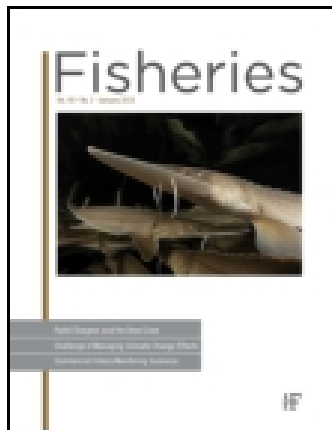


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Broadening the Regulated-River Management Paradigm: A Case Study of the Forgotten Dead Zone Hindering Pallid Sturgeon Recovery

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Broadening the Regulated-River Management Paradigm:

A Case Study of the Forgotten Dead Zone Hindering Pallid Sturgeon Recovery



The global proliferation of dams within the last half century has prompted ecologists to understand the effects of regulated rivers on large-river fishes. Currently, much of the effort to mitigate the influence of dams on large-river fishes has been focused on downriver effects, and little attention has been given to upriver effects. Through a combination of field observations and laboratory experiments, we tested the hypothesis that abiotic conditions upriver of the dam are the mechanism for the lack of recruitment in Pallid Sturgeon (*Scaphirhynchus albus*), an iconic large-river endangered species. Here we show for the first time that anoxic upriver habitat in reservoirs (i.e., the transition zone between the river and reservoir) is responsible for the lack of recruitment in Pallid Sturgeon. The anoxic condition in the transition zone is a function of reduced river velocities and the concentration of fine particulate organic material with high microbial respiration. As predicted, the river upstream of the transition zone was oxic at all sampling locations. Our results indicate that transition zones are an ecological sink for Pallid Sturgeon. We argue that ecologists, engineers, and policy makers need to broaden the regulated-river paradigm to consider upriver and downriver effects of dams equally to comprehensively mitigate altered ecosystems for the benefit of large-river fishes, especially for the Pallid Sturgeon.

Ampliando el paradigma de manejo de la regulación de ríos: la olvidada zona muerta como obstáculo para la recuperación del esturión pálido

La proliferación de presas a nivel global durante el último medio siglo, ha llevado a los ecólogos a tratar de comprender los efectos que tiene la regulación de ríos sobre los grandes peces de agua dulce. Actualmente, gran parte de los esfuerzos dirigidos a mitigar la influencia de las presas en los grandes peces de agua dulce se han enfocado en los efectos observados en la porción inferior de las cuencas y poca atención se le ha dado a los efectos río-arriba. A través de una combinación de observaciones de campo y experimentos de laboratorio, se probó la hipótesis de que las condiciones abióticas río-arriba en las presas son el mecanismo que explica las fallas del reclutamiento del esturión pálido (*Scaphirhynchus albus*), una icónica especie de agua dulce, de gran tamaño, catalogada como amenazada. Se muestra por vez primera que la anoxia en hábitats río-arriba en los reservorios (i.e., zonas de transición entre ríos y reservorios) es probablemente responsable de las fallas en el reclutamiento del esturión pálido. Las condiciones de anoxia en la zona de transición es función de la reducción de la velocidad de flujo del río y la concentración de material orgánico fino particulado, con un alto contenido de respiración microbiana. Como se predijo, las condiciones del río por encima de la zona de transición fueron óxicas en todos los sitios de muestreo. Los resultados indican que las zonas de transición representan un sumidero para el esturión pálido. Se argumenta que los ecólogos, ingenieros y tomadores de decisiones requieren de ampliar el paradigma de la regulación de ríos, con el objeto de incluir los efectos que tienen las presas tanto río-arriba como río-abajo y, así mismo, mitigar sistemáticamente los ecosistemas afectados en beneficio de los grandes peces de agua dulce, especialmente el esturión pálido.

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INTRODUCTION

The proliferation of dams within the last century has been a response to human population growth in order to provide services such as flood control, hydropower, irrigation, water supply, navigation, and recreation. For example, dams account for 12–16% of the world's food production and generate 19% of the world's electricity—approximately one third of the countries in the world obtain 50% of their electricity from hydropower (World Commission on Dams [WCD] 2000). An estimated 60% of the world's rivers have been affected by dams and diversions (WCD 2000) with the contemporary number of reservoirs estimated at 16.7 million greater than 0.01 km² (2,249 km³) and 2,094 greater than 10 km² (5,820 km³; Lehner et al. 2011). Dams influence more than 40% of the global discharge (Vörösmarty et al. 2003) and fragment the ecological integrity of river ecosystems (Nilsson et al. 2005). Given human population growth projections and global climate change, dam construction will continue, especially in developing countries because the most appropriate dam sites have already been exploited in developed countries (WCD 2000). Undoubtedly, dams provide benefits to human development, but these benefits come at a cost to the natural environment.

Within approximately two human generations, Pallid Sturgeon distribution and abundance has been reduced such that it was listed as endangered in the United States in 1990.

