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Journal

Environmental Biology of Fishes, 102(5)

ISSN

0378-1909

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Publication Date

2019-05-01

DOI

10.1007/s10641-019-00873-8

Peer reviewed



Behavioral responses of juvenile white sturgeon (*Acipenser transmontanus*) to manipulations of nutritional state and predation risk

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Received: 10 May 2018 / Accepted: 21 March 2019
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Abstract Predation and reduced energetic intake have been highlighted as potential mechanisms of recruitment failure in sturgeon populations. These two factors may interact, as foraging carries with it costs of increased predation risk, requiring behavioral trade-offs. We expect that juvenile sturgeon should express predator avoidance behaviors while they are within vulnerable size ranges, yet these behaviors should be modified by nutritional state. To evaluate behavioral trade-offs of juvenile white sturgeon, we designed an experiment to test the interacting effects of acute nutritional state and predation risk on the spatial distribution and movement of small groups ($n = 6$). Groups were assigned to one of four treatments, designed as a full factorial of nutritional state (well-fed or starved 24-h) and predation risk (largemouth bass present or absent), and eight replicates were conducted for each treatment. Juvenile sturgeon displayed a predicted and adaptive response to predation risk and predator aggression levels by reducing activity levels and displaying marked freezing behavior. Sturgeon responded strongly to nutritional deprivation through increased activity and increased near-neighbor distance, which was likely an adaptive response to increase encounter rates with benthic food items. Both of these

responses to starvation were suppressed in the presence of predators. This study has provided experimental evidence that predators can abruptly reduce the foraging activity of white sturgeon, possibly reducing growth rates and extending the period of juvenile vulnerability. Future conservation planning should consider the interacting effects of multiple stressors experienced by sturgeon at early life-stages, as introduced predators and degraded foraging habitats may have interacting effects.

Keywords Juvenile sturgeon · Behavioral trade-offs · Predation · Foraging

Introduction

White Sturgeon, *Acipenser transmontanus*, are a semi-anadromous species that inhabits the estuaries of many northern-Pacific rivers in North America, including the Sacramento River of California. While many sturgeon populations and many other anadromous species are currently in worldwide decline (Bemis and Findeis 1994; Bemis et al. 1997; Birstein et al. 1997), white sturgeon are considered a species of Special Concern in California (Moyle et al. 2015). Population stability of anadromous species is strongly affected by mortality rates of larval and juvenile life stages (Houde 1987; Parsley et al. 2002; Coutant 2004), and whilst these mortality rates are influenced by a range of human-induced changes to their ecosystems (Parsley and Beckman 1994; Anders et al. 2002; Coutant 2004; Hildebrand et al. 2017), predation is potentially an

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important issue with juvenile sturgeon (Miller and Beckman 1996; Gadomski and Parsley 2005a, b; Caroffino et al. 2010; Flowers et al. 2011; Hildebrand et al. 2017). As with many prey species, predation on juvenile sturgeon decreases with increased size (Cowan et al. 1996; Gadomski and Parsley 2005b; Rojas and Ojeda 2010). However, at vulnerable sizes prey should express adaptive predator avoidance behaviors, which could have implications for population dynamics of both predator and prey and thus be key to future conservation planning.

While the nutrition, development, pathology and reproduction of white sturgeon have been heavily studied due to its cultural and commercial importance, remarkably little is known of the predation and behavior of juvenile white sturgeon (see review Hildebrand et al. 2017). After their eggs hatch in rocky substrate, free embryos swim up into the water column and undergo a relatively brief (compared to other sturgeon species) initial downstream dispersion (approx. 1–3 days) before settling among rocks where they complete yolk-sac absorption and develop into larvae (approx. 11 days post hatch [dph] at 18 °C: Deng et al. 2002; Van Eenennaam et al. 2001; Brannon et al. 1985; Kynard and Parker 2005). Kynard and Parker (2005) propose that the adaptive benefits of this behavior are to reduce predation risk, to help vulnerable embryos reach suitable substrate, and to reduce conspecific density prior to initiation of foraging. Variations in this drift behavior may be determined by differences in interstitial habitat (McAdam 2011) and if suitable interstitial habitat exists upon hatching embryos have been found to immediately hide without drifting (Bennett et al. 2007). Upon development into larvae, white sturgeon lose their photonegative tendency and move out of the interstitial spaces between rocks to forage on the substrate (for approximately the next 30 days; Brannon et al. 1985; Kynard and Parker 2005). Fish show neither attraction nor repulsion to light at this stage and, as they can forage at depths of up to 45 m (Parsley et al. 1993; McCabe and Tracy 1994), vision is likely ineffective or unnecessary for capturing their benthic prey (primarily *Corophium* spp. and Diptera larvae/pupae in the lower Columbia River; Muir et al. 2000). Instead they primarily rely on chemosensory mechanisms (Brannon et al. 1985). White sturgeon tend to forage nocturnally (although not exclusively so), which may be a strategy to avoid threats from visual predators foraging during the day (Lucas and Baras 2001; Alvarez and Nicieza 2003;

Fraser et al. 2004; Kynard and Parker 2005). Early life-stage white sturgeon undergo a second dispersal (primarily nocturnal) after they have developed into juveniles (50–60 dph), actively swimming downstream (Kynard and Parker 2005; McAdam 2012; Howell and McLellan 2014). Fish at this life-stage are still in a size class shown to be vulnerable to predation (Gadomski and Parsley 2005a, 2005b).

