

An investigation into the effects of electric fields on *Nephrops norvegicus*

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Experiments conducted on aquarium and natural colonies of *N. norvegicus* have shown that the species can be induced to leave its burrows by electrical stimulation. The reaction does not appear to be an involuntary one and depends upon the stimulation being sufficiently strong to cause the animal to use its normal avoidance mechanism, which is a strong tail flick able to carry the animal rapidly backwards out of its burrow and clear of the electric field. The forms of electric stimuli required in aquarium and natural conditions were different, and in the aquarium a weaker form of stimulus was effective. The stimulus required in natural conditions was bursts of d.c. pulses which intermittently induced muscular tetanus, and in the intervals between bursts the animals could take avoiding action. The emergence times were sufficiently short to suggest that electrically stimulated emergence from burrows could be utilised in the commercial capture of *N. norvegicus*.

Introduction

Studies of the behaviour of the mud dwelling crustacean *Nephrops norvegicus* have shown that this species excavates burrows (Chapman and Rice, 1971a, b). The burrows are often extensive, with many side branches, and can cover an area of up to 1 m² and penetrate to 30 cm below the surface of the mud. The animals can spend a large proportion of their time in these burrows, in which they are safe from capture, and this aspect of their behaviour is reflected in large diurnal and seasonal variations in commercial trawl catches on the same grounds (Anderson 1962; Simpson 1965; Figueireido and Thomas, 1967). Any means of inducing *N. norvegicus* to leave their burrows would be likely to increase their vulnerability to capture by trawls, and it was postulated that stimulation by an electric field might have this effect.

The responses of some other species of crustacea to electrical stimulation have been studied from a similar viewpoint. *Penaeus duorarum* Burkenroad, *Penaeus aztecus* Ives (Klima, 1968) and *Crangon crangon* (Boonstra and De Groot, 1970) are all species which evade capture at certain times by burrowing into the bottom. They do not construct tunnels however, but wallow under the surface of the substrate material. Electrical stimulation causes a contraction of the tail muscles, and this involuntary movement forces the animal up off the bottom. These species of shrimp have been found to respond most strongly to stimulation at approximately 5 Hz by exponentially shaped current pulses with a pulse length of

around 0.2 ms, (Kessler, 1965; Boonstra and De Groot, 1970). It was considered that forced contraction of the tail muscles of *N. norvegicus* by an electric field would be unlikely to lead to emergence, because of the complexity of the burrows. The animal might be expected to collide with the tunnel sides and become trapped. Pilot tests on aquarium animals demonstrated however, that *N. norvegicus* could be forced by an electrical stimulus to vacate their burrows.

In this paper experiments on the response of burrowed *N. norvegicus* to stimulation by pulsed electric fields are described. Observations were made on an aquarium colony and by dives on a natural colony in a sea loch. The aquarium colony was established in a tank containing mud from ground inhabited by *N. norvegicus* in Upper Loch Torridon. The reactions of several members of the colony were also studied in an aquarium tank not containing mud (referred to below as the "open" tank) in order to investigate the reaction mechanism in detail. The natural colony was in Little Loch Broom, Wester Ross.

Experimental methods

Aquarium experiments

A 3.7 m diameter tank was filled to a depth of 10 to 15 cm with Loch Torridon mud, under continuously circulating sea water. A population of 12 creel-caught specimens of *N. norvegicus*, mixed in age and sex, and all tagged for identification, was introduced into

the tank, and these animals soon started to dig burrows. The group contained 8 males and 4 females with carapace lengths ranging from 25 to 45 mm. The tank was faintly illuminated for 12 h each day, except during tests when slightly stronger illumination was required. Two mild steel plates, 26 cm wide by 30 cm high, were used as electrodes. They were mounted vertically, 38 cm apart, on a wooden frame. A dexion frame was erected around the tank to support a moving platform to carry the electrodes, so that they could be moved easily to any part of the tank and held with the edges of the plates just touching the surface of the mud. The resistance presented by these electrodes was between 1 and 2Ω , depending on the depth of water.