Unfortunately, large-river fishes, such as species in the Order Acipenseriformes (sturgeon and Paddlefish), live in regions of the world where rivers are highly regulated (Billard and Lecointre 2001; Nilsson et al. 2005; Lehner et al. 2011). Because of dams and overharvest (the primary mechanisms), 26 of the 27 species in the Order Acipenseriformes are listed as vulnerable, endangered, or critically endangered (Billard and Lecointre 2001; Lorke and Yew 2005; also see International Union for Conservation of Nature Red List of Threatened Species at www.iucnredlist.org). Contemporary conservation of Acipenseriformes has focused on conservation propagation and altering dam discharge to simulate natural flow and temperature regimes (Billard and Lecointre 2001).

Elucidating the effects of dams on downriver habitat and aquatic biota has been an area of active science (e.g., Poff et al. 1997, 2010; Bunn and Arthington 2002) because it has been suggested that flow is the key variable that influences the patterns and processes observed in rivers (e.g., Power et al. 1995; Bunn and Arthington 2002). Furthermore, Poff et al. (2010) stated, “It is now widely accepted that a naturally variable regime of flow, rather than just a minimum low flow, is required to sustain freshwater ecosystems ... and

this understanding has contributed to the implementation of environmental flow management on thousands of river kilometres worldwide. ...” (p.149). Given that much of the focus has been on downriver responses to flow management, less is understood regarding the upriver effects of dams on aquatic biota, especially on recruitment of large-river fishes such as the Pallid Sturgeon (*Scaphirhynchus albus*).

The Pallid Sturgeon is endemic to the Missouri and Mississippi rivers and fossilized ancestors of the contemporary *Scaphirhynchus* spp. date 75–80 million years before the present (Grande and Hilton 2006, 2009; U.S. Fish and Wildlife Service 2014); however, within approximately two human generations, Pallid Sturgeon distribution and abundance has been reduced such that it was listed as endangered in the United States in 1990 (U.S. Fish and Wildlife Service 2014). It is estimated that fewer than 175 naturally produced adult Pallid Sturgeon (i.e., heritage fish) live in the free-flowing Missouri River above Lake Sakakawea (hereafter termed upper Missouri River, which also includes the Missouri River above Fort Peck Reservoir; U.S. Fish and Wildlife Service 2014). An important causal factor for the population reduction in the upper Missouri River is the lack of survival in naturally produced Pallid Sturgeon (hereafter termed recruitment). After spawning, eggs hatch and the free embryo Pallid Sturgeon drift for long distances (approximately 200 to 500 km depending on water temperature and velocity), near the substrate, and in the river thalweg (Braaten et al. 2010, 2012). The transformation of the upper and middle Missouri River from a free-flowing river to one fragmented by six large mainstem dams is likely the cause for the lack of recruitment because there is not enough available drift distance for free embryos to mature and settle out of the ichthyoplankton before entering reservoirs (Braaten et al. 2012). For example, the distance from the known spawning locations to the river–reservoir transition zone (hereafter termed transition zone, an area where the lotic ecosystem transforms to a lentic ecosystem) of Lake Sakakawea at full pool was approximately 37 km (Braaten et al. 2012); similarly, the majority of adult Pallid Sturgeon telemetry locations were within 75 km of the transition zone above Fort Peck Reservoir (Richards 2011). Despite this knowledge, how the transition zone influences recruitment failure of Pallid Sturgeon was not understood.

Millions of U.S. dollars are spent annually on research, conservation propagation, and habitat alterations (i.e., modification of discharge from the dams and creation of habitat) for the recovery of Pallid Sturgeon; furthermore, it is estimated to cost approximately \$239,000,000 to implement all recovery tasks (U.S. Fish and Wildlife Service 2014). The vast majority of funding is related to understanding the downriver effects of dams on Pallid Sturgeon; we argue that fisheries biologists, river managers, and policy makers must consider the upriver effects of dams to ensure successful recovery. We hypothesized that the upriver effects of dams (i.e., reservoirs and the associated transition zone) are as equally detrimental to the continued existence of many large-river species as the downriver effects. Thus, we focused our research efforts on the transition zone as an ecological sink for pallid sturgeon. Here we present the first evidence, via field measurements and laboratory experiments, that environmental conditions in the transition zone are the mechanism for the lack of Pallid Sturgeon recruitment, which underscores the importance of considering upriver effects on large-river fishes.

METHODS

In 2012, a pilot study was initiated and water samples were collected at three depths (surface, 50% maximum depth, and 100% maximum depth) using a Van Dorn sampler (Alpha water sampler 2.2 L, Wildco, Yulee, FL) in the river and transition zone above Fort Peck Reservoir, Montana. Samples were collected on 19 and 20 June 2012 when water temperatures in the river were optimal for Pallid Sturgeon spawning and embryo survival (Kappenman et al. 2013). Samples were emptied into an 18.9-L plastic container and dissolved oxygen (DO), temperature, pH, and unionized ammonia were measured using a YSI (Yellow Springs Instrument, Inc., Yellow Springs, OH) Professional Plus meter. We were concerned about the dissolved oxygen measurements in 2012 because the meter would not stabilize for samples near the substrate (i.e., at low dissolved oxygen). Thus, in 2013, we used the YSI ProODO, which uses an optical sensor to measure dissolved oxygen and reduced uncertainty in our measurements.

