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Research Article

The efficacy of killing developing common carp embryos with electricity: using a laboratory evaluation to assess a potential means of reducing the recruitment of an invasive fish

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Abstract

Concern about electrofishing inadvertently harming the embryos of species of conservation concern has motivated much of the research that describes what electrical conditions can kill fish embryos. As a result, targeted electrofishing might be underutilized as a potential control method to reduce the recruitment of nuisance fishes like common carp (*Cyprinus carpio*), one of the most widely distributed invasive fish in North America. We evaluate the efficacy of using electricity to reduce common carp recruitment by examining embryonic survival while manipulating the transfer of electric power to developing carp embryos. Embryos were shocked in water from a carp-occupied area (ambient conductivity 127 µS/cm) using a variety of voltage gradient and waveform treatments common to commercial electrofishing units and generators. Survival of electroshocked common carp embryos was ≤ 50% at power densities (12,700 µW/cm^3) and voltage gradients (10 V/cm) that failed to cause significant mortality in other cyprinid species; however, embryonic resistance to electroshock was first noted at almost 3 d after fertilization (survival ≤ 50% at 79,375 µW/cm^3). Power transfer theory was used to explore optimal water conductivities for the deployment of electrical control of fish embryos at shallow endorheic lakes by using conditions at Malheur Lake as an example. Power transfer theory suggests that at relatively high water conductivities it becomes more difficult to achieve power transfer thresholds sufficient to kill small fish embryos without exceeding the power capabilities of commercially-available electrofishing equipment, and that power transfer to the embryo drops below 50% of the total power applied when water conductivities exceed 325 µS/cm. Thus, water chemistry conditions most amenable to killing carp embryos with electricity in an arid, endorheic lake like Malheur Lake would most likely occur at lake inflows or more generally when the lake level is elevated. However, when spawning is dispersed or more spawning habitat is available during higher lake levels, the resulting increase in areas that require treatment may present logistical challenges. Managers considering the use of electrofishing to control recruitment of an invasive fish like common carp should consider the spatio-temporal arrangement of spawning sites, the spatial scale of the necessary control treatment, how compensatory effects may influence the overall population response, and the need for concurrent control methods targeting other life stages.

Key words: invasive species control, integrated pest management, embryonic development, electric waveform, water conductivity, power transfer

Introduction

Common carp (*Cyprinus carpio* Linnaeus, 1758) are one of the most popular freshwater food fishes in the world and have been cultured and introduced extensively outside their native range (Balon 1995). Range expansion by invasive common carp throughout North America (Fritz 1987) is aided by their ability to thrive under a variety of abiotic conditions (Edwards and Twomey 1982) and food resources (Garcia-Berthou 2001), to grow quickly (Vilizzi and Walker 1999; Phelps et al. 2008), and their high fecundity (Swee and McCrimmon 1966; Tempero et al. 2006). Common carp (henceforth "carp") feed by

sifting through aquatic sediments to consume invertebrates (Sibbing et al. 1986; Roberts et al. 1995) which often uproots aquatic plants and disturbs the sediment, leading to increased turbidity. The suspension of nutrients trapped in aquatic sediments and excretion by carp may facilitate nutrient cycling and eutrophication in aquatic systems (Drenner et al. 1998; Khan et al. 2003; Parkos et al. 2003; Weber and Brown 2009). These activities can lead to ecosystem phase shifts at high carp densities where shallow lakes change from a clear water system dominated by macrophytes to turbid systems dominated by phytoplankton (Zambrano and Hinojosa 1999; Zambrano et al. 2001; Matsuzaki et al. 2009). Carp-induced changes in the state of these aquatic systems are often associated with declines in the abundance of other fish (Jackson et al. 2010) and waterfowl (Cahoon 1953; Haas et al. 2007; Bajer et al. 2009). Carp often achieve greatest abundance when introduced into shallow, nutrient rich lakes (Egertson and Downing 2004; Jackson et al. 2010; Bajer et al. 2015b). Once they have become established, the control of carp is often time consuming, expensive, and complicated. Managers often attempt to treat carp-infested waters through use of piscicides (Schrage and Downing 2004) or by commercial netting (Rose and Moen 1953; Neess et al. 1957; Fritz 1987; Bajer et al. 2011; Colvin et al. 2012). These methods are challenging because repeated treatments are often required to achieve the level of carp reduction needed to restore ecosystem function or to prevent recolonization (Barton et al. 2000). Even when significant efforts are made to remove carp or other undesirable fish, the majority of biomanipulation projects are often not considered successful (Moyle et al. 1950; Meronek et al. 1996; Meijer et al. 1999). Efforts to control carp populations in shallow lakes will likely require an integrated approach that targets multiple life stages (e.g., Weber et al. 2011).