The pulse generator used was a pulse amplifier producing square or exponential pulses, or bursts of 50 Hz sine wave. The voltage between the electrodes could be varied up to 30 V; the time constant of the exponential pulses was variable between 0.1 and 40 ms; the width of the square pulses was variable between 50 ms and 500 ms and the pulse repetition frequency was variable from 0.25 to 50 Hz.

In each test the pulse conditions were set, the electrodes placed beside the burrow and a shock administered at a pre-determined voltage until the animal emerged or 60 s had elapsed. The emergence time, taken as the time from the application of the stimulus until the animal was clear of its burrow, was recorded by stopwatch. The angle of the electric field vector with respect to the burrow seemed, in the initial trials, to have no influence on the response of the animals. In order to standardise experimental conditions the electrodes were always placed on either side of the burrow so that the field vector was at right angles to the burrow. If possible an animal was tested only once on any given day, and sometime several days elapsed between tests. Data was obtained over a period of 4 weeks.

The resistivity of the mud was measured and found to be the same as that of sea water. The electric field between the electrode plates should not have been distorted therefore, nor the *N. norvegicus* shielded against its effects.

The best known reaction of fish to electric fields is probably electrotaxis, in which a fish in a d.c. electric field is compelled to swim to the anode (Bary, 1950). This type of reaction can have practical applications, and so a taxis experiment was attempted in the mud tank. The plate electrodes were removed from the wooden frame and placed 3.7 m apart at diametrically opposite sides of the tank. The electric field in the tank was then highly non-uniform. The stimulation used was 200 ms square or 40 ms exponential pulses at 1.4 or 5 Hz.

The open tank (without mud) was 2 m in diameter. The same set of electrodes and the same pulse generator were used for the tests. A plastic mesh cage was constructed (15×90 cm in area) to confine the *N. norvegicus* to a straight track. The plate electrodes were positioned on either side of this cage and the animals were stimulated when they walked between the plates. After each animal was introduced to the cage it was left for several hours to adjust to its new surroundings before its response to electrical stimulation was studied.

Field experiments

Area

N. norvegicus is rarely found at depths under 30 m and in order to carry out this experiment a shallow site was required. The test procedure in natural conditions requires a diver to locate an occupied burrow, move a pulse generator and electrode array to it, place the electrodes over the burrow, apply the field and observe reactions. The time taken for each test averages about 5 min, and consequently to carry out enough measurements to obtain reliable information, a relatively dense colony, in shallow water where diving time would not be limited by decompression needs had to be selected. Various sites were surveyed, and a site in Little Loch Broom, Wester Ross (Lat. $57^{\circ}51'N$ Long. $5^{\circ}14'W$) was chosen for experiments in September and November 1972.

The experimental area was a slope with a gradient of around 30° , reducing to a nearly flat zone at a depth of 25 m. The bottom was composed of a thick sticky mud with a very fine easily disturbed surface layer; the type of bottom on which *N. norvegicus* is normally found. Isolated occupied burrows were found in as little as 17 m, and from 20 m downwards the burrow density was greater, with a burrow every 2 to 3 m along a straight line. The colony was mixed in size and sex. Large males with carapace length of 70 mm, and small animals of carapace 25 mm were seen.

Burrows containing other crustaceans (eg *Goneplax rhomboides*) or gobiid fish were found in the same area, dispersed amongst the *N. norvegicus* burrows. It was not always possible to distinguish between the burrow types during selection for tests.

