Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus**

David H. Secor
Troy E. Gunderson
Chesapeake Biological Laboratory
Center for Environmental and Estuarine Studies
The University of Maryland System
P.O. Box 38, Solomons, Maryland 20688-0038
E-mail address: secor@cbl.umces.edu

Abstract.—Hypoxia in Chesapeake Bay has increased during the past century, coincident with the disappearance of Atlantic sturgeon spawning stocks. We hypothesized that Atlantic sturgeon young-of-the-year (YOY) might be more susceptible than other estuarine fishes to high temperature and low oxygen conditions, now prevalent in Chesapeake Bay. Atlantic sturgeon (10–70 g) were reared under conditions of hypoxia (2–3 mg/L dissolved oxygen) and normoxia (6–7 mg/L) at 19°C and 26°C for 10 days. High-temperature hypoxia resulted in lower survival (mean=6.3%) and respiration rate (mean=0.136 mg O_2/(g·h)). Low-temperature hypoxia resulted in a mean survival of 78% and mean respiration rate of 0.212 mg/(g·h). Under hypoxia, mean weight-specific growth rate was 1.27%/d, ca. threefold less than growth under normoxia. Temperature alone did not significantly affect growth rates. When sturgeon were denied access to the surface, growth rates were significantly diminished in both normoxic and hypoxic treatments. At low ambient oxygen levels and high temperature, denial of surface access was fully lethal within 30 hours. We conclude that increased incidence of summertime hypoxia during this century has degraded sturgeon nursery habitats in Chesapeake Bay.

Manuscript accepted 6 October 1997.
Fishery Bulletin 96:603–613 (1998).

An economically important population of Atlantic sturgeon, *Acipenser oxyrinchus*, once inhabited Chesapeake Bay. During the late nineteenth century, Chesapeake Bay supported the second greatest caviar fishery in the eastern United States (Murawski and Pacheco, 1977). In the early 1900s, the population collapsed. In Maryland, fishery landings declined from 74,500 kg, in 1904, to 320 kg in 1920 (Hildebrand and Schroeder, 1928). Atlantic sturgeon have not recovered in Chesapeake Bay (Spier and O'Connell, 1996). The last fish legally harvested in Chesapeake Bay, a mature female, was captured in 1970 from the Potomac River. The spawning population of Atlantic sturgeon may have been extirpated from Chesapeake Bay (Speir and O'Connell, 1996; Grogan and Boreman[1]).

State, federal, academic, and nonprofit organizations have begun to mobilize public interest and support for an aquaculture-based restoration program for Atlantic sturgeon in Chesapeake Bay. A principal assumption for Atlantic sturgeon restoration is that deleterious conditions that led to the extirpation of the population (e.g. loss of habitat or over fishing) are now abated. Therefore, it is critical to evaluate possible causes for Atlantic sturgeon extirpation from Chesapeake Bay before state and federal agencies move forward with a large-scale aquaculture-based restoration program.

We hypothesize that increased hypoxia in Chesapeake Bay resulted in reduced habitat for Atlantic sturgeon and contributed to their decline. During this century, periodic increases (albeit small) in Atlantic sturgeon abundances have occurred in the southern and northern extent of the species' range (Murawski and Pacheco, 1977). However, no evidence exists for periodic recoveries of Atlantic sturgeon in Chesapeake Bay. The period of population decline and low abundance in Chesapeake Bay corresponds to a period of poor water quality, from 1950 to present, caused by increased nutrient loading and increased spatial and temporal frequency of hypoxia (Officer et al., 1984; Mackiernan, 1987; Jordan et al., 1992; Kemp et al., 1992; Cooper and Brush, 1993).

* Contribution 3060 of the Chesapeake Biological Laboratory, Center for Environmental Science, University of Maryland, Solomons, MD 20688-0038.

[1] Grogan, C. S., and J. Boreman 1997. Determining the probability that historical populations of fish species are now extirpated. Unpubl. manuscr., U. Mass. Amherst, MA, 25 p.

The goal of the study was to investigate the effects of dissolved oxygen and temperature on growth, survival, and respiration of juvenile (young-of-the-year) Atlantic sturgeon. High temperatures are known to amplify negative effects of hypoxia on growth and survival of estuarine fishes (Coutant, 1985). Habitats in Chesapeake Bay that satisfy both temperature and dissolved oxygen (DO) preferences of Atlantic sturgeon may be limiting during the summer as have been demonstrated for striped bass (Coutant and Benson, 1990; Brandt and Kirsch, 1993). In this study we define hypoxia as oxygen concentrations <4.0 mg/L. Hypoxia has been defined previously as <2 mg/L for Chesapeake Bay (Phil et al., 1991; Harding et al., 1992), an ambient oxygen level that is detrimental to benthic infaunal production. This definition, however, may be too stringent for fishes because oxygen concentrations at this level are often lethal (Brett, 1970; Jordan et al., 1992).

A nested-multifactorial experiment was designed to investigate the effects of temperature and dissolved oxygen on growth, respiration, and survival of young-of-the-year Atlantic sturgeon. During the course of our experiments we observed that fish in hypoxic conditions frequently surfaced, often breaking the surface of the water with their snout. Therefore we included surface access as a third factor in our investigation—whether this behavior might benefit growth and survival under conditions of oxygen stress.