Historically efforts aimed at reducing carp recruitment have focused on the disruption of spawning by dewatering spawning habitat (Shields 1958), deploying barriers such as nets to exclude carp from spawning areas (Hillyard et al. 2010; Taylor et al. 2012), or using barriers to trap fish inside spawning areas where they can easily be killed (Bonneau and Scarnecchia 2014). Recently bluegill (*Lepomis macrochirus* Rafinesque, 1819) have successfully been used as a biocontrol for carp larvae in the Midwestern United States, and such control may be effective in deeper waters where winter hypoxia events are uncommon and in lakes where macrophyte cover is available (Poole 2018). However, in large and shallow endorheic lakes denuded of aquatic vegetation where carp can be broadly distributed and water levels can be difficult to manipulate, additional tools that specifically target recruitment may be needed to implement an integrated pest management plan. For example, cloverleaf traps have been effective at passively trapping age-0 carp. However, large scale trapping of young carp in lakes could require a substantial effort because baiting young fish into traps has not yet been successful (Carl et al. 2016).

Killing early life stages with targeted electrofishing may be underutilized as a potential control method for nuisance or invasive fishes (Nutile et al. 2013; Gross et al. 2015; Simpson et al. 2016). In fact, concern about electrofishing inadvertently harming the embryos of species of conservation concern has motivated much of the research that describes what electrical conditions can kill fish embryos (Muth and Ruppert 1997; Snyder 2003; Bohl et al. 2009). Using electricity to suppress the recruitment of invasive fish that lay eggs in discrete nests and have relatively large embryos, like salmonids, may be a viable control measure in certain habitats (Gross et al. 2015; Simpson et al. 2016; Brown et al. 2017). However, it is uncertain whether suppressing the recruitment of broadcast spawning invasive fish with relatively small embryos, such as so-called Asian carp (of the genera *Hypophthalmichthys* or *Mylopharyngodon*) and other introduced cyprinids, can be done effectively in situ with electricity (Bohl et al. 2010; Nutile et al. 2013; Simpson et al. 2016). Carp have specific habitat requirements for spawning – and can aggregate in shallow or seasonally flooded areas with abundant vegetation – thus adult spawners, eggs, and embryos can be spatially and temporally clumped in some situations (Penne and Pierce 2008). However, if the resistance to electroshock exhibited by some other cyprinids (Nutile et al. 2013) is shared with carp then it could be an impediment to the electrical control of carp recruitment.

We conducted a controlled laboratory experiment where we quantified the electrical power and voltage gradient required to kill carp embryos in an effort to understand the conditions under which electrofishing may be deployed as a tool to control carp in situ. Treatments were applied across developmental stages of carp as a means to determine how long embryos were vulnerable to electroshock. The transfer of electric power to the embryos was manipulated in small aquaria by creating homogenous electric fields in water from Malheur National Wildlife Refuge (NWR) using a variety of voltage gradient treatments. Waveform types typically emitted by boat electrofishers and electric generators were also used as treatments, reasoning that use of commercially-available equipment would be the most convenient way of using electricity to kill carp embryos in situ.

Power transfer theory was the used to explore optimal water conductivities for the deployment of electrical control of fish embryos at shallow endorheic lakes by using conditions at Malheur Lake as an example. Water conductivity is a key determinant for how electricity is transferred to target species (Kolz 1989; Kolz 2006), and is seasonally and spatially variable in endorheic lakes, like Malheur Lake. Therefore, we calculated 1) how much power must be applied to water to maintain deadly levels of power transfer to carp embryos based on the range of water conductivities observed at Malheur Lake (Reynolds 2015), and 2) at what water conductivity does power transfer to the embryo become relatively inefficient due to the reflection of applied power (Gross et al. 2015).

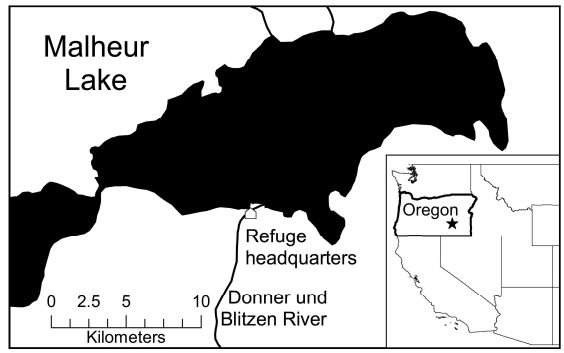

Figure 1. Map of Malheur Lake and Malheur National Wildlife Refuge. The inset shows the State of Oregon and the lake (star) relative to the western United States.

