

ARTICLE

Can behavioral fish-guidance devices protect juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from entrainment into unscreened water-diversion pipes?

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Abstract: Entrainment through water-diversion structures is a major passage challenge for fishes in watersheds worldwide. Behavioral guidance devices may be effective in passing fish by diversion inlets, thereby decreasing entrainment without reducing water-diversion rates, but data on their effectiveness is limited. In California's central valley, out-migrating Chinook salmon (*Oncorhynchus tshawytscha*) are a species at risk for entrainment through unscreened, small-scale water-diversion pipes. Therefore, we tested entrainment susceptibility and behavior of juvenile Chinook salmon in a large-river-simulation flume at a "river" velocity of 0.15 m·s⁻¹ with a 0.46 m diameter pipe diverting water at 0.57 m³·s⁻¹, during the day and night. Compared with control conditions (no fish deterrent devices present), mean fish entrainment increased by 61% (day) and 43% (night) when underwater strobe lights were active, decreased by 30% when using a metal vibrating (12 Hz) ring during the night, and was unaffected by velocity cap attachments. Fish entrainments started at water velocities of 0.8 m·s⁻¹ and decreased by 54% from spring to summer, possibly resulting from decreased pipe-passage frequency and smaller fish-school sizes. Our findings suggest that substantial entrainment can occur if fish repeatedly pass within 1.5 m of active unscreened diversions, with an estimated 50% of fish lost after encountering 18 pipes in spring and 50 pipes in summer.

Résumé : L'entraînement dans des ouvrages de déviation d'eau constitue une importante difficulté associée au passage des poissons dans les bassins versants du monde entier. Des dispositifs de guidage comportemental pourraient s'avérer efficaces pour favoriser le passage outre par les poissons des entrées de déviation, diminuant du coup le taux d'entraînement sans réduire les débits de déviation d'eau. Les données sur l'efficacité de ces dispositifs sont toutefois limitées. Dans la vallée centrale de Californie, les saumons quinnats (Oncorhynchus tshawytscha) en dévalaison constituent une espèce à risque d'entraînement dans les petits tuyaux de déviation d'eau non grillagés. Nous avons donc vérifié la vulnérabilité à l'entraînement et le comportement de saumons quinnats juvéniles dans un canal simulant une grande rivière à une vitesse d'écoulement de cette « rivière » de 0,15 m·s⁻¹, avec un tuyau de 0,46 m de diamètre servant à dévier l'eau à un débit de 0,57 m³·s⁻¹ durant le jour et la nuit. Comparativement aux conditions de référence (aucun dispositif de dissuasion des poissons), l'entraînement moyen des poissons augmentait de 61 % (jour) et 43 % (nuit) quand des lampes stroboscopiques sous l'eau étaient actives, diminuait de 30 % quand un anneau vibrateur (12 Hz) métallique était utilisé durant la nuit et n'était aucunement influencé par des plaques de déviation apposées à l'entrée des tuyaux. L'entraînement de poissons commençait à des vitesses d'écoulement de 0,8 m·s⁻¹ et diminuait de 54 % du printemps à l'été, possiblement en raison de la diminution de la fréquence des passages devant les tuyaux et de la taille des bancs de poissons. Nos résultats donnent à penser qu'un important entraînement peut avoir lieu si des poissons passent de manière répétée dans un rayon de 1,5 m de déviations actives non grillagées, le passage devant 18 tuyaux au printemps et 50 tuyaux à l'été entraînant la perte estimée de 50 % des poissons. [Traduit par la Rédaction]

Introduction

Fragmentation of aquatic habitats by anthropogenic barriers (e.g., dams or weirs) or water diversions (e.g., unscreened agricultural diversion pipes) is associated with extirpations and extinctions of fishes (Nehlsen et al. 1991; Slaney et al. 1996; Sheer and Steel 2006) and can lead to negative ecosystem-level consequences (Fahrig 2003; Nilsson et al. 2005; Layman et al. 2007). These obstacles impede safe passage of migratory and resident fishes as well as other aquatic species by interrupting watershed connectivity, altering local or regional hydraulics, limiting downstream flows,

removing planktonic and nektonic organisms from the system thereby reducing productivity, and directly through fish entrainment. Surface water diversions can entrain (draw in) large numbers of fish during their operation, and in California, surface water diversions supply 80% of the agricultural, environmental, and urban water users (Hanak et al. 2011) with an estimated 10 million acre-feet (1 acre-foot = 1233.482 m³) of water annually. Fish screens and louver arrays are used to protect fish from entrainment at most large-volume water diversions (e.g., the California State Water Project and the Federal Central Valley Project), but 95% of approximately 3700 water diversions on the Sacramento

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and San Joaquin Rivers and their tributaries, as well as in the Sacramento–San Joaquin Delta and Suisun Marsh, remain unscreened (Calfish 2012). Screens are less frequently installed on small-scale water diversions because of high construction and maintenance costs, potential disruption of water intake rates and damage to pumping equipment (i.e., clogging with debris), a lack of regulation requiring screens for historic diversions, and the general belief that fish mortality occurring at small-scale water diversions is a minor contributor to mortality overall (reviewed in Moyle and Israel 2005).

The decline of fish populations in California's central valley has been linked to numerous stressors, including climate change (i.e., reduced stream flow, increased river temperatures, and loss of tidal habitats), loss of genetic diversity due to hatchery propagation, habitat alteration, and harvest (Moyle et al. 2011; Katz et al. 2013). Entrainment losses at water diversions have also been implicated in the population declines of several fish species, including Chinook salmon (Oncorhynchus tshawytscha; Moyle 2002), delta smelt (Hypomesus transpacificus; Moyle 2002), striped bass (Morone saxatilis; Stevens et al. 1985; Kimmerer et al. 2001), and green sturgeon (Acipenser medirostris; Mussen et al. 2014), and we have previously shown that juvenile Chinook salmon are susceptible to entrainment into unscreened water diversions in laboratory simulations (Mussen et al. 2013). In nature, these fish may encounter numerous water diversions during their seaward out-migration, compounding their entrainment risk (Walters et al. 2012). With the majority of California salmon populations in rapid decline (Katz et al. 2013), and multiple California Chinook salmon runs listed as threatened or endangered by the National Marine Fisheries Service (California Department of Fish and Wildlife 2013), it is important to protect these fishes from manageable mortality sources.

