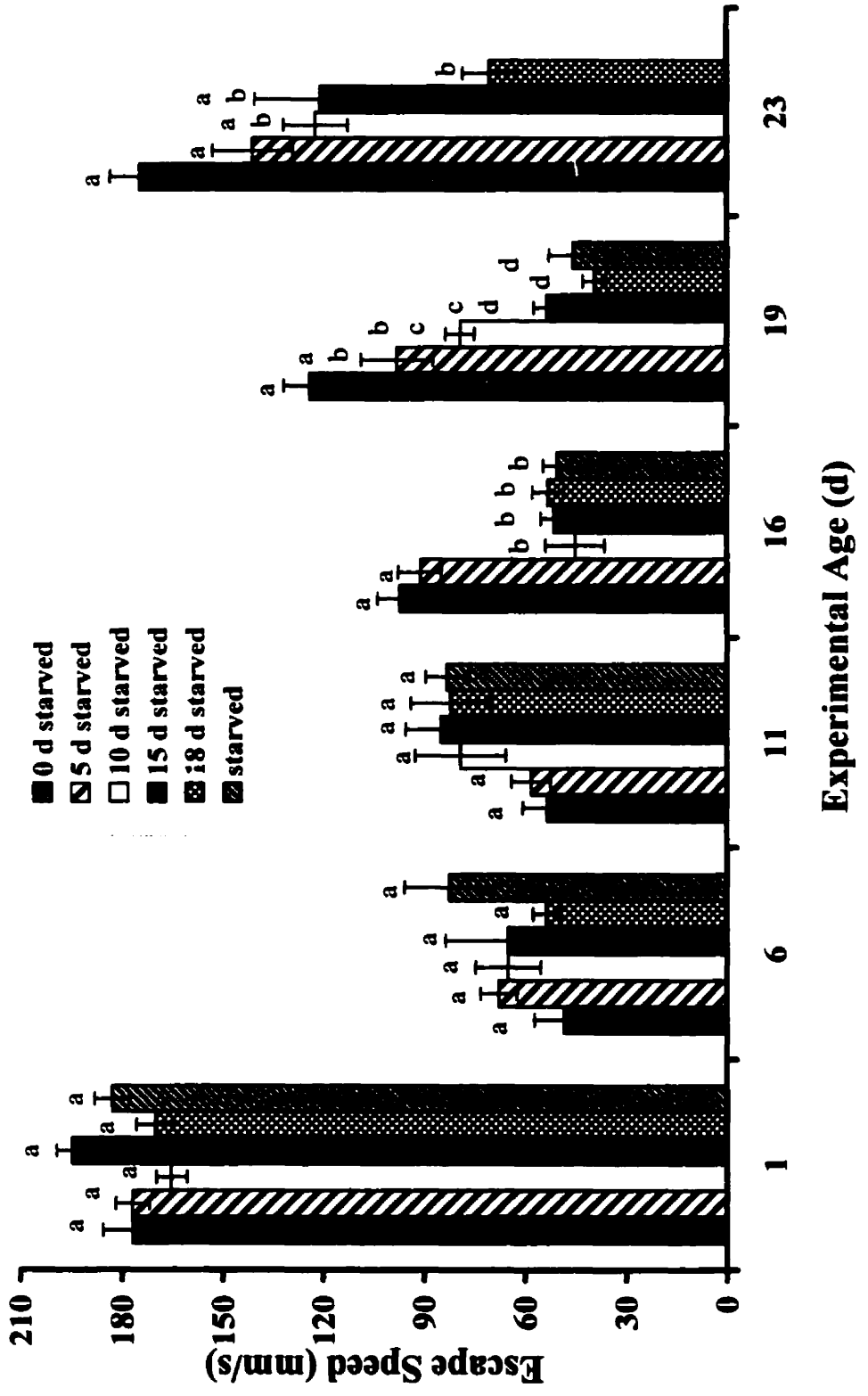
Escape Speed (mm/s)
210
180
150
120
90
60
30
0
1
6
11
16
19
23
Experimental Age (d)
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved

Figure 3.6

Figure 3.7 *Escape Speed to Tactile Stimulation.* Maximum escape speeds for larval shortnose sturgeon *Acipenser brevirostrum* in each delayed feeding treatment over the experimental period. Groups with different letters are significantly different ($P < 0.05$) at that sample period. Error bars represent ± 1 standard error.

