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True Electrotaxis and Threshold Voltages in the American Crayfish *Procambarus clarkii*

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Abstract: Experiments were conducted to obtain detailed information on the behavioral responses of American crayfish, *Procambarus clarkii* to DC electric stimuli in the form of voltage gradients. Four different arrangements of electrodes producing different electric fields were tested in both indoor and outdoor tanks. The electrical intensity used was varied from 0.02 to 0.46 V cm⁻¹. We determined two threshold voltages: threshold voltage I, which induced parallel orientation of the animal to the electric field and forward crawling toward the anode (0.04-0.10 V cm⁻¹) and threshold voltage II, which induced flicking of the tail and backward swimming toward the anode (0.12-0.16 V cm⁻¹). The crayfish that displayed true electrotaxis moved to the anode when stimulated within the space enclosed by the electrodes. However, when the electrodes were elevated 5 or 10 cm off the bottom of the tank, the crayfish moved to the anode, crawled through the gap beyond it and out of the electric field. This movement beyond the anode cannot be explained by positive electrotaxis, but it can be interpreted as repulsion from the cathode. Anodal movement was most effective at 0.24-0.30 V cm⁻¹ in the indoor tank and from 0.16-0.24 V cm⁻¹ in the outdoor tank. The crayfish suffered electronarcosis when stimulated at 0.32-0.46 V cm⁻¹ in the indoor tank and at 0.28-0.46 V cm⁻¹ in the outdoor tank. They recovered from narcosis several minutes after the electric current was switched off. Thus, crayfish can be herded into a trap or net when stimulated by direct current of 0.24-0.30 V cm⁻¹, taking care not to induce electronarcosis.

Key words: American crayfish, *Procambarus clarkii*, electrotaxis, electronarcosis, threshold voltage, anodal movement

INTRODUCTION

In Japan, the introduction of exotic species such as the American crayfish *Procambarus clarkii* as live feed for the edible frog *Rana catesbeiana* that was cultivated in rice fields has had adverse ecological effects on the Japanese crayfish *Cambaroides japonicus* by competing with them for habitat, shelters and resources (Saito and Hiruta, 1995; Usio *et al.*, 2001; Nakata *et al.*, 2006) and has caused economic losses to rice farmers by damaging the crop and the dikes in paddy fields. In order to remove this exotic species, an effective low-cost harvesting method is needed.

At the same time, a new harvesting method is needed by the crayfish aquaculture industry. The crayfish after all is an important aquaculture commodity in many countries, though not in Japan and supports a large industry in Louisiana, USA. Currently, crayfish are harvested by professional trappers who receive about half of the gross revenue, but there are not enough trappers during the peak

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harvest season (Cain and Avault, 1983; Huner and Barr, 1991; Romaine, 1995). The baits used for the traps are expensive, need freezing and must be cut into small pieces. Another problem is that low temperatures reduce the activity of the crayfish and they are no longer attracted to the baits.

The shrimp industry in Japan has developed a variety of electric shockers, one of which is attached to a drag net that is pulled over the pond bottom and forces shrimp to leap out of the sand substrate and into the net (Shigueno, 1975). Similar methods have been used in other crustacean fisheries (Pease and Seidel, 1967; Ko *et al.*, 1972; Salia and Williams, 1972; Stewart, 1975; Seidel and Watson, 1978; Fievet *et al.*, 1996; Polet *et al.*, 2005). All these methods relied on electric stimulation of the shrimp's body that results in a strong contraction of the abdomen and forces the shrimp out of the burrow or hiding place and into a net. Researchers in Louisiana developed a prototype electric push net as an alternative harvesting method for crayfish (Cain and Avault, 1983) but there are no reports on its commercial use. Electricity has been used to control the movement of diseased crayfish *Aphanomys astaci* in Sweden or Arizona, to exclude them from certain areas by means of electrical barriers (Unestam *et al.*, 1972; Soderhall *et al.*, 1977; Hyatt, 2004). Electrofishing is also being used as a removal method for the possible eradication of the American signal crayfish *Pacifastacus leniusculus* from rivers (Sinclair and Ribbens, 1999; Reeve, 2004).

A direct electric current (DC) is a preferred type of current because it has the least potential to harm individual fish (Lamarque, 1990; Beaumont *et al.*, 2002; Snyder, 2003). When exposed to a DC current, fish tend to assume a position parallel to the electric field, with their heads pointing toward the anode and swim in the direction of that electrode; this behavior is known as electrotaxis or galvanotaxis and is used to catch fish (Bary, 1956; Klima, 1972; Lamarque, 1990).