Unlike many stressors on migratory fish populations that are difficult to constrain, it may be possible to reduce migratory and resident fish entrainment at water diversions without altering the amount of water extracted. Small-scale water-diversion pipes in California's central valley are variable in construction and orientation, but typically are "over-the-levee" style pipes that project down the levee bank into the water at a 0.5 slope and are located \sim 0.3 m above the river bottom. The location and orientation of water-diversion pipes may affect fish entrainment susceptibility, and changing the shape of diversion pipe inlets or their position in the water column may be mechanisms to reduce fish entrainment risk without reducing water-diversion rates. For example, coastal power-plant water intake pipes have used velocity caps (a flat plate directing water entry from the sides of the intake) to reduce fish entrainment (Thomas et al. 1980), but their effectiveness has not been tested in freshwater habitats or when attached to relatively small-sized water diversions.

Fish-guidance devices emitting repulsive sensory stimuli may also be able to direct fish past water-diversion pipes at distances far enough to avoid the high inflow water velocities near pipe inlets. Different types of behavioral fish-guidance devices have been installed to repel fish from entering large-scale water diversions, dams, and locks. Strobe lights can repel juvenile Chinook salmon swimming in relatively large, low-velocity water bodies (Brown 2000; Johnson et al. 2005) and in laboratory tanks or raceways with still water (Nemeth and Anderson 1992; Mueller et al. 2001; Richards et al. 2007), but few studies have evaluated their effectiveness in river simulations, where hydraulic conditions may also influence and direct fish movement. Chinook salmon smolts will avoid low-frequency vibrations in laboratory experiments, hypothesized to simulate the tail-beats of an approaching predatory fish (Knudsen et al. 1997), but initial field experiments found vibratory repulsion to vary substantially by species (Maes et al. 2004).

The primary objective of this study was to determine if behavioral fish-guidance devices (strobe lights or a vibrating ring) or pipe inlet modifications (velocity cap or an upturned pipe extension) could significantly reduce juvenile Chinook salmon entrain-

ment risk during the day and night without affecting the waterdiversion rate through a small-scale, unscreened, water-diversion pipe. Behavioral deterrent experiments were conducted at a sweeping (river) velocity of 0.15 m·s⁻¹ and with a water-diversion rate of 0.57 m³·s⁻¹, a flow combination selected because it had been previously shown to entrain high numbers of Chinook salmon (Mussen et al. 2013). The location, school size, timing, and total number of fish passing the pipe were compared with those that became entrained to determine the relative entrainment risk for each device. Because previous studies with larger Chinook salmon using the same river simulation flume and methodologies found that entrainment is affected by different combinations of sweeping and diversion flows (Mussen et al. 2013), we also assessed fish entrainment risk at modified flow combinations as a secondary study objective. We tested a high water velocity treatment (0.61 m·s⁻¹ and 0.57 m³·s⁻¹) and a low water-diversion rate treatment (0.15 m·s⁻¹ and 0.37 m³·s⁻¹).

Materials and methods

We tested age-0 Chinook salmon acquired from the California Department of Fish and Wildlife's Feather River Hatchery (Oroville, California) and the US Fish and Wildlife Service's Coleman National Fish Hatchery (Anderson, California) in March 2011. Fish from both hatcheries were equally distributed between two 455 L flow-through circular tanks at UC Davis' Center for Aquatic Biology and Aquaculture.

Experiments tested fish swimming behavior near fish-deterring devices (strobe lights, vibrating ring), pipe modifications (velocity cap, upturned pipe inlet with velocity cap), and control conditions where no fish deterrent devices were present in a 18.29 m long, 3.05 m wide, and 3.20 m high outdoor flume (experimental equipment, procedures, operational details, and flume diagrams closely followed those of Mussen et al. 2013). A 0.15 m·s⁻¹ sweeping velocity was generated to simulate a river current, and water was diverted at 0.57 m³·s⁻¹ through a 0.46 m diameter pipe located near the flume's center. Other flow combinations were tested in two additional treatments without guidance devices: a high water velocity treatment (0.61 m·s⁻¹ sweeping velocity with a 0.57 m³·s⁻¹ water-diversion rate) and a low water-diversion rate treatment (0.15 m·s⁻¹ sweeping velocity with a 0.37 m³·s⁻¹ water-diversion rate). Experiments were conducting during the day and at night, and most treatments were repeated six times with 80 naive fish tested during each 2 h experiment. The complete experiment list is detailed in Table 1. Owing to changes in fish size and behavior over the course of this study, experimental treatments were categorized into spring (15 May to 15 June 2011) and summer (16 June to 27 July 2011) periods and compared with control experiments conducted during each period (Table 1). Within each experimental period, fish-guidance devices, pipe modifications, and different flow combination treatments were tested in series, while control experiments were conducted randomly throughout the period to control for changing entrainment susceptibility due to fish growth. Flume water depth was maintained at 2.2 m for most experiments. Flume depth was 2.6 m during the upturned pipe experiments (necessary to achieve the 0.57 m³·s⁻¹ water-diversion rate) and 1.8 m in the reduced water-diversion experiments (necessary to achieve the 0.57 m³·s⁻¹ water-diversion rate with a 0.15 m·s⁻¹ sweeping velocity). Mean (±SE) light levels above the flume were 3700 ± 195 lx during the day and 0.25 ± 0.01 lx during the night, water temperature was 18.4 ± 0.17 °C, dissolved oxygen was 9.5 ± 0.12 mg·L⁻¹, pH was 8.12 ± 0.04 , and ammonia levels were $0.01 \pm 0.004 \text{ mg} \cdot \text{L}^{-1}$.

