

Hypoxia and Sturgeons

Report to the Chesapeake Bay Program Dissolved Oxygen Criteria Team

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ABSTRACT

In this essay, three lines of evidence are developed that sturgeons in the Chesapeake Bay and elsewhere are unusually sensitive to hypoxic conditions: 1. In comparison to other fishes, sturgeons have a limited behavioral and physiological capacity to respond to hypoxia. Basal metabolism, growth, and consumption are quite sensitive to changes in oxygen level, which may indicate a relatively poor ability by sturgeons to oxyregulate. 2. During summertime, temperatures >20 C amplify the effect of hypoxia on sturgeons and other fishes due to a temperature*oxygen "squeeze" (Coutant 1987). In bottom waters, this interaction results in substantial reduction of habitat; in dry years, nursery habitats in the Chesapeake Bay may be particularly reduced or even eliminated. 3. While evidence for population level effects by hypoxia are circumstantial, there are corresponding trends between the absence of Atlantic sturgeon reproduction in estuaries like the Chesapeake Bay where summertime hypoxia predominates on a system-wide scale. Also, the recent and dramatic recovery of shortnose sturgeon in the Hudson River (4-fold increase in abundance from 1980 to 1995) may have been stimulated by improvement of a large portion of the nursery habitat that was restored from hypoxia to normoxia during the period 1973-1978.

CRITICAL EFFECTS OF HYPOXIA AND TEMPERATURE ON STURGEONS

Sensitivity by sturgeons and other fishes to temperature, oxygen and their interaction has been evaluated experimentally through respirometry. As an example, basal metabolism of the stellate sturgeon *Acipenser stellatus*, measured over a range of temperatures and oxygen levels shows that metabolism increases with temperature, but is only affected by oxygen only at lower oxygen levels, above which there is no response (Figure 1). The point of inflection in the curve of metabolic response to dissolved oxygen is called the critical concentration. Oxygen levels below that point will constrain metabolism, growth, swimming activity, and consumption (Fry 1971; Chiba 1988; Kaufmann and Wieser 1992). As basal metabolism increases due to increased temperature, the critical concentration becomes higher (Figures 1-3). In other words, as basic metabolic requirements increase with temperature, so too will oxygen demand. This increase in oxygen demand will outpace increased oxygen availability at higher temperatures (i.e. due to increased vapor pressure).

At very low oxygen concentrations, metabolism decreases rapidly to nil and the fish dies. This is termed the threshold concentration (Figures 1-3). Both critical and threshold concentrations were substantially higher for sturgeons in comparison to freshwater fishes (Figure 3). Critical concentrations for Eurasian sturgeons (*A. güldenstädtii*, *A. baeri*, *A. stellatus* and the hybrid *Huso huso* x *A. ruthenus*) ranged between 25-60% saturation, increasing with temperature. At 20 C, critical concentration was 3.6 mg/L (42% saturation) (Figures 2,3), which was c. 20% higher than that reported for rainbow trout. At 24 C, critical concentration was 4.5 mg/L (54% saturation) for the Eurasian sturgeons. The heightened response of metabolism to oxygen levels may be characteristic of sturgeons, and has been ascribed to an inefficiently functioning oxyregulatory system. Klyashtorin (1982) concluded that ancestral morphological and physiological traits caused sturgeons to be less efficient in respiration than other fishes. These traits included less efficient gill ventilation and lower affinity of hemoglobin to oxygen.

In experiments on Atlantic and shortnose sturgeons *A. oxyrinchus* and *A. brevirostrum*, Niklitschek (2001) observed substantial reductions in routine metabolism, consumption, feeding metabolism, growth, and survival at 40% v. 70% DO (Figures 4-7). Again the degree of effect due to oxygen level was conditional on temperature. In comparison to normoxia at 20 C, 40% DO saturation (3.3 mg/L) yielded a 76% and 54% reduction in growth, a 29% and 27% reduction in consumption, and an 23% and 17% reduction in

routine metabolism, for Atlantic and shortnose sturgeons, respectively. At 27 C and 40% saturation (2.9 mg/L), there was 86% and 51% reduction in growth, and 35% and 34% reduction in consumption, and a 28% and 21% reduction in routine metabolism, for Atlantic and shortnose sturgeons, respectively. Because routine metabolism was investigated rather than basal metabolism, estimates of critical concentrations were not possible. Secor and Gunderson (1998) reported c. 2- and 4-fold reductions in growth rate due to hypoxia at 26 and 19 C, respectively.

Few studies have addressed lethal effects of hypoxia on sturgeons (Table 1). Jenkins et al. (1994) observed 86 - 100% mortality for 25-64 day old fish in an acute 6 hr exposure to 2.5 mg/L at 22.5 C (30% saturation). Older juveniles 100-310 days old experienced 12-20 % mortality under the same conditions. Short-term exposure to 3.0 mg/L (35% saturation) resulted in 18-38% mortality for juveniles ranging 20-77 days in age. No mortality was observed for exposures to > 3.5 mg/L (42% saturation). Long term exposure (10 days) of Atlantic sturgeon young-of-the-year juveniles (c. 150-200 days old) to hypoxia at 26 C (37%-44% DO saturation; 2.8 - 3.3 mg/L) resulted in complete mortality over a ten day period in three of four replicates (Secor and Gunderson 1998). The fourth replicate experienced 50% mortality. At 20 C and hypoxia at 27%-37% saturation (2.3 - 3.2 mg/L), they observed 12-25% mortality over the 10 day period. No mortality was observed for normoxic treatments. In preliminary experiments, Niklitschek (2001) observed lethality for young-of-the-year Atlantic and shortnose sturgeon reared at 30% oxygen saturation (27 C; 2.3 mg/L) for 24 hours. Thus, he selected 40% saturation to observe sub-lethal physiological effects and avoid loss and suffering of experimental animals. At this "sub-lethal" level (2.8 mg/L at 28 C; 3.3 mg/L at 20 C), daily survival rates were significantly reduced in comparison to survival under normoxia (Figure 6). Threshold oxygen levels (levels below which basal metabolism cannot be sustained) reported for Eurasian sturgeons occurred at 1.7-2.0 mg/L (c. 25% saturation) for temperatures 20-24 C (Figure 2; Klyashtorin 1975). At 20 C, threshold oxygen concentrations were c. 20% higher for rainbow trout than for Eurasian sturgeons, but at temperatures less than 18 C, threshold values were quite similar between the sturgeons and rainbow trout (Figure 3).

