Electrofishing Power Requirements in Relation to Duty Cycle

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Abstract.—Under controlled laboratory conditions we measured the electrical peak power required to immobilize (i.e., narcotize or tetanize) fish of various species and sizes with duty cycles (i.e., percentage of time a field is energized) ranging from 1.5% to 100%. Electrofishing effectiveness was closely associated with duty cycle. Duty cycles of 10-50% required the least peak power to immobilize fish; peak power requirements increased gradually above 50% duty cycle and sharply below 10%. Small duty cycles can increase field strength by making possible higher instantaneous peak voltages that allow the threshold power needed to immobilize fish to radiate farther away from the electrodes. Therefore, operating within the 10-50% range of duty cycles would allow a larger radius of immobilization action than operating with higher duty cycles. This 10-50% range of duty cycles also coincided with some of the highest margins of difference between the electrical power required to narcotize and that required to tetanize fish. This observation is worthy of note because proper use of duty cycle could help reduce the mortality associated with tetany documented by some authors. Although electrofishing with intermediate duty cycles can potentially increase effectiveness of electrofishing, our results suggest that immobilization response is not fully accounted for by duty cycle because of a potential interaction between pulse frequency and duration that requires further investigation.

Electrofishing involves the conduction of electrical current between immersed metal electrodes having opposite polarities, thereby creating a voltage gradient, current density, and power density within a volume of water. The field size and strength surrounding the electrodes determine electrofishing effectiveness. Electrofishing fields are created by the dispersion of energy carried by electrical charge carriers around and between electrodes, resulting in heterogeneous fields, where strength is greatest next to the electrodes and rapidly dissipate as horizontal and vertical distance from the electrodes increases (Reynolds 1996). The actual field strength encountered by a fish is determined by the size of the electric field and the fish's position within the field.

Size and strength of an electrofishing field depends on the amount of electrical power that can be transmitted between electrodes, which in turn, hinges on water conductivity, electrode size and shape, electrode separation, and the voltage and current capabilities of the power source (Novotny 1990; Kolz 1993). Moreover, size and strength of an electrofishing field is influenced by the waveform delivered through the electrodes. Pulsing the delivery of DC helps increase field strength by producing large bursts of peak power that are of short duration and intercalated with recovery periods that allow the transformer and capacitor components time to store the energy required for the next burst (Novotny 1990). By releasing the stored energy in short bursts, pulsed DC (PDC) is capable of delivering higher voltage because the instantaneous power level is increased substantially above the mean power. Thus, pulsing DC can increase field size by allowing higher instantaneous peak voltages that allow the threshold power needed to immobilize fish to radiate farther away from the electrodes and, thus, an expanded radius of immobilization action. In addition to size and strength of an electric field, different waveforms may elicit diverse responses from the fish's nervous system (Lamarque 1990; Sharber and Black 1999) and thereby mediate the power required for immobilization.

Lamarque (1990) hypothesized that injury may result from severe muscle contractions during tetany. Tetany (fish immobilized, muscles rigid, and no breathing motions) is the last stage in a series of three general behavioral responses recognized in fish exposed to electroshock. It is preceded by narcosis (fish immobilized, muscles relaxed, still breathing), and fright (sporadic swimming). Some authors (e.g., Vibert 1967; Lamarque 1990) have suggested that injuries can be avoided if electrofishing equipment is operated at voltages that in-

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duce narcosis but not tetany. Our own observations indicate that tetanized fish exhibited higher mortality rates (Dolan and Miranda 2004, this issue). Unidentified factors other than tetany probably have a strong influence on incidence of injury and mortality, but operating equipment to produce power densities that induce narcosis rather than tetany may help reduce injury and mortality until the mechanisms for harm are better understood.

A diversity of DC pulses may be delivered by manipulating pulse duration (time on for one pulse) and frequency (pulses per time). Under controlled laboratory conditions, we measured the electrical power needed to immobilize (i.e., narcotize or tetanize) fish of various species and sizes with a selection of pulse frequencies and durations, and therefore duty cycles. The duty cycle indicates the percentage of time the electrofishing field is energized. Our objective was to identify those duty cycles that (1) required low peak power to immobilize fish, and (2) had a large margin of difference between the electrical power required to narcotize and that required to tetanize fish. Such duty cycles would tend to be most desirable for electrofishing because they would allow the maximum radius of immobilization action with the minimum amount of power and potentially produce the least injury.