Methods

Experimental material

Juvenile Atlantic sturgeon were obtained from the U.S. Fish and Wildlife Service, Northeast Fishery Center, Lamar, Pennsylvania (Hendrix, 1995). During June 1995, Center personnel collected a large female (2.4-m total length) and three male Atlantic sturgeon from the Hudson River near Hyde Park (River km 135). Fish were transported to the Center for artificial spawning and for larval rearing. Larvae and early juveniles were reared at the Center at 17°C and 1 ppt salinity. A failure in the water heating system at the Center caused juveniles, age 45 to 60 days after hatching, to experience low water temperatures, ca. 10°C. At 60 days after hatching, 500 juveniles (0.3–2.0 g wet weight) were transported in an oxygenated container to Chesapeake Biological Laboratory and acclimated to 19°C and 2 ppt salinity over a 10-d period. Juveniles were reared in sixteen 40-liter tanks and fed Biokyowa© fry feed (700–2000 μm diameter) ad libitum until they were ca. 5 grams wet weight (>10 cm total length) and large enough to be handled with little or no stress for scute-clips (see below).

Nested growth and survival experiments

A nested multivariate experiment (Fig. 1) evaluated survival and growth rates in relation to access to surficial water (sealed or unsealed tank), temperature (~20°C and ~26°C), dissolved oxygen (~3 mg/L or ~7 mg/L), and tank replication. The nested design directed the analysis of variance to occur in hierarchical order at four levels. The model of the nested design for growth rate was

$$y_{ijklm} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \theta_{\lambda(ijk)} + \varepsilon_{(ijkl)m},$$

where y_{ijklm} = the growth rate response by individual juveniles;
μ = overall mean;
τ_i = the effect of the ith surface access category;
$\beta_{j(i)}$ = the effect of the jth temperature;
$\gamma_{k(ij)}$ = the effect of the kth oxygen level;
$\theta_{l(ijk)}$ = the effect of the lth tank (replicate); and
$\varepsilon_{(ijkl)m}$ = the random error component.

The model of the nested design for survival rate was

$$S_{ijkl} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{l(ijk)},$$

where S_{ijkl} = the arcsine-transformed survival rate for each replicate.

Statistical significance for factors was accepted at $\alpha = 0.05$ (type-I sum of squares for type-I error). To remove possible effects due to differences in fish size among experiments and experimental levels, initial fish weight was included in ANOVAs as a covariate. Calculations of variances and significance tests were performed by using PC-SAS, PROC NESTED (SAS, 1982). Survival data were arcsine transformed to meet assumptions of normally distributed error.

Four 10-day experiments were conducted under the four combinations of surface access, temperature, and dissolved oxygen, each replicated twice. In the high-temperature hypoxia treatments, high mortality was observed. Because we wished to have greater confidence in associating low survival with high-temperature hypoxia, we repeated the treatments with surface access and high temperature (at both low and high DO levels) for a total of four replicates (Fig. 1).

Experimental tank dimensions were 78-cm diameter, 46-cm height, and 220-liter volume. External

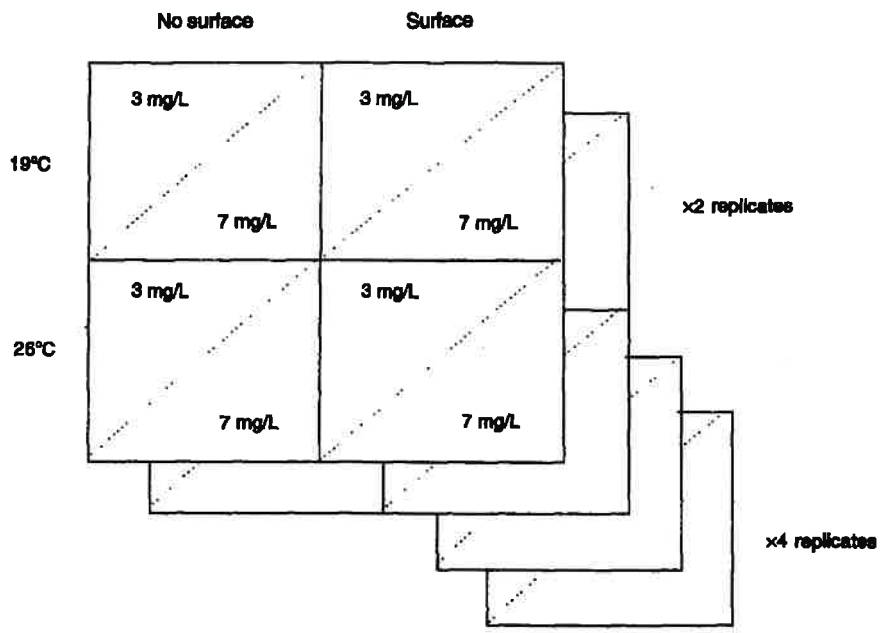

Figure 1

Nested experimental design. Replicates are presented as layers. Dissolved oxygen rates (3 or 7 mg/L) were nested within temperature and surface access levels.

stand-pipes for flow-through water allowed sturgeon to use the entire bottom surface. During the experiments clear plexiglass lids were attached to the tanks with clamps and duct tape. A large hole (5-cm diameter) in each lid, fitted with a stopper, permitted access to the tank for feeding of fish, for periodic checks of water quality, and for removal of dead individuals. Hoses for air and water supply also passed through the lid. In the tanks that permitted access to the air-water interface, water level was maintained at 5 cm below the lid. In treatments designed to limit access to the surface, lids were sealed to the tank and tanks were filled completely. Two head tanks delivered water at either 19°C or 26°C to experimental tanks, each maintained at a rate of 1.2 –1.5 L of flow-through water/min. Dissolved oxygen was controlled by maintaining hypoxic conditions in head-tanks and by adding aeration directly to normoxic treatment tanks. Hypoxic levels (2.5–3.0 mg/L) were maintained in head-tanks by mixing hypoxic well water (<2 mg/L) with oxygenated Patuxent estuary water (6 mg/L). Thus, salinity varied slightly between experiments but was always within the range 1.5–3 ppt. When necessary, water was aerated to bring oxygen levels to 2.5 mg/L in the head-tank. Normoxic treatment water was a mixture of well water and Patuxent estuary water. Dissolved oxygen levels were well mixed (homogenous) in the tanks owing to their shallow design, flow-through water, and constant swimming of YOY sturgeon. Lighting was provided on a 12:12 h light:dark cycle.