Some crustaceans also exhibit similar directional responses in a DC field. A strong electrical stimulation causes the contraction of the abdominal muscles of crustaceans and this involuntary movement forces the animal either up off the bottom, or in the direction of the anode. Higman (1956) showed that pink grooved shrimp *Penaeus duorarum* in a seawater tank flicked their tails toward the anode when subjected to an electrical field of pulsed DC. Westman *et al.* (1978) conducted sampling for the European crayfish *Astacus astacus* by means of non-pulsating DC and reported that the crayfish moved toward the anode by either swimming backward with rapid tail flicks, or by crawling slowly forward out of their hiding places. The Australian spiny lobster *Panulirus cygnus* was sensitive to the polarity of the electric field and either faced or propelled itself towards the anode (Philips and Scolari, 1980). The American lobster *Homarus americanus* exhibited true electrotaxis in a pulsed DC electric field, where it was compelled to swim to the anode (Koeller and Crowell, 1998). The brown shrimp *Crangon crangon* reacts strongly to the anode of pulsed DC (Polet *et al.*, 2005).

However, Saila and Williams (1972) observed no electrotaxis but only tail flick in the American lobster subjected to DC. In the Norway lobster *Nephrops norvegicus*, an electric field induced avoidance behaviour but no electrotaxis (Stewart, 1974; Newland and Neil, 1990). Thus electrotaxis in crustaceans is still questionable and the different results may have been due to the different arrangements of the electrodes in the various experimental designs.

We conducted this study to obtain detailed information on the behavioral responses of the American crayfish to various DC electric stimuli, which could be applied to develop economical harvesting and eradication methods for this species.

MATERIALS AND METHODS

Animals

For the indoor experiment, 10 American crayfish (42-48 mm carapace length and 85-98 mm body length), were obtained from a local supplier. They were kept in a 240 L PVC tank with tap water and an undergravel filter at 28°C and fed twice a week with crayfish pellets (Japan Pet Drugs, Tokyo).

For the outdoor experiment, five laboratory-reared crayfish (34-37 mm carapace length and 72-87 mm body length) were used. Individuals were used repeatedly within the same experiment. The crayfish were handled according to methods prescribed by the Kagoshima University's Guide for the Care and Use of Laboratory Animals.

Apparatus for Indoor Experiment

The indoor experiment was done at the Laboratory of Fishing Technology, Faculty of Fisheries, Kagoshima University during June-July 2005. A polyvinyl chloride (PVC) tank (190×42×40 cm) was used with a sand substrate bottom (2.5 cm thick) and an undergravel filter system (Nisso, Tokyo) and filled with 240 L of tap water (30 cm deep) (Fig. 1A). The tank was divided into five equal zones (each zone 38×42×40 cm): anode zone, middle zone, cathode zone and both end zones beyond the electric fields (Fig. 1). Water temperature during the experiments was 28.0°C and the conductivity of water was 625 $\mu\text{S cm}^{-1}$ determined with a conductivity meter (YSI-85, YSI Inc., USA).

Two types of electrodes were adopted: large stainless steel plate electrodes (40 cm wide, 30 cm high, 1.0 mm thick) and small ones (20 cm wide, 18 cm high, 0.8 mm thick). In the first experiment, the two large electrodes, an anode and a cathode, were placed in the tank, upright on the bottom 114 cm apart and completely partitioning its long axis by placing two PVC partitions (arrangement E1, Fig. 1). Movements of the crayfish were restricted within the space between the electrodes. In the second and third experiments, the large electrodes were raised 5 cm or 10 cm above the bottom (E2 and E3). In the fourth experiment, the small electrodes were placed upright on the bottom (E4). Since there were gaps, the crayfish were able to go out of the electric field beyond the electrodes.

The DC electric stimulus was produced by a specially made electric converter-stimulator (Hitachi, Tokyo). By adjusting the voltage of the electric converter-stimulator, the voltage gradient

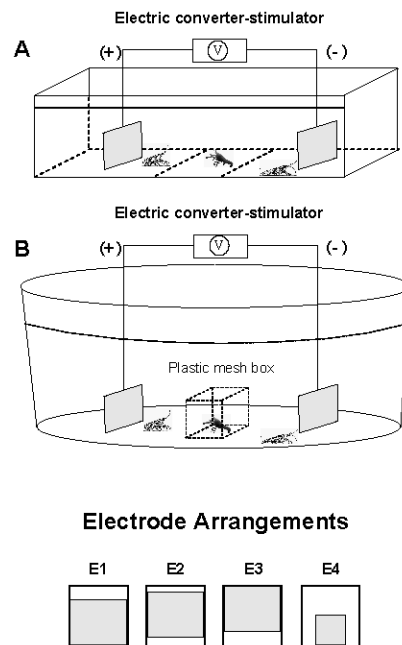


Fig. 1: Experimental apparatus for indoor (A) and outdoor (B) experiments and electrode arrangements. E1, electrodes placed standing on the bottom, no gaps from the tank walls; E2, electrodes 5 cm above the bottom; E3, electrodes 10 cm above the bottom; E4, small electrodes placed standing on the bottom with gaps from the walls

applied on the crayfish was varied from 0.02 to 0.46 V cm⁻¹. Voltage gradients were created by alternately reversing the polarity of the electrodes. The electric field intensity was measured with an electric tester (Custom Corp. CDM-2000D, Tokyo) throughout the tank to determine the voltage gradients at different locations. The signal was displayed on an oscilloscope (Iwatsu SS-5704, Tokyo) for accurate measurements. The electrodes were periodically cleaned to prevent measurement error caused by the gas bubbles on their surfaces.

