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# ARTICLE

# Juvenile green sturgeon (*Acipenser medirostris*) and white sturgeon (*Acipenser transmontanus*) behavior near water-diversion fish screens: experiments in a laboratory swimming flume

Jamilynn B. Poletto, Dennis E. Cocherell, Natalie Ho, Joseph J. Cech, Jr., A. Peter Klimley, and Nann A. Fangue

**Abstract:** Water diversions that extract fresh water for urban, industrial, and agricultural uses, as well as export to southern California, are prevalent throughout the Sacramento–San Joaquin watershed. Many water diversions are fitted with fish-exclusion screens designed to prevent fish from entrainment (i.e., being drawn in). The impact of fish screens on the behavior of migrating juvenile fishes remains largely unknown, especially for threatened species such as sturgeon. We placed individual juvenile green (*Acipenser medirostris*) or white (*Acipenser transmontanus*) sturgeon in a laboratory swimming flume in the presence of standard fish screens (2 mm bar spacing) at two field-relevant water velocities (20.4 ± 0.1 and 37.3 ± 0.3 cm·s⁻¹). Fish were tested at 18 °C for 15 min during the day or night and in the presence of possible behavioral deterrents. Behavioral responses, including screen contacts, impingements, and time spent near screens were quantified. Green sturgeon contacted and impinged upon the screens twice as frequently as white sturgeon and also differed in how their behaviors were altered by water velocities and time of day. Our results are informative in developing effective management strategies to mitigate the impacts of water diversions on sturgeon populations and suggest that effective restoration strategies for both species should be considered separately.

**Résumé :** Les déviations de cours d'eau pour l'extraction d'eau douce pour des usages urbains, industriels ou agricoles et pour l'exportation vers le sud de la Californie sont répandues dans tout le bassin versant de Sacramento–San Joaquin. De nombreuses déviations de cours d'eau sont dotées de grilles d'exclusion des poissons conçues pour prévenir l'entraînement de poissons (c.-à-d. leur entrée dans la déviation). L'impact de ces grilles sur le comportement des poissons migrateurs juvéniles demeure largement méconnu, particulièrement en ce qui concerne des espèces menacées comme l'esturgeon. Nous avons placé des esturgeons verts (*Acipenser medirostris*) ou blancs (*Acipenser transmontanus*) juvéniles dans un canal de nage en laboratoire, en présence de grilles à poissons normales (espacement des barreaux de 2 mm) et à deux vitesses du courant pertinentes en ce qui concerne les conditions de terrain (20,4 ± 0,1 et 37,3 ± 0,3 cm·s⁻¹). Les essais avec les poissons ont été menés à 18 °C pendant 15 min durant le jour ou la nuit et en présence d'éléments pouvant avoir un effet dissuasif. Les réactions comportementales, y compris les contacts avec les grilles, les collisions et le temps passé près des grilles, ont été quantifiées. Les contacts et les collisions des esturgeons verts avec les grilles étaient deux fois plus fréquents que ceux des esturgeons blancs, et les modifications des comportements selon la vitesse de l'eau et le moment de la journée étaient également différentes pour les deux espèces. Nos résultats fournissent de l'information utile pour l'élaboration de stratégies de gestion efficaces visant à atténuer les impacts des déviations de cours d'eau sur les populations d'esturgeons et donnent à penser que des stratégies de rétablissement efficaces devraient être examinées séparément pour les deux espèces. [Traduit par la Rédaction]

## Introduction

Barriers to fish passage and risks to fish migration are a concern for fish populations in altered aquatic ecosystems throughout the world (e.g., Larinier 1998; Mallen-Cooper and Brand 2007; Pelicice and Agostinho 2008). In particular, water projects (i.e., hydroelectric dams, large government pumping stations, and smaller agricultural diversions) throughout rivers and estuaries have contributed to the fragmentation and degradation of suitable habitat for native fish (Morita and Yamamoto 2002; Schrank and Rahel 2004). In California, the number of water diversions located throughout the Sacramento–San Joaquin watershed alone exceeds 3300 (Herren and Kawasaki 2001). Anadromous fishes must pass by or through these diversion structures as they migrate between their spawning and rearing grounds in the upper reaches of the freshwater rivers to the more saline estuaries and ocean environments in which they spend the majority of their lives. Fish entrainment into water diversions can

affect the spawning migrations of adult fishes as well as the recruitment of juveniles for a given year (Grimaldo et al. 2009; Kimmerer 2008). Indeed, interactions with water diversions are implicated in contributing to decreases in the population numbers of some threatened species in California, such as Chinook salmon (*Oncorhynchus tshawytscha*; Moyle 2002), delta smelt (*Hypomesus transpacificus*; Bennett 2005), striped bass (*Morone saxatilis*; Stevens et al. 1985), and green sturgeon (*Acipenser medirostris*; Mussen et al. 2014).

Many pumping facilities and similar water diversions are fitted with screens to physically exclude fish from becoming entrained, or they are equipped with louver systems (i.e., vertical bars evenly spaced apart) designed to safely guide fish movements (Taft 2000). Increased interactions with water projects magnify the risk for mortality of individual fish or may lead to injuries that result in compromised survival and fitness (Swanson et al. 2004, 2005). It has been shown that fish screens can cause detrimental effects if

**J.B. Poletto, D.E. Cocherell, N. Ho, J.J. Cech, Jr., A.P. Klimley, and N.A. Fangue.** Department of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Avenue, Davis CA 95616, USA.

**Corresponding author:** Nann A. Fangue (e-mail: nafangue@ucdavis.edu).

fish are unable to avoid contact with these devices or repeatedly become impinged (i.e., becoming "stuck") on screen faces (Young et al. 2010). Screen encounters also may reduce subsequent swimming performance or alter behavior in a manner that leaves fish more susceptible to predation (OTA 1995). Crucial to understanding how fish interact with screens is knowledge of how environmental factors such as flow velocity or time of day affect these interactions. Water velocity has been shown to be an important factor affecting contact with fish screens in some species (Boys et al. 2013a; Danley et al. 2002), and light levels have also been shown to affect fish passage, though the effect of light is species-specific (Kemp et al. 2006; Boys et al. 2013a). In addition to physical barriers, many diversions also employ behavioral deterrents to prevent or reduce fish interactions with diversion structures, such as strobe lights or mechanical vibrations (reviewed in USBR 2006). The efficacy of these devices has been investigated in a few fish species with equivocal results (Johnson et al. 2005; Sager et al. 2000), and empirical data supporting or refuting claims of their function are needed.