Methods

Test equipment.-All testing was conducted indoors in a polyethylene tank, 2.0 m long, 0.5 m wide, and 1.0 m deep. The tank was filled to a depth of 10 cm with well water. The crosssectional profile of the tank was faced with two 1.6-cm-thick aluminum-plate electrodes positioned 65 cm apart and perpendicular to the longitudinal axis of the tank. These electrodes prevented possible distortion that would preclude a homogeneous electrical field. Electricity was supplied to the plates via a Smith-Root 15-D POW unit (Smith-Root, Inc., Washington) that was modified to allow continuous rather than discrete voltage control and was equipped with supplementary smoothing capacitors to eliminate spikes and reduce ripples at the peak of rectangular pulses (i.e., ripples averaged \pm 6% of the amplitude). Conditions within the tank produced a homogeneous electrical field with a constant voltage gradient. Specific conductivity (C_s ; μ S/cm) and ambient water temperature (T_w) were recorded with a YSI 30/ 10 FT meter (Yellow Springs Instruments, Ohio). The meter read C_s at specific temperature (T_s; 25°C). Ambient water conductivity (C_w) was estimated from C_x , T_x , and T_w (Reynolds 1996):

$$C_w = \frac{C_s}{1.02^{T_s - T_w}}.$$
 (1)

Electrical treatments and test fish.—Ten electrical treatments consisting of a wide range of pulse frequencies and duration were considered (Table 1). These pulse frequencies and durations were selected because they (1) represented settings throughout the range of adjustments commonly available in commercial electrofishing units, and (2) encompassed a wide range of duty cycles. Peak voltage (V_{pk}), pulse frequency, and pulse duration were measured within the energized field with a Tektronix THS720A oscilloscope (Tektronix, Inc., Oregon). Following Kolz and Reynolds (1989), V_{pk} was used to calculate power density (Pd; μ W/ cm³) in the water:

$$Pd = C_{w} \left(\frac{V_{pk}}{\hbar}\right)^{2}.$$
 (2)

Distance between electrodes (h) was 65 cm, except when treating the two smallest species with PDC 15 Hz,1ms, when it became necessary to reduce hto 48 cm to increase Pd. Duty cycle was computed as the product of pulse duration (ms) and pulse frequency (Hz) divided by 1,000 and expressed as a percentage.

We applied the 10 electrical treatments to various sizes of eight fish species selected because they represented a wide range of sizes and shapes and were readily available from local fish culture facilities and streams (Table 1). However, limited fish availability did not allow application of all electrical treatments to a balanced combination of species and sizes. Before testing, fish were seined from culture ponds or from local streams; held in concrete raceways or polyethylene circular tanks for at least 2 weeks; and maintained in good condition on a diet of live or prepared food, depending on the species. During testing, fish were indiscriminately dipped from the holding tank, transferred one at a time to the test tank and confined in the area between the two electrodes. After allowing 3-10 s for the fish to orient and when the fish was positioned perpendicular to the electrodes, the current was switched on for 15 s. As individuals, fish were treated only once and to a single voltage, but as a group, fish were exposed to voltages incrementing from near zero to the highest levels allowed by our equipment. Two thresholds were identified: (1) status at 3 s, recorded as 0 for TABLE 1.—Electrical treatments (DC and pulsed DC [PDC]), duty cycles, species, and sizes included in this evaluation. The first number in parentheses represents the mean total length (mm) and the second number is the sample size. In all, 1,796 fish were included.