Figure 2 shows the electric field intensities in the experimental tanks, especially between electrodes arrangement E3 and E4. A uniform electrical field intensity was present in the E1

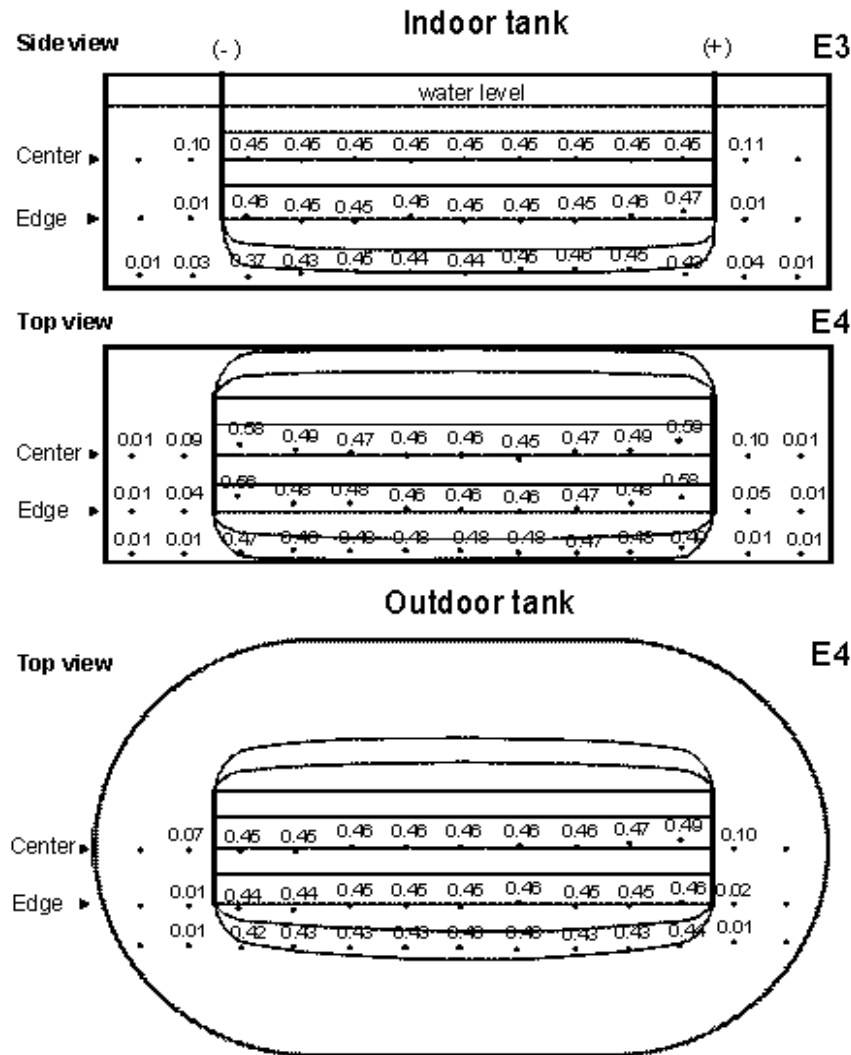


Fig. 2: Electric field intensities measured in the indoor tank with electrode arrangements E3 (side view) and E4 (top view). Electric field intensities in the outdoor tank with electrode arrangement E4 (top view)

arrangement (0.46 V cm^{-1}). In the E2 arrangement, the intensity at the 5 cm gap off the bottom was 0.46 V cm^{-1} , equal to that at the center between the electrodes. In E3, the intensity was 0.44 V cm^{-1} at the gap 10 cm off the bottom. With the small electrodes in E4, the intensities at the lower part of the electrodes (0.49 V cm^{-1}) and close to the tank walls (0.48 V cm^{-1}) were higher than at the center between the electrodes (0.46 V cm^{-1}). A small electric field was detected behind the electrodes but it was near zero, with the wave forms on the oscilloscope fluctuating between 0.01 and 0.09 Volts.