Achieving life-history events (e.g. sexual maturation) requires the acquisition of sufficient energy for both maintenance and growth, motivating animals to seek out food. Foraging behavior invariably leads to costs such as increased predation risk (Abrahams and Dill 1989; Lima and Dill 1990; Houston et al. 1993), resulting in a series of trade-offs. Hungry fish are known to increase risky behavior for energetic reward (Magnhagen 1988; Pettersson and Brönmark 1993; Damsgård and Dill 1998). They have been observed to increase activity (Metcalf et al. 1987), leave refuges earlier (Krause et al. 1998), alter voluntary swimming speeds (Hansen et al. 2015a), increase near-neighbor distance, and form smaller shoals (Morgan 1988; Krause 1993; Reeb and Saulnier 1997; Hansen et al. 2015b). The balance between energetic requirements and predation risk is a cornerstone of behavioral ecology (Sih 1982; Dill 1983; Lima and Dill 1990; Houston et al. 1993; Anholt et al. 2000) and a major explanatory factor for the movement and distribution of individuals, groups, and populations. Juvenile white sturgeon have a fast growth rate in their first year of life (Moyle 1976), likely driven by strong selection to reduce the period of vulnerability to predation. To support this fast growth rate, juvenile white sturgeon display continuous feeding (Brannon et al. 1985) and thus nutritional state is likely a major determinant of young sturgeon behavior.

In this study we designed a simple trade-off experiment to explore the interacting effects of nutritional state and predation risk on the spatial distribution and movement of groups of juvenile white sturgeon. We exposed starved (24 h) or well-fed juvenile white sturgeon to largemouth bass predators and recorded space use (a measure of spatial predator avoidance), activity level (a proxy for foraging behavior and predator exposure), and group cohesion (a measure of anti-predator behavior). Previous work on a similar species, the shovelnose sturgeon, *Scaphirhynchus platyrhynchus*, suggested that sturgeon were initially unresponsive to risk of predation by a catfish predator, but after a negative interaction (being chased or bitten) sturgeon were more likely to display

predator-avoidance behavior (Hintz et al. 2013). Thus, as well as monitoring prey spatial distribution and activity rates, we also collected data on predator activity. We recorded the same behavioral metrics for starved or well-fed juvenile white sturgeon in the absence of a predator. While white sturgeon are primarily benthic and therefore most likely to be consumed by benthic predators such as catfish and sculpin (Parsley et al. 1995), we used largemouth bass, *Micropterus salmoides*, as *Micropterus* species have been shown to consume juvenile sturgeon (French et al. 2010), and largemouth bass are opportunistic predators that consume both pelagic and benthic prey (Hodgson and Kitchell 1987; Schindler et al. 1997). We tested three hypotheses: 1) regardless of nutritional state, activity and near-neighbor distance will decrease under predation risk and white sturgeon will spatially avoid largemouth bass; 2) starved white sturgeon will show a relative increase in activity and near-neighbor distance measures when compared to well-fed white sturgeon; 3) predator activity, in addition to predator presence, will be a strong predictor of white sturgeon activity and space use.

Methods

Juvenile white sturgeon were held at the University of California Davis, Center for Aquatic Biology and Aquaculture (CABA). Fish were spawned in May 2017 at the Sterling Caviar Farm (Sacramento, California, USA) before being transferred to CABA at 20 days post-hatch (dph) and reared at 18 ± 0.5 °C in 815 L round fiberglass tanks with continuous flows of aerated, non-chlorinated fresh water from a dedicated well. Fish were initially fed daily with semi-moist pellets (Rangen, Inc., Buhl, Idaho)

then weaned onto a dry pelleted diet (Silver-Cup) at ~60 dph. Adult largemouth bass were used as predators and obtained from electrofishing operations at Clifton Court Forebay, Tracy, CA, administered by the California Department of Water Resources. Twice a week bass were fed live fathead minnows, *Pimephales promelas*, (five per predator) while being acclimated to captivity at 18 °C in 2420 L round fiberglass tanks.