For many species, juvenile fish may be the most susceptible to entrainment into diversions or to impingement on screens (Danley et al. 2002; Grimaldo et al. 2009). Additionally, some native fish species that encounter water diversions may be disproportionately impacted by or particularly vulnerable to the new environmental challenges they create (Moyle 2002). For example, the green sturgeon is an anadromous fish species with two distinct population segments (DPS; Israel et al. 2004); the southern DPS was listed as "Threatened" under the Endangered Species Act by the National Marine Fisheries Division of NOAA in 2006. The closely related white sturgeon (*Acipenser transmontanus*) is a semi-anadromous sympatric species facing similar challenges, though it is not currently listed as a threatened species in California. Sturgeon may be particularly susceptible to such interactions because they are thought to be relatively poor swimmers as compared with salmonids (Peake et al. 1997). Sturgeon have a reduced critical swimming speed and lowered ability for sustained high-speed swimming compared with many teleosts (Deslauriers and Kieffer 2011), constraining their ability to overcome water diversion intake velocities. In particular, juvenile green sturgeon at the size they undertake migrations to the ocean have lower critical swimming velocities compared with several other species of sturgeon (summarized in Deslauriers and Kieffer 2011), perhaps because of energetic constraints imposed on green sturgeon during their physiological preparations for entry into salt water (Allen et al. 2006). Green sturgeon also show much higher entrainment rates into unscreened diversions (Mussen et al. 2014) compared with Chinook salmon (Mussen et al. 2013) when tested in the laboratory, suggesting that they are less adept at detecting the disturbances in velocity caused by diversions and altering their swimming paths to avoid them. Furthermore, green sturgeon do not exhibit avoidance behaviors in response to unscreened diversions, further reducing their ability to avoid entrainment (Mussen et al. 2014).

While fish-exclusion screens reduce entrainment into diversions (Gale et al. 2008; Simpson and Ostrand 2012; Boys et al. 2013a), few studies have examined the behavior of sturgeon in the presence of screens, including impingement, screen contacts, or swimming performance near screens. We therefore sought to investigate the behavior of juvenile green and white sturgeon near fish-exclusion screens in a laboratory setting. Owing to the differences in their early life history strategies and consequent differences in swimming performance and behavior, we predicted that green sturgeon (anadromous) and white sturgeon (semi-anadromous) would differ in their behavioral responses to fish screens, particularly in their responses to water flow velocity and time of day. We hypothesized that white sturgeon would show reduced screen interactions, including reduced overall screen contacts and impingements relative to green sturgeon. We also predicted that both species would differ in their

behavior during the day and night and that green sturgeon would show increased screen interactions during nighttime trials relative to white sturgeon. We further hypothesized that sensory deterrents affixed to screens would reduce screen interactions relative to those of control, providing species-specific information for managers seeking to reduce fish interactions with screens.

## Materials and methods

Juvenile green and white sturgeon were held at the University of California, Davis (UC Davis), Center for Aquatic Biology and Aquaculture (CABA). Green sturgeon (F2, northern DPS) were spawned from UC Davis broodstock in May 2009 (methodology described in Van Eenennaam et al. 2001) and reared at 18 °C in 815 L round fiberglass tanks with continuous flows of aerated (dissolved oxygen 8.5 ± 1.0 mg $O_2 \cdot L^{-1}$), nonchlorinated fresh water from a dedicated well. Fish were fed daily to satiation with semimoist pellets (Rangen, Inc., Buhl, Idaho) and eventually weaned onto a dry pelleted diet (Silver-Cup) at ~60 days posthatch (dph). White sturgeon were spawned in June 2011 at the Sterling Caviar Farm (Sacramento, California) before being transferred to CABA at 20 dph and reared as described above. All handling, care, and experimental procedures used were reviewed and approved by the UC Davis Institutional Animal Care and Use Committee (IACUC No.17017).

All experiments were performed in an indoor, elliptical, flow-through, fiberglass swimming flume outfitted with a variable-frequency pump to adjust flume water velocity (Fig. 1; Mussen and Cech 2012). Two wedge-wire stainless steel screens (1 m × 1 m, 2 mm bar spacing) were suspended in a 60° V-configuration in the flume with the apex pointed downstream. A stainless steel (wire mesh 0.635 cm²) screen was positioned 1.5 m upstream from the apex of the wedge-wire screens, creating an enclosed testing area in which fish were placed (Fig. 1). Water temperature was maintained at 18 °C. Before trials began, water velocity was measured (Marsh-McBirney, Model 523 flow meter) every 30 cm from the upstream screen to the apex of the wedge-wire screens and every 23 cm from the outside to inside portion of the screen in a grid layout, at 5 cm from the bottom of the flume and 5 cm below the water surface.

To test the efficacy of commonly used deterrents, a strobe light (Monarch Instruments, DB Plus) was positioned above the flume so as to direct light into the testing area, and pneumatically operated vibrators (NTK25 Netter Vibrations, Model 55252) were affixed to each wedge-wire screen above the water's surface. The strobe light was operated at 300 flashes per minute and the wedge-wire screens were driven to vibrate at a frequency of 10 Hz, with only one of the two screens vibrating during an experiment.