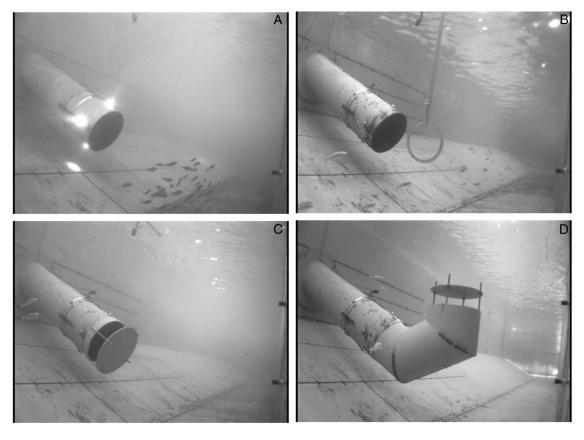
Strobe light experiments used four synchronized LED lights (Rotan, QuasarDot), each emitting >200 lumens when active, with a flash pattern of four rapid flashes over 0.5 s, followed by 0.5 s of darkness. Strobe lights were attached to the top, bottom, and each

Table 1. Experimental conditions for treatments.

Treatment	Season	Day-night	Sweeping velocity (m·s ⁻¹)	Diversion rate (m ³ ·s ⁻¹)	Reps.	Fish fork length (cm, ±SE)	Fish mass (g, ±SE)	Naive fish tested
Control (no device)	Spring	Day	0.15	0.57	4	7.6±0.2	5.2±0.6	Yes
High velocity (no device)	Spring	Day	0.61	0.57	6	8.5±0.5	7.7±1.6	Yes
Inside strobe	Spring	Day	0.15	0.57	6	8.0±0.1	6.1±0.3	Yes
Outside strobe	Spring	Day	0.15	0.57	6	8.8±0.1	8.5±0.4	Yes
Vibrating ring	Spring	Day	0.15	0.57	6	8.6±0.7	8.8±2.4	Yes
Control (no device)	Spring	Night	0.15	0.57	4	8.8±0.2	8.0±1.2	Yes
Control (no device)	Summer	Day	0.15	0.57	7	10.3±0.3	14.2±1.2	Yes
Low diversion (no device)	Summer	Day	0.15	0.37	6	10.4±0.1	14.0±0.2	Yes
Velocity cap	Summer	Day	0.15	0.57	6	9.7±0.2	11.6±0.5	Yes
Upturned pipe with cap	Summer	Day	0.15	0.57	6	9.7±0.1	11.1±0.3	Yes
Control (no device)	Summer	Night	0.15	0.57	7	10.8±0.2	15.9±0.7	No
Outside strobe	Summer	Night	0.15	0.57	6	10.6±0.2	14.8±1.0	No
Vibrating ring	Summer	Night	0.15	0.57	6	11.0±0.1	17.8±0.4	Yes
Upturned pipe with cap	Summer	Night	0.15	0.57	6	9.3±0.1	10.3±0.3	Yes

Note: Experiments were grouped into spring and summer periods to account for fish growth and seasonal effects. The seasonal grouping was decided after the spring period, resulting in fewer repetitions of spring control experiments. Most experiments tested naive fish (no previous experience in the flume), but two summer night experiments reused fish previously tested once in spring day experiments.

Fig. 1. View inside the flume channel, 2.1 m downstream of the water-diversion pipe from the flume's sidewall, displaying the tested fish-deterring devices: (A) outside strobe lights; (B) vibrating ring; (C) velocity cap; (D) velocity cap on an upturned pipe extension.



sidewall of the water-diversion pipe, placed 14 cm behind its inlet (Fig. 1A). Experiments were conducted with strobe lights attached inside the diversion pipe during the day, outside of the diversion pipe during the day, and attached outside of the pipe at night. Vibrating ring experiments (designed to simulate low-frequency vibrations analogous to tail-beats of approaching predatory fish) used a 38.1 cm diameter, 3.2 cm wide, 2 mm thick steel ring, welded to the end of a 2.4 m long, 7.5 cm wide, 4 mm thick suspension rod, with the top of the ring positioned 5 cm below and 19 cm in front of the top of the pipe inlet (Fig. 1B; Knudsen et al. 1997; Maes et al. 2004; Mussen and Cech 2013). The ring's

width was oriented parallel to the length of the pipe to project vibrations upstream and downstream of the inlet and minimize water intake obstruction. An industrial pneumatic vibrator (Martin, NTK 25) attached to the suspension rod 60 cm above the water surface generated 12 Hz vibrations in the upstream and downstream directions. An electric timer (Tork, ACT120S) and solenoid (Bosch Rexroth, TC15) were used to set the vibration period to cycle 6 s on and 6 s off during the 2 h experiments. A steel box (7 cm \times 7 cm \times 5 cm) containing three 1 cm diameter metal balls was attached to the rod 15.2 cm above the metal ring to create rattling sounds when the rod was vibrated.

In velocity cap experiments, a circular, 52 cm diameter, 2 cm thick steel plate was mounted on threaded rods directly in front of the water-diversion inlet (Fig. 1C). The plate was set at the closest distance possible to the pipe inlet that caused no reduction in water-diversion rate, determined to be 15.2 cm in empirical tests. The velocity cap was designed to reduce the diversion's maximum intake velocity by blocking water inflow from directly in front of the pipe (where inflow velocities are generally highest) and redistributing the inflow around the periphery of the pipe and velocity cap. The velocity cap was also tested in combination with an upturned pipe extension, which positioned the pipe inlet 62 cm higher in the flume and diverted water horizontally from all sides of the inlet (Fig. 1D). Flume water depth was increased by 24 cm to compensate for head loss from the two 58° angle bends in the upturned pipe and maintain a 0.57 m³·s⁻¹ water-diversion rate.

Underwater cameras (Speco, CVC320, 252K pixels, 30 frames per second (fps)) were positioned just under the water's surface, above the pipe inlet and the flume walls, lateral to the pipe inlet, to record fish swimming behaviors and entrainment starting locations during day experiments. A camera mounted 2.1 m downstream of the pipe inlet on the flume's sidewall also recorded a wide view of the flume channel to record fish traveling past the diversion pipe. A floating 1.2 m², clear-acrylic view-plate and a camera (Sony, CCD-TRV108, 250K Pixels, 30 fps) were used during upturned pipe experiments to view and record a larger section of the flume's surface above the diversion pipe inlet. The center of the pipe inlet was located 50 cm above the base of the flume and 0.3 m above the riverbank simulation ramp in all conditions except the upturned pipe experiments, where it was increased to 112 cm.