With the exception of the 26°C and no-surface-access treatment, temperature and oxygen concentrations were maintained within 10% of their prescribed levels (19 or 26°C, 3 or 7 mg/L). In the 26°C sealed experiment, aeration supplied to the head-tank was insufficient to attain oxygen conditions close to 7 mg/L for the normoxic treatment (mean replicate dissolved oxygen concentrations were 5.10 and 5.25 mg/L). In the hypoxic sealed treatment (mean replicate dissolved oxygen concentrations were 3.76 and 4.44 mg/L), dissolved oxygen was deliberately held above 3 mg/L because this level with high temperature had been observed previously to be lethal in unsealed tanks. Despite these elevated "hypoxic" conditions, the combination of high temperature and low oxygen was fully lethal in the sealed tanks (see below).

Juveniles (8 to 30 grams wet weight) were acclimated to experimental conditions over a 4-d period. On day 0 of each experiment, lengths and wet weights (juveniles weighed in water on a top-loading balance) were recorded and a dorsal scute(s) clipped to identify each individual. In preliminary trials, we found that scute clips did not significantly affect growth

rate. Regeneration of the scute did not obscure the clip during the 10-d experiments. Six to eight juveniles were placed in each experimental tank and fed the formulated diet (2-mm pellets) at 2.5% body weight per day. Fish were fed at 06:00, 10:00, 14:00, 18:00, and 20:00 h. Water quality was checked during feeding times and any remaining food or feces were siphoned prior to feeding. Food amounts were adjusted when mortalities occurred. On day 10 of the experiment, individual weights and lengths were recorded. Weight-specific absolute and instantaneous growth rates were determined for the experimental period according to Ricker (1975). In instances where juveniles died before the end of the experiment, individuals surviving >3 days of experimental conditions were included in the analysis of treatment effects on growth.

Respiration experiment

Respiration was estimated over a 42-h period for four combinations of temperature (19 or 26°C) and dissolved oxygen (~3 or ~7 mg/L) each replicated once. Juveniles were acclimated for a 4-day period and starved 12 h prior to the start of respiration measures. Seven juveniles were weighed (in water) and placed in each tank "respirometer." The tanks were sealed (no air gap). Oxygen levels were maintained by aerating the head-tanks, rather than each experimental tank. There was no feeding during the 42-h experiments. Inflow and outflow temperature, salinity, oxygen content, and flow rate were measured in experimental and control "blank" tanks (Cech, 1990) at 06:00, 10:00, 14:00, 18:00 and 22:00.

Experimental conditions of temperature were maintained within 1°C of the prescribed treatment level (19 or 26°C) (Table 1). Oxygen levels varied substantially from the prescribed levels between temperatures. For the hypoxic treatments, oxygen was provided at significantly higher levels (P=0.001) at 26°C (4.09 ±0.07 mg/L) than at 19°C (2.51 ±0.05 mg/L). This was intentional because survival and growth experiments had shown that DO levels <3.5 mg/L in concert with high temperature were lethal. Despite this precaution, all fish at 26°C and at low oxygen level perished within 24 hours. At the high-level DO treatments, oxygen conditions were ca. 1 mg/L higher at 19°C than at 26°C. Total biomass of the 7 fish per tank ranged from 157.6 to 248.2 grams (Table 1).

Respiration (i.e. oxygen uptake) was estimated (Cech, 1990) as

$$R = (M_E - M_C)/B$$

$$M_{E,C} = ((C_I - C_O)V$$

where R = weight-specific O_2 consumption rate (mg O_2/(g·h);

$M_{E,C}$ = O_2 consumption rate in experimental E or control C tanks (mg O_2/h);

B = combined wet weight (biomass) of sturgeon juveniles (g);

C_I = O_2 concentration in inflowing water (mg O_2/L);

C_O = O_2 concentration in outflowing water (mg O_2/L); and

V = water flow rate (L/h).

Results

Survival

Deaths were observed only in hypoxic treatments (Table 2). At hypoxic level, survival was substantially lower at 26°C (mean=6.3% survival) than at 19°C

Table 1

Replicate tank environmental conditions and respiration rates (mean ± standard error) for respiration experiment. Dissolved oxygen (DO) levels, low or high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Inflow oxygen and tank temperature refer to actual conditions provided to tanks. Biomass is the total initial weight of the seven sturgeon used in each replicate.

Temperature level	DO level	Inflow oxygen mg/L	Tank temperature	Biomass (g)	Respiration rate mg O_2/g·h
26°C	Low	3.762 ± 0.163	25.20 ± 0.04	216.6	0.175 ± 0.042
		4.436 ± 0.209	25.34 ± 0.02	181.3	0.103 ± 0.030
	High	6.310 ± 0.075	25.54 ± 0.02	188.1	0.245 ± 0.028
		6.259 ± 0.088	25.47 ± 0.02	179.6	0.307 ± 0.020
19°C	Low	2.536 ± 0.029	19.51 ± 0.02	196.3	0.202 ± 0.028
		2.495 ± 0.020	19.43 ± 0.02	157.6	0.214 ± 0.022
	High	7.361 ± 0.060	19.73 ± 0.06	189.5	0.228 ± 0.028
		7.273 ± 0.058	19.67 ± 0.04	249.2	0.207 ± 0.020

Table 2

Replicate tank deaths during the nested survival and growth experiment. Experiments are labeled according to the temperature treatment and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Rep. = replicate(s).