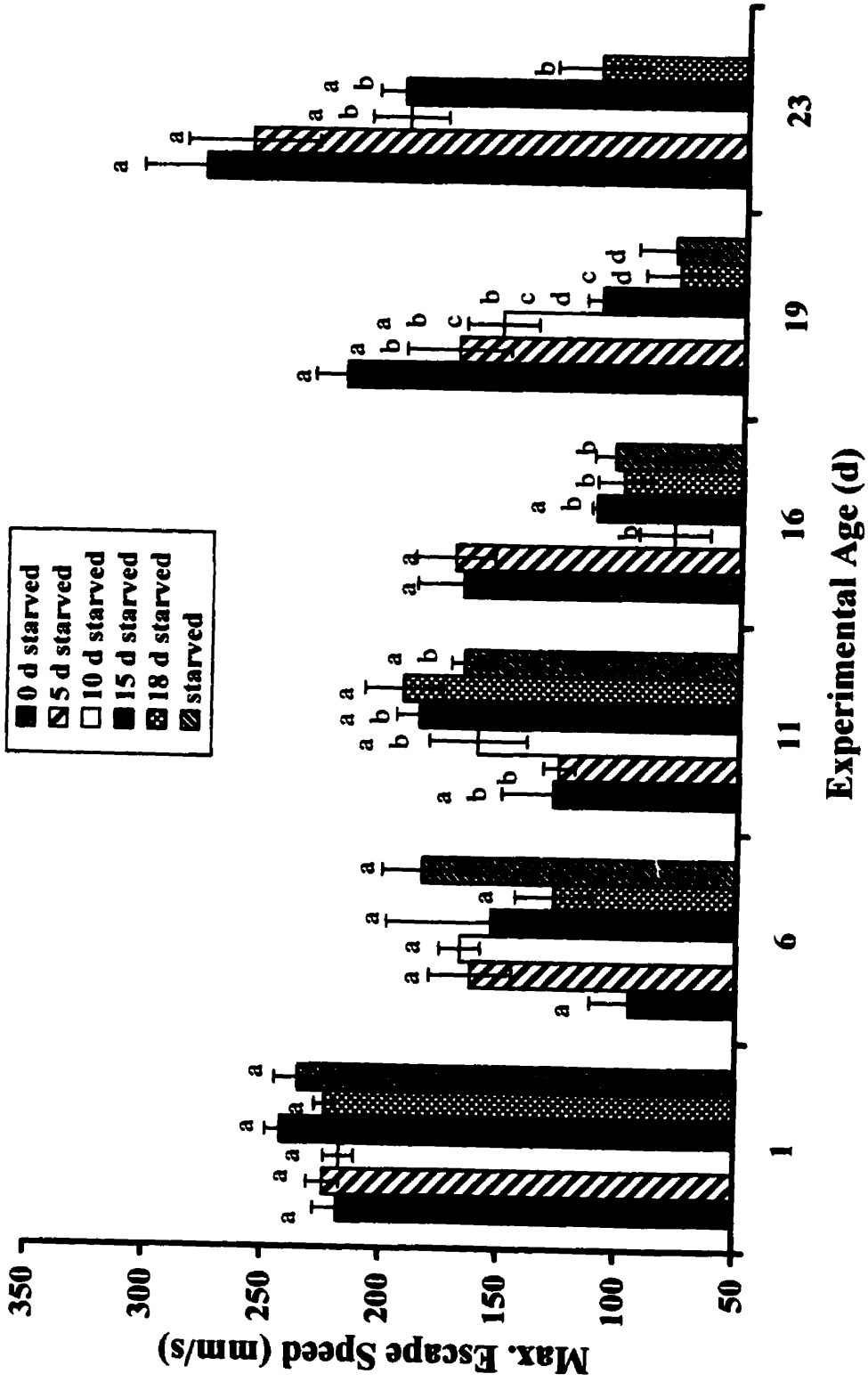
Max. Escape Speed (mm/s)
350
300
250
200
150
100
50
1
6
11
16
19
23
Experimental Age (d)
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved

Figure 3.7

Figure 3.8 *Escape Response to Mechanical Vibration.* Mean % of larval shortnose sturgeon *Acipenser brevirostrum* in each feeding treatment exhibiting escape response (to ball striking side of tank) over the experimental period. Groups with different letters are significantly different ($P < 0.05$) at that sample period. Error bars represent ± 1 standard error.

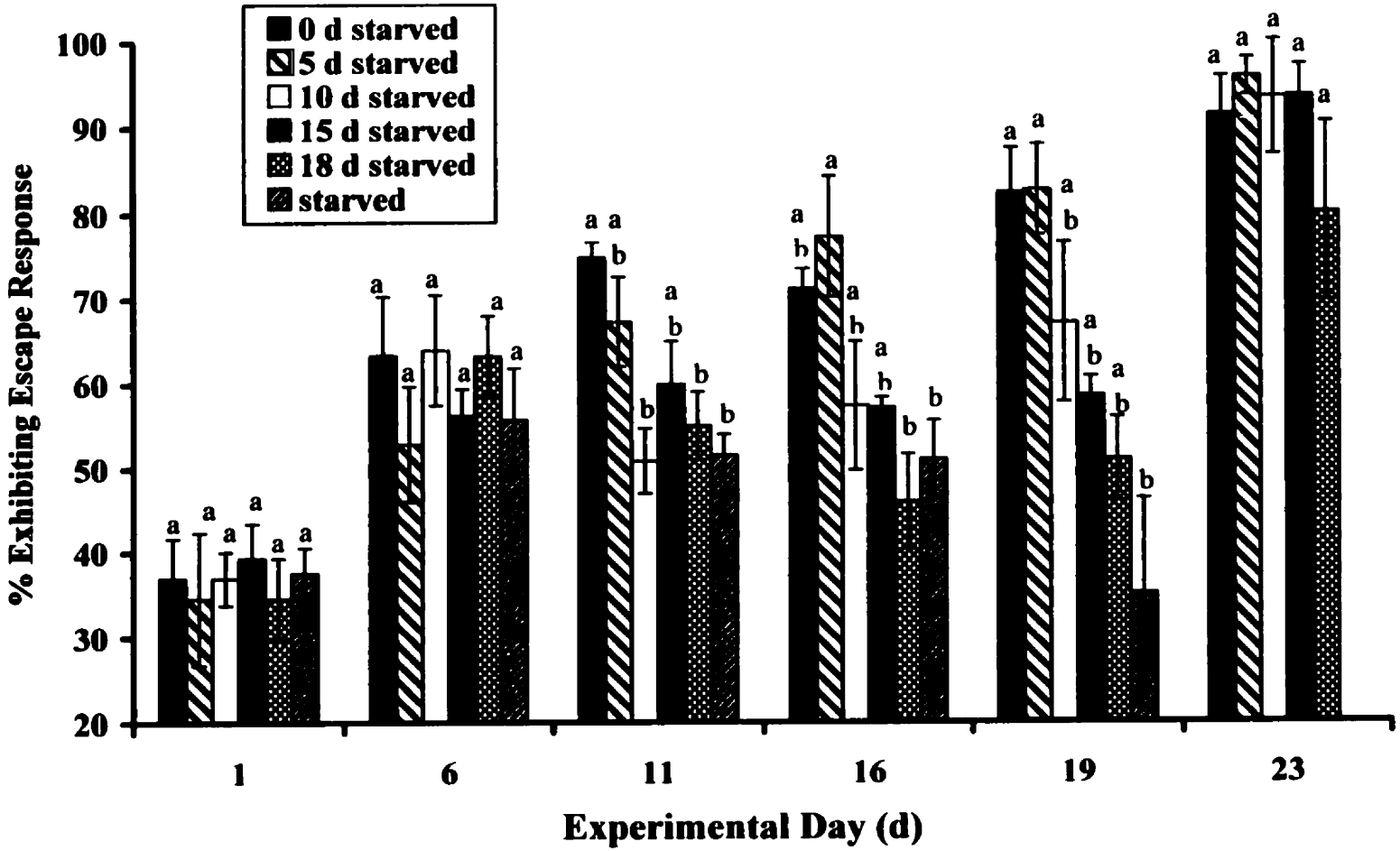
0 d starved
5 d starved
10 d starved
15 d starved
18 d starved
starved
% Exhibiting Escape Response
100
90
80
70
60
50
40
30
20
1
6
11
16
19
23
Experimental Day (d)