Experiment, Data Collection and Analysis

The crayfish were exposed to electric stimuli in the form of voltage gradients at intensities ranging from 0.02 to 0.46 V cm^{-1} . The group of 10 crayfish was used in every trial and 5 trials were done at each voltage gradient intensity. The total number of trials at different voltage gradients was 115. The animals were given time to recover after each trial: 2 min after trials with $0.02\text{-}0.10 \text{ V cm}^{-1}$; 3 min after $0.12\text{-}0.20 \text{ V cm}^{-1}$; 4 min after $0.22\text{-}0.30 \text{ V cm}^{-1}$ and 5 min after $0.32\text{-}0.46 \text{ V cm}^{-1}$.

Before each trial, the crayfish were confined in the middle zone of the tank by means of two PVC partitions. At the start of each trial was the control period, when the partitions were removed and the crayfish were allowed to move freely for 1 min. Then the partitions were put back in place and the crayfish confined again in the middle zone. The test consisted of removing the partitions and applying the voltage gradient for 1 min. During the control and test periods, the movements and numbers of crayfish were carefully noted every 15 sec in the three zones in arrangement E1, or five zones in E2, E3 and E4.

Any movement of a crayfish toward the anode upon stimulation was considered a *positive response*, whether or not the crayfish reached the anode within the 1 min test period. For quantitative analysis of the response to the electric field, the magnitude of anodal group response (%) was defined for each trial by the following formula:

$$\text{Magnitude of anodal group response (\%)} = \frac{\text{No. of crayfish with positive response}}{\text{Crayfish in test}} \times 100$$

The percent values for 5 trials at each voltage gradient were compared statistically with the percent values for the controls by the Mann-Whitney test (Conover, 1980). When the test values were significantly higher than the control value, the group response was considered positive.

Outdoor Experiment

An outdoor experiment was conducted outside the laboratory on February 2007 in a fiber-reinforced plastic oval tank ($214 \times 169 \text{ cm}$; Tanaka-Sanjiro, Fukuoka, Japan) with 1,700 L tap water (47 cm deep) and a 1.5 cm deep sand bottom (Fig. 1B). Due to the low water temperature, an electric heater (Nisso, Tokyo) was used. Water temperature during experiments varied from $12.5\text{-}17.0^\circ\text{C}$ and the water conductivity was $80\text{-}160 \mu\text{S cm}^{-1}$. The electrodes and electrical apparatus were the same as in the indoor experiment.

The average electric field intensities between the large electrodes (E1 and E2) were the same as in the indoor tank. Between the small electrodes (Fig. 2-E4), intensities were 0.46 V cm^{-1} at the center, 0.45 V cm^{-1} at 10 cm from the edge and 0.43 V cm^{-1} beyond the electrodes.

Before the electric stimulation, the crayfish were confined in a plastic mesh box at the middle zone of the tank. The control, test exposure, data collection and analysis were carried out the same way as in the indoor experiment.

Definition of Threshold

We determined two threshold voltages: threshold voltage I, which induced parallel orientation of the animal to the electric field and forward crawling toward the anode and threshold voltage II, which induced flicking of the tail and backward swimming toward the anode.

RESULTS

Indoor Experiment

Figure 3 shows the results of the indoor experiments with the electrode arrangements E1-E4. During the control period (0 V cm^{-1}) in the experiment when the electrodes were placed upright on the bottom (arrangement E1), the crayfish moved their appendages (claws, walking legs, swimmerets, antennas, antennules and mouthparts) normally and walked freely throughout the three zones, while their bodies oriented at random. The anodal control group response was only $18 \pm 4.9\%$ (mean percent $\pm$ standard error).

When a stimulus of 0.02 V cm^{-1} was applied, the crayfish showed a slight twitch of the walking legs and antennas, indicating the detection of the electric field. At 0.06 V cm^{-1} (threshold voltage I), two crayfish in five trials exhibited a clear parallel orientation to the electric field facing the anode, but the anodal group response was the same as the control ($18 \pm 3.5\%$). The Mann-Whitney test showed that the percentage remained at the same level of the control at 0.02 - 0.08 V cm^{-1} ($p > 0.05$). At 0.10 V cm^{-1} or higher, the percentage was significantly higher ($p < 0.05$) than in the control. At 0.12 - 0.14 V cm^{-1} (threshold voltage II), the crayfish showed the tail flick, due to contraction of the abdomen and swam backward toward the anode.