Experiment	DO level	Rep.	Experimental day 1	2	3	4	5	6	7	8	9	10	Survival (%)
26°C unsealed 1	Low	1			6	1	1						0
		2			2		4					2	0
		3		4			1	2	1				0
		4				1		1		1	1		50
26°C unsealed 2	High	1											100
		2											100
		3											100
		4											100
26°C sealed	Low	1	8										0
		2	7	1									0
	High	1											100
		2											100
19°C unsealed	Low	1			1		1						75
		2			1			1					75
	High	1											100
		2											100
19°C sealed	Low	1							1				88
		2						1	1				75
	High	1											100
		2											100

(mean=78.3% survival). No significant difference was found in overall survival rate between sealed and unsealed tanks (P=0.54). In unsealed tanks, deaths were distributed throughout the 10-d experimental period. In the 26°C sealed-hypoxic level tanks, all individuals succumbed within the first 30 hours of the experiment. Moribund sturgeon were observed at the air-water interface in unsealed tanks, or just below the lid in sealed tanks. Fin margins of dead individuals were perfused with blood, an indicator of oxygen deprivation (Jobling, 1995).

Growth

Across replicates, growth rates ranged in weight from 0.3% to 5.1% per day (Table 3). Sturgeon experienced positive growth in weight and length under all experimental conditions. Initial mean weights and lengths varied substantially among experiments; range was 10.94 to 69.20 g in weight and 14.59 to 26.60 cm in length. Absolute growth in weight was positively related to initial size (regression analysis; P<0.01); tanks with fish having initial mean weights greater than 50 g showed the highest absolute growth rates (>1.0 mg/d). Because initial size covaried with growth rate, initial weight was used as a covariate in statistical analyses of treatment effects.

Analysis of variance of instantaneous growth rate showed significant effects due to surface access and oxygen level (Table 4); temperature, replicate, and individual fish did not explain significant variance, although at 7 mg/L DO there was a trend for lower growth rates at 26°C than at 19°C (Fig. 2, Table 3). Mean growth rates were 2.9 times less at 3 mg/L (1.27%/d) than at 7 mg/L (3.62%/d). Sealed tanks showed consistently lower growth rates than those with surface access. The effect was greatest at 3 mg/L oxygen. Only 0.3%/d weight-specific growth was observed in the 19°C sealed tanks, and all fish perished before growth determinations could be made in the 26°C sealed tanks. Absolute growth in weight was significantly affected by surface access, temperature, surface access in combination with temperature interaction, and by oxygen level. Absolute growth rate was higher when surface access was allowed and at the higher DO level; absolute growth rate was inversely related to temperature.

Respiration

Respiration rates measured over the entire experiment ranged from 0.05 to 0.55 mg O_2/(g·h) (Fig. 3). Respiration rates were normally distributed for the high oxygen treatment with a mean of 0.245 ± 0.013

Table 3

Growth rates (mean ± standard error) of Atlantic sturgeon during the laboratory experiment. Growth rates in weight and length are instantaneous rates. Absolute growth rates in weight is presented under the heading mg/d. Experiments are labeled according to the temperature level and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. *n* = number of individuals in each tank. Rep. = replicate(s).

Experiment	DO level	Rep.	Growth rate in weight (per day)	mg/d	Growth rate in length (per day)	*n*
26°C unsealed	Low	1	0.023 ± .006	0.345 ± 0.094	~0	2
		2	0.013 ± 0.003	0.202 ± 0.056	~0	6
		3	0.006 ± 0.005	0.093 ± 0.062	0.003 ± 0.001	4
		4	0.029 ± 0.019	0.324 ± 0.192	0.003 ± 0.001	8
	High	1	0.037 ± 0.004	0.524 ± 0.076	0.010 ± 0.001	8
		2	0.037 ± 0.006	0.643 ± 0.116	0.012 ± 0.002	8
		3	0.036 ± 0.007	0.587 ± 0.112	0.012 ± 0.002	8
		4	0.036 ± 0.004	0.789 ± 0.117	0.015 ± 0.001	8
26°C sealed	Low	1	Lethal			0
		2	Lethal			0
	High	1	0.029 ± 0.001	2.220 ± 0.059	0.006 ± 0.001	6
		2	0.025 ± 0.001	2.015 ± 0.178	0.007 ± 0.001	6
19°C unsealed	Low	1	0.013 ± 0.002	0.185 ± 0.029	0.005 ± 0.001	7
		2	0.011 ± 0.003	0.129 ± 0.037	0.005 ± 0.001	7
	High	1	0.050 ± 0.005	0.721 ± 0.057	0.014 ± 0.001	8
		2	0.045 ± 0.002	0.719 ± 0.044	0.015 ± 0.001	8
19°C sealed	Low	1	0.003 ± 0.001	0.072 ± 0.030	0.004 ± 0.001	8
		2	0.003 ± 0.001	0.071 ± 0.031	0.004 ± 0.001	8
	High	1	0.028 ± 0.003	1.887 ± 0.253	0.009 ± 0.001	6
		2	0.031 ± 0.002	2.270 ± 0.197	0.008 ± 0.001	6

Table 4

Nested analysis of variance of surface access, temperature, oxygen level, replicate and individual effects on growth rate. Initial weight was used as a covariate in the analyses. Sealed refers to whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Designated temperature and oxygen levels were 19°C and 26°C, and 3 mg/L and 7 mg/L, respectively. Factors in parentheses indicate the nesting procedure. For example "Oxygen (Sealed-Temperature)" refers to variance explained by oxygen level nested within combinations of surface access and temperature.