All experimental trials (hereafter simply ‘trials’) were conducted in four 940 L circular tanks (157 cm in diameter, water depth 44 cm). Each tank was designed as a low velocity flow-through system using ground water, with tanks maintaining a mean temperature of 19.1 °C ± 0.72 SD. Water turnover was set to approximately 3.8 L min^{-1} to maintain water quality throughout the trials. A 6 mm wire mesh barrier was installed across the center of each tank with a 100 mm gap at the bottom allowing sturgeon to pass underneath but constraining the predators to a single side (Fig. 1). Eight standard masonry bricks were used in each tank to create simplified habitat structure. Tanks were located in an open-air structure, and each was surrounded by white vinyl curtains to reduce impacts of external disturbance and to improve video images. Each tank was equipped with a single video camera (4MP, model QTH8071b, Qsee, Anaheim, CA) to record the trials and also transmit a live video stream to a monitor located away from the experimental tanks.

Two main treatment effects were used in a full factorial design, resulting in four treatments: well-fed with predator, starved with predator, well-fed without predator, starved without predator. In the starved treatment, sturgeon were fasted for 24 h before the trial began (adequate time for juvenile fish to empty gut; Silva and Anderson 1994), and in the well-fed treatment,

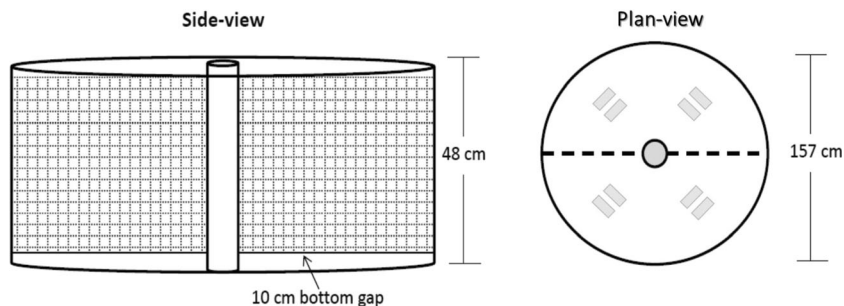


Fig. 1 Experimental tank design in side and plan view. Four circular blue fiberglass tanks (940 L) with central stand-pipes were fitted with a central partition made of 6 mm wire mesh and a 100 mm gap between the mesh and the tank bottom. Eight

masonry bricks provided simplified structure (indicated as small rectangles in plan-view). A video camera, not shown, was mounted directly above the center of the tank

sturgeon were allowed to eat ad libitum until approximately 30 min prior to the trial beginning. Largemouth bass ranging from 330 to 430 mm FL were obtained from the wild and held in captivity for three or more months on live feed. Once moved to experimental tanks, these predators were acclimated for at least three days to reduce possible effects of handling, and to allow habituation to the new environment. We elected to allow the predators greater acclimation time to increase the likelihood of active foraging during experiments, as pilot data collection had shown that handling and transport stress often caused bass to temporarily cease feeding. Bass were fed live fathead minnows in the experimental tank prior to trials, then placed in a minimum 48-h fasting period prior to trials to induce predation activity. Each bass was used in four trials, except for one which showed signs of illness after two trials and was replaced (a total of five individual predators were used in the experiment). Eight replicated trials of each of the four treatments were completed between 1 Aug 2017 and 11 Aug 2017. Each replicate included six naïve juvenile white sturgeon (mean fork length = 87 mm \pm 0.85 SD, mean mass = 4.75 g \pm 1.24 SD, 67–77 dph). On each day, four trials were conducted simultaneously, with two tanks assigned well-fed sturgeon and two tanks assigned starved sturgeon. Two four-day sets of trials were conducted, beginning with 2 days of trials with predators present and ending with 2 days of trials with predators absent.

Trials began in the morning at approximately 10:00 and lasted 270 min to assess how both predator and prey behaviors may change after multiple interactions over time. To initiate a trial, six naïve sturgeon (starved or well-fed) were transferred from the holding tanks to the experimental tank, with three introduced to either side of the central division. After an initial 30 minutes to allow sturgeon to acclimate to the tank and predator, each trial was observed for 5 minutes to record the number of times sturgeon passed under the partition. These observations were repeated once every 60 min for the duration of the trial. In addition to direct activity measures, every 30 minutes a remote observation was made to record the number of sturgeon on each half of the tank. A screenshot was also collected for later analysis of sturgeon spatial distribution, resulting in nine images per trial. At the end of the trial all remaining white sturgeon were removed to be euthanized, weighed, measured, and assessed for external

injury. After all trials were completed, the first hour of each trial video was analyzed in greater detail to quantify the degree of predator activity. The sum total of predator attacks, captures, and ingestions was used as an index of predator activity in the subsequent statistical analyses. The first hour was selected to evaluate activity because this was the peak of activity for both predator and prey (Fig. 1b), and thus provided an opportunity to evaluate differences between predators.