In 2013, DO, water temperature, and velocity were systematically measured along transects in the river and transition zone above Fort Peck Reservoir, Montana (Figure 1). Water velocity, substrate, and channel characteristics were used to delineate the river and transition zone. River was defined as having surface water velocity ≥ 0.5 m/s, sand substrate, and a river channel within the riverbanks. The transition zone was defined as having a surface water velocity ≥ 0.1 m/s and < 0.5 m/s, silt substrate, river channel not well confined, and the reach resembled a lentic environment. The transition zone habitat has been previously described by Thornton (1990). As in 2012, measurements were collected on 18 June when water temperatures in the river were optimal for Pallid Sturgeon spawning (Kappenman et al. 2013). Transects within each habitat type were spaced approximately 1 km apart.

Measurements at 50, 75, and 100% of the maximum depth were collected in the thalweg and immediately outside the thalweg on river left and right along each transect. In addition, vertical profile measurements were collected in the thalweg, and DO, water temperature, and velocity were measured at 0.25-m increments. All DO and water temperature measurements were measured using a YSI ProODO meter, and velocity was measured using a Marsh McBirney Flo-Mate 2000 (Hach, Loveland, CO). Unlike 2012, we collected all measurements in 2013 in situ because meter sensors were attached to a sounding weight attached to the boat via cable. Measurements at the maximum depth were 14 cm above the substrate because meter sensors were attached to the hanger bar for the sounding weight. Kruskal-Wallis test was used to compare dissolved oxygen concentration between habitat types and among depths because these data were not normally distributed.

Sediment samples were collected from the surface of the benthos in the thalweg on 18 June 2013 by scraping the benthos using a 250-mL plastic bottle attached to a metal rod. Sediment was collected in the river (i.e., sand; $N = 5$) and transition zone (i.e., silt; $N = 8$) at the same locations as the DO, water temperature, and velocity measurements. Approximately 10 mL of sediment (only fine-grained) was placed in separate 50-mL screw-top centrifuge tubes and stored on ice in the dark until samples were analyzed in the lab for sediment respiration rates. Additionally, river water was collected in the same area and stored on ice in dark conditions until analysis. Laboratory analysis followed methods outlined by Hill et al. (2000). Sediment samples were transferred from ice to ambient conditions, set upright for the sediment to settle, and the water was decanted. Each tube was filled to the top (being careful to leave room for air bubbles) with filtered (0.7 μm pore size) river water, sealed, and incubated for at least 2 h in ambient temperatures (mean 23.8°C) in the dark.

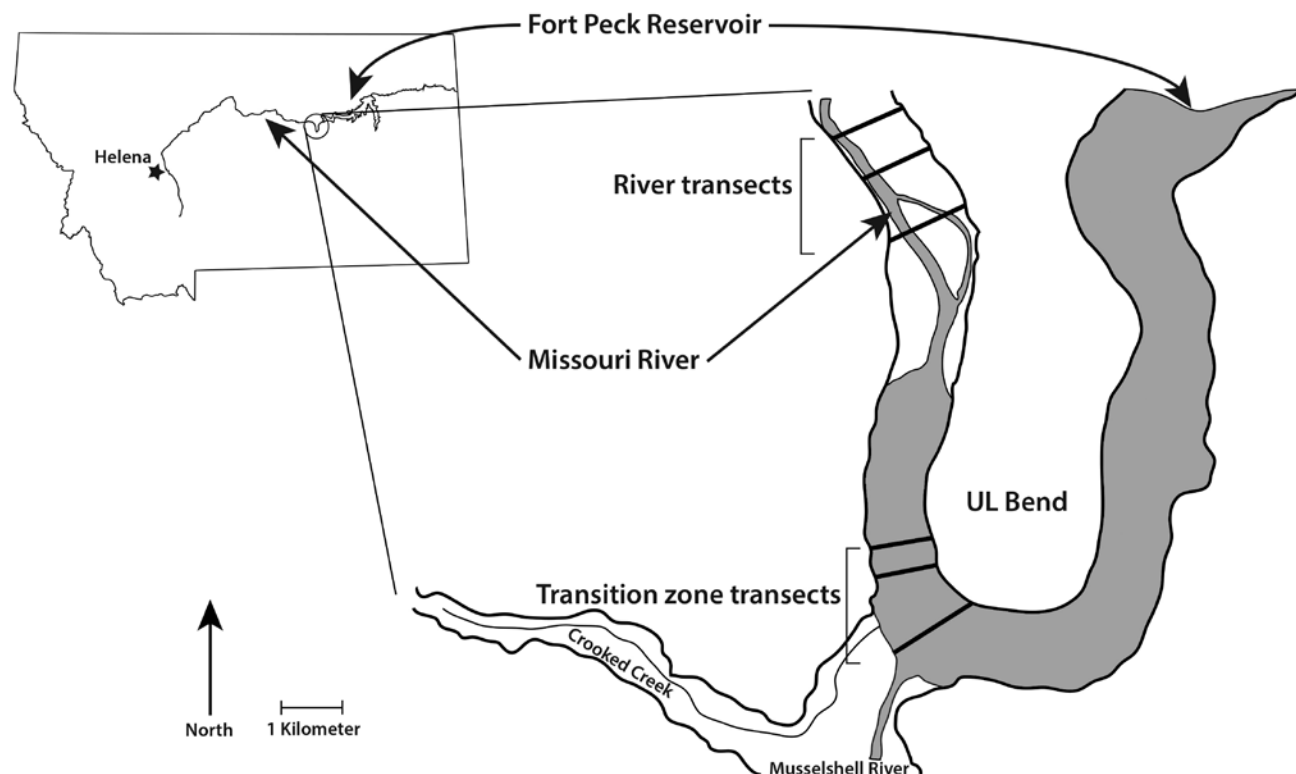


Figure 1. Sampling locations in the Missouri River and river-reservoir transition zone in Fort Peck Reservoir, Montana.