Treatment number	Pulse frequency (Hz)	Pulse duration (ms)	Duty cycle (%)	Test species	Total volume (cm ³)
				Channel catfish	
DC	None ^a	None ^a	100	Ictalurus punctatus	4(56,32), 31(163,22), 303(311,31), 312(313,21), 318(317,17)
				Bluegill	
				Lepomis macrochirus Largemouth bass	12(67,26), 109(159,23)
				Micropterus salmoides	6(73,34), 189(221,22)
				Morone hybrid ^b	101(180,34)
				Black crappie	
				Pomoxis nigromaculatus	83(155,28)
PDC110-6	110	6	66	Channel catfish	5(69,32), 31(160,25), 309(311,25)
				Bluegill	12(68,28), 104(156,23)
				Largemouth bass	6(75,30), 186(220,21)
				<i>Morone</i> hybrid ^b	96(175,25)
				Bluntnose minnow	
				Pimephales notatus	2(55,32)
				Black crappie	70(142,29)
PDC110-1	110	1	11	Channel catfish	4(57,36), 32(166,22), 303(310,34),
					336(327,17)
				Bluegill	12(68,27), 118(168,25)
				Largemouth bass	6(72,30), 166(207,21)
				Morone hybrid ^b	96(174,28)
				Bluntnose minnow	2(57,30)
	(1)		24	Black crappie	77(151,21)
PDC60-6	60	6	36	Channel cathsh	31(158,25)
				Bluegill	12(67,30)
	60	,	6	Changemouth bass	4(02,30)
FDC00-1	00	1	0	Channel Callish Dhuasill	51(101,21), 505(510,22), 507(512,20)
				L argemouth base	12(09,50)
				Plack grappie	4(U2,20) 93(155-25)
PDC30-1	30	1	3	Channel antfish	306(312,25)
PDC20-1	20	1	2	Channel catfish	303(310.24)
PDC15-6	20	6	0	Channel catfish	4(63.31) - 30(159.21) - 310(313.28)
IDC15-0	12	U	,	Bluegill	12(68,36) - 93(148,25)
				Largemouth bass	6(75, 34) = 197(222, 22)
				Morone hybrid ⁶	100(176.28)
				Bluntnose minnow	2(61.32)
				Black Crannie	86(159.26)
				Creek chub	
				Semotilus atromaculatus	4(63,31)
PDC15-4	15	4	6	Black crappie	87(158.25)
				Redfin darter	
PDC15-1	15	1	1.5	Etheostoma whipplei	3(53,30)
				Channel catfish	5(67,30), 31(164,27), 305(311,31), 330(328,22)
				Bluevill	12(68.31) - 104(157.20)
				Largemouth bass	6(75.43), 189(215.21)
				Black crappie	85(157.33)
				Creek chub	4(62,34)
				·····	······································

 $^{\rm a}\,{\rm DC}$ is on continuously.

^b White bass *M. chrysops* \times striped bass *M. saxatilis*.

no immobilization or 1 for immobilization; and (2) status at 15 s, recorded as 0 for no discernable effect, fright, or narcosis, or 1 for tetanus. The 3-s period estimated the time within which, if the fish was not immobilized, it would probably escape the electrical field. The immobilization re-

sponse represented either narcosis or tetany, but the real status was unknown because the field remained energized for another 12 s. The 15-s period estimated the maximum amount of time that a fish would be exposed to electricity in an actual field setting, and after the field was deenergized, it was

TABLE 2.—Regression models descriptive of the power that was transferred into the study fish (Pt_{0.95}) to narcotize them within 3 s or tetanize them within 15 s. The parameters correspond to the model log₁₀ Pt_{0.95} = $\beta_0 + \beta_1 \log_{10}$, $D_i + \beta_2 \log_{10}$, $D^2_i + \beta_3 \log_{10}$, V_j , where D = duty cycle (%) and V = fish volume (cm³). All parameters were significantly different from zero at $P \le 0.01$. Standard errors are given in parentheses. For each model N = 66 and df = 62.

	Immobilization status at			
Parameter	3 s	15 s		
β0	5.451 (0.205)	5.234 (0.173)		
βı	-3.636 (0.338)	-3.230 (0.526)		
Bo	1.265 (0.146)	1.268 (0.153)		
βī	-0.513 (0.071)	-0.428 (0.106)		
F	70.64	45.61		
\mathbb{R}^2	0.78	0.72		

 $(F_{1, 61} = 2.09, P = 0.14)$ and not significant for the 15-s model $(F_{1, 61} = 0.12, P = 0.71)$; thus, they were excluded from the final models.

The coefficients of determination ($R^2 = 0.78$ and 0.72) indicated the models adequately described the effect of duty cycle on power requirements while accounting for fish size. Nevertheless, for both models, a plot of the residuals against duty cycle and volume revealed a possible lack of fit, wherein residuals for PDC 15 Hz, 4 ms and PDC15 HZ, 6 ms tended to be higher than zero and residuals for PDC 60 Hz, 1 ms tended to be less than zero. This lack of fit would cause the models to overestimate the power requirements for PDC 60 Hz, 1 ms and underestimate the power requirements for PDC 60 Hz, 4 ms and PDC 15 Hz, 6 ms.