We looked for evidence of the influence of acute nutritional state and predator presence on three types of prey behavior (activity level, spatial avoidance, and aggregation behavior). Generalized linear mixed models (GLMM) were used to evaluate the main treatment effects while accounting for inter-individual variation among predators and changes in behavior over time. The hierarchical structure of the models allowed us to account for repeated measures of behavior within a trial, and non-independence of predators across trials. All analysis was completed in R (R Core Team 2017), using the ‘lme4’ (Bates et al. 2015) and ‘MuMIn’ packages (Barton 2017). All possible subsets of each full model were compared using Akaike information criterion, corrected for small sample sizes (AICc; Hurvich and Tsai 1989; Burnham and Anderson 2002) to assess the explanatory value of each fixed effect. Those predictor variables that did not contribute to improved AICc scores were removed from the final models. A random intercept was included in each model for the effect of trial nested within predator identity (one of five individuals) to account for repeated measures and potential clustering of observations due to the experimental design. Model residuals were graphically assessed for normality and homoscedasticity. Final parameter values were considered significant at $\alpha < 0.05$.

To evaluate changes in activity levels, we recorded the number of times sturgeon crossed under the central partition during each five-minute observation period. We then constructed a GLMM using a log transformation of the activity level and a Gaussian error distribution, as a Poisson distribution was inappropriate due to overdispersion of the data. The model tested the main effects of predator presence, acute nutritional state, and their interaction on this metric of activity, and included an index value of predator activity as assessed from video recordings of the first hour of the trial, as well as an effect of time into the trial to account for changing mean activity levels through time.

To evaluate the degree to which juvenile white sturgeon showed spatial avoidance of predators, we quantified the proportion of individuals in a trial that were on the predator-occupied half (focal side) of the experimental tank at each 30-min interval. For control trials without a predator present, we assigned a focal side of the tank for calculation of comparable metrics. We then constructed a GLMM with a binomial error distribution to test the main effects of predator presence, acute nutritional state, and their interaction on this metric of avoidance. The full model also included an index value for predator activity level and time into the trial.

To evaluate the aggregation behavior demonstrated by the juvenile sturgeon, we measured the six near-neighbor distances (distance from centroid of an individual to the centroid of its nearest neighbor) for each image captured throughout trials at 30 min intervals. The x and y coordinates of each sturgeon were quantified using the software ImageJ (1.51n, NIH, USA). The median near-neighbor distance for each image was calculated and will be referred to as the NND hereafter. We then constructed a GLMM with a Gaussian error distribution to test the main effects of predator presence, acute nutritional state, and

their interaction on NND. The full model also included an index value for predator activity level and time into the trial as predictor variables.

Results

A total of 32 trials were conducted, and of the 16 conducted with predators, only two white sturgeon were consumed (2%) and thirteen were injured by predators. Injuries were identified by visual inspection and ranged from mild (e.g., skin abrasions or slight bruising visible in fins) to moderate (e.g., kinked spine due to trauma). Analysis of activity levels (using a log-transformation and Gaussian GLMM) indicated that nearly all the variables considered (time into trial, predator presence, nutritional state, and interaction of predator presence and nutritional state) had significant effects on the juvenile white sturgeon activity levels. Sturgeon reduced their activity when in the presence of a predator ($\beta = -2.04 \pm 0.314, p < 0.001$; Table 1, Fig. 2b), and increased their activity when they had been starved ($\beta = 1.02 \pm 0.315, p = 0.003$). Yet there was a significant

Table 1 Estimates of effect sizes and uncertainty for three final models of anti-predator behavioral metrics (activity level, spatial avoidance, and near-neighbor distance, NND). Final models were selected from full models containing all fixed predictors using AICc. Overall variance (σ^2), group variance (τ_{00}), and interclass correlation (ICC) are presented for the random effect of trial ID

nested within predator ID in each model. Confidence intervals (95%) are computed with standard errors calculated according to the delta method (Oehlert 1992), and *p*-values are computed using the Kenward-Roger approximation (Kenward and Roger 1997) using the sjPlot package in R (Ludecke 2018)

	Activity (<i>ln transformed</i>)			Spatial avoidance			NND		
	<i>B</i>	<i>CI</i>	<i>p</i>	Odds Ratio	<i>CI</i>	<i>p</i>	<i>B</i>	<i>CI</i>	<i>p</i>
Fixed predictors									
(Intercept)	3.80	3.33–4.27	<0.001	1.06	0.80–1.41	0.690	21.05	17.32–24.78	<0.001
Starved 24-h	1.02	0.40–1.64	0.003	-	-	-	8.95	3.67–14.23	0.002
Predator Present	-2.04	-2.66 – -1.43	<0.001	0.78	0.49–1.23	0.285	4.37	-0.91 – 9.65	0.116
Time into Trial	-0.16	-0.20 – -0.12	<0.001	-	-	-	-	-	-
Predator Activity Index	-	-	-	0.98	0.97–0.99	0.002	-	-	-
Starved x Predator Present	-1.25	-2.12 – -038	0.008	-	-	-	-13.29	-20.75 – -5.82	0.002
Random predictors									
σ^2	0.434			n/a			158.461		
τ_{00} , Trial-ID nested within Pred-ID	0.309			0.258			11.399		
ICC, Trial-ID nested within Pred-ID	0.416			0.073			0.067		
Error distribution	Gaussian			Binomial			Gaussian		
Observations	160			288			288		
R^2 / Ω_0^2	0.872 / 0.872			Deviance: 303.378			0.177 / 0.165		