Materials and methods

Study site

Malheur Lake in SE Oregon State is the largest freshwater marsh in the western United States (approximately 20,114 ha; Figure 1), and is an example of a large, productive lake where introduced common carp have a devastating effect on the aquatic ecosystem. Water depths in this shallow lake are most often near 1 m, but infrequently lake depths can approach 0 m during extremely dry years and 6 m during uncharacteristically wet conditions (Cornely et al. 1985). Specific conductivity on the lake has been measured ranging between 200 and 3540 µS/cm from April through June (Hubbard 1975, unpublished data), and in the central unit of the lake where spawning is often observed specific conductivity has reached 1880 µS/cm. The relatively isolated location of the Malheur Lake within an arid landscape has made it a disproportionally important stop along the Pacific Flyway for migratory birds. Historically Malheur Lake may have supported 50 percent of the Pacific Flyway's migrating waterfowl and produced over 100,000 ducklings annually (Ivey et al. 1998). Declines in waterfowl production at Malheur NWR to 25% of its historic capacity has been attributed to the near disappearance of aquatic vegetation in Malheur Lake since carp became established in the 1950s (Cornely 1982; Ivey et al. 1998). There are no water control structures on this closed (i.e., endorheic or terminal) lake, so the Malheur NWR sought to address this problem through application of the piscicide rotenone on eight different occasions between 1955 and 1992. Although approximately 2.5 million carp were killed by these treatments there has been no long term decline in carp abundance due to populations rebounding in the years after each piscicide application (Ivey et al. 1998).

Experimental apparatus and electrical delivery systems

A closed water recirculation system was constructed to incubate carp embryos both before and after electroshock. The recirculation system consisted of two 2-L conical upwelling incubators to rear embryos pre-treatment, two 1.2-m-diameter circular tanks that were each filled with 660 L of water for rearing embryos post-treatment, water aeration, and sump tanks and pumps to recirculate water through the system. Water from the recirculation system came from Marshall Pond at the Malheur NWR headquarters and was replaced daily during the experiment (temperature = 18.8 ± 0.9 °C, ambient conductivity = 135 ± 8µS/cm, DO = 73 ± 5% [mean ± SD]), which ran between May 27th and June 1st, 2015.

Two electrical waveforms – alternating current (AC) and pulsed direct current (PDC) – were selected as treatments based on their high root-mean square (RMS) voltage gradients (Simpson et al. 2016, Figure 2) and their use in commercially-available electrofishers and generators. A sine-shaped AC waveform was generated by running grid power through a transformer device that was constructed (see Simpson et al. 2016 for a complete description). A PDC waveform with a square shape was generated using a Coffelt VVP-15 electrofisher. Both electrical delivery systems (AC and PDC generators) were wired to a shocking tank constructed from a 9.5 L glass aquarium fitted with two aluminum plate electrodes. The shocking tank was also fitted with a submerged oscilloscope probe to ensure the electrical field was homogeneous and the shape and peak voltage gradient of the waveforms were consistently repeated (see Simpson et al. 2016).

Delivery systems settings were adjusted so both waveforms had the same frequency (60 Hz). The square PDC waveform had a pulse width of 8.33 ms,

equivalent to a 50% duty cycle. The AC sine wave had a pulse width of 16.67 ms. Each positive and negative departure of the AC sine wave from 0 V lasted 8.33 ms.

Obtaining embryos from carp

Carp were dip netted from sites where they were actively spawning near the mouth of the Donner und Blitzen River on May 27th, 2015 at Malheur NWR (Figure 1). These sites were primarily backwater areas with flooded terrestrial vegetation. Captive fish were examined in holding tanks for ripeness (i.e., expressing eggs when the belly was gently depressed). Spawning began by stripping the eggs of one ripe female carp into a dry bowl. Milt from two male carp was added to the eggs, and the resulting mixture was stirred for one minute with a feather. Fertilization was initiated by adding water treated with urea salt (4g NaCl/L; 3g urea/L) to the mixture. The mixture was gently stirred for an hour while additional urea salt solution was added as the fertilized eggs swelled and hardened. The fertilized eggs were then rinsed in water treated with tannic acid (0.5g tannic acid/L) for 20 seconds to remove any remaining stickiness, and finally rinsed with fresh water (Jhingran and Pullin 1985; Rottmann et al. 1991). The fertilized eggs (diameter 2.13 ± 0.06 mm [mean ± SD]) were stocked into the upwelling incubators in the water recirculation system.

Experimental design

Fish were shocked or sham shocked (control) at five different embryonic stages (blastula [8 h post-fertilization], gastrula [17 h], organogenesis [35 h], active movement [50 h] and pigmentation [69 h]; Korwin-Kossakowski 2008), using two waveform shapes (AC or square PDC) that were adjusted to produce five peak voltage gradients (0, 10, 15, 20, or 25 V/cm). Peak voltage gradients were chosen based on the ranges of survival rates observed for other cyprinids exposed to square PDC waveforms (Nutile et al. 2013). The development of embryos were tracked by periodically selecting a sample of unshocked embryos from incubators, fixing them in 10% neutral-buffered formalin solution, and examining them under a dissecting stereo-microscope (George and Chapman 2013). Once embryos reached the desired developmental stage, a sample of embryos (N = 15 per sample) was removed from the incubators and placed into "exposure" baskets (cf. Nutile et al. 2012). These baskets were submerged in the aforementioned shocking tank filled with 5L of water from the water recirculation system (tank depth = 12 cm; temperature