Table 1. Results of lethality experiments on shortnose and Atlantic sturgeon.				
Species, temperature	age (days)	DO (mg/L)	Survival	Ref/Comments
Shortnose, 22.5 C	46	2.0	8%	Jenkins et al. 1994, Figure 2, mean of 6 repl.s, run for 6 hr. duration.
	110	2.0	78%	
	25	2.5	0%	
	32	2.5	3%	
	64	2.5	14%	
	104	2.5	88%	
	20	3.0	62%	
	39	3.0	82%	
	77	3.0	67%	
	103	3.0	100%	
	19	3.5	78%	
90	3.5	100%		
Atlantic, 26 C	150-200	2.8-3.3	12.5%	Secor and Gunderson 1998, mean of 4 repl.s run for 10 day duration, tanks open to air.
Atlantic, 20 C	150-200	2.3-3.2	78%	Secor and Gunderson 1998, mean of 4 repl.s run for 10 days duration, tanks sealed and open to air
Atlantic, 20-26 C	150-200	>5.0	100%	Secor and Gunderson 1998

In a direct comparison between juvenile white sturgeon and striped bass, growth rate was substantially more depressed under hypoxia in white sturgeon *A. transmontanus* (Cech et al. 1984). Growth rates under hypoxia (90 torr ~ 4.5 mg/L) and temperatures 20-25 C were 20-25% lower than those under normoxia (130 torr ~ 7 mg/L) for sturgeon. Striped bass reared under identical conditions experienced 7-9% growth depression under hypoxia. During the 34-day long experiment, higher mortalities of both species occurred under relatively mild hypoxia in comparison to normoxic treatments.

Beyond metabolic response, sturgeons undertake other important physiological and behavioral responses to hypoxia. Niklitschek (2001) observed that egestion levels for Atlantic and shortnose sturgeon juveniles increased significantly under hypoxia, indicating that consumed food was incompletely digested. This

response could serve as a useful means to shunt energy towards respiration and other life support functions (Figure 7). Behavioral studies indicate that Atlantic sturgeon and shortnose sturgeon are quite sensitive to ambient conditions of oxygen and temperature. In a series of choice experiments, juvenile sturgeons consistently selected normoxic over hypoxic conditions (Figure 8; Niklitschek 2001). On the other hand, larval stage Siberian sturgeon *A. baeri* did not actively avoid or disperse from experimental hypoxic conditions (2-3 mg/l at 19 C; Khakimullin 1988). Beyond escape or avoidance, sturgeons respond to hypoxia (< 40% saturation) through increased ventilation, increased surfacing (to ventilate relatively oxygen-rich surficial water), and decreased swimming and routine metabolism (Nonnette et al. 1993; Croker and Cech 1997; Secor and Gunderson 1998; Niklitschek 2001). Historically, sturgeons were at the center of a debate on whether or not fishes could oxyconform to hypoxia: that is, could fish tolerate declines in dissolved oxygen delivery to their tissues? (Burggren and Randall 1978; Klyashtorin 1982; Nonnette et al. 1993). Oxyregulation by the typical vertebrate mechanism of anaerobic metabolism has been since demonstrated for sturgeons (Nonnette et al. 1993; McKenzie et al. 1995), providing solid evidence against physiological oxyconformity. Still, behavioral means to oxyregulate in sturgeons may be relatively more important since critical concentrations are higher for sturgeons than other teleosts (Klyashtorin 1982). As evidence of this, white sturgeon juveniles were 3- to 9-fold less active under hypoxia (80 mm Hg ~ 5 mg/L or 50% saturation @ 16 C) than under normoxia (Croker and Cech 1997). Secor and Gunderson (1998) observed that lethality to hypoxia increased when surfacing behavior was blocked.

In summary, sturgeons endemic to the Chesapeake Bay, and sturgeons in general, are unusually sensitive to hypoxia in terms of their metabolic and behavioral responses. The critical concentration at which sturgeons metabolically respond to dissolved oxygen is higher or similar to that of rainbow trout. Bioenergetic and behavioral responses indicate that young-of-the-year juveniles (~30 to 200 days old) will experience lost production in those habitats with less than 60% saturation. For summertime temperatures (22-27 C), this level corresponds to c. 4.3 - 4.7 mg/L. Acute and chronic lethal effects for shortnose and Atlantic sturgeons were observed for levels \leq 3.3 mg/L at summertime temperatures. Threshold concentrations for Eurasian sturgeons were somewhat lower ranging between 1.7 and 2.0 mg/L for temperatures 20-24 C.

A HABITAT SQUEEZE FOR CHESAPEAKE BAY STURGEONS?

Coutant and Benson (1990) proposed that habitats of Chesapeake Bay striped bass were severely curtailed during summer months due to thermal preference compounded by hypoxia. During summer, striped bass adults selected narrow lenses within the water column characterized by < 25 C water and normoxia (Cheek et al. 1985). In many instances, it was expected that such summertime refugia would curtail prey availability and growth. Coutant's concept, known popularly as the "habitat squeeze," was a prevailing hypothesis on the decline of striped bass during the 1980s. Using bioenergetic models (Hartman and Brandt 1995), Brandt and Kirsch (1993) mapped habitat suitability for striped bass in the Chesapeake Bay and predicted substantial habitat restrictions in summer, leading to negative or static growth during summer months.

Sturgeons are particularly vulnerable to a habitat squeeze (i.e. synergism between temperature and dissolved oxygen effects on habitat availability) due to their demersal lifestyle and unique bioenergetic responses to hypoxia. While sturgeons do occasionally surface, they depend almost exclusively on benthic substrates and bottom waters for spawning, feeding, migration, and refuge from predation or stressful environments (e.g. flow and temperature refugia). Their specialized underslung jaw, diets, electrosensory and olfactory systems, poor vision, body form, and heterocercal tail are but a few features that attest to their demersal lifestyle (Burggren 1978; Bemis and Kynard 1997; Carlson and Simpson 1987; Haley 1999; Secor et al. 2000). Atlantic sturgeons are known to occur at depths between 1 m to greater than 25 m; shortnose sturgeons have been observed between 1 and 12 m (Kieffer and Kynard 1997; Savoy and Shake 2000; Welsh et al. 2000). In the Chesapeake Bay during winter, Atlantic sturgeon selected deeper habitats occurring in the deep channel (Secor et al. 2000; Welsh et al. 2000). Thus, sturgeons are not limited by bathymetry within the Bay and would be expected to utilize sub-pycnocline waters contingent upon water quality.

In dissertation research, Niklitschek (2001) developed spatially explicit bioenergetic models for both Chesapeake Bay sturgeons to evaluate the influences of water quality parameters on sturgeon habitats. This is particularly appropriate for sturgeons because opportunities to directly observe habitat use is curtailed given their threatened or extirpated status. Habitat value was assigned based upon expected growth and survival responses, predicted by a bioenergetics model filtered through Chesapeake Bay Program Monitoring data (1990-1999).

Potential production rates for young-of-the-year Atlantic and shortnose sturgeons in the Chesapeake Bay reflected the strong seasonal cycle in potential production driven by the interaction of temperature, salinity and dissolved oxygen. Summer represented the most critical season in which hypoxia and high temperature conditions caused severe habitat fragmentation for both species, restricting suitable habitat to a small fraction of the Bay. Negative potential production areas closely mirrored hypoxic regions occurring in the middle mainstem, as well as the lower Patuxent, Potomac and Rappahannock rivers (Figures 9-10). Negative production areas were also predicted near the Bay mouth where very high salinities masked the otherwise improved conditions of dissolved oxygen and temperature. As a result, null or positive production was restricted to very limited areas, which coincide only in part between sturgeon species (Figure 9).