At 0.16 to 0.30 V cm^{-1} , movement of claws, walking legs, swimmerets, tail fan and antennae became more pronounced. This was followed by reorientation of the crayfish to face the cathode,

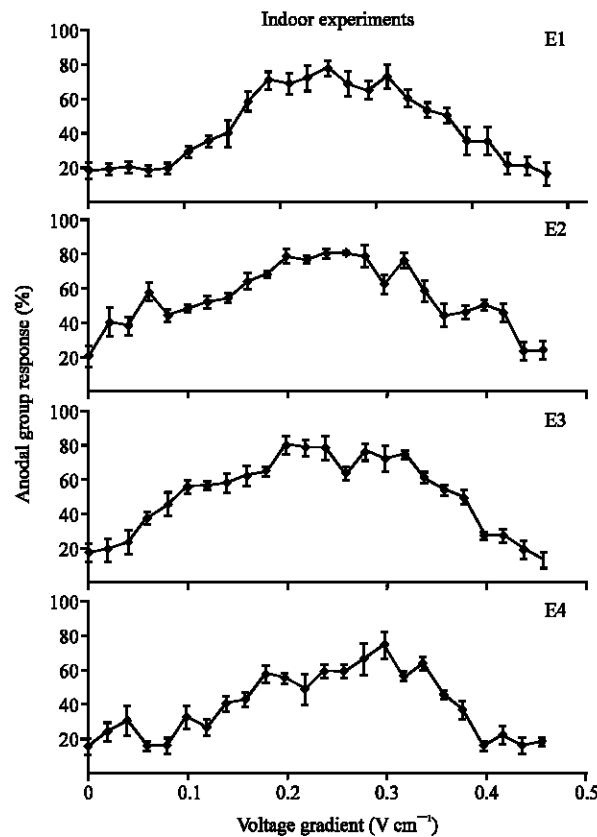


Fig. 3: Anodal group response (mean % $\pm$ SE) under various electric field intensities in the indoor tank with electrode arrangements E1, E2, E3 and E4

then the onset of the involuntary tail flick and a resultant movement toward the anode. The maximum anodal group response ($77 \pm 4.2\%$) toward the anode was elicited by electrical intensity of 0.24 V cm^{-1} (Fig. 3, E1).

At $0.32\text{-}0.46 \text{ V cm}^{-1}$, the crayfish exhibited abnormal behavior such as unbalanced walking, extreme tail flick and lying on their dorsal side. Two to four of 10 crayfish showed the tail flick, twitched their tail fans rapidly, swam backward only a short distance and then sometimes lay on their dorsal side. When the electric current was switched on at high voltages ($0.40\text{-}0.46 \text{ V cm}^{-1}$), the crayfish jerked their tail, then laid motionless on their dorsal side and stayed in that position for several seconds or minutes after the current had been switched off. If the crayfish moved again, there was no orientation. Lying on the back with muscular rigidity was a sign of narcosis and 3-5 crayfish were affected during the different trials at high electrical intensity.

In the experiments with the electrodes 5 cm (E2) or 10 cm (E3) off the bottom, the crayfish during the control period freely crawled around and some passed under the electrodes; the anodal group response was $20 \pm 6.3\%$. There was no change in behavior at $0.02\text{-}0.04 \text{ V cm}^{-1}$, only that 3-4 crayfish walked slowly to both the anode and cathode zones and then left the electric field through the gaps under the electrodes. The Mann-Whitney test showed that the percentage was significantly higher ($p < 0.05$) than the control at 0.04 V cm^{-1} in the E2 arrangement and at 0.06 V cm^{-1} in E3; these were thus the threshold voltage Is.

At $0.12\text{-}0.16 \text{ V cm}^{-1}$, the animals raised one or both claws facing the cathode and slowly moved backward, or walked around the anode zone and then passed beneath the anode out of the electric field; this was threshold voltage II.

At $0.18\text{-}0.32 \text{ V cm}^{-1}$, 6-8 crayfish swam backward with rapid tail flicks, or swam rapidly forward with their abdomen and tail fan elevated and both claws raised, then left the electric field. Two to four animals moved for a short distance or settled on the bottom facing the anode.

High positive anodal group responses ($79 \pm 3.9\%$) ($p < 0.05$) were obtained at $0.20\text{-}0.26 \text{ V cm}^{-1}$ in E2 and at $0.20\text{-}0.24 \text{ V cm}^{-1}$ in E3 (Fig. 3, E2 and E3). Thus, about 80% of the crayfish tested showed the same tendency to crawl away from the cathode toward the anode and under the anode out of the electric field. This result suggests that the crayfish were not attracted by the anode, but just repelled by the cathode. Overstimulation occurred at $0.34\text{-}0.46 \text{ V cm}^{-1}$ and crayfish behaved as if narcotized.

In the experiment with the small electrode arrangement E4, the crayfish moved almost the same way as described above, but they crawled away from the electric field through the gaps between the electrodes and the walls ($16 \pm 4.0\%$). At $0.02\text{-}0.08 \text{ V cm}^{-1}$, only 2-3 crayfish crawled slowly out of the electric field and the others crawled around in the anode or the cathode zones. Sometimes the crayfish stayed right next to the electrodes, or climbed the anode without being shocked. The Mann-Whitney test showed that the percentage was significantly higher ($p < 0.05$) than the control at 0.10 V cm^{-1} (threshold voltage I) and swam backward toward the anode by flicking their tails at $0.14\text{-}0.16 \text{ V cm}^{-1}$ (threshold voltage II).