Video recordings were analyzed with a video editor (Sony, Movie Studio 10) to determine the numbers, timing, approximate depths, swimming orientations (relative to the sweeping current), and school sizes of fish that successfully traveled past the diversion pipe. Video playback was done in real time until a fish was observed swimming near the pipe, at which time the video was tracked frame by frame to determine if the fish became entrained. The starting and ending locations of each fish entrainment event were also determined as described in Mussen et al. (2013). Successful pipe passage events (defined as each time a fish traveled past the water-diversion pipe from upstream to downstream, or from downstream back upstream, at any distance without becoming entrained) were analyzed and used to calculate entrainment risk per pipe passage risk for each experiment. Fish passing the pipe were categorized as follows: fish traveling downstream and swimming with the sweeping current (negative rheotaxis), fish facing into the sweeping current and being carried downstream (positive rheotaxis), or fish swimming upstream into the current (also displaying positive rheotaxis). Still images of fish entrainment events were created from recorded video to determine the starting locations of fish entrainment events relative to the center of the diversion pipe inlet and the associated water velocities at the locations.

The mean fish entrainment risk per pipe passage was calculated for each day treatment by dividing the number of entrained fish by the observed number of pipe passages that occurred during the experiment (including both successful passage and passages resulting in entrainment), multiplied by 100. The percentage of fish lost to entrainment following repeated encounters with unscreened diversion pipes was estimated by repeatedly multiplying the product of a variable (starting at 100) by the calculated fraction of fish diverted during pipe passage and summing the resulting differences between the starting value and product for each iteration (representing repeated pipe passages). As an example, after 15 pipe passages, with 3.9% entrainment risk per passage, the percentage of fish entrained was estimated to be 44.9%, from $\{100 \times [1-(1-0.039)^{15}]\}$.

Data were analyzed using ANOVA models, with alpha set at 0.05, and Tukey's post hoc tests. Separate two-way ANOVAs were used to compare mean fish fork length and mass between en-

trained and non-entrained fish and among treatments. Mean fish entrainment counts and school sizes among treatments were analyzed using separate ANOVAs with Poisson distributions. Separate ANOVAs with normal distributions were used to compare mean successful pipe passage rates, entrainment starting distances, and water velocities at fish entrainment locations. The mean percentage of fish at each swimming orientation (downstream movement, positive rheotaxis; downstream movement, negative rheotaxis; upstream movement, positive rheotaxis) was compared between entrained fish and fish that successfully traveled past the diversion pipe for each treatment using χ^2 tests (alpha set at 0.05).

Results

Fish sizes

Mean fish fork lengths and masses did not differ between entrained and non-entrained fish (length $F_{[1,135]} = 0.63$, P = 0.428; mass $F_{[1,135]} = 0.95$, P = 0.331), but differed among treatments (length $F_{[1,135]}$ = 24.4, P < 0.001; mass $F_{[1,135]}$ = 25.4, P < 0.001), with no entrainment by treatment interaction (length $F_{[1,135]} = 0.14$, P = 1.0; mass $F_{[1,135]} = 0.17$, P = 1.0). Mean length and mass was similar between fish tested during the day and night in the same season $(P \ge 0.087)$, but fish in the summer control experiments were heaver and longer than those tested in the spring control experiments (P < 0.001; Table 1). Among treatments, mean fish length and mass were similar between control fish and those in most other treatments conducted during the same season and time of day $(P \ge 0.060)$. There were two exceptions; fish in the summer day control were heavier than those tested in the summer upturned pipe treatment (P = 0.013), and fish in the summer night control were longer and heavier than those tested in the night upturned pipe treatment ($P \le 0.025$; Table 1).

Influence of season, time of day, and water flow on entrainment

The number of juvenile Chinook salmon entrained in swimming experiments differed among treatments ($F_{[13,68]}=55.4$, P<0.001; Fig. 2). Season largely influenced the number of fish entrained, with significantly fewer fish entrained in day control experiments in the summer compared with those in the spring (P<0.001). Entrainment rates were similar at night between fish in the spring and summer control experiments (P=0.180), and correspondingly more fish were entrained during the day than night in summer control experiments (P=0.035). In spring day experiments, fewer fish were entrained in the high water velocity ($0.61~\text{m·s}^{-1}$) treatment compared with those in the control ($0.15~\text{m·s}^{-1}$) treatment (P<0.001). In the summer day experiments, fewer fish were entrained in the low water-diversion rate ($0.37~\text{m}^3\cdot\text{s}^{-1}$) treatment compared with those in the summer control ($0.57~\text{m}^3\cdot\text{s}^{-1}$) treatment compared with those in the summer control ($0.57~\text{m}^3\cdot\text{s}^{-1}$) treatment (P<0.001).

Influence of fish-guidance devices on entrainment

Some fish deterring devices were effective at decreasing the numbers of fish entrained through the diversion pipe, but others had little effect or increased the number of fish entrained (Fig. 2). Compared with fish in the spring day control, more fish were entrained in the inside strobe light treatments (P = 0.001), and similar numbers of fish were entrained in the outside strobe light treatments (P = 0.284). During the summer night experiments, more fish were entrained in outside strobe light treatments compared with those in the control (P = 0.026). In spring, fish in the daytime vibrating ring experiments showed similar entrainment rates compared with those in daytime control experiments (P = 0.096), and in the summer, significantly fewer fish were entrained at night in vibrating ring experiments compared with those in the night control experiments (P < 0.001). Similar numbers of fish were entrained when the velocity cap was attached to the pipe inlet and when it was absent (P = 1.0). The velocity cap tested in combination with the upturned pipe also had similar numbers of

Fig. 2. Mean + SE number of Chinook salmon entrained through an unscreened diversion pipe, out of 80 fish tested per replicate, during 2 h day (open bars) and night (black bars) experiments in the spring and summer (n = 6 replicates tested per treatment with some exceptions; see Table 1). Experiments were tested at 0.15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate, except for the high water velocity treatment (0.61 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate) and the low water-diversion treatment (0.15 m·s⁻¹ sweeping velocity and 0.37 m³·s⁻¹ water-diversion rate). Significant differences in the mean number of fish entrained among treatments are marked with different letters (P < 0.050 for all significant pairwise comparisons).