Figure 3.8

Chapter 4: Discussion

Temperature and Developing Yolk-sac larvae

Temperature significantly affected timing of development in larval shortnose and Atlantic sturgeon. At low water temperatures, a slow yolk utilization rate, delayed development of escape response, and slow growth through ELH stages, may all contribute to higher risks of predation. In contrast, yolk-sac utilization efficiencies within each species stayed the same between test temperatures. Similar studies of larval white sturgeon *A. transmontanus* reported that conversion of yolk proteins to tissues were similar between 11-17 °C yet were lower at 20 °C (lipid and ash content varied between temperatures; Wang *et al.* 1987). Similar efficiencies may be a very important adaptation for survival of these two species and possibly others as well. Since temperatures normally fluctuate in natural environments, the physiological mechanism in larval shortnose and Atlantic sturgeon which balances yolk partitioning may allow an equal chance of survival. It must be considered, however, that temperature may have a direct affect on the successful functioning of swimming and escape abilities (Batty *et al.* 1986; Shepherd *et al.* 2000). For example, swimming speeds of some fish species are strongly temperature dependent (Fry 1971; Hunter 1981; Fukuhara 1990). Others have attributed differences in escape and swimming speeds to temperature mediated growth (Batty *et al.* 1993). Additional studies (like Shepherd *et al.* 2000) may be required to fully understand how temperature affects the swimming and escape performance, as well as other indirect factors of mortality, of these species.

Temperature may also affect the potential for starvation in natural environments. It has been reported that in cold water years, copepod reproductive timing is delayed,

whereas warm water years result in peaks of prey abundance much earlier relative to the abundance of larval fish (Gotceitas *et al.* 1996). This underlying contributor to 'match' or 'mismatch' of prey items may play an important role in determining larval survival and subsequent recruitment (Cushing 1972). I found that higher rearing temperatures decreased stage durations, including the switch to exogenous feeding and time to 100 % starvation, for both shortnose and Atlantic sturgeon larvae. Depending on seasonal weather conditions, fluctuating river levels below hydroelectric facilities can cause rapid changes in water temperatures (Cushman 1985). For example, low water years, which may result in more water being retained for hydorelectric purposes, may cause an increase in river temperatures. In light of this, it is possible that accelerated development in larval shortnose and Atlantic sturgeon in low water years may result in a 'mismatch' of suitable prey items to occur. Although rapid growth through these stages may reduce the vulnerability to predation by reducing stage durations, it may also result in a critical dependence on suitable exogenous foods due to minimal energy reserves (Taylor and Freeburg 1984). It seems likely that shortnose and Atlantic sturgeon larvae have conditioned a steady rate of development, combined with similar efficiencies and body size, to allow the adequate match of suitable prey items.

Starvation and Growth

Growth of larval shortnose sturgeon following yolk absorption was arrested by starvation, which could give rise to factors of size dependent predation (Bailey and Houde 1989; Miller *et al.* 1988). Larvae SGRs of dry weight in those treatments starved the longest (15 and 18d) were higher than those starved for shorter periods. This may be reflective

of a compensatory mechanism present in larval shortnose after long periods of starvation. It may, however, be an artifact of feeding rate, where those starved the longest simply eat more until satiation (Jobling and Koskela 1996). The latter seems more likely since the SGRs of standard and dry weight of those treatments starved the least were all significantly higher at the end of the experiment.