At $0.18\text{-}0.30 \text{ V cm}^{-1}$, the crayfish quickly swam forward between the electrodes and the tank walls out of the electric field; swam sideways crossing the electric field; or swam backward with rapid tail flicks toward the anode. The maximum anodal group response ($72 \pm 7.3\%$) ($p < 0.05$) occurred at 0.30 V cm^{-1} (Fig. 3, E4). Overstimulation at $0.32\text{-}0.46 \text{ V cm}^{-1}$ also narcotized the crayfish.

Outdoor Experiment

Figure 4 shows the results of the outdoor experiment with three electrode arrangements (E1, E2, E4). In the experiment with the electrodes upright on the bottom (Fig. 4, E1), the crayfish in the control period moved slowly at a low water temperature of 12.5°C and moved faster when water temperature was raised to 13.5°C . The group anodal response during the control period was $27 \pm 6.7\%$.

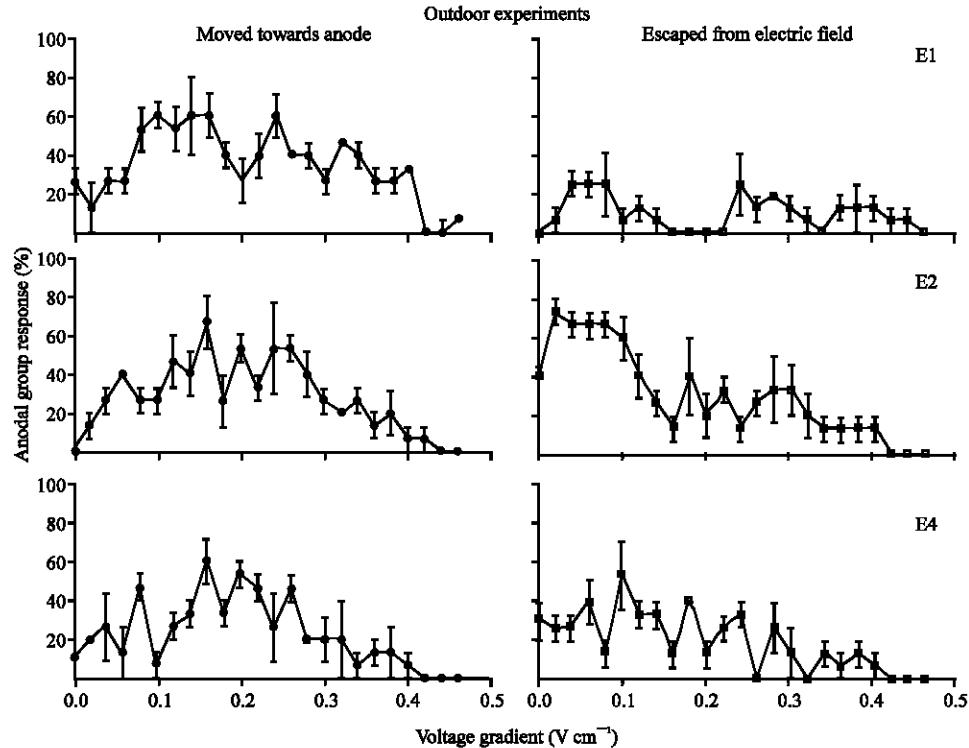


Fig. 4: Anodal group response (mean % $\pm$ SE) under various electric field intensities in the outdoor tank with electrode arrangements E1, E2 and E4. Left panels show anodal movement; right panels show crayfish that crawled away from the electric field beyond the anode

With stimulation at 0.02-0.06 V cm^{-1} , the group anodal response was the same as the control. The Mann-Whitney test showed that the group response at 0.08 V cm^{-1} (threshold voltage I) was significantly higher ($p < 0.05$) than the control. The animals swam back toward the anode by flicking their tails at 0.14-0.16 V cm^{-1} (threshold voltage II). High positive anodal group response ($60 \pm 11.5\%$) was obtained at 0.24 V cm^{-1} .

At 0.28 V cm^{-1} or higher, the crayfish struggled and could not remain upright. Two crayfish lay narcotized in the anode zone. Beyond the electric field at 10 cm, crayfish were still affected by the electric current and crawled sideways or turned and moved back away from the electric field. Farther from the field, they crawled along the side of the tank or settled their bodies on the bottom.