Table 1 . Results of dissolved oxygen (mg/L), temperature (°C), and velocity (m/s) field measurements by depth (values in parentheses are 95% confidence intervals).

Year	Location ^a	Variable	Percentage of maximum depth		
			50	75 ^a	100 ^b
2012	Transition zone thalweg	Dissolved oxygen	8.55 (0.17)		1.32 (1.49)
		Temperature	18.30 (0.00)		17.83 (0.32)
	River thalweg	Dissolved oxygen	8.25 (0.37)		7.61 (1.02)
		Temperature	18.15 (0.08)		18.03 (0.11)
2013	Transition zone thalweg	Dissolved oxygen	7.95 (0.07)	7.93 (0.07)	0.00 (0.00)
		Temperature	20.6 (0.3)	20.6 (0.2)	19.9 (0.2)
		Velocity	0.34 (0.04)	0.30 (0.05)	0.08 (0.06)
	Outside thalweg	Dissolved oxygen	8.02 (0.06)	7.94 (0.12)	0.00 (0.00)
		Temperature	20.9 (0.6)	20.6 (0.7)	20.5 (0.7)
		Velocity	0.25 (0.12)	0.19 (0.08)	0.04 (0.07)
	River thalweg	Dissolved oxygen	7.94 (0.01)	7.91 (0.05)	7.92 (0.01)
		Temperature	21.9 (0.3)	21.9 (0.3)	21.9 (0.3)
		Velocity	0.68 (0.09)	0.59 (0.07)	0.38 (0.14)
	Outside thalweg	Dissolved oxygen	7.96 (0.02)	7.96 (0.02)	7.96 (0.02)
		Temperature	22.0 (0.2)	22.0 (0.2)	22.0 (0.2)
		Velocity	0.57 (0.10)	0.52 (0.10)	0.27 (0.15)

^a No measurements were made outside the thalweg and at 75% of maximum depth in 2012.

^bIn 2013, measurements were 14 cm above the substrate given where the meter sensors were attached to the sounding weight.

The dissolved oxygen concentration and temperature of the filtered water were recorded before filling the samples to get an estimate of beginning water properties. Dissolved oxygen concentrations were measured using a YSI ProODO after at least 2 h of incubation to estimate the changes of oxygen concentrations attributed to sediment respiration. Additionally, eight blanks consisting only of filtered river water with known DO and temperature were incubated and analyzed to account for changes in DO concentrations not associated with the sediment (i.e., those changes due to respiration by organisms in the filtered water). Following incubation, samples were corrected for changes unattributed to sediment respiration (by using the DO measurements in the blank samples), divided by sample volume, and divided by total time incubated to obtain estimates in oxygen consumption per hour (mg O₂/h).

Following respiration measurements, sediment was saved for analysis of ash-free dry mass (AFDM). Sediments were transferred to aluminum drying pans and oven dried (60°C, 5 days), weighed, and combusted (600°C, 4 h) in a muffle furnace. Following combustion, samples were rewetted with distilled water to rehydrate clays, dried (60°C, 5 days), and reweighed to estimate AFDM. The percentage of organic matter in the samples was estimated by dividing AFDM by dry mass. Ash-free dry mass and dry mass estimates were then used to estimate sediment respiration rates (mg O₂/g AFDM h), allowing us to correct for differences in the volume of sediment among samples. Kruskal-Wallis test was used to compare sediment respiration between substrate types because these data were not normally distributed. Correlation analysis was used to evaluate the relationship between percentage organic matter and oxygen consumption.

All laboratory experiments were conducted at the U.S. Fish and Wildlife Service, Bozeman Fish Technology Center, Bozeman, Montana. Desired DO concentrations were achieved using a gas-stripping column (Mount 1964). Oxygen was removed from water in the column with a vacuum pump to achieve a minimum DO level of 1.5 mg/L. The deoxygenated water was then distributed to McDonald-type hatching jars (tanks) at a rate of 1 L/min, and complete tank turnover occurred in 3 min. Based on the assigned treatment level, the deoxygenated water was mixed with untreated (i.e., oxygen rich; 7 mg/L) water from the Bozeman Fish Technology Center to maintain the needed DO level in each tank. We monitored DO levels each day of an experiment with a YSI model 55/12 FT handheld DO meter (Yellow Springs, Yellow Springs, OH).