Type of variable	Variable	df	Sum of squares	Significance level (*P*)
Instantaneous growth rate in weight				
Covariate	Initial weight	1	0.3892	0.0001
Class variables	Sealed	1	0.0392	0.019
	Temperature (sealed)	2	0.0086	0.54
	Oxygen (sealed-temperature)	3	0.0981	0.0039
	Tank (sealed-temperature-oxygen)	7	0.0097	0.99
	Individual (sealed-temperature-oxygen-tank)	14	0.0077	0.99
Absolute growth rate in weight				
Covariate	Initial weight	1	0.0839	0.0001
Class variables	Sealed	1	0.0445	0.0001
	Temperature (sealed)	2	0.0523	0.0002
	Oxygen (sealed-temperature)	3	0.7734	0.0001
	Tank (sealed-temperature-oxygen)	7	0.0293	0.17
	Individual (sealed-temperature-oxygen-tank)	14	0.0194	0.92

mg O_2/(g·h). In relation to the high oxygen treatment, hypoxic oxygen treatment respiration rates were skewed towards lower rates with a mean of 0.174 ±0.016 mg O_2/(g·h). Two individual tank respiration rates for the hypoxic treatment were exceptionally high (Fig. 3). These data were measured at 0 hours from tanks at 19°C and 26°C and may have reflected an insufficiently long period of acclimation prior to the experiments. Therefore, we chose to exclude measures taken at 0 hours in the analysis of variance on respiration rates.

Respiration rates were significantly influenced by oxygen level (P=0.001), by the interactions between temperature and oxygen (P=0.04), and by the interaction among temperature, oxygen, and replicate (P=0.04). Mean respiration rates were 0.187 ± 0.012 and 0.247 ± 0.015 mg O_2/(g·h) under hypoxia and normoxia, respectively (Table 1). At high oxygen levels, 26°C respiration rates (mean=0.281 ±0.023 mg O_2/(g·h)) tended to be higher than 19°C respiration rates (mean=0.210 ±0.021 mg O_2/(g·h)). However, the converse was true at hypoxic levels; mean respiration rate at 26°C (0.136 ±0.027 mg O_2/(g·h)) was significantly lower than at 19°C (0.212 ±0.021 mg O_2/(g·h)). For all but the 26°C and hypoxic-level combination, replicate rates were similar. Respiration for the second replicate for the 26°C and hypoxic-level combination was substantially lower than other replicates that may have produced the significant interaction among temperature, oxygen, and replicate factors in the analysis of variance. In a procedure to reduce bias associated with deviations of actual inflow DO levels from those prescribed, an analysis of variance was conducted for which the inflow oxygen concentration was a covariate. After viariance associated with individual tank DO conditions was removed, the effect of oxygen level (high or low) remained significant (P=0.04).

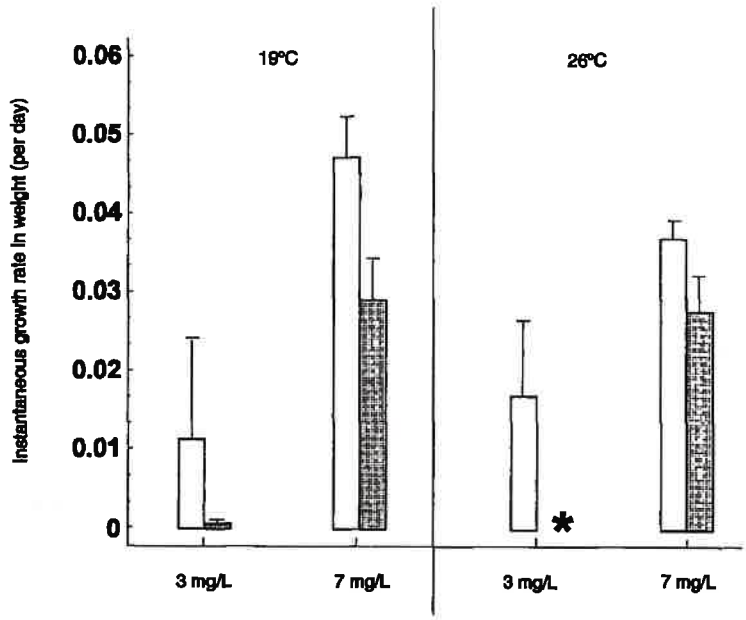

Figure 2

Effects of dissolved oxygen concentration on instantaneous growth rates in weight (per day) (mean ± 95% confidence interval) of young-of-the-year Atlantic sturgeon at two temperatures and different tank configurations. Stippled bars indicate treatments denying surface access. Replicate tanks were combined for each treatment level comination. The asterisk indicates that complete mortality occurred for that treatment.

Discussion

Juvenile Atlantic sturgeon were vulnerable to conditions of high temperature and low oxygen. In five out of six replicates (sealed and unsealed tanks combined) at 26°C and ~3 mg/L DO, all juveniles died. All sturgeon that died showed a perfusion of blood along the margins of their fins, indicative of oxygen deprivation (Jobling, 1995). Reduced oxygen levels resulted in a threefold reduction in growth rate and a 50% reduction in routine respiration rate. At 19°C, respiration rates were similar between hypoxic and normoxic treatments. But, at the 26°C hypoxic treatment, mean respiration rates dropped below 2 mg O_2/(g·h) and all sturgeon died. We speculate that these fish were unable to supply sufficient oxygen to their tissues at this level of reduced respiration.