For Atlantic sturgeon, summer refuges for an average year were restricted to the upper Bay between the Magothy River and the Susquehanna Flats. Slightly negative areas were expected around Fishing Bay-Nanticoke River, between the Severn and Choptank rivers and in the upper Potomac River. For shortnose sturgeon, most suitable habitat in the mainstem would be restricted to the Bay head above Sassafraz River. Other areas of positive production included the upper sections of the Potomac and James rivers, as well as most of the Nanticoke River. The total area supporting positive production (suitable habitat) under average July conditions corresponded to 1,586 and 1,076 km², for Atlantic and shortnose sturgeons, respectively. These surfaces represent 8.5% and 5.8% of the total surface area of the mainstem and tidal sections of its tributaries. The best summer condition for both sturgeons was predicted for 1996, where suitable habitat reached circa 4,200 km² for Atlantic sturgeon and 2,050 km² for shortnose sturgeon. In 1996, average temperature and salinity were the second lowest in the studied period, while average dissolved oxygen conditions were above the average. This year also exhibited the highest July freshwater inflow of the studied period. The worst conditions for Atlantic sturgeon were observed in July 1999, where suitable habitat was close to 1 km². In 1999, overall salinity was highest in the time series. This higher than usual salinity reduced the habitat value of the upper Bay section, which is typically the most productive section of the Chesapeake Bay due to favorable temperature and oxygen conditions.

In summary, due to avoidance, sub-lethal, or lethal effects, sturgeon summertime habitats are expected to be restricted in comparison to historical times when hypoxia was less prevalent (Officer et al. 1984; Cooper et al. 1991). The habitat squeeze phenomenon is particularly relevant to sturgeons due to the synergism of temperature, dissolved oxygen and salinity during their first year of life. In dry years, the interaction of

high salinity, warm temperatures, and hypoxic waters reduces sturgeon habitats and in some years can virtually eliminate all habitats for Atlantic sturgeon. The fragmented distribution and small volume of productive habitats imposed by summertime hypoxia represents a substantial hurdle to overcome in the restoration of Chesapeake Bay sturgeons.

CHESAPEAKE BAY STURGEONS: WHERE ARE THEY NOW?

Shortnose sturgeon are in all probability extirpated from the Chesapeake Bay. Those shortnose recently observed in the region of Susquehanna flats and in the Potomac River have been confirmed to be immigrants from the Delaware Bay population, presumably having migrated through the C&D Canal (Wirgin et al. in review). The status of Atlantic sturgeon in the Chesapeake Bay is less certain (Grogan and Boreman 1998). There has been no evidence of reproduction in the Maryland portion of the Chesapeake Bay for over 25 years (Secor 1995). Recently, evidence of reproduction (capture of young-of-the-year Atlantic sturgeon) occurred for the York and Rappahannock Rivers (NMFS 1998). Based upon historical catch data, Secor (in press) estimated that 19th century adults may have numbered > 100,000 in the Chesapeake Bay. Their numbers were decimated by over-exploitation at the turn of the 19th-20th century. During the past 100 years, there has been no evidence of recovery.

Secor and Gunderson (1998) hypothesized that due to their unusual sensitivity to hypoxia, Atlantic sturgeon may have been extirpated in Maryland waters due in part to the increased prevalence of hypoxia in the 20th century. Atlantic sturgeon populations recovered in South Carolina estuaries and in the Hudson River after the intensive 19th century fishery (Smith et al. 1985; NMFS 1998) but not in the Chesapeake Bay. Secor (in press) recorded that cycles of overfishing and recovery for this species occur over a 50 year period. Prevalence of hypoxia increased in critical habitats of sturgeons due to post-WWII agricultural practices (industrial fertilizers) and residential development (increased waste water). These factors may have curtailed any 20th century cycle of recovery within the Chesapeake Bay. Still, there are other important factors which also may have prevented recovery, including lost spawning grounds due to siltation and reductions in abundance due to incidental catch (there has been no directed fishery for sturgeons in over a century in the Chesapeake Bay). Circumstantial evidence for a relationship between increased hypoxia and loss of sturgeons this past century includes the absence of sturgeons in systems that are prevalently hypoxic in summer (Collins et al. 2000).

The recent recovery of shortnose sturgeon abundance in the Hudson River is also consistent with the idea that hypoxia may be important in controlling sturgeon populations. Bain et al. (2000) have compared mark-recapture population estimates for the period 1980 - 1995. During this period, sub-adult and adult shortnose sturgeon increased from c. 13,000 to 57,000 - a four-fold increase in abundance! This yields a population growth rate of 10% per year that is remarkably high for a long-lived, late maturing species such as shortnose sturgeon. Prior to 1974, a pervasive hypoxic/anoxic summertime region known as "Albany Pool" (Figure 11) overlapped c. 40% of the expected nursery habitat for shortnose sturgeon (i.e. 40% of tidal freshwater). Levels of pervasive hypoxia (<30% saturation) would have been lethal to shortnose sturgeon juveniles (Figures 12, 13). Few fish, sturgeon or otherwise, were documented in the in the 60 km river stretch during July - October (Leslie et al. 1988). In 1974, >80% of the region's wastewater received secondary and tertiary treatment, and in less than two years the system recovered fully to normoxia (Figures 12, 13). Monitoring data showed a dramatic faunal recovery in the number of fish species returning to the Albany Pool region (Leslie et al. 1988). In 1983, a relatively strong year-class (high abundances of juveniles) was reported by two independent studies (Carlson and Simpson 1987; Dovel et al. 1992). This year-classes may have stimulated recovery of Hudson River shortnose sturgeon during the past 20 years.

In summary, absence or diminished populations of sturgeons correspond to systems where summertime hypoxia is prevalent. Recovery of normoxia to the Hudson River estuary corresponded with a remarkable recovery of shortnose sturgeon there. These case studies provide circumstantial evidence that summertime hypoxia might substantially diminish population recovery or perhaps even lead to extirpation. Sturgeons represent the only threatened or extinct resource species in the Chesapeake Bay. Future recovery of sturgeons that was coincident with improved water quality in the Chesapeake Bay would be a quite a success story.

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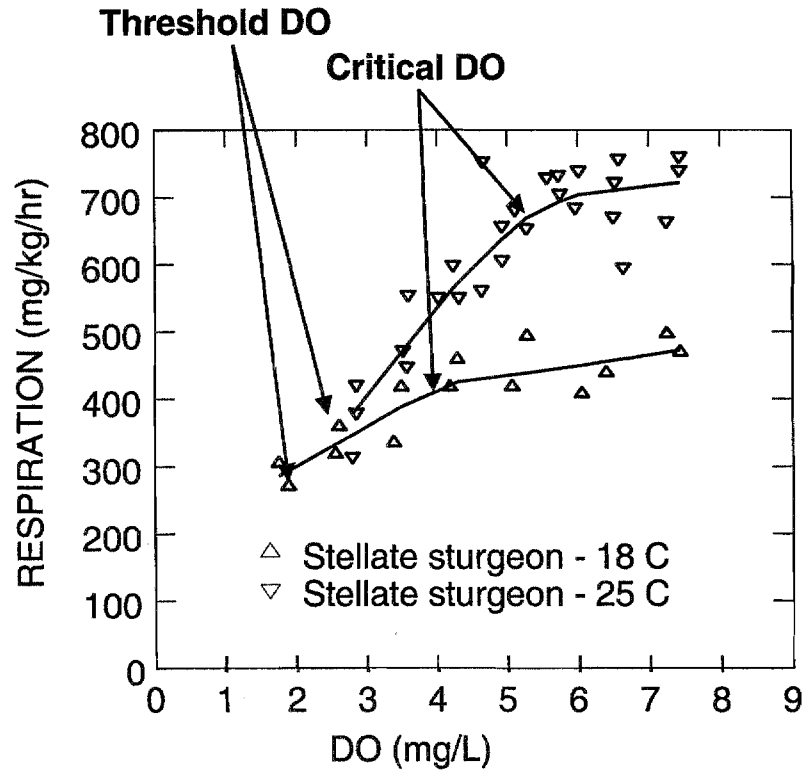