Experimental Procedure

An underwater pulse generator was constructed for the tests (Stewart and Cameron, in prep.). This was capable of feeding pulses up to 75 V in amplitude into sea water loads presenting resistances as low as

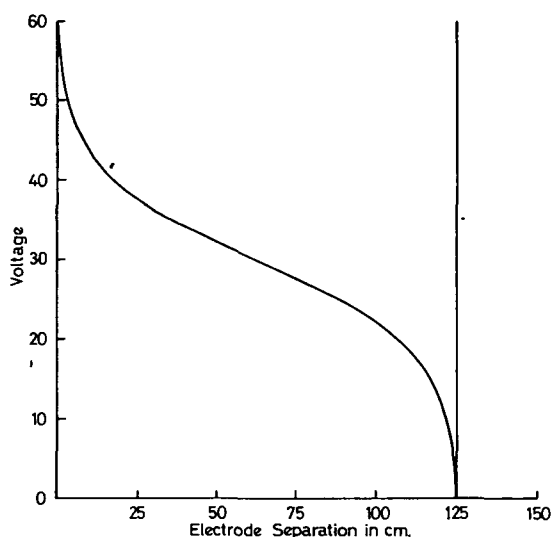


Figure 1. Theoretical voltage distribution between electrodes used in underwater experiments (60 V applied).

80 m Ω . The pulse generator was mounted in a steel housing carried on a frame for easy handling, and was supplied with power via a cable from the surface. The pulse generator was buoyed with floats so that it could be easily moved around the bottom by divers. Control of the unit was provided by an underwater switch on a long cable, and two small housings with inspection windows were provided to allow the divers to monitor the operation of the unit and read the amplitude of the voltage on the electrodes. The electrodes were mounted on a Tufnol frame 1.25 m apart, and were 1 m long pieces of 1 cm diameter stainless steel wire linked to the pulse generator by 6 m of heavy copper cable. The calculated voltage distribution between the electrodes is shown in Figure 1. Laboratory measurements showed that the actual voltage distribution was very close to that predicted. It should be noted that in the central 75 cm the electric field is nearly constant. The resistance presented by the electrodes was approximately 0.3 Ω . In the first series of tests the pulse generator supplied exponential shaped pulses at 2, 10 or 20 Hz with durations of 40, 40 and 20 ms respectively. In the second series the unit supplied exponential shaped pulses at 2, 10, 30 and 50 Hz, both continuously and in bursts at 0.5 and 1 Hz. The pulse patterns produced by the generator in the continuous and burst firing modes are sketched in Figures 2a and 2b respectively. The drop in amplitude in Figure 2b is a characteristic of the unit, and was retained during this exercise as it prevented over-severe tetanus (see below).

The procedure adopted was to survey the area,

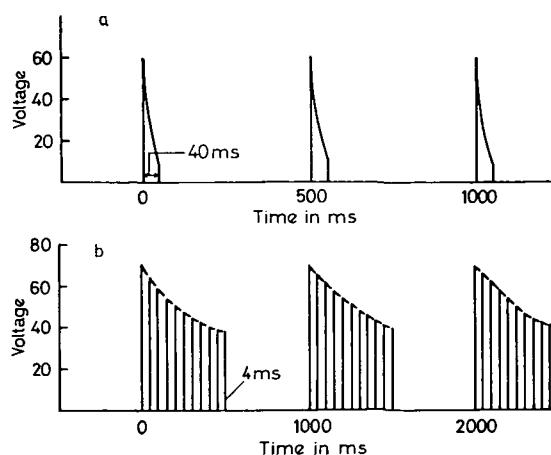


Figure 2. Pulse patterns used in underwater experiments. a) 40 ms exponential pulses at a continuous 2 Hz b) 1 s duration bursts of 4 ms exponential pulses at 50 Hz, with a repetition frequency of 0.5 Hz.

mark out suitable regions of occupied burrows, then move the pulse generator to such a region and lay the electrode frame over a burrow. Energy was then switched to the electrodes and reactions observed. Although the main entrance of a burrow was generally obvious, the layout of the tunnels and subsidiary entrances had to be guessed by the diver when positioning the electrodes. When current was being passed, bubbles were generated by electrolysis at the electrodes, and the bursts of bubbles corresponding to pulses at 2 Hz were easily seen. The electrodes were in contact with the surface of the mud. A core sample was taken and the mud found to have a resistivity comparable to that of the sea water. Tests were carried out with the electrodes parallel to, and at right angles to, the main tunnels of burrows, without any obvious difference in reaction.