Exposure experiments were designed as a 2 × 3 factorial in which larvae at each of two ages, free embryo and 40-day posthatch (40 DPH), were exposed to three treatments. Treatments were 1.5, 2.5, and 7.0 mg/L (control) and fish were exposed for a period of 6 (free embryo) or 5 (40 DPH) days. At the start of each experiment, experimental tanks were randomly assigned to one of the three treatments, with each treatment replicated three times. Larvae were collected in a 1-L glass beaker from 1.83-m (diameter) round holding tanks and randomly assigned to experimental tanks. One hundred free embryos and twenty 40 DPH were distributed to each tank. In the case of the 40-DPH Pallid Sturgeon, there were 10 per tank. Water temperature in the tanks varied between 18°C and 20°C. Mortality was determined by recording the number of living fish in each tank at the end of the experiment and calculating the difference from the initial number introduced into the tank. A two-way analysis of variance was used to evaluate the

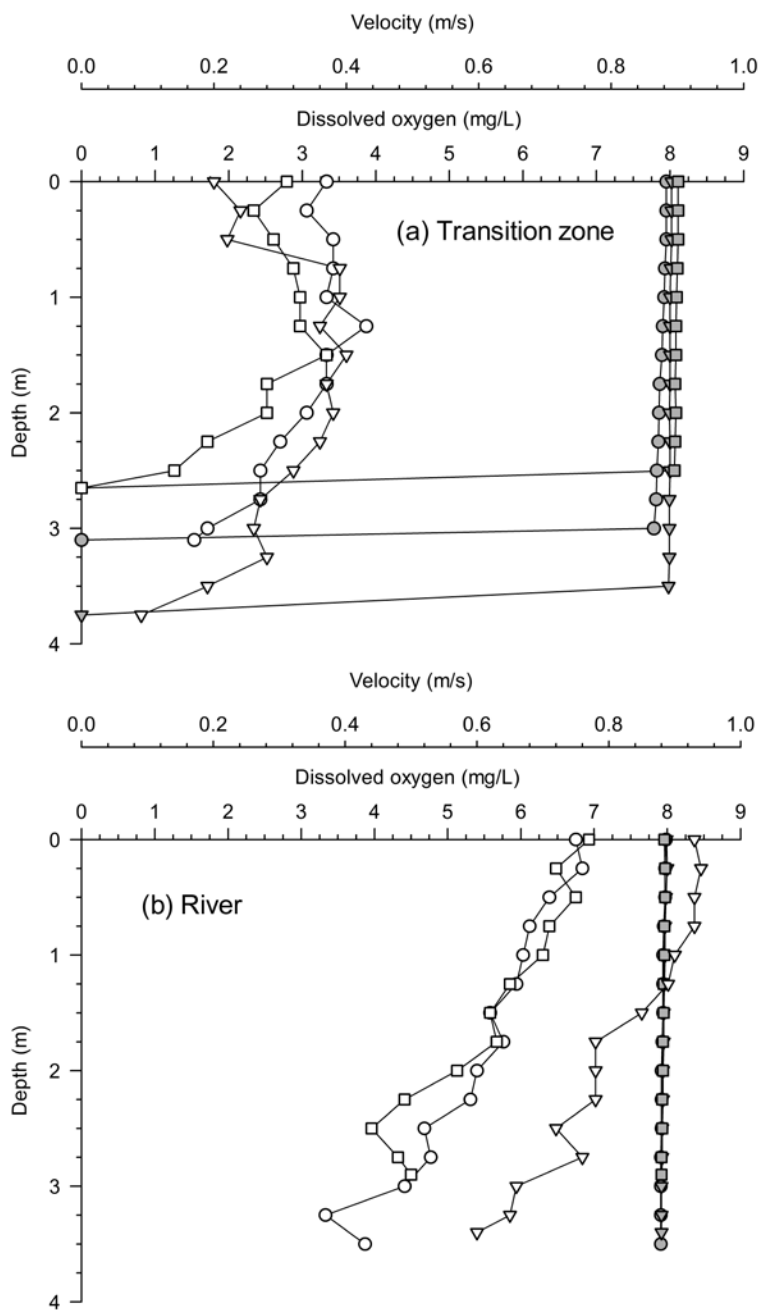


Figure 2. Dissolved oxygen and velocity profiles for the (a) transition zone and (b) river. Shaded symbols delineate dissolved oxygen measurements and open symbols delineate velocity measurements. Symbol shapes correspond to dissolved oxygen and velocity measurements collected in the same profile. The variation in where conditions become anoxic in the transition zone is a function of varying maximum depth (see main text). Symbols for dissolved oxygen are overlaid in the river because of similarities in the measurements.

influence of age and DO treatment on mortality. All analyses were evaluated for normality and homogeneity of variances. All statistical analyses were performed using R (R Development Core Team 2012) and $\alpha = 0.05$.

RESULTS

The transition zone was hypoxic or anoxic near the substrate in and outside the thalweg (Table 1). Conversely, in the river (i.e., representing natural conditions), DO concentrations were

greater than 7 mg/L at all depths and lateral locations (Table 1). Dissolved oxygen differed significantly near the substrate (i.e., 100% of maximum depth) between the river and transition zone (2013; Kruskal-Wallis $\chi^2 = 24.9$, $P < 0.0001$, $df = 1$), but DO did not differ between the river and transition zone at shallower depths (2013; Kruskal-Wallis $\chi^2 = 0.33$, $P = 0.56$, $df = 1$ for 75% of maximum depth; Kruskal-Wallis $\chi^2 = 1.93$, $P = 0.16$, $df = 1$ for 50% of maximum depth). A clinograde DO distribution occurred in the transition zone, whereas DO was homogenous among depth in the river (Figure 2). Similar to the transect data, DO profiles only differed between the transition zone and river near the substrate (Figure 2). As expected, velocity was lower in the transition zone compared to the river (Table 1, Figure 2).