Figure 1. Basal metabolic responses by young-of-the-year stellate sturgeon (*A. stellatus*). Data from Winberg 1956, Figure 20. Critical DO is given for inflection point indicating the point of metabolic responsiveness. Threshold DO indicates lethality where basal metabolism can no longer be maintained..

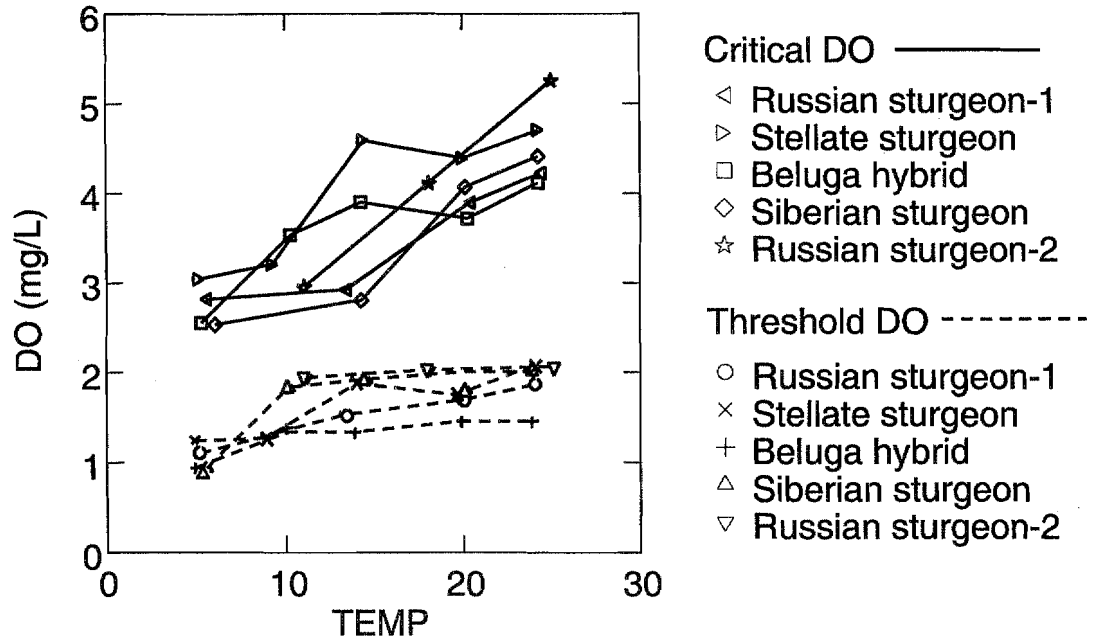


Figure 2. Critical DO concentrations for Eurasian sturgeons (*A. gueldenstaedtii*, *A. stellatus*, *H. huso* X *A. ruthenus*, *A. baeris*). Data from Klyashtorin 1976, Figure 3 (DO levels were recalculated from partial pressures to concentration). Critical DO is given for inflection point indicating the point of metabolic responsiveness. Threshold DO indicates lethality where basal metabolism can no longer be maintained. Russian sturgeon-1 and Russian sturgeon-2 designate two separate experiments. All data for young-of-the-year stage sturgeons.

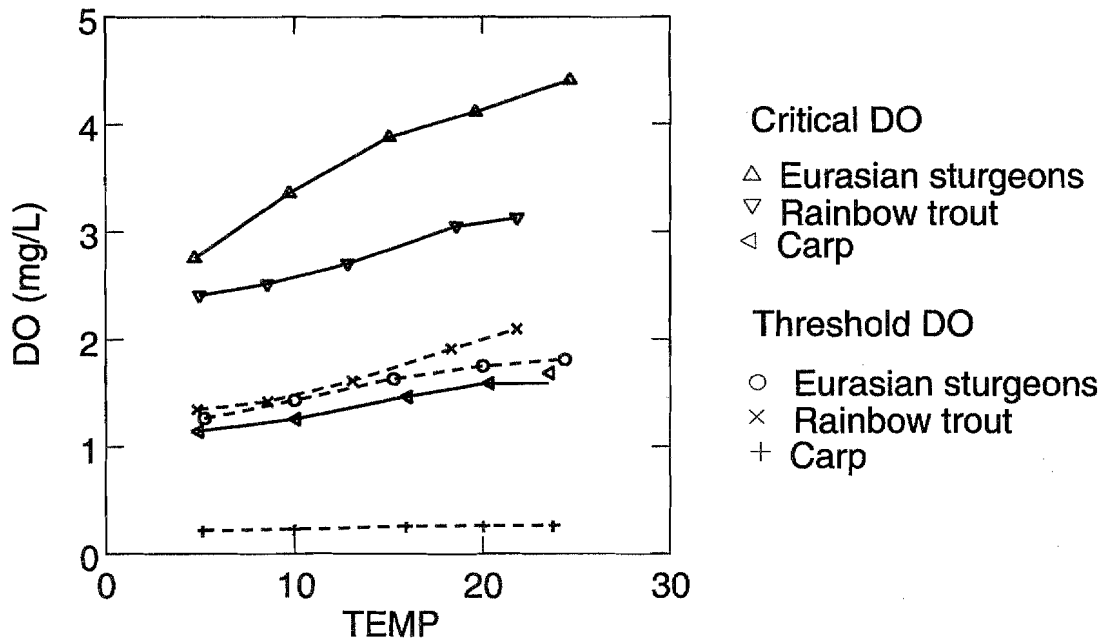


Figure 3. Critical DO concentrations for Eurasian sturgeons (*A. gueldenstaedtii*, *A. stellatus*, *H. huso* X *A. ruthenus*, *A. baeris*). Data from Klyashtorin 1976, Figure 6 (DO levels were recalculated from partial pressures to concentration). Critical DO is given for inflection point indicating the point of metabolic responsiveness. Threshold DO indicates lethality where basal metabolism can no longer be maintained. Data for Eurasian sturgeons represents a pooled mean response. All data for young-of-the-year stage sturgeons, trout and carp.