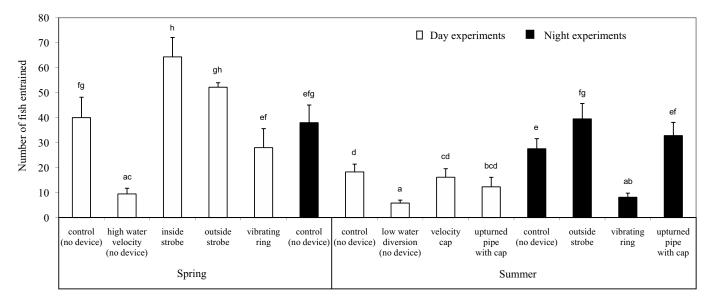
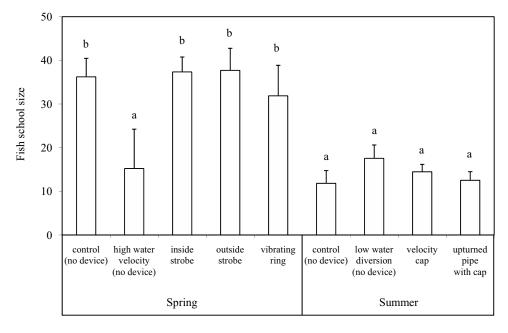


Fig. 3. Mean + SE Chinook salmon school sizes during day experiments in the spring and summer (n = 6 replicates tested per treatment with some exceptions; see Table 1). Experiments were tested at 0.15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate, except for the high water velocity treatment (0.61 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate) and the low water-diversion treatment (0.15 m·s⁻¹ sweeping velocity and 0.37 m³·s⁻¹ water-diversion rate). Significant differences in mean school size among treatments are marked with different letters (P < 0.050 for all significant pairwise comparisons).



fish entrained compared with those in control experiments during the day (P = 0.303) and night (P = 0.900).

Influence of fish-guidance devices on swimming behaviors

In day experiments, fish school sizes varied among treatments ($F_{[8,44]} = 31.0$, P < 0.001) and were mostly larger in the spring (mean = 36 fish) compared with those in the summer (mean = 14 fish; P < 0.001), with the exception of fish in the high water velocity (no device) experiments, where fish swam in smaller

schools (Fig. 3). The number of times fish traveled past the water-diversion pipe also differed among treatments in day experiments ($F_{[8,44]} = 5.8$, P < 0.001), with fewer fish passing the pipe in the high water velocity treatment compared with those in the control, strobe light, or vibrating ring treatments ($P \le 0.031$; Fig. 4).

By calculating mean fish entrainment risk during one pass of the pipe, fish entrainment risk can be compared among the daytime treatments without the influence of varied pipe encounter rates. Entrainment risk per pipe passage differed among treat-

Fig. 4. Mean + SE number of Chinook salmon that successfully traveled past the diversion pipe during day experiments (n = 6 replicates tested per treatment with some exceptions; see Table 1). Experiments were tested at 0.15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate, except for the high water velocity treatment (0.61 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate) and the low water-diversion treatment (0.15 m·s⁻¹ sweeping velocity and 0.37 m³·s⁻¹ water-diversion rate). Significant differences in the mean number of fish passing the pipe among treatments are marked with different letters ($P \le 0.001$ for all significant pairwise comparisons).

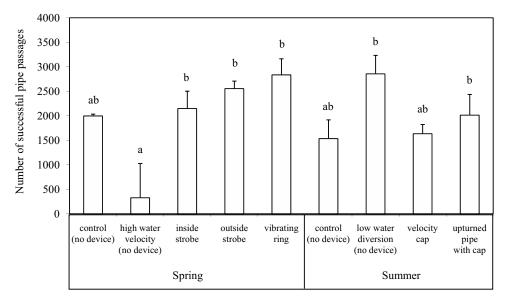
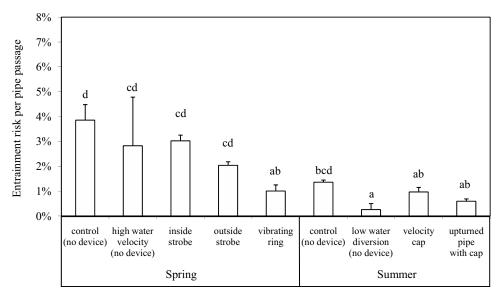


Fig. 5. Entrainment risk percentage (mean + SE) calculated per pipe passage for fish traveling past the diversion pipe. Experiments were tested at 0.15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate, except for the high water velocity treatment (0.61 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate) and the low water-diversion treatment (0.15 m·s⁻¹ sweeping velocity and 0.37 m³·s⁻¹ water-diversion rate). Individual fish could pass the diversion pipe more than once during an experiment, and 80 fish were tested in each replicate (n = 6 replicates tested per treatment with some exceptions; see Table 1). Significant differences in the mean percentage of fish entrained among treatments are marked with different letters ($P \le 0.046$ for all significant pairwise comparisons).