Mass-normalized microbial respiration rates were approximately four times higher in the transition zone (i.e., silt substrate) than in the river (i.e., sand substrate; Figure 3a), and respiration rates differed significantly between substrate type (Kruskal-Wallis $\chi^2 = 7.7$, $P = 0.005$, $df = 1$). The transition zone substrate had a higher proportion of organic matter than the river substrate (Figure 3b). Furthermore, percent organic matter was significantly correlated with oxygen consumption ($P = 0.0005$, $r = 0.82$, $df = 12$).

In our laboratory experiments, Pallid Sturgeon experience 100% mortality at dissolved oxygen concentrations of 1.5 mg/L at the free embryo and 40-DPH life stages (Figure 4). Mortality differed significantly among DO treatments ($P \leq 0.0001$, $F = 110.2$, $df = 2$) and there was no influence of age ($P = 0.23$, $F = 1.52$, $df = 1$), but there was a significant treatment by age interaction ($P \leq 0.0001$, $F = 16.9$, $df = 2$). The interaction was a function of higher mortality in the control than the 2.5 mg/L dissolved oxygen treatment for the free embryo Pallid Sturgeon. Nevertheless, mean mortality at the 2.5 mg/L treatment and control were half the mortality at the 1.5 mg/L treatment. Pallid Sturgeon typically died within 1 h after exposure to the 1.5 mg/L DO treatment, which can be considered a maximum duration for DO levels below 1.5 mg/L.

DISCUSSION

Given that free embryo Pallid Sturgeon drift into transition zones (see Braaten et al. 2012), we have provided data necessary to explain the mechanism for Pallid Sturgeon recruitment failure in the upper Missouri River. Prior to the fragmentation of the Missouri River by dams, Pallid Sturgeon free embryos would drift for hundreds of kilometers near the thalweg and settle out of the drift as they aged and could negotiate the flow (Figure 5a). Patches of suitable habitat (low velocity with high DO) existed within the thalweg, most likely behind velocity breaks such as woody debris or underwater sand dunes (Figure 5a). Under natural conditions, it is believed that drifting near the thalweg substrate

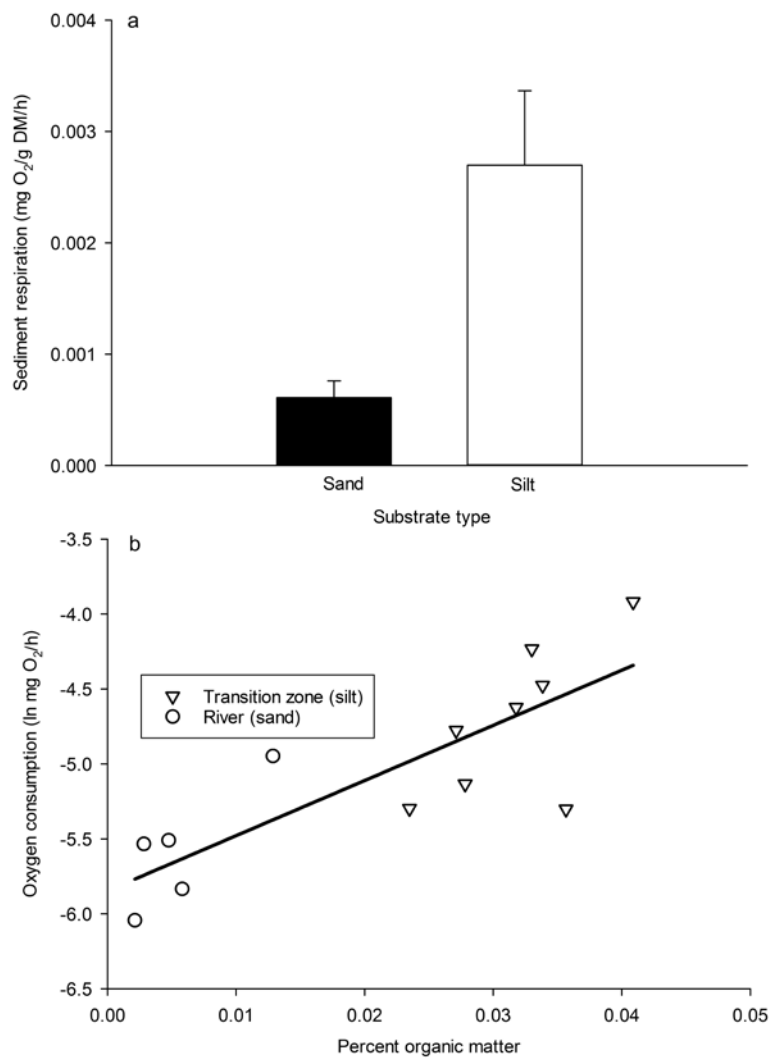


Figure 3. (a) Mean (standard error) sediment microbial respiration estimates per dry mass (DM) (mg O₂/g DM/h) for sand and silt. (b) Relationship between natural log of oxygen consumption and percentage of organic matter for all empirical samples.