Atlantic
sturgeon

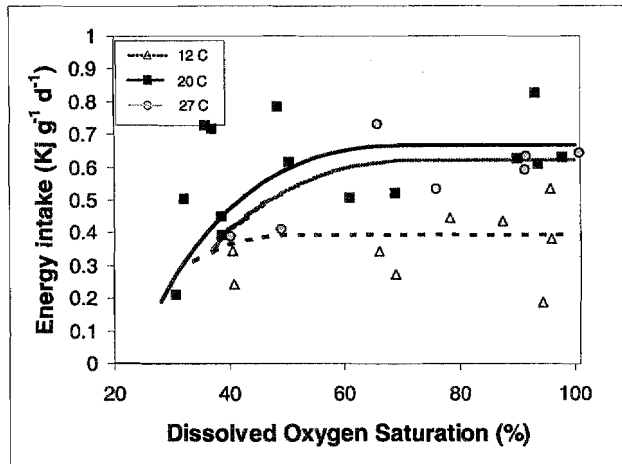
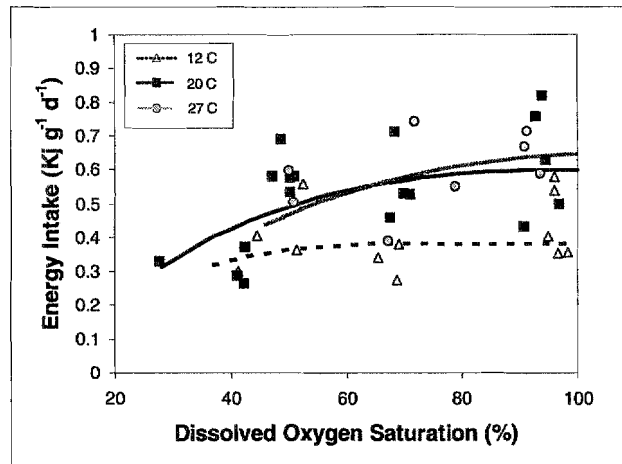


Figure 4. Effect of DO and temperature on consumption by Atlantic and shortnose sturgeon young-of-the-year. 10-d laboratory experiments conducted by Niklitschek (2001).

Shortnose
sturgeon



17

Atlantic
sturgeon

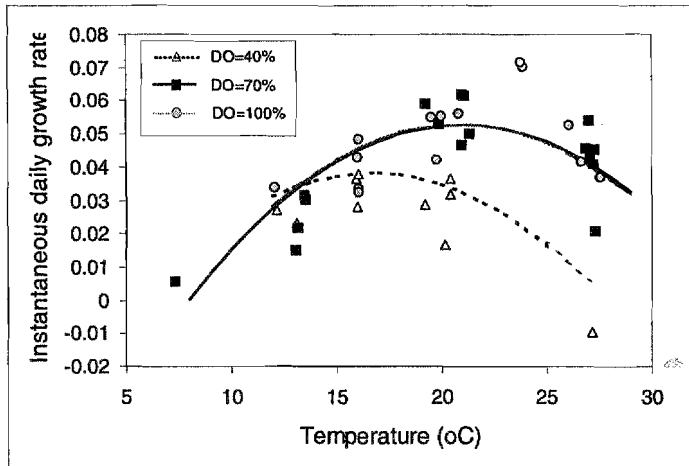
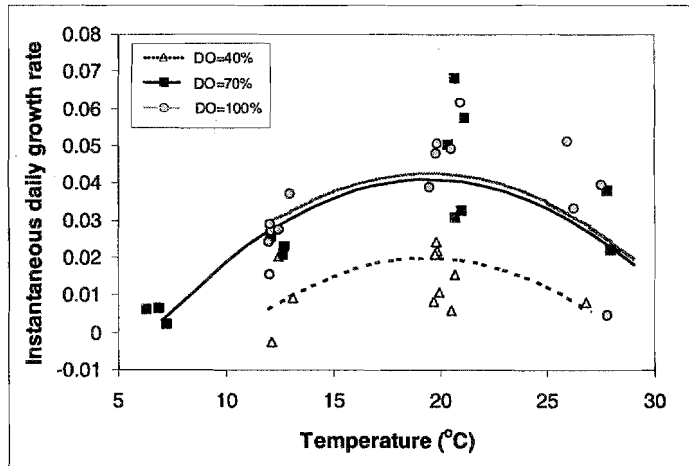


Figure 5. Effect of DO and temperature on growth by Atlantic and shortnose sturgeon young-of-the-year. 10-d laboratory experiments conducted by Niklitschek (2001).

18

Shortnose
sturgeon



Atlantic sturgeon and Shortnose sturgeon
(pooled response)

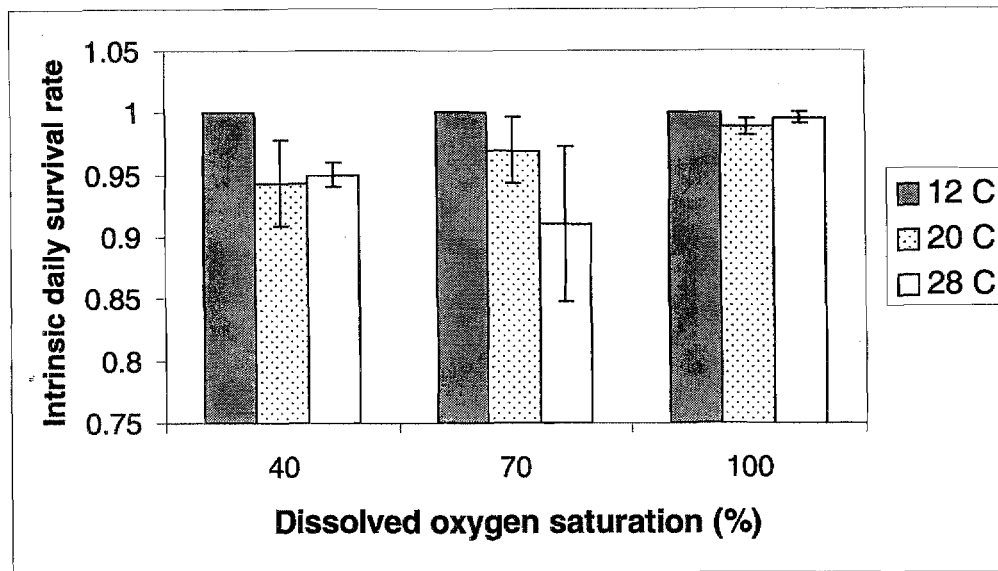


Figure 6. Effect of DO and temperature on long-term survival (20-45 d trials) by Atlantic and shortnose sturgeon young-of-the-year. Laboratory experiments conducted by Niklitschek (2001). Bars represent standard errors.