It is also important to keep in mind that growth of larval fish is limited by their ability to capture and process prey items (Grover and Olla 1986). Since swimming speeds are shown to be lowered in many species during food deprivation (Chick and Van Den Avyle 2000; Jonas and Wahl 1998) the difficulty in prey capture must be considered. Artemia spp. *nauplii* (used in this experiment) are less in nutritive value (Bolla 1989) and easier for a larva capture than copepod *nauplii*, primarily due to their larger size, slower swimming ability, and bright coloration (Fulton and Wear 1985; Drost *et al.* 1988). As a result, the increase in swimming speeds required to successfully capture these faster and more translucent natural prey items, may deplete valuable energy needed during this time. Further study is needed to identify such interactions with natural prey items of larval shortnose, as well as spatial and temporal concentrations of prey items on nursery grounds.

Starvation and Vulnerability to Predation

The extent to which larval fish are able to effectively forage, avoid predator attacks, and resist long periods of food deprivation may determine the probability of long-term survival through ELH stages (Jonas and Wahl 1998). In addition, there is increasing evidence that fish take an active role in determining outcomes for their

survival. For example, despite increasing the risks of predation, fish show the ability to increase activity levels to locate prey items in order to avoid starvation (Blaxter and Ehrlich 1974; Rice *et al.* 1987). Therefore, in the presence of food deprivation, larvae may be faced with some potentially conflicting survival strategies: 1) reduce all metabolic expenditures to conserve energy while maintaining a high level of escape capability; 2) maintain high risk responsiveness as well as increase search speeds and activity levels to increase chances of finding a food source; 3) reduce activity levels as well as responsiveness to predators to conserve energy; or 4) increase activity levels to find a food patch, yet make a trade-off by lowering risk responsiveness. The strategies adopted by shortnose sturgeon larvae changed depending on the degree of starvation. For example, those larvae completely deprived of food exhibited increasing levels of activity with increasing degree of starvation, while risk responsiveness (through swimming and escape abilities) was maintained until PNR. This may be strategy utilized in order to reduce predatory threat, while increasing the means by which food is located. Directly following feeding, however, larvae reacted quite differently depending on the length of starvation. Behavior following feeding shifted from low activity levels, combined with low risk responsiveness, in those larvae starved short periods, to higher activity levels and risk responsiveness as starvation progressed. Beyond the first feeding stage, however, most fed larvae reduced their activity levels and swimming speeds, while greatly increasing escape speeds to the end of the experiment. Since shortnose larvae hatch in swift current environments, it makes sense that a larva may need to reduce swimming speeds and activity, once food is located, in order to remain in a food patch.

Since escape velocity is very important in determining the outcome of predatory attacks (Browman *et al.* 1989; Fuiman 1989), the escape abilities of shortnose, relative to other species, may be very important in determining survival. Shortnose exhibited similar swimming and escape speeds as a number of species with common ELH stages. For example, the swimming and mean and maximum escape speeds of larval shortnose in normally fed treatments were as high as 1.4 $BL \cdot s^{-1}$, 11.4 $BL \cdot s^{-1}$, and 19.4 $BL \cdot s^{-1}$ respectively. This is similar to the 0.9-1.2 $BL \cdot s^{-1}$ swimming speeds of larval striped bass *Morone saxatalis* (Chick and Van Den Avyle 2000), as well mean and maximum escape speeds of 5.7-8.6 $BL \cdot s^{-1}$ and 12.1 to 16.1 $BL \cdot s^{-1}$ reported for several other marine fish species (Yin and Blaxter 1987a). These findings contradict the assertion that sturgeon possess relatively poor acceleration ability and should be considered "slow" fish (Gershanovich and Taufik 1992). This is also not likely, since the environment these fish are located requires the ability to maintain position or swim against swift currents.