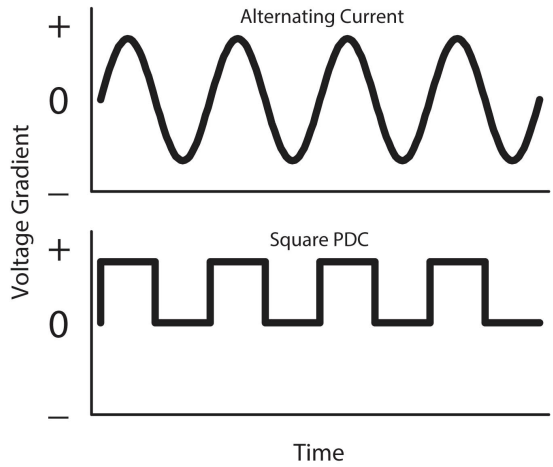

Figure 2. Shape of the two waveforms used in electroshocking treatments with common carp embryos. The duration of each AC sine wave was 16.67 ms. The pulsed DC (PDC) waveform is at 0 V for half of the duty cycle (50%, pulse width = 8.33 ms).

18.8 ± 0.9°C; ambient conductivity 127 ± 3 µS/cm [mean ± SD]) and exposed or sham exposed (0 V/cm) to electricity for 30 seconds. After a sample of embryos was shocked, their floating exposure basket was placed in one of the circular tanks. Each waveform shape × voltage gradient combination was replicated six times at each developmental stage. The entire set of electrical exposures at each developmental stage occurred within a narrow time period (i.e., 85 to 105 min for each stage) to help ensure that the embryos remained at the same developmental stage during treatment. Fish survival was determined by counting the number of living embryos and hatched embryos under a dissecting stereo-microscope with 40× magnification after approximately 50% of the embryos had successfully hatched across all treatments (120 h post-fertilization).

Analysis

Differences in the proportion of carp embryos surviving electroshock at voltage gradient and waveform type treatments were evaluated at each developmental stage using a two-factor generalized linear model with an interaction term, quasibinomial errors, and a logit link function (Fitzgerald et al. 2016). Peak voltage gradient was analyzed as a quantitative independent variable and both waveforms were assumed to have the common intercept represented by the control (sham shock) treatment. Significant voltage gradient × waveform interactions were used to indicate that waveform-specific regression coefficients were different as suggested by Piepho et al. (2006) for

Table 1. Results of general linear model analyses assessing the effects of voltage gradient (VG) and voltage gradient × waveform interaction on the survival of electroshocked common carp embryos during five stages of embryonic development. Only the interaction was included because the waveforms shared a y intercept (control or 0 volt group). No embryos survived the square wave electroshock during organogenesis, producing a large parameter estimate for the interaction.

Developmental stage	Effect	Coefficient	SE	P
Blastula	VG	−0.110	0.035	**0.003**
	VG × Waveform	−0.046	0.045	0.310
Gastrula	VG	−0.062	0.037	0.101
	VG × Waveform	−0.071	0.058	0.230
Organogenesis	VG	−0.372	0.052	**< 0.001**
	VG × Waveform	−1.833	272.9	0.995
Active Movement	VG	−0.230	0.036	**< 0.001**
	VG × Waveform	−0.179	0.087	**0.045**
Pigmentation	VG	−0.090	0.021	**< 0.001**
	VG × Waveform	−0.007	0.016	0.673

augmented factorial designs. Model simplification was achieved using *F*-tests based on analysis of deviance (Crawley 2007). All analyses were done in R (R Core Team 2015). The relative importance of each treatment combination (peak voltage gradient × waveform type × developmental stage) on the survival of electroshocked carp embryos were made by comparing the mean survival and 95% confidence intervals among treatment types. Confidence intervals for mean survival of each treatment combination were created with bootstrap resampling of replicates 1,000 times.

The lowest peak voltage gradient that resulted in a ≤ 50% survival was determined for each developmental stage, and was deemed a treatment that effectively kills carp embryos in subsequent analyses. This voltage gradient was used to calculate the power density applied to the water in the effective laboratory treatment using the equation $D_a = E^2\sigma$, where D_a is applied power density (in μW/cm^3), E is a peak voltage gradient (in V/cm), and σ is ambient water conductivity (in μS/cm). The applied power density actually transferred from the water to the embryos (D_m) in the effective laboratory treatment was calculated using an equation from Kolz (1989): $D_m = D_a\,[4q/(1+q)^2]$, where D_m is the power transferred to the embryo, and q is the ratio of ambient water conductivity and the immersion conductivity of fish embryo. The immersion conductivity of a fish is related to its cross-sectional area relative to the cross-sectional area of the water body it inhabits (Kolz 2006), and for simplicity 115 μS/cm is often used to represent this value for adult and juvenile fish (Miranda and Dolan 2003). Because fish embryos have smaller cross-sectional areas than juveniles and adults, a representative value at the lower end of the range of conductivities measured for adult fish was used (56 μS/cm; Miranda and Dolan 2003). The amount of applied power density, and accompanying voltage gradient, necessary to kill carp embryos under Malheur Lake conditions were calculated with the equation by holding constant the deadly power transfer value generated from the laboratory experiment and the immersion conductivity of the fish embryo while imputing values of ambient conductivities observed at the lake (< 100 μS/cm to 1000 μS/cm). Finally, we examined changes in efficiency with which power is transferred to embryos by observing how the reflection of applied power changes across lake conductivities, as represented by the difference between applied power and the power transferred to the fish embryo.