With electrodes 5 cm over the bottom (Fig. 4, E2), the crayfish during the control period stayed in the center zone or moved to the cathode zone, but none moved into the anode zone. At 0.04 V cm^{-1} (threshold voltage I), four crayfish in three trials clearly oriented parallel to the electric field and faced the anode. Below 0.10 V cm^{-1} , about 67-73% of the crayfish crawled away from the electric field beyond the anode. At 0.12-0.14 V cm^{-1} (threshold voltage II), the crayfish flicked their tails and swam back toward the anode. Stimulation at 0.16 V cm^{-1} induced ($67 \pm 13.3\%$) of the animals to move toward the anode, but higher intensities of 0.20-0.26 V cm^{-1} induced only (53 ± 12.4) to do so. Electroneurosis set in at 0.28 V cm^{-1} . Beyond the electric field, the crayfish crawled freely around the tank or rested on the bottom. These results again showed that crayfish were not attracted to the anode, but avoided the cathode and tried to escape the electric field.

With the small electrodes (Fig. 4, E4), the anodal group response in the control period was $7 \pm 8.0\%$. The percentage was significantly higher ($p < 0.05$) than the control at 0.08 V cm^{-1} (threshold

Table 1: Threshold voltage for the anodal orientation (I), movement (II) and the most effective electric field that induced the highest anodal group response and electronarcosis in the American crayfish

Test tank (Water temperature)	Arrangement of electrodes	Threshold voltage (V cm^{-1})		Most effective electric field (V cm^{-1})	Electro narcosis (V cm^{-1})
		I	II		
Indoor tank (28.0°C)	Electrodes upright on the bottom (E1)	0.06	0.12-0.14	0.24	0.32
	Electrodes 5 cm off the bottom (E2)	0.04	0.12-0.16	0.26	0.34
	Electrodes 10 cm off the bottom (E3)	0.06	0.12-0.16	0.24	0.34
	Small electrodes (E4)	0.10	0.14-0.16	0.30	0.32
Outdoor tank (12.5-17.0°C)	Electrodes upright on the bottom (E1)	0.08	0.14-0.16	0.24	0.28
	Electrodes 5 cm off the bottom (E2)	0.04	0.12-0.14	0.16	0.28
	Small electrodes (E4)	0.08	0.14	0.16	0.30

voltage I). Half of the crayfish ($47 \pm 6.7\%$) moved toward the anode and crawled away from the electric field beyond the anode. The crayfish flicked their tails and swam backward at 0.14 V cm^{-1} (threshold voltage II). A maximum anodal group response ($60 \pm 11.5\%$) occurred at 0.16 V cm^{-1} and declined with increasing voltage. Two animals showed narcosis at the anode zone at $0.30\text{-}0.46 \text{ V cm}^{-1}$. These results also suggested that crayfish were not attracted by the anode but repelled by the cathode.

During the control periods, the crawling speeds of the crayfish were $1.95\text{-}2.60 \text{ cm s}^{-1}$ and they never swam backward. When stimulated at intensities ranging from $0.26\text{-}0.32 \text{ V cm}^{-1}$ the crayfish swam backward toward the anode at speeds of $6.67\text{-}19.5 \text{ cm s}^{-1}$.

Table 1 summarizes the threshold voltages for the anodal orientation and movement, most effective electric field intensity and electronarcosis in the crayfish. Threshold I ranged $0.04\text{-}0.10 \text{ V cm}^{-1}$ and threshold II $0.12\text{-}0.16 \text{ V cm}^{-1}$. The most effective electric field intensity that induced anodal group response was $0.24\text{-}0.30 \text{ V cm}^{-1}$, when the conductivity of water was $625 \mu\text{S cm}^{-1}$ in the indoor tank at 28.0°C and was $0.16\text{-}0.24 \text{ V cm}^{-1}$, when the conductivity was $80\text{-}160 \mu\text{S cm}^{-1}$ in the outdoor tank at $12.5\text{-}17.0^\circ\text{C}$. Electronarcosis set in between 0.32 and 0.46 V cm^{-1} in the indoor tank and between 0.28 and 0.46 V cm^{-1} in the outdoor tank. The crayfish recovered from electronarcosis several minutes after the electric current had been switched off.

DISCUSSION

This study clearly demonstrated in the tank experiment that in a uniform electric field, the American crayfish were sensitive to the electric field and showed a slight twitch of the walking legs indicating detection of the weak electric field at 0.02 V cm^{-1} . Crayfish within moderate electric fields of $0.12\text{-}0.30 \text{ V cm}^{-1}$ showed positive electrotaxis or movement toward the anode. In the E1 electrode arrangement (upright on the bottom), the crayfish oriented to the anode, flicked the tail, moved toward the anode and continuously flicked the tail after reaching the anode. However, in the E2 and E3 electrode arrangements (5 and 10 cm over the bottom), the crayfish moved to the anode and crawled beyond it out of the electric field. Such movement beyond the anode cannot be explained as positive electrotaxis and can be interpreted as repulsion from the cathode.