Despite reduced survival and respiration in conditions of low dissolved oxygen, feeding continued and fish grew. Apparently, Atlantic sturgeon were able to reduce activity but still feed and allocate some energy to growth. In unsealed tanks, weight gain ranged from 1.1% to 2.9%, and from 3.6% to 5.0% body weight per day, at ~3 and ~7 mg O_2/L, respectively. Cech et al. (1984) also observed continued growth by juvenile white sturgeon (*Acipenser transmontanus*) (ca. 0.5 to 5 g) under conditions of hypoxia. Daily weight-specific growth rates of white sturgeon varied between 1.6% (15°C) and 2.9% (25°C) under normoxic conditions and between 0.6% (15°C) and 2.3% (25°C) under hypoxic conditions. Growth rates measured by Cech et al. (1984) under hypoxia were substantially higher than those that we ob-

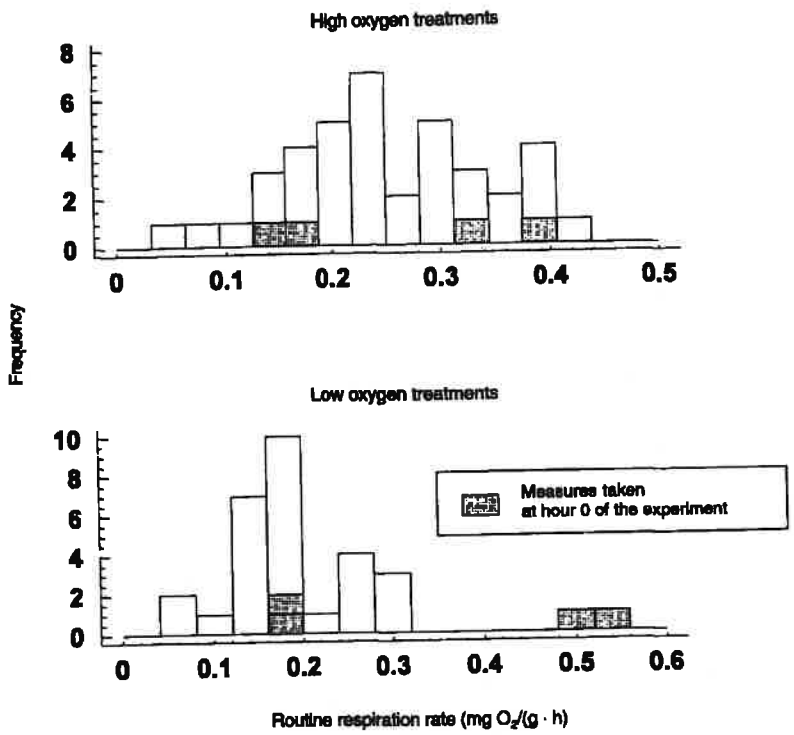

Figure 3

Frequency histogram of respiration rates for young-of-the-year Atlantic sturgeon exposed to either high (7 mg/L) or low levels (3 mg/L) of dissolved oxygen. Measures taken at the initiation of the experiment (hour 0) are stippled.

served. This may be attributable to a higher designated oxygen level for hypoxic treatments (<5 mg/L), differences between the two species, or an ontogenetic effect. Juvenile white sturgeon were substantially smaller (initial weight 0.5 grams) than those used in our study (mean initial weight=23.7 grams).

Our study was unique in examining the effects of long-term hypoxia on routine metabolism. Other studies have examined the effects of hypoxia on sturgeon respiration in short-term respirometry studies (Table 5). Investigations on white sturgeon and Siberian sturgeon (*Acipenser baeri*) have indicated reduced rates of respiration under hypoxic conditions. An ontogenetic trend of decreasing routine metabolic rates with increased mass, which is typical in fishes, was also suggested in the comparison of studies. Metabolic rates under normoxic conditions ranged from 0.9 mg O_2/(g·h) (1–2 g fish) to 0.055 mg O_2/(g·h) (1800-g fish). Metabolic rates (0.2

Table 5

Summary of studies on hypoxia and routine metabolism for sturgeons. Oxygen concentrations and consumption rates have been converted to common units (mg O_2/L or mg O_2/(g·h) from reported units (e.g. mm Hg or µmol O_2/kg(g·h) for several of the studies. Wt = wet weight; Hyp = hypoxia treatment; Norm = normoxia treatment; Swim = velocities were provided in respirometer to induce swimming velocities; S = salinity; and T = temperature.

Species	Wt (g)	Treatments	Routine metabolism mg/(g·h)	S (ppt)	T (°C)	Study duration	Reference
Acipenser transmontanus	0.5–5	Hyp: 4.7 - 5.7 mg/L Norm: 6.8 - 8.2 mg/L	Not measured	0	15, 20, 25	30 d	Cech et al., 1984
A. baeri	1–2	High density Low density	0.3 to 0.5 0.4 to 0.9	0	22–24	2–12 h	Khakimullin, 1987
A. baeri	3–7	Routine Swim: 5–30 cm/sec	0.3 to 0.7 0.4 to 3.6	0	22–24	3 h	Khakimullin, 1988
A. oxyrinchus	12–69	Hyp: 2.5–4.4 mg/L Norm: 6.3–7.4 mg/L	0.1 to 0.2 0.2 to 0.3	1.8–2.5	19, 26	10 d	This study
A. transmontanus	950	Hyp: 1.7–6.3 mg/L Norm: 9.8 mg/L	~0 to 0.015 0.079	0	15	4.5 h	Burggren and Randall, 1978
A. baeri	1800	Hyp: 1.3–3.8 mg/L Norm: 8.2 mg/L	0.023 0.055	0	15	3.5 h	Nonnotte et al., 1993
A. transmontanus	2000	Hyp: 4.7–5.9 mg/L Norm: 7.7–8.9mg/L	0.090 0.098	0 0	18	24 h	Ruer et al., 1987

to 0.3 mg O_2/(g·h) and fish sizes (12 to 69 g) in our experiments were both intermediate within this range.

Surface behavior

In the nested growth and survival experiment, surface access influenced both growth and survival rates. Eliminating surface accesses in tanks reduced growth rates by ca. 35%, and fivefold at high and low levels of DO, respectively. The effects of denying surface access under "hypoxia" at 26°C was fully lethal within a 30-h period. In the 26°C hypoxic treatments that allowed surface access, the majority of juveniles survived the first 5 days of exposure, although they too eventually died.