Results

Survival of common carp embryos was strongly related to developmental stage at electroshock. The mean survival of electroshocked carp embryos were relatively low in the four developmental stages before pigmentation (mean survival across all voltage gradients = 0–42%); however, at the pigmented stage carp embryos were much more resistant to electroshock (mean survival 37–50% at 25 V/cm; Figure 3).

The mean survival of electroshocked carp embryos was negatively related to voltage gradient across all developmental stages (P < 0.01; Table 1) except for at the gastrula stage. Mean embryo survival of controls for the first two developmental stages, blastula and gastrula, was relatively low (blastula = 40%, gastrula = 16%, Figure 3) and variable (range across replicates 0–80%). Survival during gastrulation was almost uniformly low, and low survival of the control group may have limited our ability to detect a statistically significant treatment effect at that stage. Mean embryo survival was below 50% at the lowest voltage gradient treatment, 10 V/cm, at all

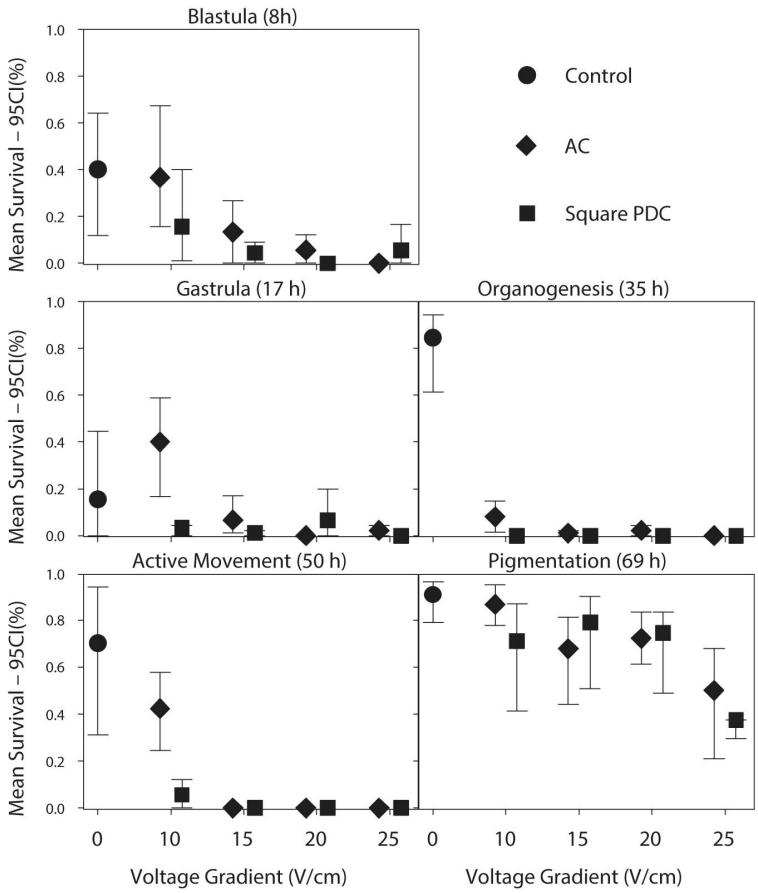

Figure 3. Mean survival (percentage ± 95 CI) of common carp embryos exposed to electrical treatments. Embryos were electroshocked using alternating current [AC] or square pulsed direct current [square PDC] at one of four peak voltage gradients (V/cm) or a sham exposure [control] across five developmental stages. Hours post-fertilization of the treatments are indicated next to name of each developmental stage.

developmental stages except pigmentation, where mean survival ranged from 71 – 87% (Figure 3).

The waveform-specific regression coefficients were only significant ($P < 0.05$; Table 1) at the active movement stage because of higher survival of embryos shocked with AC waveforms at 10 V/cm (Figure 3). The gastrula stage did not have significantly different waveform-specific coefficients despite visibly higher survival of AC electroshocked embryos at 10 V/cm, in part because of the low survival of controls. Otherwise survival was similar between waveform types across developmental stages (Figure 3).