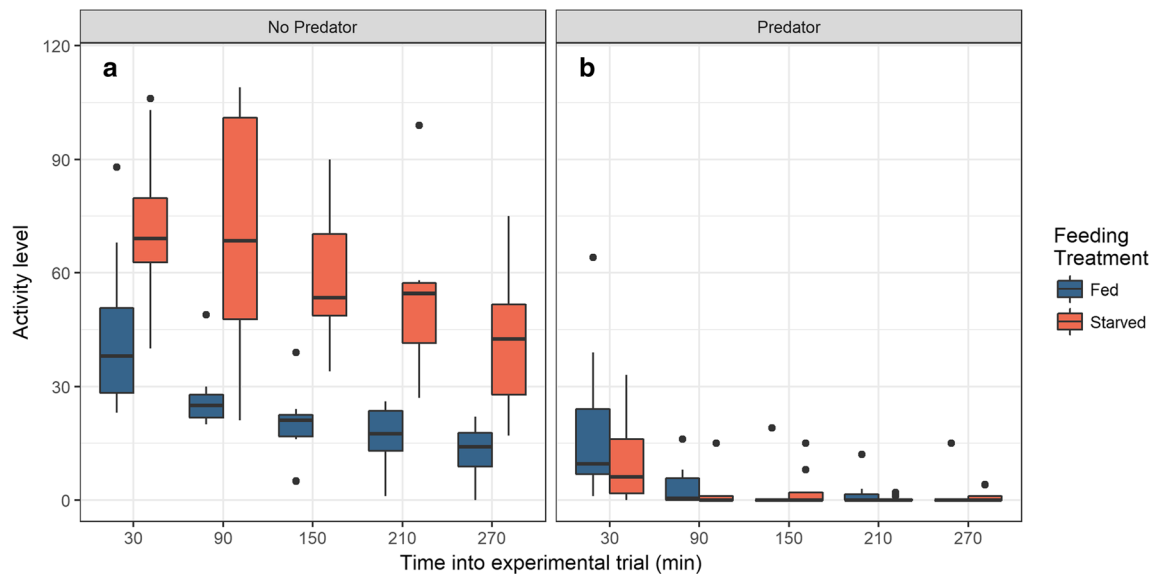


Fig. 2 Activity level through time of juvenile white sturgeon without a predator (**a**) and in the presence of a predator (**b**). Activity was quantified by the number of times individuals crossed underneath the central division in the experimental tank during each 5-min observation period. Blue indicates activity of well-fed

sturgeon, while red indicates activity of starved sturgeon. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to $1.5 \times \text{IQR}$. All points beyond the whiskers are shown. Each trial included six individuals, and each treatment was replicated eight times

interaction between nutritional state and predator presence. A post-hoc test (Tukey HSD) indicated significantly increased activity levels due to starvation in the absence of a predator ($p = 0.015$) but not in the presence of a predator ($p = 0.995$). Sturgeon activity levels also significantly decreased over time ($\beta = -0.16 \pm 0.018$, $p < 0.001$).

The analysis of spatial avoidance of predators by juvenile white sturgeon showed that space use was related to both predator presence and activity index (measured as the number of pursuits and attacks on white sturgeon within the first hour of a trial), while nutritional state and time into the trial had no significant effect. When a predator was absent, sturgeon were equally likely to be on either side of the tank (Fig. 3a). When a predator was present, the binomial GLMM analysis estimated that sturgeon were 22% less likely to be on the side with the predator, although there was high uncertainty in the effect size and direction (odds ratio: 0.78 [0.49–1.23], $p = 0.285$; Table 1, Fig. 3b). The more aggressive a predator was, the less likely the prey was to be on the same side, with a 2% decrease in probability for each additional pursuit or attack observed during the first hour (odds ratio: 0.98 [0.97–0.99], $p = 0.002$).