Many fishes surface in hypoxic environments to convey relatively oxygen-rich water, located at the air-water interface, across their gills. In laboratory experiment, access to surface waters may have increased the effective level of DO above nominal levels, resulting in improved growth and survival. Alternatively, aerial respiration cannot be ruled out for sturgeon that are physostomous. Histological studies should be undertaken to investigate whether the swim bladder of Atlantic sturgeon contains a vascular structure, apart from the gas gland, which meets the criteria for an aerial respiratory organ. No such structure has been identified in any sturgeon species.

Reasons for decline of Atlantic sturgeon in Chesapeake Bay

We conclude that increased frequency of hypoxia in Chesapeake Bay during this century (Officer et al., 1984; Cooper and Brush, 1993) was detrimental to Atlantic sturgeon production. Recent water quality monitoring has shown that during summer months (mid-June through mid-September), temperatures >25°C and DO levels <4.0 mg O_2/L are prevalent in Chesapeake Bay benthic habitats (Breitburg, 1990, 1992; Phil et al., 1991). Our laboratory experiments showed that juvenile Atlantic sturgeon were less tolerant of summertime hypoxia than were other juvenile estuarine species. Young-of-the-year spot, *Leiostomus xanthurus* (total length 10–20 cm), survived long-term (>1 week) experimental exposure of 2.4–3.0 mg/L at 25°C, but 0.8–1.0 mg/L DO was fully lethal (Phil et al., 1991). Juvenile and adult hogchokers, *Trinectes maculatus* (Phil et al., 1991), and naked gobies, *Gobiosoma bosc* (Brietburg, 1992), can tolerate several-day periods of 0.5–1.0 mg/L DO.

Our laboratory experiments did not consider behaviors that can 1) reduce exposure to hypoxic waters and 2) compensate for reduced dissolved oxygen levels. Phil et al. (1991) and Brietburg (1992) have provided field evidence that fish will escape hypoxic conditions through local migrations. These include vertical or shoalward emigrations from hypoxic or anoxic bottom habitats. Following hypoxic events, bottom habitats are recolonized. Further, short-term episodic hypoxia may benefit bottom-feeding fish. Burrowing macrobenthic prey will emerge at DO levels <2 mg/L, increasing their vulnerability to predation by fish that can tolerate short-term excursions into hypoxic waters (Phil et al., 1992). If unable to escape hypoxic conditions, sturgeon may be able to compensate by either surfacing to exploit higher oxygen concentrations in surficial water or in the atmosphere or by adjusting their metabolic rate (e.g. through reduced swimming [Cech et al., 1984]).

Hudson River "strain" Atlantic sturgeon, used in our experiment, might have exhibited a different response to hypoxia than a strain native to Chesapeake Bay. The Hudson River rarely becomes hypoxic (Cooper et al., 1988). Therefore, Hudson River Atlantic sturgeon may not have been adapted to hypoxic conditions. An aquaculture study by Serov et al. (1988) on stellate sturgeon (*A. stellatus*) showed that heterozygosity in the LDH gene conferred survival advantages to hypoxia and high temperature. Therefore, it is conceivable that selection of Chesapeake Bay Atlantic sturgeon to hypoxic conditions could have occurred over several generations. However, because generation time is extremely high in Atlantic sturgeon (c.a. 29 years [Stevenson and Secor, 1996]) and because hypoxia increased rapidly during this century in the Chesapeake Bay, Chesapeake Bay Atlantic sturgeon may not have been able to recoup historical abundances by dint of selection to low-oxygen conditions. In addition, Hudson River Atlantic sturgeon juveniles >80 cm TL are known to visit Chesapeake Bay during summer months (Dovel and Berggren, 1983). Presumably, these fish could have adapted to Chesapeake Bay conditions. Serov et al.'s (1988) observation that water quality experienced by juveniles in culture influences genotypic frequencies has important implications for the use of hatchery-produced sturgeon in restoration programs and merits additional research.

Scientists and managers are now considering a restoration program for Atlantic sturgeon in Chesapeake Bay and elsewhere (St. Pierre, 1994; Secor, 1995). The feasibility of a sturgeon restoration program must address the same issues that led to the sturgeon's decline. If these conditions persist in Chesapeake Bay, a restoration program cannot be easily justified. Necessary conditions for population recovery must include increased population abundance, and improvement in the quality and size and number of essential habitats. Population abundance

can be increased by deliberately releasing artificially produced progeny (parentage from an outside population like the Hudson River population), by imposing a moratorium on sturgeon harvests, and by making efforts to reduce sturgeon taken as bycatch in other fisheries.

A critical and unresolved question is whether habitat quality remains sufficient at present in the Chesapeake Bay to support Atlantic sturgeon growth, survival, and reproduction. An encouraging finding has been a trend in improved water quality and macrobenthic production in Chesapeake Bay tributary nursery habitats, the apparent result of nutrient abatement programs (Dauer, 1995).

Acknowledgments

This research was supported by Maryland Department of Natural Resources Chesapeake Bay Research and Monitoring Division through funds made available by the National Marine Fisheries Service (Anadromous Fish and Great Lakes Conservation Act). We are especially grateful to Mike Hendrix and Jerre Mohler at U.S. Fish and Wildlife Service (Northeast Fishery Center, Lamar PA) for their assistance in providing hatchery-produced young-of-year Atlantic sturgeon used in our experiments. Jill Stevenson and Erik Zlokovitz (Chesapeake Biological Laboratory) provided assistance in the laboratory. We thank Ed Houde, Ron Klauda, and Paul Miller for their comments on an earlier draft of this manuscript. Letty Fernandez assisted with preparation of this report.

Literature cited

Brandt, S. B., and J. Kirsch.
1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Trans. Am. Fish. Soc. 122:845–869.