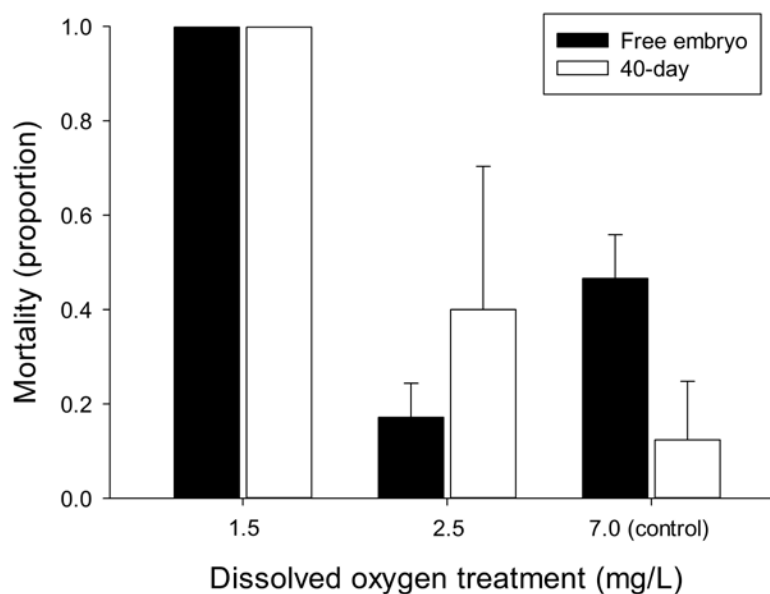


Figure 4. Mortality of free embryo and 40-day-old Pallid Sturgeon by dissolved oxygen treatment.

was a mechanism to avoid predation, which evolved over millions of years (Braaten et al. 2012). In the current human-altered ecosystem, the river enters the transition zone, velocity significantly decreases, and fine particulate organic matter settles to form a flocculent that is anoxic (i.e., dead zone) because of high microbial respiration (Figure 5b). This is also the area where free embryo Pallid Sturgeon prematurely settle (Figure 5b) because the needed drift distance is hindered by river fragmentation from dams (Braaten et al. 2012).

For the upper Missouri River, the fine particulate organic matter that concentrates in the transition zone is naturally occurring and likely lower than historical conditions given the dominate land use and occurrence of reservoirs on several tributaries in the upper Missouri River basin. The size of the transition zone is currently unknown because we did not measure the most downriver extent because of monetary and logistic constraints. Is it possible for free embryos to drift through the transition zone? We argue that this is highly unlikely. For example, our study reach was approximately 3 km long and it would take approximately 2.5 h for a Pallid Sturgeon free embryo to drift between the first and last transects—using the mean drift velocity for Pallid Sturgeon free embryos calculated as 95% of mean column velocity in the thalweg from our study (see Braaten et al. [2012] for using values slightly less than full velocity). This estimate is the best-case scenario because free embryos drift near the bottom and it would take approximately 10 h using the 95% mean bottom velocity. Both drift velocity estimates would be lethal for Pallid Sturgeon free embryos given that we discovered 100% mortality within 1 h of being exposed to DO concentrations at 1.5 mg/L.

Others have suggested that reservoirs can influence fish assemblages (e.g., Martinez et al. 1994; Matthews et al. 1994; Falke and Gido 2006). Furthermore, Winston et al. (1991) hypothesized that recruitment failure in Speckled Chub (*Macrhybopsis aestivalis*) and Plains Minnow (*Hybognathus placitus*) may be a function of free embryos drifting into reservoirs, the U.S. Army Corps of Engineers generally described the transition zone in the Missouri River mainstem water quality report but provided no empirical measurements (U.S. Army Corps of Engineers 2006b), and Cole and Hannan (1990) describe the likelihood of low DO in the transition zones—hence, the “forgotten dead zone” in our title. We believe that our study is unique from those listed above because we make direct links between human-induced changes in sediment transport and the subsequent effects on DO and the survival of an endangered species. This underscores the need for a better understanding of upriver effects of dams on aquatic biota.