Prior to each experiment, ten randomly chosen juvenile green or white sturgeon were captured and transferred to a single holding tank (140 L). Green sturgeon (n = 239) juveniles were aged 150–198 dph, while white sturgeon (n = 319) were 170–192 dph. Green sturgeon were 29.6 ± 0.2 cm (mean ± SE) in fork length (FL) and had a mass of 147.1 ± 3.1 g; white sturgeon were 27.4 ± 0.2 cm FL and had a mass of 154.0 ± 3.6 g. For each trial, individual fish were first removed from the holding tank and placed into the testing area of the flume for a period of 5 min without water flow or any stimulus presentation. This acclimation period allowed the fish to explore the testing area without any additional stimuli. Immediately following the acclimation period, treatment conditions, including water velocity, were induced, starting the trial period. Fish were exposed to treatment conditions for 15 min. Fish were observed during each experiment, and if a fish became impinged on a screen (having more than two-thirds of its body pinned flush against the screen face) for ≥30 s in a manner where the fish was unable to free itself from the screen, the experiment was terminated and not included in subsequent analyses. No fish were excluded based on this endpoint criterion. Experiments included the following treatment conditions, conducted at one of two water velocities (mean ± SE: 20.4 ± 0.1 or 37.3 ±

**Fig. 1.** Overhead diagram of the laboratory swimming flume. The wedge wire screens are indicated by thick dashed lines placed in a 60° conformation, and the testing area is enclosed by steel mesh placed upstream. Solid arrows indicate water flow direction. For behavioral analyses, the test area was divided into an outside, inside, and upstream section, designated by dotted lines.
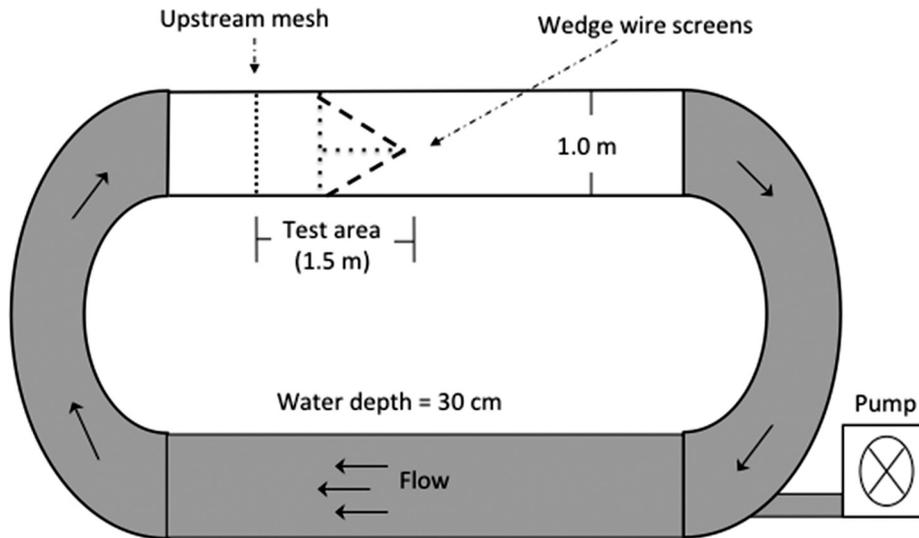


0.3 cm·s$^{-1}$): control (no stimulus), strobe light, screen vibrations (one screen only), or a strobe light and screen vibrations combination (where only one screen was randomly chosen to vibrate). The water velocities we used were roughly one-third and two-thirds of the critical swimming velocities for similarly sized green sturgeon (D. Cocherell, B. DeCourten, J. Cech, Jr., and N. Fangue, unpublished data). Similar swimming performance data for size-matched white sturgeon are not available, but the flow velocities used in our study were nearly one-third and more than one-half the critical swimming velocities of slightly smaller white sturgeon (~25 cm total length; D. Cocherell, B. DeCourten, J. Cech, Jr., and N. Fangue, unpublished data). Sturgeon have been shown to exhibit station-holding behaviors in response to high water velocities to reduce swimming effort (Deslauriers and Kieffer 2012a), but in our study all individuals exhibited swimming behavior during the trials, and we did not observe any form of station-holding behavior within the testing area. These experiments were also performed during the day under normal light conditions and at night under full dark conditions. Experimental conditions (treatment and water velocity) for trials performed during the day or night were randomized with respect to order of administration.

Trials were recorded using a video camera (Sony DCR DVD-505) mounted directly over the testing area. Nighttime trials were illuminated with two infrared LED flood lights mounted over the swimming flume and recorded using the camera's low-light setting. Following each trial, the fish was removed from the flume, measured for length (FL (cm)) and mass (g), and euthanized following IACUC guidelines. Each fish was used only once, eliminating the possibility for fish to modify their behavior based on previous experience.

Three different behavioral indices were quantified: the number of screen contacts (both tail and body contacts), the number of impingements, and the amount of time spent near screens or upstream of the screens (residence time, min). Body and tail contacts were counted as any physical contact the fish made with a screen. The proportion of contacts made by fish with their bodies or their tails is reported as the proportion of body contacts relative to total contacts ($P_{Body}$); frequency of tail contacts is therefore $1 - (P_{Body})$. Impingements were counted when more than two-thirds of the body of the fish remained flush against a screen for >10 s. The testing area of the flume was divided into outside and inside sections of equal sizes (2.2 m² each) and a larger upstream section (6.3 m²); the residence time in each area was cal-culated. Residence time is reported as the proportion of time fish spent near screens relative to upstream of the screens ($T_{Screen}$); time spent upstream of screens is therefore $1 - (T_{Screen})$. All indices of behavior were recorded using JWatcher version 1.0 during the 15 min trial period; no behaviors were quantified during the acclimation period.