Breitburg, D. L.
1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. Estuarine Coastal Shelf Sci. 30:593–609.
1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbances. Ecol. Monogr. 62:525–546.

Brett, J. R.
1970. The metabolic demand for oxygen in fish, particularly salmonids, with a comparison with other vertebrates. Respir. Physiol. 14:151–170.

Berggren, W. W., and D. J. Randall.
1978. Oxygen uptake and transport during hypoxic exposure in the sturgeon *Acipenser transmontanus*. Respir. Physiol. 34:171–183.

Cech, J. J.
1990. Respirometry. *In* C. B. Schreck and P. B. Moyle (eds.), Methods for fish biology, p. 335–362. Am. Fish. Soc., Bethesda, MD.

Cech, J. J., S. J. Mitchell, and T. E. Wragg.
1984. Comparative growth of juvenile white sturgeon and striped bass: effects of temperature and hypoxia. Estuaries 7:12–18.

Cooper, J. C., F. R. Cantelno, and C. E. Newton.
1988. Overview of Hudson River Estuary. Am. Fish. Soc. Monogr. 4:11–24.

Cooper, S. R., and G. S. Brush.
1993. A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. Estuaries 16:617–626.

Coutant, C. C.
1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. 114:31–61.

Coutant, C. C., and D. L. Benson.
1990. Summer decline in habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. Trans. Am. Fish. Soc. 119:757–778.

Dauer, D. M.
1995. Long-term trends in macrobenthos of the lower Chesapeake Bay (1985–92). *In* P. Hill and S. Nelson (eds.), Toward a sustainable watershed: the Chesapeake experiment. Chesapeake Research Consortium Publ.149, Edgewater, MD.

Dovel, W. L., and T. J. Berggren.
(1983). Atlantic sturgeon of the Hudson Estuary, New York. NY Fish and Game J. 30:140–172.

Harding, L. W., M. Leffler, and G. E. Mackiernan.
1992. Dissolved oxygen in the Chesapeake Bay: a scientific consensus. Maryland Sea Grant, College Park, MD, 18 p.

Hendrix, M. A.
1995. Update—U.S. Fish and Wildlife Service and Atlantic sturgeon. Sturgeon Notes 3:10–11.

Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of the Chesapeake Bay. U.S. Bureau of Fisheries, Washington, D.C., 388 p.

Jobling, M.
1995. Environmental biology of fishes. Chapman and Hall, New York, NY, 455 p.

Jordan, S., C. Stenger, M. Olson, R. Batiuk, and K. Mountford.
1992. Chesapeake Bay dissolved oxygen goal for restoration of living resource habitats. Maryland Department of Natural Resources, Annapolis, MD, 81 p.

Kemp, W. M., P. A. Sampou, J. Garber, J. Tuttle, and W. R. Boynton.
1992. Seasonal depletion of oxygen form bottom waters of Chesapeake Bay: roles of benthic and planktonic respiration and physical exchange processes. Mar. Ecol. Prog. Ser. 85:137–152.

Khakimullin, A. A.
1987. Intensity of gas exchange in individuals and groups of juvenile siberian sturgeon, *Acipenser baeri*. Vop. Ikht. 6:978–983.
1988. Intensity of gas exchange of hatchery siberian sturgeon, *Acipenser baeri*, under muscular load. Vop. Ikht. 1988:282–288.

Mackiernan, G. B.
1987. Dissolved oxygen in the Chesapeake Bay: processes and effects. Maryland Sea Grant, College Park, MD, 177 p.

Murawski, S. A., and A. L. Pacheco.
1977. Biological and fisheries data on Atlantic sturgeon,

Acipenser oxyrhynchus (Mitchill). National Marine Fisheries Service, NOAA, Highlands, NJ, 69 p.

Nonnotte, G., V. Maxime, J. P. Truchot, P. Williot, and C. Peyraud.
1993. Respiratory responses to progressive ambient hypoxia in the sturgeon, *Acipenser baeri*. Respir. Physiol. 91:71–82.

Officer, C. B., B. B. Biggs, J. L. Taft, L. E. Cronin, M. A. Tyler, and W. R. Boynton.
1984. Chesapeake Bay anoxia: origin, development, and significance. Science 223:22–27.

Phil, L., S. P. Baden, and R. J. Diaz.
1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar. Biol. 108:349–360.

Phil, L., S. P. Baden, R. J. Diaz, and L. C. Schaffner.
1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustaceans. Mar. Biol. 112:349–361.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Canada Fisheries and Oceans, Ottawa, Ontario, 382 p.

Ruer, P. M., J. J. Cech and S. I. Doroshov.
1987. Routine metabolism of the white sturgeon, *Acipenser transmontanus*: effect of population density and hypoxia. Aquaculture 62:45–52.

SAS.
1982. Statistical analysis system user guide: statistics. SAS Institute, Inc., Cary, NC, 585 p.

Secor, D. H.
1995. Chesapeake Bay Atlantic sturgeon: current status and future recovery. Chesapeake Biological Laboratory, Solomons, MD, 10 p.

Serov, D. V., S. I. Kikonorov, and E. S. Asadullaeva.
1988. Genetic selection in young stellate sturgeon. Rybn. Khov. 4: 64–65.

Speir, H., and T. O'Connell.
1996. Status of Atlantic sturgeon in Maryland's Chesapeake Bay. MD Dep. Natur. Resources, Annapolis, MD, 7 p.

St. Pierre, R. A.
1994. The national strategy for the management and conservation of paddlefish and sturgeon species in the United States. *In* V. J. Birstein (ed.), The international conference on sturgeon biodiversity and conservation. Hudson River Foundation, New York.

Stevenson, J. T., and D. H. Secor.
1996. Demographic analysis of Atlantic sturgeon fisheries in the New York Bight. Chesapeake Biological Laboratory, Solomons, MD, 17 p.