The $Pt_{0.95}$ required to tetanize fish within 15 s was generally higher than that needed to immobilize fish within 3 s. Nevertheless, the margin of difference between the two power values changed relative to duty cycle. For some low duty-cycle treatments, fish could not be immobilized within 3 s without tetanizing them by the end of the 15-s period. Conversely, for high duty-cycle treatments there was a wider margin of power requirements between immobilized within 3 s remained only narcotized by the end of the 15-s period. This effect is illustrated by a plot of the two models (Figure 2).

Discussion

Although our tank experiments controlled for many sources of variability commonly associated with field electrofishing, some estimation errors could not be avoided. We strived to maintain am-



FIGURE 2.—Relationship between duty cycle and power transferred to immobilize 95% of fish (Pt_{0.95}) within 3 s or tetanize them within 15 s. Curves, derived with the equations in Table 2, were based on D = 1.5-100%and V = 10 and 300 cm³. The figure illustrates how, for fish of a given size, the margin of difference in power needed to immobilize within 3 s or tetanize within 15 s increases directly with duty cycle. Thus, immobilization of fish using low duty cycles is more likely to produce tetany.

bient conditions as constant as practicable, but variability in water temperature had to be accepted owing to the seasonal availability of test fish. The 10°C range of experimental temperatures, which possibly influenced effective fish conductivity and reaction thresholds, could have introduced variability. Furthermore, identification of the immobilization threshold relied on an observer's ability to discern the moment fish were immobilized. As duty cycle decreased, fish exhibited a vigorous forced swimming behavior that sometimes made it hard to assert whether the fish had been immobilized within 3 s, even after reviewing recorded videos. Despite these inaccuracies, error around our explanatory model, which included both experimental error as well as model lack of fit, was relatively small.

The lack of fit appeared to be contributed mainly by the PDC 15 Hz, 4 ms and PDC 15 Hz, 6 ms treatments. Residual analyses showed that the power needed to immobilize fish with these low pulse frequencies was greater than that required by higher frequency treatments of similar duty cycles. This discrepancy suggests that immobilization response is not fully accounted for by duty cycle but is also affected by a potential interaction between pulse frequency and pulse duration. We were unable to further examine this effect because of the unbalanced nature of our treatment combinations. Nevertheless, this lack of fit was trivial in the context of our conclusions about duty cycles that maximize radius of immobilization action and minimize power requirements.

In addition to the effect of duty cycle, our descriptive models identified a lack of species effect and a strong size effect. The absence of a species effect possibly reflects the overwhelming importance of fish size. Dolan and Miranda (2003) suggested that although some species differences could be expected because of differences in fish conductivity, most of the variability in immobilization response is attributed to fish size.

Power densities needed to immobilize fish within 3 s and tetanize them within 15 s decreased with increases in fish size and duty cycle but increased rapidly at duty cycles lower than about 10%. Similarly, Lamarque (1967) reported that varying the pulse duration of a fixed 100 Hz waveform resulted in an increase in the threshold of anodic taxis only when duty cycles were less than 10%. Novotny and Priegel (1974) indicated that 25% and 50% duty cycles produced similar results and that a 10% duty cycle was less effective. Kolz and Reynolds (1989) reported a decrease in the power density required to immobilize 6-9-cm goldfish Carassius auratus as they varied duty cycle from 100% to 10%, but they did not consider duty cycles lower than 10%. Given our results and those reported by other authors, effectiveness of electrofishing can be maximized with duty cycles between 10% and 50%. Such a strategy would allow an increase in the radius of immobilization action by operating with duty cycles that allow higher peak power to be transmitted further away from the electrodes and requiring less peak power to immobilize fish. The increase in the radius of action is a result of pulsing the delivery of DC, which by generating higher instantaneous peak voltages, allow the threshold power needed to immobilize fish to radiate with higher strength farther away from the electrodes (Novotny 1990; Reynolds 1996). The decreased peak power requirements at intermediate duty cycles reflect changes in response to different electrical stimuli by the fish's nervous system, but the mechanisms are not well understood and are currently being debated in the literature (Lamarque 1990; Sharber et al. 1995; Sharber and Black 1999).