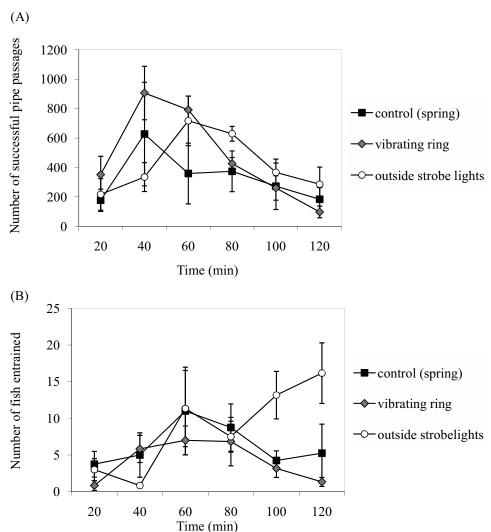


ments ($F_{[8,44]} = 7.8$, P < 0.001; Fig. 5). Fish in the summer control treatment showed a nonsignificant reduction in entrainment risk per pipe passage compared with those in spring control experiments (P = 0.073). In the spring, a lower percentage of fish in the vibrating ring treatments were entrained during pipe passage than those in the control treatment (P = 0.012). In summer, a lower percentage of fish were entrained in the low water-diversion rate treatment compared with those in the control treatment (P = 0.024). Fish entrainment risk was similar between fish in the strobe light, velocity cap, and upturned pipe inlet (with velocity cap) treat-

ments and those in the corresponding control treatments for each season ($P \ge 0.241$).

In most experiments, relatively few fish passed or became entrained into the diversion pipe in the first 20 min. The numbers of passing or entrained fish generally increased during the 40 and 60 min periods and then gradually declined until experiment completion (see Figs. 6A, 6B; the spring control data are representative of this general pattern). More fish traveled past the pipe in the first 60 min of the vibrating ring experiments compared with those swimming in the spring control treatment, but similar

Fig. 6. Mean \pm SE number of fish that successfully passed the diversion pipe (A) or became entrained into the pipe (B) calculated in 20 min intervals during spring day experiments at 0.15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate (n = 4 replicates for the control and 6 replicates for the strobe light and vibrating ring treatments).



numbers of fish were entrained (Figs. 6A, 6B). Few fish traveled past the pipe in the first 40 min of the strobe light treatment (Fig. 6A), reducing mean fish entrainment rates compared with those in the control treatment (Fig. 6B). But pipe passage rates increased in the outside strobe light treatment after the first 40 min and again in the last 40 min, corresponding to higher fish entrainment rates in the last 40 min compared with those in the control (Fig. 6B).

Locations, water velocities, and swimming orientations at

Fish entrainment starting distances varied among treatments $(F_{[8,43]} = 6.6, P < 0.001)$ because fish in the upturned pipe inlet with velocity cap experiments started to become entrained at a greater distance from the pipe $(40 \pm 2.4 \text{ cm})$, compared with those in all of the other treatments $(P \le 0.047)$. In the non-upturned pipe treatments, entrainments began at 30 ± 1.1 cm from the center of the diversion pipe and were not different among treatments $(P \ge 0.233)$. The mean water velocity fish experienced at the start of entrainment events was similar among all treatments $(F_{[8,40]} = 1.9, P = 0.087)$ with a value of $0.82 \pm 0.04 \text{ m} \cdot \text{s}^{-1}$. Detailed locations of

each entrainment event occurring at day are presented by treatment as supplemental material (Figs. S1–S8¹).

The percentage of fish entrained at each swimming orientation (1: downstream passage, negative rheotaxis; 2: downstream passage, positive rheotaxis; 3: upstream passage, positive rheotaxis) was significantly different from the swimming orientations of fish that successfully passed the pipe in every treatment (P < 0.001), except for those tested in the high water velocity treatment (data not shown). In the control experiments, only $2.8\% \pm 1.0\%$ of fish successfully passed the pipe with negative rheotaxis, but $28.9\% \pm 3.3\%$ of fish entrainment events started with negative rheotaxis. At $0.61 \, \text{m·s}^{-1}$ sweeping velocities, 49.3% of successful pipe passages occurred with negative rheotaxis, resulting in similar percentages of fish successfully passing the water-diversion pipe and becoming entrained at each swimming orientation (P = 0.539).

Discussion

Entrainment relative to swimming speeds

Chinook salmon have been shown to avoid entering rapid water accelerations (Kemp et al. 2005a; Enders et al. 2009) and darkened

water intake structures (Kemp et al. 2005b), which are both characteristics of the active water-diversion pipe in our experiments. Some fish in our experiments, however, entered the high velocity zone determined to be located 30 cm from the pipe inlet's center by the fish entrainment starting locations, where the intake velocities exceeded 0.82 m·s⁻¹. This inflow velocity is within the range previously described for older, larger juvenile Chinook salmon (0.6–0.9 m·s⁻¹; Mussen et al. 2013). Portz (2007) determined the maximum (burst) swimming velocity for juvenile Chinook salmon (10.3 cm total length) to be 0.60 m·s⁻¹ in startle experiments, indicating that the entrained fish in our experiment were likely unable to escape from the high velocity inflow zone near the pipe inlet after entering it.

Intake velocity

Reduced water intake velocities through diversion pipes may allow more juvenile Chinook salmon to avoid entrainment; however, the percentage of water extracted from the river is not directly proportional to the percentage of fish removed from the habitat (Hanson 2001; Mussen et al. 2013). Based on the results of our summer experiments (Fig. 5), reducing a pipe's water-diversion rate from 0.57 m³·s⁻¹ (1.357% entrainment risk) to 0.37 m³·s⁻¹ (0.0026% entrainment risk) and operating it for 1.54 times longer (to divert an equivalent amount of water) would reduce the risk of entrainment for fish passing the pipe by 70.5%, calculated as follows: ({[(0.0026 × 1.54)/1.357] × 100} – 1). While reductions in water-diversion rates may decrease fish entrainment, irrigators would likely prefer alternate methods to reliably reduce fish entrainment without decreasing water-diversion rates.