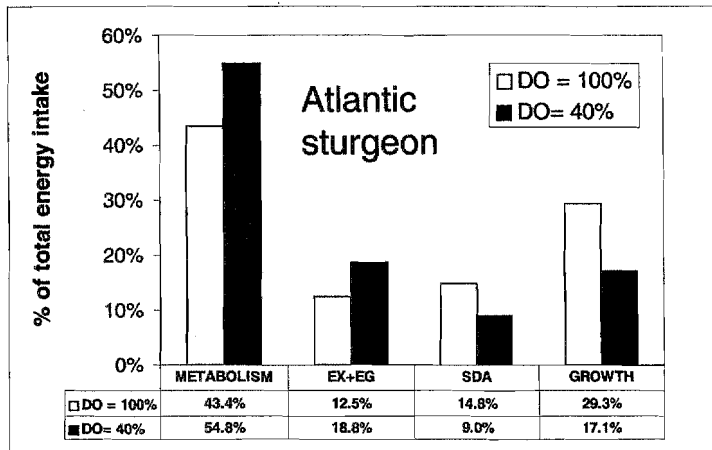
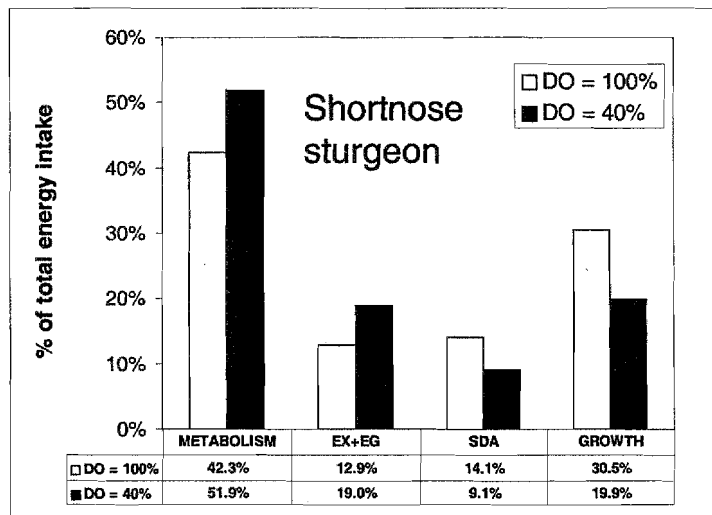
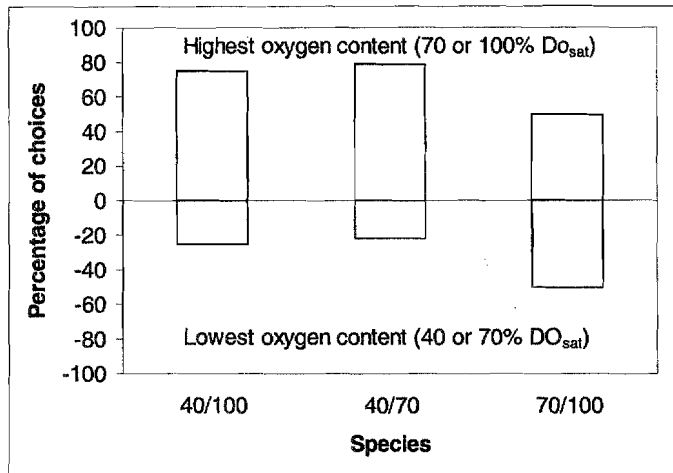


Figure 7. Effect of DO on energy allocation patterns for Atlantic and shortnose sturgeon young-of-the-year, based upon laboratory experiments by Niklitschek (2001). Allocation modeled for temperature=20 C and salinity=8 ppt.

20



Atlantic sturgeon



21

Shortnose sturgeon

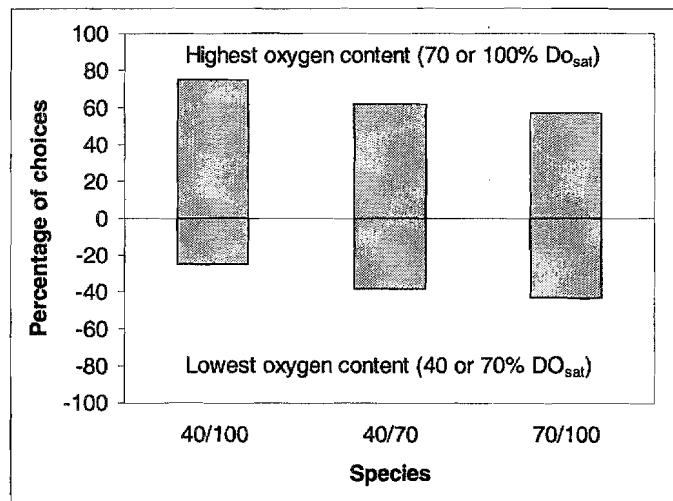


Figure 8. Selection of hypoxia (40% saturation) over normoxia (70 or 100% saturation) by Atlantic and shortnose sturgeon young-of-the-year. Based upon selection experiments conducted by Niklitschek (2001). Positive % of choices indicates selection of higher DO, negative % indicates selection of lower DO level.