Stream electrofishing equipment sometimes re-

lies on battery-powered electrofishers. Because battery power is limited and battery life is finite, use of intermediate duty cycles would increase the time between battery charges in backpack electrofishing units. Beaumont et al. (2000) reported that battery longevity in their backpack equipment was extended tenfold by reducing the pulsed duration of PDC 60 Hz from 6 ms (duty cycle = 36%) to 0.5 ms (duty cycle = 3%), and extended threefold when a gated burst with 30 Hz and 0.9 ms (duty cycle = 2.7%) was applied.

Although power requirements and capture efficiency are important considerations in selecting waveforms for electrofishing, increased taxis (attraction towards the anode or positive electrode) and thrashing can influence the choice of waveform. Reynolds (1996) commented that continuous DC can induce taxis, given appropriate thresholds were reached, but the taxis responses to PDC were less predictable. In our tests, we noted that the continuous DC treatment caused fish to exhibit forced swimming towards the anode before being immobilized within 3 s. This attraction occurred immediately upon electrification of the field and was highly conspicuous in some species, although it occurred in all species and sizes treated with continuous DC. However, at high levels of DC, fish were immobilized instantly once the field was electrified, displaying no obvious forced swimming towards the anode. Attraction towards the anode was observed in a few fish treated with PDC but was not as striking as with continuous DC. The high power levels required for immobilizing fish with low duty cycles tended to encourage forced swimming and thrashing rather than immobilization. This observation is consistent with those made by Corcoran (1979) and Gilliland (1988) who reported that low duty cycles made ictalurids easier to detect, because of thrashing, but that collection often required a chase boat because fish were not immobilized.

A central finding of our study was the changing margin of difference between the amount of electrical power required to tetanize fish within 15 s and that required to immobilize them within 3 s. At high duty cycles, there was a large margin of difference so that power could be applied in a way that it immobilized fish within 3 s and produced only narcosis within 15 s, allowing the fish to resume swimming when power was deactivated. Contrastingly, at low duty cycles the margin of difference decreased to the extent that the power needed to immobilize fish within 3 s would almost inevitably produce tetany within 15 s. Higher levels of injury and mortality have been reported for fish that are tetanized by electrofishing (Lamarque 1990; Reynolds 1996; Dolan and Miranda 2004). Thus, electrofishing with intermediate to high duty cycles can potentially reduce harm to fish by providing improved ability to avoid tetany. Nevertheless, injury and mortality are not fully accounted for by tetany, and sources of injury are not fully understood.

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possible to determine whether the fish was tetanized. As many as 18–35 fish were used per treatment, depending on ease of identifying the thresholds. The reactions of each fish were observed and recorded, as well as video-taped via a camera positioned over the tank to allow review of responses and verify the accuracy of live observations.

Estimation of thresholds.—Field strength has traditionally been described as voltage gradient, current density, or power density (voltage gradient \times current density). More recently, Kolz (1989) suggested that the success of electrofishing depends on the fraction of the power density that is transferred to the fish. The power-transfer model has been shown to reduce variability of survey data (Burkhardt and Gutreuter 1995) and to adequately predict power levels required to immobilize fish over a wide range of water conductivities (Kolz and Reynolds 1989; Miranda and Dolan 2003).

For each electrical waveform, species, and size combination the dependent 3-s binary immobilization response y (0 or 1) recorded for each fish was regressed on the independent variable Pd applied to each fish by using the logistic regression model

$$logit(y) = \beta_0 + \beta_1 \log_e Pd, \qquad (3)$$

where β_0 represents the intercept parameter, and β_1 the slope parameter for $\log_e Pd$. After regression, the logit(y) was transformed to the probability P(y) by rearranging equation (3):

$$P(y) = \frac{e^{\beta_0 + \beta_1 \log_e \mathrm{Pd}}}{1 + e^{\beta_0 + \beta_1 \log_e \mathrm{Pd}}}.$$
 (4)