**Statistical analysis**

Data were analyzed using R Studio version 2.15.2 (R Development Core Team 2012) and SigmaStat 3.0 software packages. To ensure no side bias was present, the number of times green and white sturgeon contacted one screen versus the other screen and the amount of time spent near one screen versus the other were compared using Student's $t$ tests. Statistical analyses in R were performed using the R core package (R Development Core Team 2012) and "MASS" package (Venables and Ripley 2002). Because the data did not fit Gaussian distributions and because we were interested in several two- and three-way interactions between variables, we chose to analyze the data using individual generalized linear models (GLMs) for each behavioral metric. Predictor variables included species, velocity, time of day, treatment (behavioral deterrents), and fish size. Species was a categorical variable with two levels (green and white); velocity was a categorical variable with two levels (high and low); time of day was a categorical variable with two levels (day and night); treatment was a categorical variable with four levels (control, strobe light, vibrations, strobe light–vibration combination); fish size (mass) was continuous. We included main effects of the predictor variables and several two-and three-way interactions determined a priori in our initial models, to test our hypotheses regarding the behavioral differences between species, the effects of velocity and time of day, and the efficacy of the treatments. The best-fitting model for each behavioral measurement was assessed using log-likelihood ratio tests, and data assumptions were evaluated graphically. The mean number of times fish contacted the screens was investigated using a negative binomial GLM with a log-link function to account for the distribution of the data, using the predictor variables described above. The proportion of screen contacts made by the body of the fish ($P_{Body}$) and the amount of time fish spent near screens ($T_{Screen}$) were both analyzed separately using GLMs with binomial error distributions and log-link functions, using the predictor variables described above. Impingement differences between the two species were compared using a Wilcoxon–Mann–Whitney rank sum test. Statistical significance was considered at $\alpha \leq 0.05$.

**Table 1.** The predictor variables for the best-fitting model describing total screen contacts.

| Total screen contacts predictor variable | Effect size (z value) | p |
|---|---|---|
| Species | –10.447 | 2e-10*** |
| Velocity | –3.699 | 0.0002*** |
| Time of day | 2.792 | 0.005** |
| Species × velocity | 5.018 | 5.23e-7*** |
| Mass | 0.0008 | 0.29 |

**Note:** Significant p values are indicated by asterisks: **, $p < 0.01$; ***, $p < 0.001$.

## Results

No differences in screen contacts between the two screens or the amount of time spent near either screen were observed ($p > 0.05$ for comparisons), so screen contacts were combined into total screen contacts, and $T_{Screen}$ was calculated.

### Screen contacts

The predictor values for the best-fitting model of screen contacts are listed in Table 1. The significant predictors of screen contacts were species ($z = –10.447$, $p = 2e-10$), velocity ($z = –3.699$, $p = 0.0002$), time of day ($z = 2.792$, $p = 0.005$), and an interaction between species and velocity ($z = 5.018$, $p = 5.23e-7$). The variable "treatment" — the behavioral deterrents — was included in several models used to analyze mean screen contacts. The inclusion of this parameter did not significantly improve model fit, indicating there was no significant impact of the tested deterrents on the number of times a fish made contact with the screens, and was therefore not included in the final model.

Species was the most significant predictor of screen contacts. Overall, green sturgeon contacted the screens a significantly greater number of times than white sturgeon (mean ± SE: 61.2 ± 3.0 versus 28.3 ± 1.0; Fig. 2a). In any given experiment, the total number of screen contacts per fish ranged from 0 to 225 contacts for green sturgeon and 1 to 100 contacts for white sturgeon.

Overall, the time of day influenced the number of times fish made contact with screens; fish contacted the screens a greater number of times during the day compared with the night (42.9 ± 2.2 versus 41.3 ± 3.0). However, the impact of time of day on the behavior of green and white sturgeon near the fish screens was variable for the two species. For green sturgeon, mean screen contacts were slightly greater during the day (62.5 ± 3.7 versus 57.8 ± 5.0), while white sturgeon contacted the screens a greater number of times during the night (31.7 ± 1.5 versus 26.2 ± 1.4). An interaction between time of day and species, however, did not significantly improve model fit.

Velocity had an overall significant effect on the number of times fish made contact with the screens, with fish contacting the screens a greater number of times at the lower water velocity (44.2 ± 1.8 versus 38.9 ± 2.7). There was also a significant interaction between species and water velocity (Fig. 2b). Green and white sturgeon both showed differences in the total number of times they made contact with the fish screens at the two different water velocities, though the effect of velocity was different for the two species. Green sturgeon contacted the screens a greater number of times at the higher water velocity (72.9 ± 6.2 versus 55.2 ± 3.1), while white sturgeon contacted the screens a greater number of total times at the lower water velocity (33.4 ± 1.5 versus 23.0 ± 1.3).

### Proportion of screen contacts made with body versus tail

The predictor values for the best-fitting model of the proportion of screen contacts fish made with their bodies ($P_{Body}$) are listed in Table 2. The significant predictors of $P_{Body}$ were species ($z = –8.914$, $p = 2e-10$) and an interaction between species and time of day ($z = 2.448$, $p = 0.014$). Time of day, velocity, and treatment were all included in the model as predictor values, but were found to be nonsignificant, indicating that these variables had no significant impact on the manner in which fish made contact with the screens. Each treatment is listed independently in Table 2, and the effect size for each is that relative to the control.

Species was the most significant predictor of $P_{Body}$. Overall, green sturgeon contacted the screens significantly more frequently with their bodies than white sturgeon did and thus had a significantly greater overall $P_{Body}$ value than white sturgeon (0.75 ± 0.01 versus 0.34 ± 0.01). There was a large amount of variation in this measurement, which ranged from 0.0 to 1.0 for green sturgeon and 0.0 to 0.93 for white sturgeon.

The interaction between species and time of day was also a significant predictor of how fish made contact with the screens — time of day had a different effect on $P_{Body}$ for the two species (Fig. 3). For green sturgeon, the time of day had a small impact on $P_{Body}$, with little difference in the proportion of body contacts between the day and night (0.73 ± 0.02 versus 0.79 ± 0.01). However, white sturgeon displayed significantly greater $P_{Body}$ values during the night as compared with the day (0.52 ± 0.01 versus 0.24 ± 0.02).

### Residence time

The predictor values for the best-fitting model of $T_{Screen}$ are listed in Table 3. The significant predictors of screen contacts were species ($z = –4.175$, $p = 2.98e-5$) and an interaction between species and velocity ($z = 2.336$, $p = 0.018$). Velocity, time of day, and mass were all included in the model as predictor values, but were found to be nonsignificant, indicating they had no significant impact on the amount of time fish spent near screens. There was no significant impact of treatment on $T_{Screen}$.