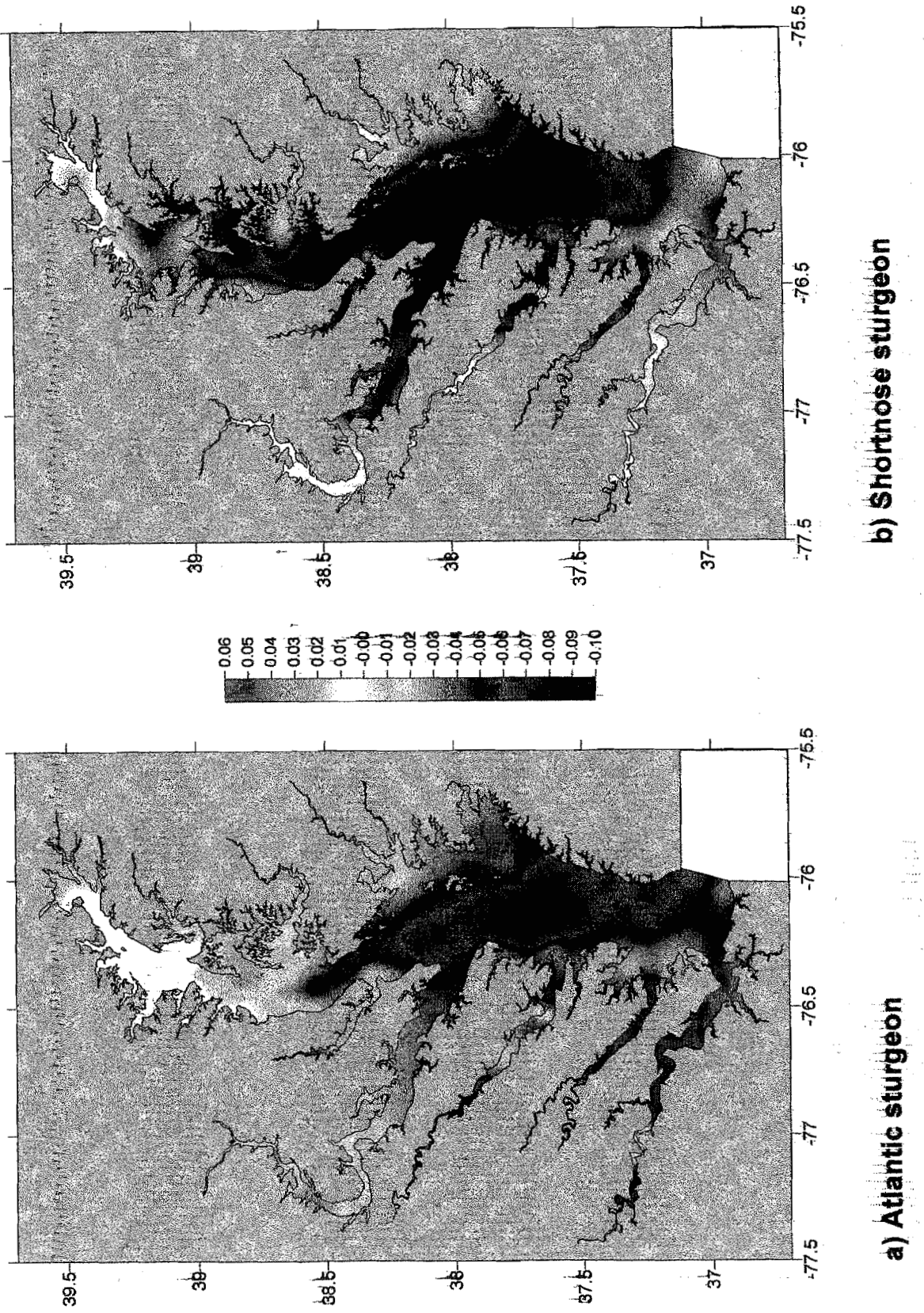


Figure 9. Spatially explicit maps of habitat suitability (potential production) by Atlantic and shortnose sturgeon young-of-the-year in the Chesapeake Bay during July (1990-1999). From Niklitschek (2001).

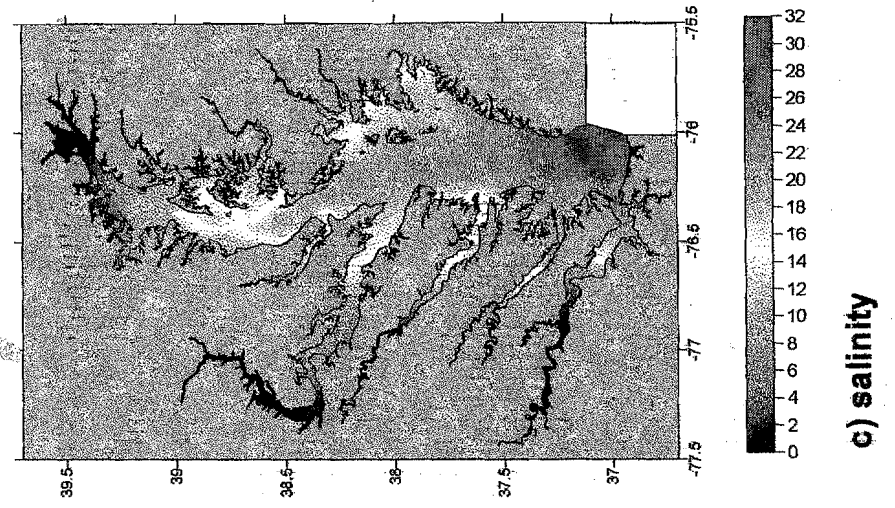
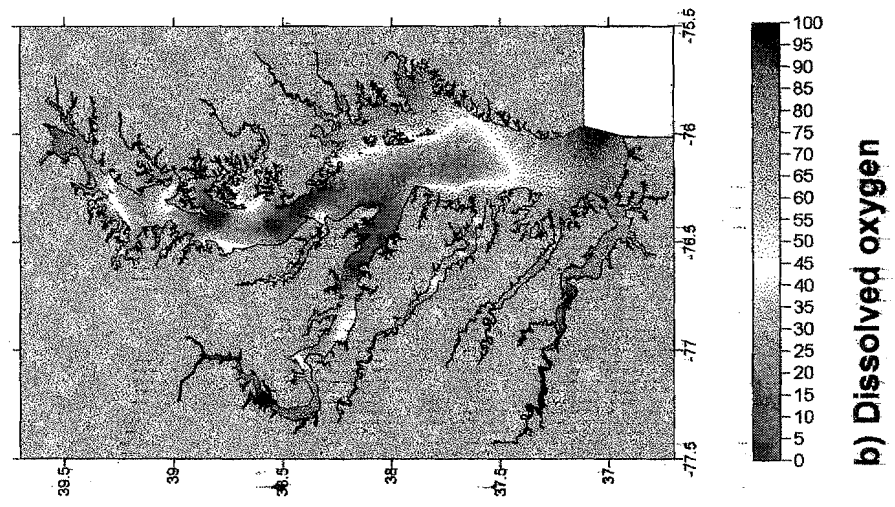
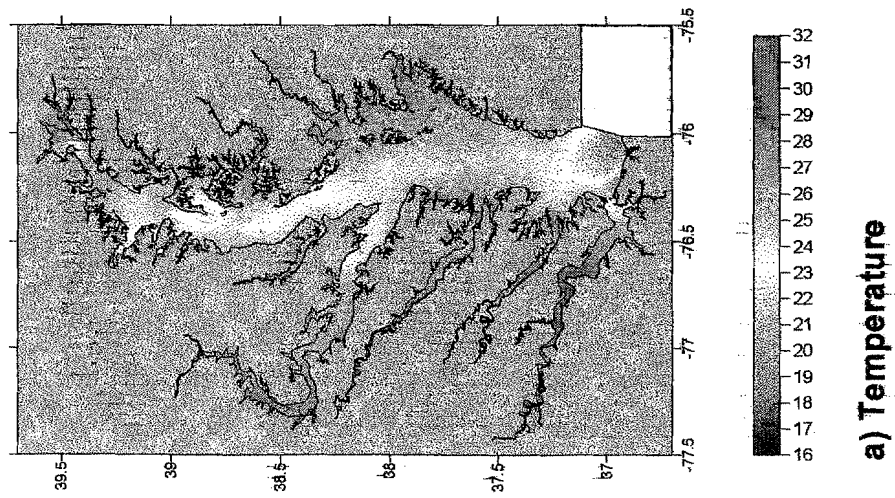


Figure 10. Bottom water quality conditions in the Chesapeake Bay. From Niklitschek (2001).

The Albany Pool

“Below the dam at Troy, open sewers from that city face upon the river like so many giant backsides. Without question this stretch of the river is the most polluted part of the Hudson, exceeding even New York City in concentrated filth. Indeed, the river here can be so awesomely foul that it is a source of wonder to sanitary engineers, and in the trade they speak of the place, almost fondly, as the *Albany Pool*.”

There are sturgeon and striped bass and occasional shad which buck up against Troy dam with ancestral fury, while the spring runoff from the Adirondacks thunders downstream. But then the runoff slows, and death comes to the Albany Pool with the first hot spell...”