In the laboratory experiment, mean survival of pre-pigmented carp embryos was ≤ 50% when 12,700 μW/cm^3 was applied to water collected from Malheur NWR (127 μS/cm at 10 V/cm), and much more power had to be applied to the same water to reduce the mean survival of pigmented carp embryos ≤ 50% (79,375 μW/cm^3). Under these conditions we calculated that a power transfer of 10,788 μW/cm^3 resulted in the death of pre-pigmented carp embryos, and a much higher power transfer of 67,427 μW/cm^3 was required to kill pigmented embryos.

The applied power density necessary to transfer enough power to kill carp embryos increased at an extremely high rate when ambient water conductivities fell below the immersion conductivity of embryos (Figure 4) due to the increase in voltage gradient that is required to maintain power transfer. When maintaining constant power transfer (D_m: 10,788 μW/cm^3, 67,427 μW/cm^3) to embryos in water with a conductivity greater than the immersion conductivity of the embryo, the power density required to be applied to the water increases almost linearly with increasing ambient conductivity (D_a, Figure 4). This is due to the increasing reflection of applied power away from the embryo at high water conductivities, as represented by the increasing difference between D_a and D_m. As a result, the efficiency with which applied power is transferred to the embryo becomes relatively poor (≤ 50%) at or above an ambient water conductivity of 325 μS/cm. As a result, the amount of applied power required to kill embryos at conductivities of 1000 μS/cm became extremely high (pre-pigmented = 53,706 μW/cm^3, pigmented = 335,671 μW/cm^3).

Discussion

Successfully controlling or removing invasive common carp may require deploying a variety of techniques that target different life stages (Brown and Walker 2004; Weber and Brown 2009; Bajer et al. 2015b; Lechelt and Bajer 2016). In situ experiments have shown that significant shifts from a clear water system to a turbid water system can occur at carp densities of 174–300 kg/ha, and that dramatic declines in aquatic vegetation cover can occur at densities of 100 kg/ha (Vilizzi et al. 2015). A negative relationship between the abundance of juvenile carp and adult carp has been observed (Weber and Brown 2013) and strong density-dependent controls on recruitment are often assumed in carp population models (e.g., Brown and Walker 2004; Lechelt and Bajer 2016; Pearson et al., unpublished). Gear used to capture and remove carp by most commercial netters targets adult fish, with the potential unintended consequences that a relaxation of density dependent recruitment processes can result in fast-growing juvenile carp that quickly replace the removed adult fish (Weber and Brown 2013), or that carp removal can result in compensatory survival (Weber et al. 2016). Simulations suggest efforts to control carp by direct removal may be more successful in shallow, productive lakes if they focus on removing multiple life stages (Brown and Walker 2004; Weber et al. 2011) or if adult removal is done in areas that experience recruitment bottlenecks (Lechelt and Bajer 2016), like where carp recruitment is regulated by fish that consume carp eggs and larvae (Bajer and Sorensen 2010; Bajer et al. 2012; Silbernagel and Sorensen 2013; Bajer et al. 2015a, b). As a result, integrated pest management that pairs commercial fishing with population control methods that also target spawning aggregations of carp or kill carp embryos and larvae could increase the likelihood of successful carp control, especially when such efforts target the reproductive source in populations exhibiting source-sink dynamics (e.g., Dauphinais et al. 2018). Simulation modeling of the carp population at Malheur Lake indicates that active control methods that concurrently target adults and embryos – or all life stages – were most likely to achieve a desired population reduction (Pearson et al., unpublished).

Using electrofishing to effectively kill embryos of invasive carp has been viewed as a questionable proposition (Nutile et al. 2013; Simpson et al. 2016). In part this is because the peak voltage gradients required to reduce survival below 50% in small pre-pigmented embryos can be relatively high compared to fish with larger embryos that are more sensitive to electroshock, like salmonids (Bohl et al. 2010; Gross et al. 2015;

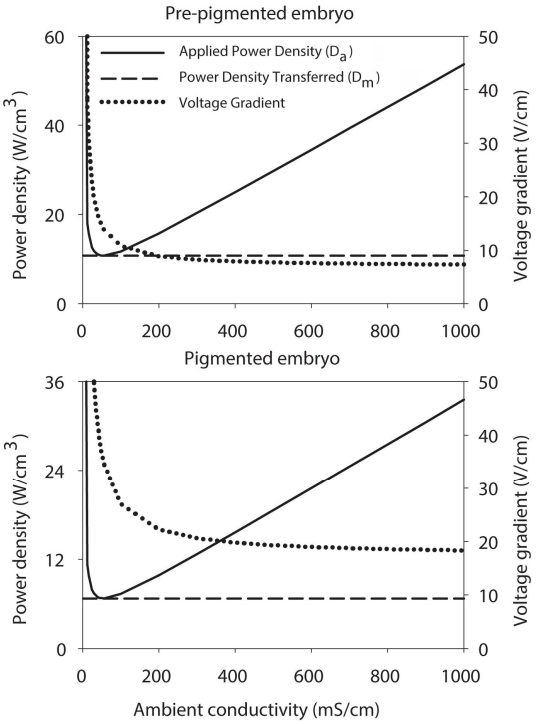

Figure 4. The applied power density (left axis, solid line) required to maintain the transfer of enough power to kill common carp embryos (left axis, dashed line) across water conductivities that could be observed at Malheur Lake, and the voltage gradient associated with those conditions (right axis, dotted line). Pre-pigmented embryos are depicted on the top pane, and pigmented embryos are depicted on the bottom pane.