Predator presence mediated the effect of nutritional state on the aggregation of juvenile white sturgeon, measured through near-neighbor distances (NND). Overall, a Gaussian GLMM estimated that distances between individuals were larger when sturgeon were starved ($\beta = 8.95 \pm 2.693$, $p = 0.002$; Table 1), and there was no significant difference based solely on the presence of a predator. However, to evaluate the significant interaction between these terms a post-hoc test (Tukey HSD) indicated that when predators were absent, there was a significant effect of nutritional state, with starved sturgeon maintaining larger NND compared to well-fed sturgeon ($p = 0.013$; Fig. 4). It also indicated that starved and well-fed individuals had statistically similar NND when a predator was present ($p = 0.389$). All other effects considered had low explanatory value and were removed from the final model.

Discussion

Behavioral plasticity is adaptive in animals living in dynamic environments (Komers 1997; Snell-Rood 2013), and indeed, white sturgeon activity and near-neighbor distance was affected by both nutritional state and predation threat, indicating that both factors are

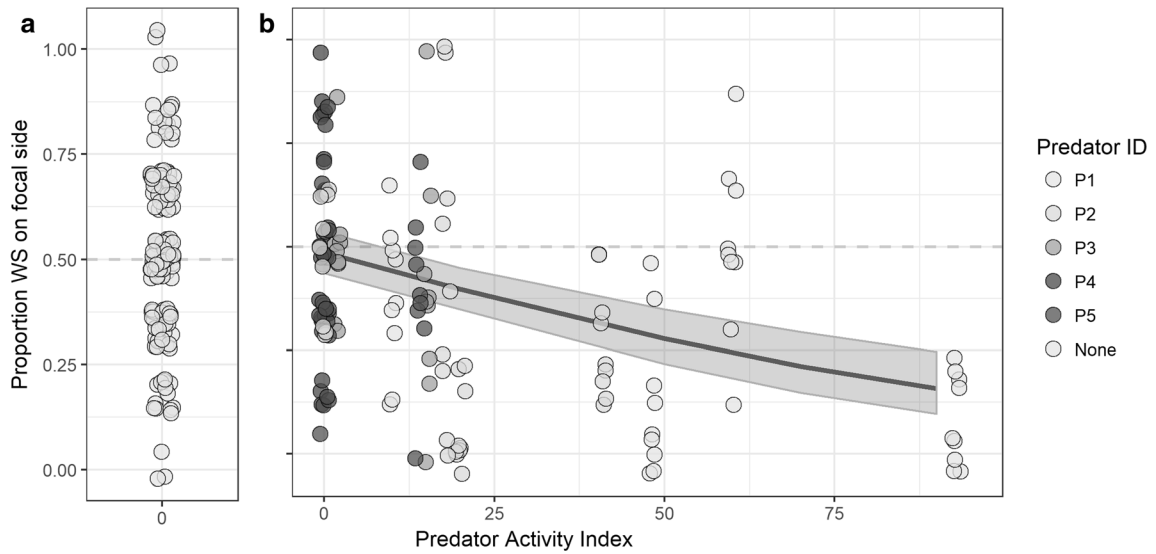


Fig. 3 White surgeon (WS) spatial distribution on focal side without a predator present (**a**) and with a predator present as a function of predator activity index (**b**). Predators were confined to one half of the tank (focal side), and sturgeon could move freely between predator-free and predator-present sides. When no predators were used in the trial (**a**), the focal side was randomly selected to allow comparison with predator-present trials. Point

colors (**b**) indicate results from each of the five predators (P1-P5) used during the experiment. Trend line indicates predictions resulting from the binomial GLMM, and corresponding 95% confidence interval. Data are aggregated through time and across surgeon feed treatments because binomial GLMM showed no effect of time or nutritional state on space use. Data points are jittered to allow better visualization