River velocity

Faster out-migration rates at higher river discharges and velocities have been shown in many fishes, including Chinook salmon in the Sacramento River (Youngson et al. 1989; Vøllestad et al. 1986; McCormick et al. 1998; Smith et al. 2002; Michel et al. 2013). Juvenile Chinook salmon do occasionally pause their downstream migration, holding in areas of low water velocity, near shore and often during the day (Chapman et al 2012; Zajanc et al. 2013). During these holding periods, fish may repeatedly encounter water diversions located along the riverbank. Svendsen et al. (2011) determined that a water diversion caused Atlantic salmon (Salmo salar) to slow their migration speed and perform milling behaviors with fish swimming back upstream or in circles near the water-diversion entrance. The longer fish remained near the diversion, the more likely they were to enter it and fail to migrate. Fish in our experiments passed the pipe more frequently at the slower sweeping velocity (Fig. 4), but the risk of entrainment per pipe passage was not significantly different between high and low sweeping velocities (Fig. 5). If faster river currents encourage juvenile Chinook salmon to out-migrate through river systems more rapidly, limiting the time they spend in shoreline habitats that may contain unscreened diversions, higher river velocities may decrease fish entrainment by decreasing their likelihood of encountering active water diversions.

Seasonal changes in entrainment

In spring control experiments, a small percentage of fish became entrained during each pipe passage event during the day, but repeated pipe encounters resulted in roughly 50% of the fish becoming entrained during these experiments. A seasonal reduction in pipe passage rates likely explains why more fish were entrained during the spring than summer, when overall entrainment fell to 23%. A further reduction in pipe passage and entrainment rates has been shown for older and larger fish tested in late summer (Mussen et al. 2013) and is consistent with the idea that entrainment susceptibility declines as these fish grow. As the outmigration season progresses, migratory readiness, the degree of

smoltification, and altered rheotactic responses likely play key roles in entrainment susceptibility (McCormick et al. 1998). Importantly, we showed that smaller fish are four to five times more susceptible to entrainment compared with larger fish tested under similar hydraulic conditions in previous studies (Mussen et al. 2013). The tendency of juvenile Chinook salmon to swim in larger schools may have also contributed to the increased number of fish entrained during the spring than summer. Most of the Chinook salmon traveled downstream with negative rheotaxis at 0.15 m·s⁻¹ sweeping velocity, swimming head-first with the current. Although few fish passed the pipe with positive rheotaxis, a surprisingly large percentage of fish became entrained with positive rheotaxis. As schooling fish approached the diversion's intake area, fish near the front and sides of the school would occasionally switch orientations, presumably to swim towards the middle of the school, but this behavior frequently resulted in entrainment.

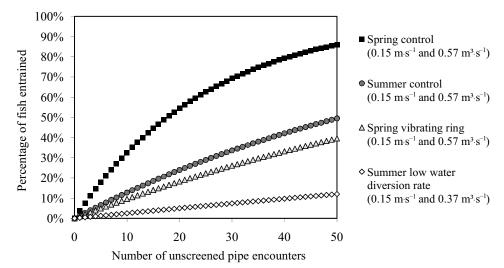
Strobe lights

Strobe light systems may be less effective at repelling juvenile Chinook salmon in rivers where water flow direction and speed may direct fish movement. Sager et al. (2000) found that two perciform fishes showed less avoidance to strobe lights at higher water flow rates (from 0.2 to 0.5 m·s⁻¹), although one species of clupeid fish showed no difference in strobe light avoidance among tested velocities. In our studies, juvenile Chinook salmon appeared to be repelled by the outside strobe lights for the first 40 min of the experiment, indicated by low numbers of fish observed passing the pipe. Chinook salmon have been shown to avoid strobe lights up to 7.3 m from their projected source (Richards et al. 2007), but avoidance may delay fish from migrating downstream, possibly increasing their risk of predation (Perry et al. 2010). In our experiments, fish appeared to avoid strobe lights for the first 40 min, but as the experiments proceeded they may have been attracted to the lights, indicated by the extremely high number of fish entrained during the final 20 min of the outside strobe light treatment (Fig. 6B). Kock et al. (2009) also found that strobe light illumination increased juvenile steelhead (Oncorhynchus mykiss) entrainment at turbine induction slot inlets compared with unlit intakes and proposed that strobe light exposure might have induced a "torpor-like" state in the steelhead at close distance, increasing their susceptibility to entrainment (Flamarique et al. 2006). We suspect that juvenile Chinook salmon were temporarily stunned by exposure to strobe lights at close proximity to the pipe inlet, reducing the fish's ability to escape from the water inflow and increasing entrainment.

Vibrating ring

Vibratory stimuli has been shown to elicit flight responses and avoidance behaviors in fishes (Knudsen et al. 1994, 1997), but the effectiveness of vibrations at guiding fish past unscreened waterdiversion pipes has not previously been tested. Atlantic salmon were found to avoid a 10 Hz vibration source by 2 m (Knudsen et al. 1994), and vibrations initiated within 1 m of schooling Chinook salmon caused rapid avoidance responses (Knudsen et al. 1997), suggesting that vibratory repulsion may have potential to guide fish past water-diversion pipes. In our experiments, the vibratory ring produced both visual and vibratory stimuli during the day, but the low number of fish entrained at night (where vision was limited) indicates that the ring's vibrations were directing fish avoidance behaviors in low-light conditions. The vibrating rattle may have heightened the fish's awareness to a change in environment, but near-field vibrations from the ring likely generated the directional cues for avoidance responses near the pipe. During the first hour of daytime experiments, the ring may have functioned as an effective deterrent, resulting in higher fish pipe passage rates and fewer entrainments. However, after the first hour of exposure, fish appeared to habituate to the stimulus, indicated by similar pipe passage and entrainment rates to those in control

Fig. 7. Calculated percentages of Chinook salmon lost to entrainment after repeatedly encountering unscreened diversion pipes (passing within 1.5 m of the pipe's inlet) in spring with and without a vibrating ring at 15 m·s⁻¹ sweeping velocity and 0.57 m³·s⁻¹ water-diversion rate and in summer under control (0.57 m³·s⁻¹) and low (0.37 m³·s⁻¹) water-diversion rates. Values are estimated from the entrainment risk per pipe passage values (see Fig. 5).



treatments during the second hour. For out-migrating fish in rivers, habituation to vibrations may be less problematic if fish pass water-diversion pipes rapidly and only encounter pipes periodically (Knudsen et al. 1997). The effectiveness of vibrating rings may be hindered in locations with large amounts of river debris that could accumulate on the ring and dampen vibrations. Further studies investigating ring vibration frequency, amplitude, shape, size, color, orientation, and placement relative to the water intake should be considered.