Species was again the most significant predictor of the amount of time fish spent near screens, and green sturgeon spent a greater amount of time near screens as compared with white sturgeon. Green sturgeon spent a mean of 34.8% (±1.9%) of the experimental period near the fish screens, while white sturgeon only spent 18.7% (±1.1%) there. The proportion of time green and white sturgeon spent near screens during experiments ranged from 0.0 to 0.99 for green sturgeon and 0.0 to 1.0 for white sturgeon.

The impact of velocity on the proportion of time spent near screens for green and white sturgeon had varying effects (Fig. 4), and the interaction between species and velocity was a significant predictor of behavior. Velocity had a moderate impact on the behavior of green sturgeon, spending a slightly greater proportion of time near screens at the higher water velocity as compared with the lower velocity (0.36 ± 0.04 versus 0.33 ± 0.02). White sturgeon spent a greater proportion of time near screens at the lower water velocity (0.24 ± 0.02 versus 0.13 ± 0.01).

### Impingements

Green and white sturgeon displayed differences in the number of times they became impinged upon the screens. For both species, the majority of individual fish never became impinged, with impingement events per fish ranging from 0 to 15 for green sturgeon and 0 to 1 for white sturgeon. Out of the 239 green sturgeon tested overall, 40 fish became impinged at least once, and there were a total of 161 green sturgeon impingement events. The 40 impinged fish represented 16.8% of the total green sturgeon tested, and 27 of these fish (11.3% of total) became impinged more than once. Of the 319 white sturgeon tested overall, only five became impinged, and there were a total of five impingement events, as no white sturgeon impinged more than one time. Overall, the mean number of impingement events per fish was significantly different between green and white sturgeon, with green sturgeon impinging a significantly greater number of times than did white sturgeon (0.68 ± 0.1 versus 0.02 ± 0.01, $U = 43\,813.5$, $p < 0.001$).

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**Fig. 2.** (*a*) The difference between the sturgeon species in the total number of screen contacts per fish during the 15 min trial period. Green sturgeon contacted the screens more frequently (median: 53) than did white sturgeon (median: 25). Black line = median, box = interquartile range (IQ), whiskers = 1.5 × IQ, open circles = outliers. Mean total screen contacts (±SE) are reported in the text. (*b*) The effect of velocity and species on the mean number of total screen contacts made by fish during the 15 min trial period. The interaction between species and velocity was a significant predictor of behavior (*p* = 5.23e-7).
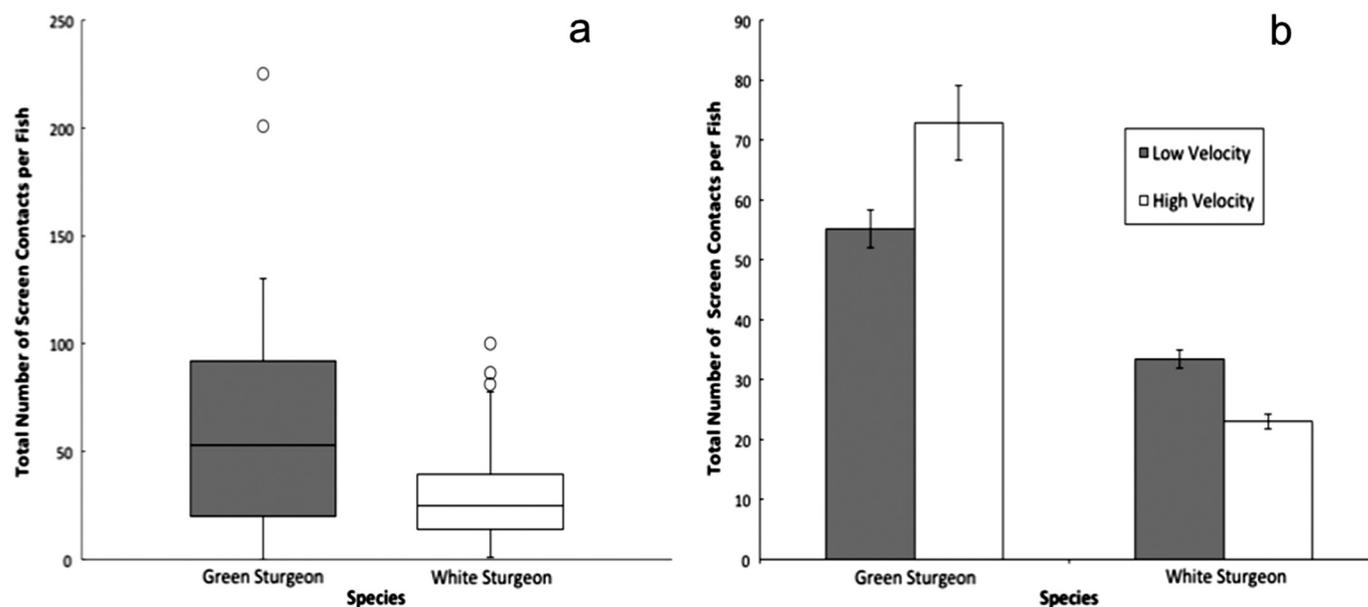


**Table 2.** The predictor variables used in the best-fitting model for the proportion of screen contacts made with the fish's body ($P_{Body}$).

| $P_{Body}$ predictor variable | Effect size (z value) | p |
|---|---|---|
| Species | −8.914 | 2e-10*** |
| Species × time of day | 2.448 | 0.014* |
| Time of day | 0.467 | 0.64 |
| Velocity | 1.659 | 0.09 |
| Treatment (strobe light) | 0.756 | 0.45 |
| Treatment (vibrations) | −0.47 | 0.64 |
| Treatment (strobe and vibrations) | 0.801 | 0.42 |

**Note:** Treatment effect sizes are in comparison with the control treatment. Significant variables are indicated by asterisks: *, $p < 0.05$; ***, $p < 0.001$.