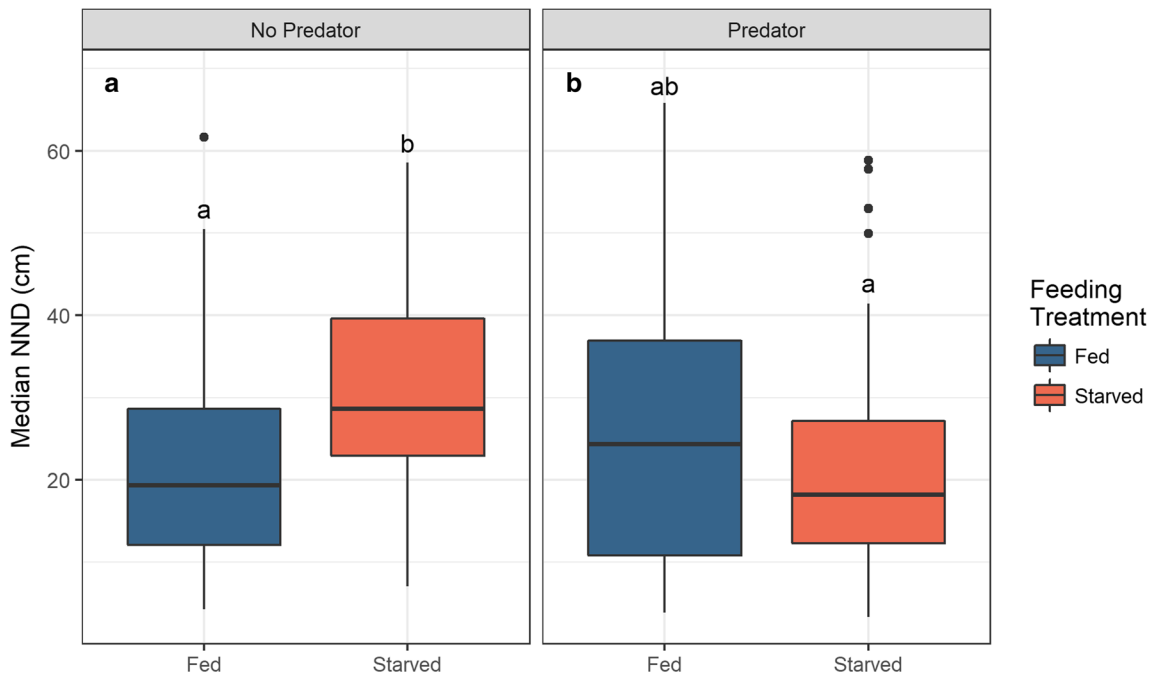


Fig. 4 Aggregation behavior of juvenile white sturgeon, as measured by median near-neighbor distance (NND) across nine time points per trial. Trials conducted without a predator (**a**) and in the presence of a predator (**b**). Blue indicates mean NND of well-fed sturgeon, while red indicates mean NND of starved sturgeon. Boxes indicate the inter quartile range (IQR), with the central line

depicting the median and the whiskers extending up to $1.5 \times IQR$. All points beyond the whiskers are shown. Each trial included six individuals, and each treatment was replicated eight times. Letters represent significant post-hoc differences between groups (GLMM, $N = 8$, $P < 0.05$)

important considerations when examining the movement and spatial distribution of juvenile sturgeon. When predators were absent from the trials, nutritional state was a strong determinant of sturgeon activity, with starved fish having activity rates approximately twice those of well-fed fish. This result was expected, considering previous observations showing similar trends (Metcalf et al. 1987) and the assumption that natural selection should favor individuals that adjust their behavior to their internal state, as the state determines the relative costs and benefits of a behavioral decision (Houston and McNamara 1999). However, the magnitude of the response to 24 h starvation was dramatic in this study. This likely relates to the white sturgeon's fast growth rates in their first year of life (Moyle 1976) and we propose this is partly a result of selection to escape a size-dependent predation window. Once white sturgeon reach approximately 120 mm, even large predators (approximately 400 mm) are unlikely to consume them (Gadomski and Parsley 2005b).

The fast growth rate and strong motivation to feed, which characterizes this species at juvenile stages, was predicted to increase risky foraging behavior in starved white sturgeon compared to well-fed sturgeon. Transgenic Atlantic salmon, *Salmo salar*, bred for increased growth rates, increased risky foraging behavior in the face of predation (Abrahams and Sutterlin 1999). However, in our study, there was a strong dampening effect of predation threat on white sturgeon activity rates regardless of nutritional state, which quickly reduced activity to close to zero, with some fish remaining frozen for hours at a time (e.g. see Fig. 2b where activity was very low after the initial 30 min of the trial). A modulation of activity is a very common predation avoidance strategy. If a switch in temporal or spatial habitat use (Werner et al. 1983; Jacobsen and Berg 1998; Alvarez and Nieceza 2003; Fraser et al. 2004) is not possible due to spatial or informational constraints (lack of knowledge about quality of other available habitats), fish often reduce the frequency of conspicuous movements and physical exposure (Dill and Fraser 1984; Metcalf et al. 1987; Gotceitas 1990). Freezing behavior, as observed in this study, is particularly common in fish (Mathis et al. 1996; Vilhunen and Hirvonen 2003; Speedie and Gerlai 2008) as many piscivorous visual systems, including that of largemouth bass, are tuned to respond to movement (Howick and O'Brien 1983).

In the absence of predators, sturgeon near-neighbor distance was greater for starved fish than well-fed fish.

This is in contrast to earlier work in the congeneric sturgeon, *Acipenser fulvescens*, where near-neighbor distance was found to be unrelated to feeding or non-feeding times in either large or small fish (Allen et al. 2009). When the same metric was measured in the presence of predators in the current study, no difference was found between fish of different nutritional states. Whilst juvenile and adult white sturgeon are commonly found in large aggregations (Hildebrand et al. 1999; Parsley et al. 2007), there is very little evidence for sociality in sturgeon, although, Allen et al. (2009) did find that *A. fulvescens* have a faster stress response when in a group. We hypothesize that after initial dispersion, any aggregations of juvenile white sturgeon are determined by a shared attraction or repulsion to abiotic factors rather than social attraction for the purposes of risk-reduction or transfer of social information (Ward and Webster 2016). We believe the pattern of near-neighbor distances observed in this study was an indirect effect of the reduced activity rates, rather than a direct effect of the predator presence. Sturgeon generally swam around the outside of the tank close to the wall, and tended to stop when they reached a stationary conspecific. Thus, under conditions of reduced activity there was a gradual accumulation of fish in the same location. Future studies could assess whether sturgeon would be as likely to stop if an abiotic feature was placed alongside the tank wall to provide similar structure without a conspecific cue.