The forward crawling and the backward swimming shown by the crayfish in the present study have also been documented earlier in the pink shrimp *Penaeus duorarum* (Higman, 1956; Kessler, 1965), the European crayfish *Astacus astacus* (Westman *et al.*, 1978), the Norway lobster *Nephrops norvegicus* (Stewart, 1974), the Australian spiny lobster *Pandalus cygnus* (Phillips and Scolaro, 1980), American lobster *Homarus americanus* (Koeller and Crowell, 1998), American crayfish *P. clarkii* (Kawai *et al.*, 2004) and the brown shrimp *Crangon crangon* (Polet *et al.*, 2005).

In this study, we determined threshold voltage I ($0.04\text{-}0.10 \text{ V cm}^{-1}$), which induced parallel orientation of the animal to the electric field and forward crawling toward the anode and threshold voltage II ($0.12\text{-}0.16 \text{ V cm}^{-1}$), which induced flicking of the tail and backward swimming toward the anode (Table 1). The threshold voltage did not vary with water temperature in this study. Kessler

(1965) reported that threshold voltages in the pink shrimp were affected by water temperature where the shrimp tested at 14°C and 36°C had higher mean threshold voltages than shrimp tested at 20°C and 28°C. The threshold voltage I of 0.04-0.06 V cm⁻¹ for the freshwater crayfish in our study was similar to that of the pink shrimp *Penaeus duorarum* (0.06 V cm⁻¹) from coastal waters and estuaries despite the fact that the conductivity of sea water is roughly 1,000 times that of freshwater.

The most effective electric field intensity that induced anodal group response in the American crayfish was higher in the indoor tank (0.24-0.30 V cm⁻¹) than in the outdoor tank (0.16-0.24 V cm⁻¹) (Table 1). This was attributable to the conductivity of tap water, which was affected by temperature. The more ions, the more conductive the water resulting in a higher electrical current. The conductivity was 625 µS cm⁻¹ at 28°C in the indoor tank and 80-160 µS cm⁻¹ at 12.5-17.0°C in the outdoor tank.

Orientation of the animal in an electric field is an important factor in inducing anodal movements. The American crayfish required a threshold voltage for anodal movement that was 1.4 times higher when they faced the cathode than when they faced the anode. Fish required more voltage to respond when facing the anode than when facing the cathode (Klima, 1972). The pink shrimp required about twice as much voltage when facing the cathode than when facing the anode (Kessler, 1965). Wathne (1967) reported that shrimp responded much more readily when their body axis was perpendicular to the electrodes than when they were parallel to them. Klima (1968) concluded that the voltage felt by shrimp varies not only with its orientation but also with its total length.

Within strong electric fields, animals are stunned (electronarcosis), injured or killed. However, American crayfish that suffered electronarcosis for 5 min at 0.46 V cm⁻¹ quickly recovered within 1 min without any ill effect or injury (and regardless of water temperature 12.5-28.0°C). At extreme field strengths of more than 20 V cm⁻¹, it was possible to cause Australian spiny lobsters to lose their legs, but no lobsters were ever killed (Phillips and Scolaro, 1980). The European crayfish *Astacus astacus* (Westman *et al.*, 1978) or the white-clawed crayfish, *Austropotamobius pallipes* (Alonso, 2001) collected by electric fishing often have no claws. Smaller crayfish are more prone to suffer cheliped loss. It also should be noted that voltage output used in this work is remarkably lower than that employed in other studies, which typically ranges between 3-7 V cm⁻¹ (Westman *et al.*, 1978; Penczak and Rodriguez, 1990; Fievet *et al.*, 1996; Bernardo *et al.*, 1997).

Knowledge of the change in behavior of crayfish with intensity of the electric field can be applied to control and catch them during electric fishing. The most effective electric field intensity (0.16-0.30 V cm⁻¹) that induces anodal group response can be used to herd crayfish to a trap or net. This intensity must be carefully adjusted to prevent electronarcosis, which occurs at just a little higher intensity, 0.28-0.34 V cm⁻¹. When crayfish are insensible in a high electric field, they have to be collected immediately before they recover from the narcosis. This requires work and time for the fishers. Although the adjustment is not easy, the difficulty might be overcome by improvement in the fishing skill.

For eradication, we can learn from previous studies (Reeve, 2004) using electrofishing for removal which appeared successful in catching all age classes of American crayfish; however, to eliminate them completely is impractical. This work is only effective in shallow creeks, wet seeded rice fields or small ponds and only catches a limited portion of the crayfish population; therefore, it is not a viable method of control. Electric fishing over fish's spawning areas should be avoided. Any captured indigenous crayfish species or other aquatic organisms should also be humanely released.

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