The applied Pd that results in a P(y) = 0.95 is the predicted Pd_{0.95}, which was used to estimate the peak power transferred into the fish (Pt_{0.95}; μ W/cm³):

$$Pt_{0.95} = Pd_{0.95} \frac{4\frac{C_f}{C_w}}{\left[1 + \frac{C_f}{C_w}\right]^2},$$
 (5)

where C_f is the estimated "effective conductivity" (Kolz and Reynolds 1989) and the quotient is the inverse of the multiplier for constant power (Kolz 1989). We fixed C_f at 115 µS/cm, as suggested by Miranda and Dolan (2003). This process was repeated to estimate the dependent 15-s binary tetanus response. The difference between these curves may be interpreted as the additional peak power required to advance narcosis to tetany or,

alternatively, the margin of error within which tetany may be avoided. In this manner, we obtained 66 estimates of the $Pt_{0.95}$ required to induce immobilization within 3 s, and 66 estimates of the $Pt_{0.95}$ required to induce tetany within 15 s. Each of these estimates required 18–35 fish. The 66 values corresponded to the 66 treatments, species, and size combinations identified in Table 1.

Effect of duty cycle.—The effects of pulse duration and frequency on power required to immobilize fish within 3 s and tetanize them within 15 s were examined by plotting $Pt_{0.95}$ against duty cycle. To account for potential differences in fish species and size that affect power requirements, fish species (S) and volume (V) were included in a model designed to assess the effect of duty cycle (D):

$$\log_{10} Pt_{0.95} = \beta_0 + \beta_1 \log_{10} D_i + \beta_2 \log_{10} D^2 i + \beta_3 \log_{10} V_j + \beta_k S,$$
(6)

where β_0 represented the model's intercept parameter, β_1 and β_2 are the slope parameters for the effect of the *i*th duty cycle, β_3 is the slope parameter for fish volume, and β_k is the effect of the kth species. Logarithmic transformations of Pt_{0.95} and V_i were needed to homogenize variances and linearize relationships, and transformation of D_i was needed to correct a skewed relationship and allow proper application of the quadratic model. Equation (6) was fit twice. In the first fit $Pt_{0.95}$ was the power required to trigger narcosis within 3 s; in the second fit $Pt_{0.95}$ was the power required to trigger tetany within 15 s. We used fish volume to index size because we had previously identified it as the size descriptor best related to the level of peak power required to immobilize fish (Dolan and Miranda 2003). Interactions among main effects were also tested. The logarithmic transformation was needed to properly fit a linear model to the relation between fish volume and $Pt_{0.95}$, and a second-degree polynomial, U-shaped model to the relation between duty cycle and Pt_{0.95}. Adequacy of the models was judged by the magnitude of the R^2 value and by inspecting residual plots.

Results

In all, 1.796 fish were included in these tests, ranging in mean total length from 53 to 328 mm (overall mean = 159 mm) and in volume from 2 to 336 cm³ (overall mean = 103 cm³). Water temperatures at which fish were held and tested ranged from $17-27^{\circ}$ C (mean = 23°C). Specific conductivity was relatively invariable at 195 ± 4 µS/cm

throughout the study. However, due to fluctuations in ambient water temperature, ambient water conductivity (equation 1) ranged from 176 to 201 μ S/ cm. Peak voltages applied in these water conditions ranged from 12 to 1,100 V, and peak power densities ranged from 7 to 147,500 μ W/cm³.

Estimates of $Pt_{0.95}$ required to immobilize fish within 3 s ranged from over 88,000 μ W/cm³ for the small-bodied redfin darter with 1.5% duty cycle to less than 50 μ W/cm³ for large-bodied fish of several species treated with 11–66% duty cycle (Figure 1). For the 3-s immobilization and 15-s tetanus thresholds, a significant U-shaped relation between $Pt_{0.95}$ and duty cycle (Table 2) indicated that power requirements were lowest at intermediate duty cycles between 10% and 50%. The models for the two thresholds identified no significant species effect, but a significant effect of fish volume suggested that any species differences were potentially overshadowed by the effect of fish size. The interaction between fish volume and duty cycle was marginally significant for the 3-s model



FIGURE 1.—Relationship between peak power transferred to immobilize 95% of fish within 3 s ($Pt_{0.95}$; μ W/cm³) and duty cycle (N = 66). Differences in circle sizes denote relative differences in the log of fish volume. The labels next to the dashed vertical lines identify the treatments listed in Table 1 and their corresponding duty cycles. For duty cycle = 6, the shaded circles represent pulsed DC of 60 Hz, 1 ms, and the unshaded circles represent pulsed DC of 15 Hz, 4 ms. The dashed curve denotes $Pt_{0.95}$ in relation to duty cycle at a fish volume of 100 cm³.