- R. Boyle. 1969. *The Hudson River*

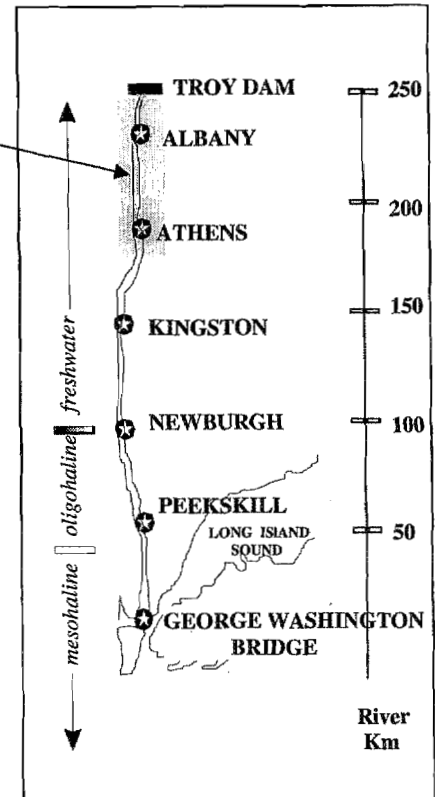


Figure 11. Region of persistent hypoxia known as Albany Pool in the Hudson River. This region overlaps broadly with shortnose sturgeon nursery habitat that occurs throughout the freshwater tidal reach of the estuary.

Albany Pool (river km 227) 1970-1978

Data from Lawler, Matusky and Skelly © 1976, and Hudson River Research Council 1980. Reported by Leslie et al. 1988 *In Fisheries Research in the Hudson River.*

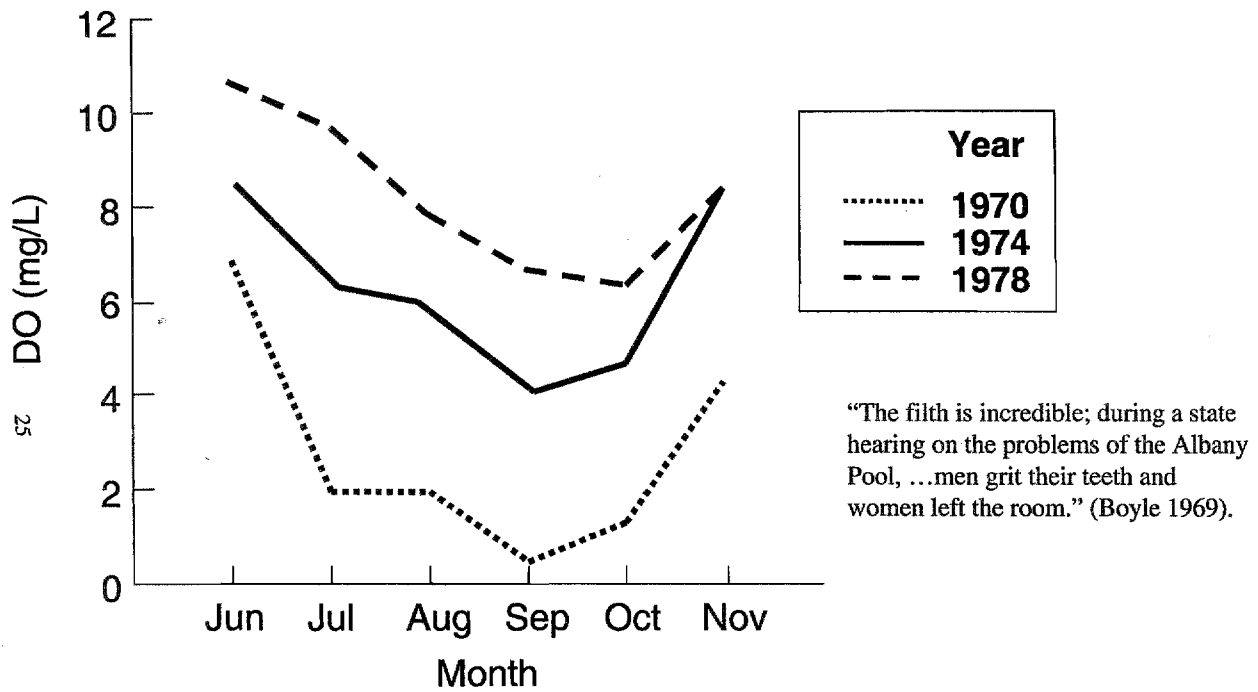


Figure 12. DO levels for an “Albany Pool” station during summer and fall months.

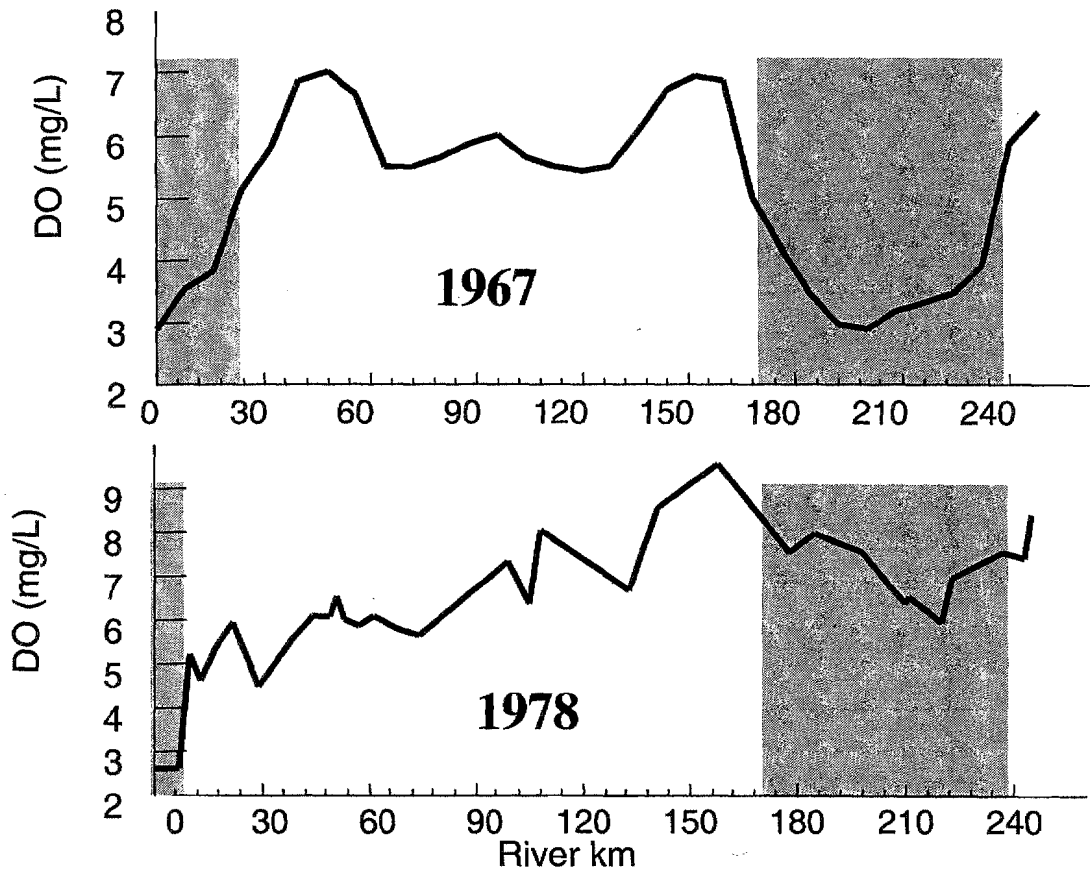


Figure 13. DO levels throughout the Hudson River estuary before (1967) and after (1978) system recovery from hypoxia. "Albany Pool" is shown in gray for upriver DO sag (1967).