## Discussion

The results from our laboratory swimming flume experiments indicate that juvenile green sturgeon interact with fish-exclusion screens more frequently than white sturgeon of the same size. Overall, green sturgeon contacted and impinged upon screens more frequently than did white sturgeon and spent a greater proportion of the experimental period near screens, indicating that despite their similar size and age, green sturgeon behave differently in response to the presence of fish screens. This is perhaps due to differences in physiology, perceptual abilities, or life history characteristics. Regardless of the mechanism, the propensity for heightened interactions with fish screens by green sturgeon leaves them comparatively more vulnerable to an accumulation of detrimental effects, as these fish may encounter multiple water diversions during outmigration or daily movements. Caution should be taken in applying these results directly to field situations, however, as our experimental design does not fully replicate field conditions, which can be quite variable in screen design, flow characteristics, and extent of interaction with fish.

The short-term and long-term effects of multiple contacts with and impingements upon screens have not been evaluated in juvenile sturgeon, despite their imperiled status. It is likely that repeated contact or impingements may reduce swimming performance, possibly because of increased physiological stress from the encounter, exhaustion and metabolic disturbance elicited during escape attempts, or physical damage to skin and fin structure. It has been previously shown in other San Francisco Bay Delta fishes, such as delta smelt and Chinook salmon, that injury and mortality can occur following multiple contacts with and (or) impingements upon exclusion screens, though susceptibility to physical injury and mortality is species-specific (Swanson et al. 2004, 2005). Plasma cortisol and hematocrit levels have been shown to increase during screen encounters in delta smelt, coupled with acidosis likely induced in response to sustained and elevated metabolic rates (Young et al. 2010). Similarly, adult white sturgeon showed elevated plasma cortisol concentrations after ascending a fishway in a laboratory setting (Cocherell et al. 2011). It has been shown that acute injections of cortisol reduced the recovery capabilities of European seabass (*Dicentrarchus labrax*) in successive critical swimming velocity tests (Carbonara et al. 2010), suggesting that stress responses induced by screen encounters may limit swimming performance characteristics of migrating fish. Another repercussion may be increased predation risk, either during or immediately following encounters. Olla et al. (1992) compared predation rates by lingcod (*Ophiodon elongatus*) on juvenile coho salmon (*Oncorhynchus kisutch*) with elevated cortisol levels induced by handling stress with those of unhandled control fish and observed higher short-term predation rates upon those fish that were handled. Fish may be particularly vulnerable to predation following screen encounters that result in elevated stress hormones, thereby limiting effective antipredator detection and appropriate behavioral responses.

Green sturgeon showed increased contact with screens as flow velocity increased, a trend that was not shared by white sturgeon; white sturgeon contacts *decreased* as flow increased. There are a number of potential explanations for the differences in behavior we observed between green and white sturgeon in response to velocity. Juvenile green and white sturgeon at this size could have different swimming capabilities, including differences in critical swimming velocities (*U*crits). The flume water velocities we tested (20.4 ± 0.1 and 37.3 ± 0.3 cm·s⁻¹) were roughly one-third and two-

**Fig. 3.** The effect of time of day and species on the proportion of screen contacts made with the fish's body relative to the tail ($P_{Body}$) during the 15 min trial period. The interaction between species and time of day was a significant predictor of $P_{Body}$ ($p = 0.014$).
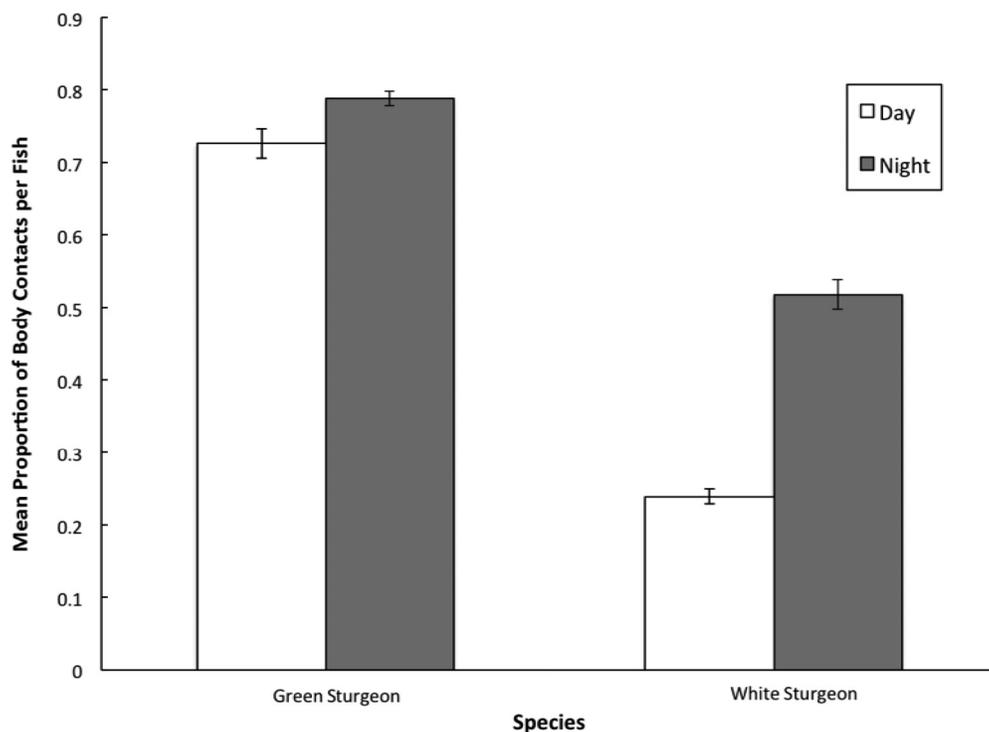


**Table 3.** Predictor values for the best-fitting model describing the proportion of time spent near screens ($T_{Screen}$).