Velocity cap

Velocity caps placed in front of water-diversion pipes decrease their maximum inflow velocity by blocking water inflow at the center of pipe inlet, instead drawing water in from the sides of the pipe. Velocity caps installed on vertically oriented coastal water intake pipes, which withdraw ocean water to cool electrical plants, can significantly reduce fish entrainment compared with those with open inlets (Thomas et al. 1980). Fish are theorized to have a stronger natural aversion to entering water intakes with velocity caps, which create dispersed horizontally oriented inflows, compared with uncapped water intakes (Watts et al. 1982). Reductions in fish entrainment using velocity caps at coastal power plants (California, USA) were greater during the day than night (Thomas et al. 1980), suggesting a visual component to the guiding stimuli. However, significantly fewer fish were entrained through the velocity caps at night compared with open inlets (Thomas et al. 1980), indicating nonvisual guidance cues are also provided by the device (possibly detected by fish lateral line systems). The upturned pipe extension and velocity cap combination created the "typical" horizontal water inflow condition that marine fish are known to avoid, while the velocity cap mounted on the pipe without the upturned orientation tested the effect of a more dispersed intake area without a horizontal intake direction. Although fewer fish were diverted from the center of the inlet in the velocity cap treatments, many fish were entrained from the sides of the pipe (Fig. S81), where water inflow velocity was beyond the fish's ability to escape. Water entered the velocity cap at 2.6 m·s⁻¹ in our experiments (calculated by 0.57 m³·s⁻¹ diversion rate / 0.22 m² inlet area), which greatly exceeds the recommended velocity cap inflow rates of 0.15 to 0.46 m·s⁻¹ for coastal water intakes (Watts et al. 1982), and was higher than the mean entrainment starting velocity of 0.82 m·s⁻¹ in our experiments. To achieve a horizontal inflow at a velocity below 0.46 m·s⁻¹ at a 0.57 m³·s⁻¹ diversion rate, the pipe inlet and velocity cap diameters would need to be substantially larger than those used in our experiments, or the cap would need to be located further from the pipe, likely lessening its effectiveness. Widened pipe inlets should be tested in future experiments to determine if reduced inflow velocities across a large intake area can reduce fish entrainment risk at unscreened water-diversion pipes.

The upturned pipe created a widely dispersed horizontal intake area in the flume, above the mean fish swimming depth in control experiments. However, the fish swam higher in the water column with the upturned pipe installed, which resulted in similar entrainment rates compared with those in the control treatment. The shift in swimming depth suggests that the juvenile Chinook salmon may have been attracted to the increased water velocity near the pipe inlet, before encountering inflow velocities approaching their maximum swimming speed (Mussen et al. 2013) or areas of rapid acceleration (Kemp et al. 2005b; Enders et al. 2009), which commonly evoke escape responses. Migratory fishes, including juvenile Chinook salmon, often move into faster flowing waters (Smith et al. 2002; Michel et al. 2013), and if these fish are attracted to water-diversion inflows, they may be equally susceptible to entrainment through unscreened diversion pipes situated at any river depth.

Implications for juvenile Chinook salmon management

Our results show that repeated encounters with unscreened water diversions have the potential to remove a significant number of out-migrating juvenile Chinook salmon. Although the number of fish entrained may be low when passing a single waterdiversion pipe, repeated pipe encounters could have substantial impacts on fish populations. For example, we estimate that 50% of out-migrating juvenile Chinook salmon could be entrained after encountering (passing within 1.5 m of the pipe's inlet) 18 active water-diversion pipes in the spring or 50 active water-diversion pipes in the summer (Fig. 7). Walters et al. (2012) estimated that 71.1% of out-migrating Chinook salmon would be mortally entrained after passing 89 unscreened water diversions in the Lemhi River, USA, using a model incorporating passive integrated transponder tag data and the proportion of water extracted at diversions. Similarly, our findings predict that 70.4% of juvenile Chinook salmon would be mortally entrained after encountering 89 unscreened diversion pipes (estimated from the calculated entrainment risk for summer control experiments). Fortunately, our

results and those of Walters et al. (2012) also suggest that fish entrainment can be substantially decreased through water-diversion management. Using our entrainment data, we estimate that after encountering 20 pipes the number of spring-migrating fish entrained would be decreased by 66.4% (from 54.5% to 18.3%) when a vibrating ring is present and the number of summer-migrating fish entrained would be decreased by 79% (from 23.9% to 5.0%; Fig. 7) if water-diversion rates are reduced from 0.57 to 0.37 m³·s⁻¹.

Understanding fish behavior is a key component to the development of successful fish passage mechanisms (Enders et al. 2009) and necessary to provide a scientific basis for management actions designed to help protect fishes. Our results suggest that some behavioral fish-guidance devices (e.g., vibrating rings) can be effective in decreasing fish entrainment through unscreened water diversions, while other devices such as velocity caps and strobe lights, which have proven to be effective in other aquatic environments, can be ineffective (velocity caps) or even harmful (strobe lights) at guiding fish safely past unscreened diversions. Decreasing water-diversion rates below 0.37 m³·s⁻¹ for 0.46 m diameter unscreened pipes can also substantially decrease entrainment risk. Fish screens have been installed at many large waterdiversion projects in California, are generally very effective at minimizing juvenile salmonid entrainment (Swanson et al. 2004; Gale et al. 2008; Walters et al. 2012), and are required in California on all new or renovated water-diversion structures in salmoninhabited waters (California Department of Fish and Wildlife 1996). However, the costs of installation, required maintenance, and legal regulations can discourage owners of existing water diversions (that are not required to be screened) from installing new fish screens. Behavioral fish-guidance devices may appeal to owners of existing water diversions because they can offer a lowcost, unregulated alternative to fish screens without decreasing water delivery rates, but further refinement of these devices and studies testing their effectiveness under alternative flow regimes, turbid water conditions, and at multiple water temperatures are recommended prior to general implementation.

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