Simpson et al. 2016). For instance, three other cyprinid species (e.g., zebrafish [*Danio rerio* Hamilton, 1822], goldfish [*Carassius auratus* Linnaeus, 1758], and fathead minnow [*Pimephales promelas* Rafinesque, 1820]) with relatively small embryo diameters like common carp (mean diameter 1.0–1.5 mm, Hsu and Goetz 1993; Bohl et al. 2010) were electroshocked using square PDC waveforms (60 Hz, 40% duty cycle) similar to those used in this study (60 Hz, 50% duty cycle), and voltage gradients of 16–24 V/cm were necessary to kill more than half of pre-pigmented embryos (Nutile et al. 2013). Killing the embryos of these cyprinids with electricity from commercial electrofishers might be difficult because voltage gradients of 16–20 V/cm have been measured within 5 cm of the anodes when shocking with traditional electrode configurations (e.g., Wisconsin ring and dropper type, Henry et al. 2003). In our laboratory experiment, carp embryos were killed within the range of voltage gradients (< 50% survival at 10 V/cm) produced by traditional electrode configurations and at voltage gradients too low to induce significant mortality in these other cyprinid species (Nutile et al.

2013), indicating it may be possible to adjust the output of commercially-available electrofishers to achieve a power transfer that will kill carp embryos. In fact, two novel mobile electrode arrays designed to kill lake trout (*Salvelinus namaycush* Walbaum, 1792) embryos have been able to reach voltage gradients of 10 V/cm over much larger areas (0.5–22.5 m^2) than traditional electrode array configurations (Henry et al. 2003; Brown et al. 2017), suggesting that such designs may help augment the performance of commercially-available electrofishing units. It is important to note that interpreting the effect of voltage gradients on the survival of fish embryos without considering water conductivity can be misleading because both factors influence the power transfer to an embryo (Reynolds 2015). Carp embryos in this study were shocked at lower water conductivities (127 µS/cm) than cyprinids in some other studies (e.g., Nutile et al. 2013 = 337–574 µS/cm), with the result that pre-pigmented carp embryos were killed at a much lower applied power density (mean at 10 V/cm = 12,700 $\mu W/cm^3$) than reported for other cyprinids (33,720–57,360 $\mu W/cm^3$, Nutile et al. 2013). We also estimated the amount of applied power necessary to kill carp embryos in situ by standardizing the power transfer that killed embryos in the laboratory experiment across potential water conductivities of Malheur Lake (Miranda 2005; Reynolds 2015). Fish embryos could be killed in situ by measuring the amount and distribution of power applied to the water by a boat electrofisher under a range of power settings, and then using the applied power goal calculated from the laboratory-generated standardized power transfer value to determine which settings would kill fish embryos (Miranda 2005; Reynolds 2015).

Power transfer theory suggests both relatively low and high water conductivities may be impediments to effectively killing fish embryos. Relatively little power is transferred to embryos at low water conductivities, especially when water conductivities are below the immersion conductivity of an embryo (assumed 56 µS/cm in our simulation). Furthermore, the transfer of applied power to the embryo becomes inefficient above ambient conductivities of 325 µS/cm due to almost linear increases in the reflection of power. In fact, embryos exposed to a constant voltage gradient may not experience great increases in mortality as water conductivities increase above 300 µS/cm (Gross et al. 2015), presumably due to this increasing reflection of the applied power away from the embryo (Kolz 1989). In addition it may become more difficult to achieve power transfer thresholds sufficient to kill small embryos without exceeding the power capabilities of commercially-available electrofishing equipment at higher lake conductivities. Therefore, deploying boat electrofishing to kill carp embryos in shallow productive lakes may be most efficient when water conductivities range between 56 and 325 µS/cm at important spawning locations.