| $T_{Screen}$ predictor variable | Effect size (z value) | $p$ |
|---|---|---|
| Species | −4.175 | 2.98e-5*** |
| Species × velocity | 2.336 | 0.018* |
| Velocity | −0.87 | 0.384 |
| Time of day | 1.268 | 0.205 |
| Mass | 0.772 | 0.44 |

**Note:** Significant predictor variables are indicated by asterisks: *, $p < 0.05$; ***, $p < 0.001$.

thirds that of average $U$crits for size-matched green sturgeon (D. Cocherell, B. DeCourten, J. Cech, Jr., and N. Fangue, unpublished data). Similar white sturgeon swimming performance data are not available for fish of this size, limiting direct comparisons. However, preliminary swimming performance data for white sturgeon slightly smaller than those used here (~25 cm total length) indicate that the water velocities tested in our study were less than one-third and more than one-half of their $U$crit (D. Cocherell, B. DeCourten, J. Cech, Jr., and N. Fangue, unpublished data). Therefore, the decrease in the number of contacts made with screens by white sturgeon at higher water velocities could indicate a greater motivation to swim into the current with strong positive rheotaxis, thus bringing the fish away from the screens. This might indicate that similarly sized green sturgeon have decreased swimming capabilities and lower $U$crits than white sturgeon, but this remains to be determined. Conversely, the lower flow velocity might not have been a strong enough cue for white sturgeon to continually swim with strong positive rheotaxis, increasing the chances for contact with the downstream screens. The positive relationship between increasing water velocity and increasing rheotactic response is well documented (e.g., Montgomery et al. 1997; Baker and Montgomery 1999). Similarly, adult white sturgeon were found to respond more quickly to faster water velocities by swimming upstream when subjected to tests in a laboratory flume (Webber et al. 2007). The importance of velocity in mediating fish

passage has also been previously documented in juvenile salmonids, and it has been shown that fish tend to avoid areas of flow acceleration or rapid changes in flow velocity (Kemp et al. 2005; Enders et al. 2009). While this behavioral response has not been extensively studied in juvenile sturgeon, it underscores the importance of velocity in altering the performance of fish species near anthropogenic devices.

Swimming performance differences between green and white sturgeon might be due, in part, to differences in their early life histories. Green sturgeon are considered to be the most truly anadromous of all the sturgeon species, meaning they spend a major portion of their life in the marine environment (Doroshov 1985; Allen and Cech 2006). White sturgeon, on the other hand, are considered semi-anadromous, spending a large majority of their time in bays and estuaries (Doroshov 1985). Green sturgeon are able to transition into full-strength salt water (33 ppt) relatively early in life, and evidence suggests they begin to move into brackish waters within the first year of life (Allen et al. 2009a, 2009b) This transition into waters with increasing salinity is preceded by a "pseudo-smoltification" in which green sturgeon begin to remodel their physiology in preparation for the osmoregulatory demands that accompany living in brackish and salt water (Allen et al. 2011). While fish are undergoing this preparation for increased salinity, it is possible that a trade-off between physiological change and other measures, such as swimming performance, may exist. Indeed, Allen et al. (2006) found that as size increased in green sturgeon that were saltwater tolerant, there was a corresponding decrease in their $U$crit. This decrease in $U$crit was seasonal, and older fish of the same size did not exhibit this negative relationship between size and $U$crit. The seawater-tolerant fish tested by Allen et al. (2006; 26–47 cm; 150 dph) were similar in size and age to those tested here. Juvenile white sturgeon of this same age, while tolerant of salinities associated with brackish water (10–15 ppt), have been shown to experience high mortality rates (up to 100%) when exposed to salinities greater than 24–25 ppt (Amiri et al. 2009; McEnroe and Cech 1985). Temperature is also an important variable to consider when com-

**Fig. 4.** The effect of velocity and species on the proportion of time spent near screens relative to time spent upstream ($T_{Screen}$) during the 15 min trial period. The interaction between species and velocity was a significant predictor of $T_{Screen}$ ($p = 0.018$).
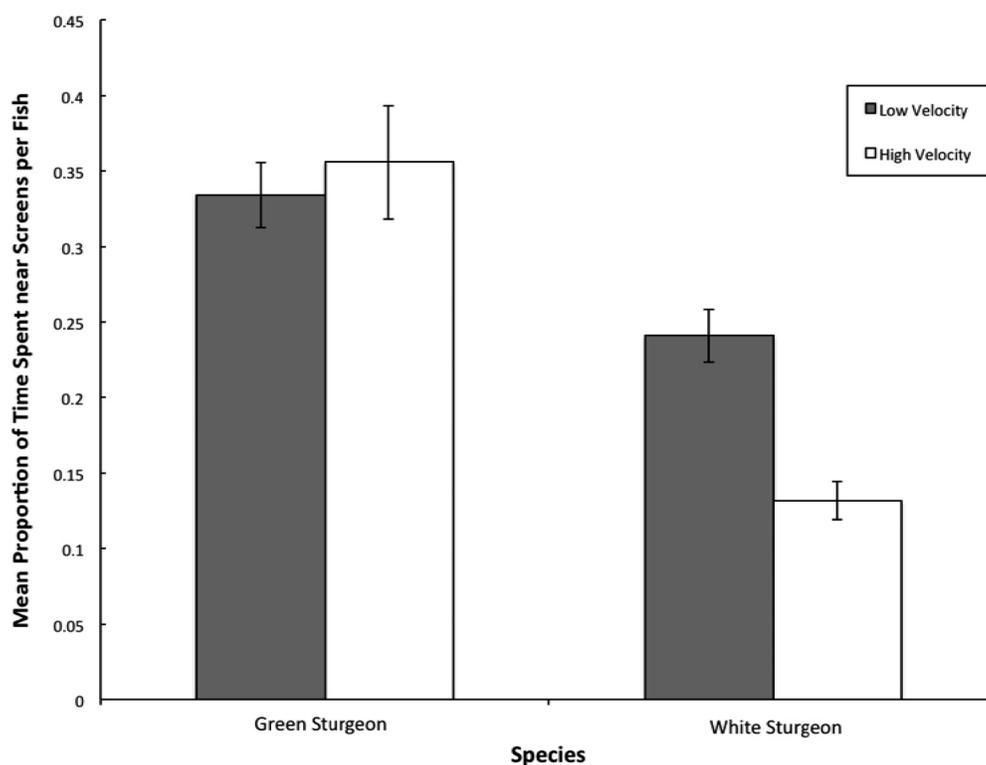
paring the swimming performance capabilities of fishes, and temperature has been previously shown to affect swimming performance in several species of sturgeon (Adams et al. 2003; Allen et al. 2006; Deslauriers and Kieffer 2012b). Our experiments were performed at a constant temperature of 18 °C, and further studies are needed to evaluate the effect of temperature on behavior near fish screens between these two sturgeon species.