Sturgeon did not universally avoid predators by aggregating on the side of the arena without the predator. However, increased activity of predators was a significant determinant of spatial predator avoidance, suggesting a degree of learning from direct predator encounters. This is similar to findings in *S. platyrhynchus* (Hintz et al. 2013) which only showed a strong anti-predator response after a negative predator interaction (chased or bitten). In this study, sturgeon were not predated upon unless they were moving, and indeed many stationary sturgeon froze very close to or even underneath largemouth bass. Movement likely triggered an innate fixed response in largemouth bass (Howick and O'Brien 1983), and unless this occurred, sturgeon were rarely bitten or predated upon. It is likely that crypsis in the form of staying stationary after an initial burst escape response is a key anti-predation strategy of sturgeon, in tandem with a rapid growth rate and armoring. However, a degree of caution should be attached to these conclusions, as manipulative laboratory experiments

inevitably have aspects of artificiality imbedded into their designs. In our experiment, sturgeon were reared in captivity and were naïve of the predatory bass. While it was not possible to use wild fish that had natural experience of predation risk, ideally, future lab experiments could use sturgeon that were reared in mesocosms with predators or were at least exposed and acclimated to predators for lengthy periods of time prior to experimental trials. Whilst we believe it is likely, it would be informative to see if the drop in activity rates due to predator presence and activity still occurs under these conditions.

Despite low mortality levels, white sturgeon did encounter predators in this experiment. Only a few were consumed but many were handled and rejected by largemouth bass which, in the wild, could cause sufficient injury to reduce fitness levels or cause death. However, the general unpalatability of white sturgeon to largemouth bass suggests that their armor likely plays a key role in reducing predation risk, even for juveniles at this vulnerable size. Their armor is well developed at even these early life stages (at about 25 mm TL, white sturgeon develop dorsal and lateral scutes; Deng et al. 2002) which is likely an energetically demanding investment; further evidence that a high food intake and adequate nutrition is key to juveniles of this species. A promising area of research in sturgeon would be to explore predator-induced phenotypic changes in body morphology and dietary selection. One could hypothesize that predation risk might alter feeding rates of food types high in specific nutrients (e.g. calcium as a key component of scutes, pers. comm. Van Eenennaam) to ensure fish absorb a sufficient amount of nutrients needed for scute development. It is possible that predation risk may be sensed via chemical signals, perhaps even at egg development stage, or passed epigenetically from the mother, and this could lead to an investment of energy or nutrients towards more developed or increased scute hardness (Brönmark and Miner 1992; Brönmark and Pettersson 1994).

In conclusion, white sturgeon displayed a predicted and adaptive response to predation presence and an increase in predator activity by reducing activity levels, and displaying marked freezing behavior. Sturgeon also responded strongly to nutritional deprivation through increased activity and greater near-neighbor distances, which were likely adaptive responses to increase encounter rates with benthic food items. However, both of these responses to starvation were suppressed in the presence

of predators. This study has provided empirical evidence that in addition to direct consumption, largemouth bass can induce behavioral trade-offs in juvenile sturgeon, resulting in abrupt reduction in foraging activity. This finding further supports work by McAdam (2015) indicating that food limitation and increased predation may be an important element of observed recruitment failure in some white sturgeon populations. Here we show that these two mechanisms may function synergistically to decrease survival of early feeding stages of juvenile white sturgeon, and thus we emphasize the importance of considering multiple stressors when designing strategies for white sturgeon management.

Acknowledgments We thank Joseph J. Cech, Jr. for advice on the manuscript, and Joel Van Eenennaam and Sterling Caviar Farms for spawning the white sturgeon. We would also like to thank the members of the Fangué Laboratory for assistance in fish rearing, maintenance, and manual labor setting up the experiment. Additionally, the manuscript was improved by comments from two anonymous reviewers. This work was supported by the University of California, Davis Agricultural Experiment Station (grant #20998), the Delta Stewardship Council (grant # 201603413), and the California Department of Water Resources (#4600010855). All work was conducted in accordance with the guidelines and approval of the UC Davis Animal Care and Use Committee.

Compliance with ethical standards The authors declare they have no conflict of interest regarding this manuscript. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the study was conducted. This article does not contain any studies with human participants performed by any of the authors.

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