The large variability in water volume and conductivity of terminal lakes can result in high water conductivities that may make electroshock control of embryos challenging. However, characteristic carp spawning behavior in combination with local water phenology and lake morphology may still provide conditions amendable to such electroshocking. Hydrologic conditions associated with carp spawning – such as rising water levels that flood low lying terrestrial vegetation (Swee and McCrimmon 1966) – or sites where rivers empty into lakes (Lougheed et al. 1998; Bonneau and Scarnecchia 2014) may be locations of seasonally low water conductivity. These situations may provide the most effective opportunity to kill fish embryos with electricity in arid endorheic environments. In the northern Great Basin of the western USA (which includes Malheur Lake), freshwater inputs are often driven by spring snowpack melt and climatic cycles that influence precipitation patterns (Grimm et al. 1997; Moore 2016). For example, the lowest lake conductivities in Malheur Lake are often found when a large spring snowmelt from Steens Mountain drives the lake level to its highest point (Hubbard 1975), and as a result a decrease in lake conductivities can coincide with carp spawning (typically in May). Under these conditions conductivities are relatively low in the lake's central basin where most river inputs drain (280–713 µS/cm), and are particularly low at the mouth of the Donner und Blitzen River where carp frequently spawn (Hubbard 1975). A trade-off may occur as higher lake levels create conditions that are more amenable to electroshock embryos, but spawning carp may become more dispersed which would make treatment more challenging. Annual differences in water conductivity and the distribution of aquatic vegetation available for carp spawning due to lake level fluctuations require a portable method to target embryos (Taylor et al. 2012). The flat topography and shallow water depth often characteristic of endorheic lakes may also aid in the electroshock control of fish embryos. Varied subsurface topography and large interstitial spaces in lake substrates may restrict the penetration of electric power to fish embryos, thereby decreasing the effectiveness of the electrical treatments (Brown et al. 2017). Uniformly shallow lakes with a homogenous substrate lacking interstitial spaces – like Malheur Lake and some other endorheic lakes – might present more suitable conditions for the use of electrofishing to control the

recruitment of invasive fish if deployed from low draft boats (e.g., airboat).

Application of any electroshock system used to kill embryos of nuisance fish requires an accounting of the rate of embryonic development and whether sensitivity to electroshock varies by developmental stage. Resistance of fish embryos to electroshock commonly peaks later in embryonic development for a variety of salmonid and cyprinid species (Godfrey 1957; Dwyer et al. 1993; Muth and Ruppert 1997; Henry and Grizzle 2004; Bohl et al. 2009; Simpson et al. 2016). Controlling carp recruitment with electroshock would likely require the treatment of embryos before they reach the last embryonic stage, pigmentation, at which ≤ 50% survival was only attained at a voltage gradient 25 V/cm under our test conditions (ambient conductivity = 127 µS/cm, mean temperature = 18.8 °C). The applied power density necessary to reach power transfer thresholds that kill embryos at the pigmentation stage in moderately conductive waters would likely exceed the power capacity of most electrofishing equipment. Carp embryos quickly became resistant to electroshock, reaching pigmentation in 69 hr of laboratory incubation (52 accumulated thermal units in °C). Carp in Malheur Lake generally spawn for two weeks, but the number of treatments required to control embryos would increase where spawning periods are more protracted. Furthermore, in settings where carp development is more rapid due to higher water temperatures (Silbernagel and Sorensen 2013), treatments would have to occur more frequently. In these situations the logistical challenges of using electrofishing to kill embryos could be significant. Whether it would be possible and practical to achieve meaningful control of carp recruitment in this context depends on a number of factors, including the spatial arrangement of spawning areas, whether spawning is synchronized across sites, and the size of the treatment area. The ability to predict carp spawning locations or anticipate where water conductivities would be suitable for electrofishing would help increase the effectiveness and reduce the cost of electrofishing as a control measure for carp. Developing habitat maps or predictive models of spawning locations based on climate forecasts and snowpack conditions might prove useful operationally (initial locations to target) and for planning (whether electrofishing should be attempted that year). Real time monitoring of carp spawning distributions with telemetry (i.e., the Judas technique, Taylor et al. 2012) could further improve operational efficiency.

Few proven methods currently exist to control carp recruitment besides dewatering or reducing access to spawning areas and poisoning spawning areas (Lennon and Berger 1970; Bonneau and Scarnecchia 2014), which may not be feasible in large lakes or those lakes without water control structures. Any potential tool under consideration for the control of fish recruitment (e.g., electrofishing, piscicide treatments, traps) can face a common set of challenges, such as how it would be implemented across a large geographic area and whether vulnerability would be influenced by the rapid development and somatic growth of carp embryos and juveniles. Our work illustrates that pre-pigmented carp embryos can be effectively killed at voltage gradients emitted by electrofishers in moderately conductive waters, and that adjusting the electrical output may reduce harm to non-target species during control efforts since the two electrical waveform treatments that effectively killed carp embryos may differ in their lethality to adult fish (Simpson et al. 2016). A firm understanding of the spawning ecology of the target carp population and water chemistry of the spawning habitat would be a prerequisite for an in situ test of electrofishing as a method to control recruitment. Population modeling that simulates the effect of killing different life stages of carp is also vitally important to determine the level of treatment required to achieve management objectives (e.g., Pearson et al., unpublished) and help evaluate the feasibility of implementation.

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