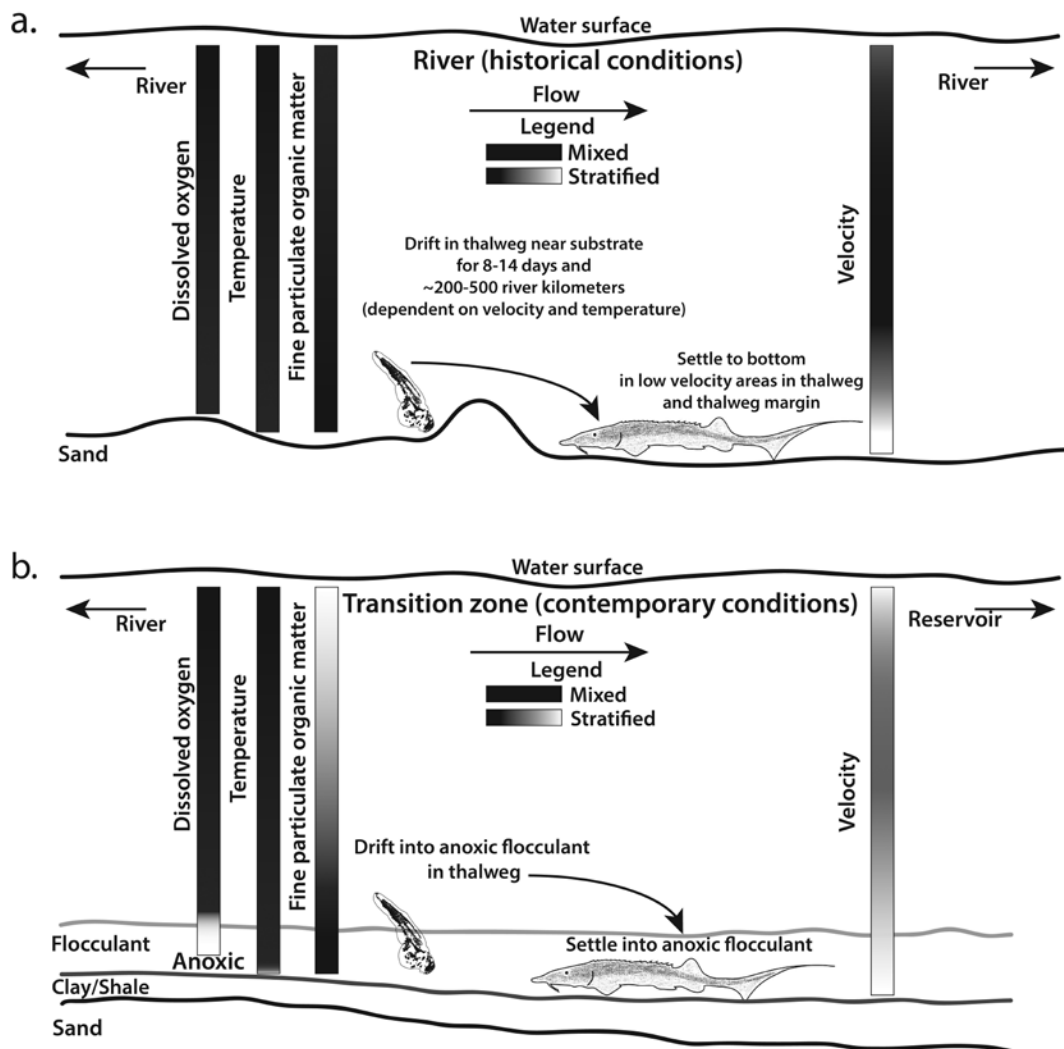


Figure 5. Schematic of historical river conditions and the contemporary ecological sink as a function of reservoirs. Historically, river habitat was dynamic with dissolved oxygen, temperature, and fine particulate organic matter mixed throughout the water column as a function of complex velocity currents. Velocity is lowest near the substrate as a function of shear stress and drag forces. Free embryos drift along the thalweg for hundreds of kilometers prior to settling at the substrate. (a) Pockets of low-velocity microhabitat with high dissolved oxygen exist in the river thalweg, and these are likely the locations that Pallid Sturgeon select once they reach an age and size where they can negotiate flow. In the current conditions, the transition zone habitat is a human-made habitat that differs from the river by having stratified dissolved oxygen concentrations and fine particulate organic matter. (b) Free embryo Pallid Sturgeon drift into these habitats because drift distance is limited and they are involuntarily exposed to habitat that is anoxic.

The upriver effects of dams likely influence other large-river species; for example, other species in the Order Acipenseriformes exhibit high mortality when exposed to hypoxic conditions (Dettlaff et al. 1993; Cambell and Goodman 2004; Niklitschek and Secor 2009). Historically, most of the species in the Order Acipenseriformes migrated long distances in rivers to complete their life history requirements (Bemis and Kynard 1997). However, given the globalization of dam construction, many species are isolated from historical spawning areas or occur in fragmented river ecosystems (Billard and Lecointre 2001). Furthermore, dams have reduced the global flux of sediment reaching the oceans by over 100 billion metric tons (Syvitski et al. 2005). We contend that sediment and anoxic conditions in transition zones are global threats to many species that evolved in large, turbid, free-flowing rivers. Ecologists, engineers, and policy makers need to broaden the regulated-river paradigm to consider upriver and downriver effects of dams

equally to comprehensively mitigate altered ecosystems for the benefit of large-river fishes.

Specifically for the Pallid Sturgeon, it is unlikely that it can be recovered in all management units as outlined in the *Recovery Plan for the Pallid Sturgeon* (U.S. Fish and Wildlife Service 2014) without sizable modifications to how mainstem reservoir water levels are managed by the U.S. Army Corps of Engineers. Is manipulating reservoir water levels to increase the drift distance available for Pallid Sturgeon free embryos a viable management action? To achieve the needed drift distance for Pallid Sturgeon free embryos, reservoirs would need to be operated at a much-reduced capacity and this would likely influence the current benefits to society that dams provide as outlined in the *Missouri River Mainstem Reservoir System Master Control Manual* (U.S. Army Corps of Engineers 2006a). If natural resource agencies are serious about recovering the Pallid Sturgeon as outlined in the recovery plan, then all

stakeholders need to begin thoughtful discussions and take action regarding innovative approaches to managing Missouri River reservoirs. We argue that creative approaches are needed to conserve Pallid Sturgeon in the upper Missouri River and could be used as a model to benefit other large-river fishes worldwide. Change is required given our results, because simply modifying discharge from dams to reflect a more natural hydrograph is presently shortsighted in terms of large-river fish conservation.

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