Species Comparison: Atlantic and Shortnose

At all stages of development, shortnose were significantly larger in size than Atlantic sturgeon larvae reared at the same temperatures. In addition, shortnose were more resistant to starvation than Atlantic larvae at different rearing temperatures. This is to be expected since starvation resistance increases with larger egg size and larger larval size at hatch (Rana 1985). Since shortnose spawn at much cooler temperatures and lower food productivity during the spring, larger larval sizes will allow shortnose to survive longer until warmer temperatures afford a match with suitable prey items. This phenomenon may be unique in these two species, since it has been suggested that many sturgeon

species, spawning at very similar temperatures, despite geographic location, have not yet evolved the mechanisms to temporally separate spawning activities (Detlaff *et al.* 1981).

The larger size of shortnose at hatch may also have advantages such as increased survival (Hare and Cowen 1997), wider range of prey sizes (Hunter 1981), as well as, better predator avoidance capabilities (Bailey 1984; Miller *et al.* 1988). However, larger larvae may have greater chances of encountering or being detected by predators (Bailey and Houde 1989; Litvak and Leggett 1992; Pepin *et al.* 1992). At lower rearing temperatures (13 and 15 °C), however, shortnose absorbed their yolk at a faster rate than Atlantic larvae, and were less efficient in converting such energy into tissue. As a consequence of higher metabolic demands, larger larvae tend to experience a decline in efficiency with continuing development (for reviews see Kamler 1992). Therefore lower efficiencies in shortnose are to be expected since they were larger at all developmental stages. This also may reflect a difference in yolk quality between the two species. It has been reported that marine species retain more protein for growth (Kamler 1992) than freshwater species. Since mature Atlantic sturgeon spend most of their time in a marine environment, the maternal influence on egg yolk quality may result in higher caloric value than that of shortnose, resulting in more body tissue incorporated as the yolk is utilized.

Vulnerability of Sturgeon to Predation

With a large body size, tough leathery skin and bony scutes sturgeon are relatively well equipped at the juvenile and adult stage to withstand starvation and attacks from predators (Cech *et al.* 1984). In addition, the presence of *tepeta lucida* (reflecting layers)

in the sturgeons eyes, coupled with rosteral barbels, allow the sturgeon to feed at night or in extremely turbid environments (Cech *et al.* 1984). This may also reduce attacks from visual predators (including avian attacks). Since starvation and predation may be insignificant in the late juvenile through adult stages, it makes sense that the survival through the ELH stages of larval sturgeon may be more important in determining the strength of a year-class. The studies conducted here were performed in an effort to understand and identify potential factors of mortality in the ELH stages of shortnose and Atlantic sturgeon. These results provide much information, indicating that water temperature as well as periods of food deprivation may significantly affect (directly or indirectly) survival and subsequent recruitment strategies of these two species. It is important to consider, however, that these effects may be more significant in wild sturgeon populations due to high energetic costs of swimming against large swift currents (0.4-1.8m sec^{-1}; for reviews see Kynard 1997), avoiding predation, and securing suitable nursery and foraging habitats (Bestgen 1996). The ability of sturgeon to produce such vast numbers of eggs (e.g. shortnose: 30,000-200,000 eggs, Dadswell 1979; Atlantic: 1-2 million eggs, Smith 1985) may be a recruitment strategy to off-set ELH mortality.

Additional Research Needs

Due to the patchiness of prey items in time and space, periods of food deprivation are common among fish resulting in high mortality through starvation (Cushing 1972; Theilacker 1986; Mehner and Wieser 1994). Starvation is a continuous phenomenon persisting over relatively long periods which results in mortality directly through death, or indirectly through starvation mediated predation (Taggart and Leggett 1987). The

ability of larval shortnose sturgeon to withstand such an extended period of food deprivation immediately following full absorption of endogenous energy reserves may be an ecological adaptation to survive periods of low or patchy food distribution, not uncommon in natural environments. While identifying possible relationships between temperature, starvation and potential predation are very important, other factors such as food quality and abundance, predator abundance, and interspecific competition may also prove to be just as important in determining survival through ELH stages (Gotceitas *et al.* 1996). All of these factors including the ones presently investigated may interact to some degree, with some being more dependent than others (Letcher *et al.* 1996). Therefore, it is necessary to further examine interactions of these agents of mortality in order to make useful assumptions on the year-class formation strategies in larval shortnose and Atlantic sturgeon.

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