Time of day reflected additional differences in green and white sturgeon behavior, with white sturgeon contacting screens more often during the night than during the day. The differences in diel behavior between the species may represent a difference in activity levels during the night and day. White sturgeon seemed to be more active during nighttime experiments, leading to an increase in the number of screen contacts they made. Indeed, white sturgeon spent a greater proportion of time near screens during the night than they did during the day, perhaps because of increased exploration around the test area. Conversely, it is possible that green sturgeon had a propensity for more directed and sustained swimming behavior during nighttime trials, thus resulting in fewer screen contacts. Laboratory evidence suggests that larval and juvenile green sturgeon increase migratory behavior during the night (Kynard et al. 2005), a phenomenon that has been observed in other species of anadromous fish, such as Atlantic salmon (*Salmo salar*; McCormick et al. 1998) and Chinook salmon (Chapman et al. 2012). An increase in migratory-type swimming behavior in green sturgeon during the night could also explain the differences observed between the species, though these reasons are not mutually exclusive.

It is important to not only consider the overall screen contacts made by green and white sturgeon, but also how they contacted the screens, including impingement events. Green sturgeon did show some difference in the number of fish that impinged at least once during the day compared with the night; while only 12 fish became impinged during the day, 28 did so at night. This may reflect a true change in the behavior of green sturgeon at night, though the low

number of impinging fish makes interpretation difficult. The way in which white sturgeon contacted screens changed based on the time of day; at night white sturgeon contacted screens more frequently with their body than they did during the day. In contrast, green sturgeon showed no variation in how often they contacted the screens or the manner in which they did so. Overall, green sturgeon consistently contacted screens more frequently with their bodies, whereas white sturgeon contacted the screens more frequently with their tails. There are several possibilities that might explain this observation. Sturgeon, like many fish species, have a lateral-line system that contains both canal and free (superficial) neuromasts. Canal neuromasts are located under the dermis, and sensory stimuli reach receptor cells via pores in the skin. Superficial neuromasts are similar in structure to canal neuromasts, but lie in shallow grooves in the skin and are exposed constantly to environmental stimuli (Bleckmann and Zelick 2009). The distribution, density, and relative abundance of the two receptor types are variable and are influenced by the hydrological environment in which a fish lives, showing variability between species (Wellenreuther et al. 2010) and among populations of the same species (Wark and Peichel 2009). Green sturgeon have an extensive lateral-line system on their heads and tails, but the neuromasts along the body are less obvious (J. Poletto and D. Cocherell, unpublished data). While morphology does not always correlate to function, the tail of a green sturgeon may be more sensitive to detecting particle motion as compared with the body, causing the fish to divert its tail away from contact with the screens. If green and white sturgeon differ in the extent of the lateral-line system on the tail and their sensitivity to sensory stimuli, this might explain the differences observed in how the two species contacted the screens. This explanation requires further investigation, as a comparative study on the morphology and function of the lateral line between these two species has not been completed. Additionally, as mentioned earlier, green and white sturgeon might also differ in the strength of their rheotactic response to velocity, thus influencing the manner in which contact was made with the fish screens and explaining the observed pattern. A relation-

ship between rheotaxis and screen contacts has been observed in other species of fish (Boys et al. 2013b) and warrants further investigation in this system.

The deterrent treatments used in this study did not significantly impact the behavior of either sturgeon species around screens. Previous studies evaluating the effectiveness of behavioral deterrents utilizing sensory stimuli have been shown to vary drastically by species and environmental type. Acoustic vibrations were very successful at repelling some species such as Atlantic herring (*Clupea harengus*), but had no effect on threespine stickleback (*Gasterosteus aculeatus*; Maes et al. 2004). Similarly, strobe lights deterred juvenile salmonids when used in slow-moving water (Johnson et al. 2005), but avoidance behavior of strobe lights decreased as water velocity increased in other species (Sager et al. 2000). The mixed results on deterrent effectiveness available to date and combined with our data here highlight the importance of laboratory testing on individual species to adequately assess the efficacy of these devices as management tools. Management strategies should be designed with caution in assuming that what will be aversive to one fish species will be similarly aversive to others. Species have specialized sensory systems to detect sensory stimuli, and care should be taken when considering how effective a deterrent may be to specific fish species.

The species-specific differences in the behavior of sturgeon around fish screens at variable water velocities and during the day or night have important management implications. For example, if green sturgeon are most susceptible to higher flow velocities near fish-exclusion screens, it is possible for water diverters to reduce flows through screens during the time of year when sturgeon are likely to encounter screens with the highest frequency. Data on the abundance and movement patterns of juvenile green sturgeon in this system are lacking, but limited catch data suggest that green sturgeon begin an outward migration from the upper reaches of the watershed into the Sacramento–San Joaquin delta from May to September (Gaines and Martin 2002). The effects of the magnitude of water diverted and the time of year during which diversions are at highest operation have been previously considered for assessing their impact on migrating juvenile salmonid species (Vogel 2011), and a similar approach for juvenile sturgeon species could help reduce water diversion interactions. Combining field data with these laboratory studies may make it possible to develop methodologies for altering water diversion activities in ways that reduce green sturgeon contact with screens, thereby lowering the risk they pose to migrating green sturgeon.

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