In order to observe the response of *N. norvegicus* to electric fields when clear of their burrows, a net cage with a Tufnol frame was constructed. Specimens were caught in creels and kept in a creel on the sea bed at a depth of 10 m. Individual animals were introduced into the cage and subjected to pulsed electric fields.

These tests were extended by using underwater TV at a depth of 30 to 40 m. A frame carrying the TV equipment was lowered from a ship and electrodes attached to the frame were suspended a few centimetres off the sea bed.

Results

Open tank experiments

The data obtained in these experiments was mainly

qualitative. The number of available specimens was limited and these could not be repeatedly stimulated by an electric field without producing in them a state of stress. In this condition they reacted strongly to even weak stimuli and their behaviour was then of little significance in the context of this investigation. Consequently each animal was subjected to the electric field a few times only with intervals of an hour or more between tests. This was enough to observe the mechanism of the response, but the limited amount of data obtained gave only general information on the relationships between the various parameters of the electrical stimulus. The information obtained however, appeared to provide a useful background for experiments on burrowed *N. norvegicus* and so the open tank experiments were not prolonged.

With a specimen in the cage between the electrodes, the electric field strength was slowly increased from zero. The first observed reaction was a twitching of the eye stalks. At a slightly higher field level weak involuntary contractions of the muscles of the tail and chelae were observed, and further increases in the field strength increased the severity of these contractions. A further increase in the field strength induced the *N. norvegicus* to escape from the field zone. They escaped in two distinct ways, either by walking slowly forwards or by flicking their tails and moving rapidly backwards. The forwards movement was very slow and awkward; the animal walking forward normally whilst experiencing involuntary tail contractions which tended to move it backwards. The backwards movement was similar to the typical escape reaction of decapod crustacea (Higman, 1956). The tail was bent upwards with the uropod fully opened, and the latter was quickly closed as the tail was brought down and forwards imparting a strong reverse thrust to the animal. The chelae were fully extended in line with the body, and in this movement the animal was relatively streamlined. The tail flick did not appear to be directly stimulated by the electrical field which seemed to act as an irritant inducing the *N. norvegicus* to use its normal escape mechanism.

The minimum electric field levels at which the *N. norvegicus* could detect the presence of the field, and at which they were induced to escape from the field were investigated. The threshold field levels were found to be inversely proportional to the size of the animals, i.e. the larger specimens reacted at lower field strengths than the smaller specimens. Square pulses 100 ms wide, and exponential pulses with time constants of 40 ms and 6 ms to 0.3 ms were used in these tests. The threshold field levels were approximately the same for pulses 40 ms or

more in duration, but the threshold levels were 2 to 3 times higher with the shorter pulses. With the longer pulses all sizes of *N. norvegicus* were made to jump clear of the field by applying field strengths in the range 10 to 26 V/m. Further reduction of the pulse width demonstrated that *N. norvegicus* could detect the presence of exponential pulses with a time constant as low as 0.3 ms, with a minimum field strength ranging from 20 to 37 V/m.

By increasing the pulse frequency from 1 Hz the onset of muscular tetanus was observed. This arises when the delay between stimulating pulses is shorter than the time needed for the muscle to relax, and results in the muscle being held in a state of tension. Tetanus occurred in *N. norvegicus* at approximately 10 Hz, regardless of the size of the animal, and caused the muscles of the tail and chelae to contract strongly. Tetanus could be induced in all specimens by exponential shaped pulses of 3 ms time constant and a field strength of 30 V/m at 15 Hz.

Electric fields were applied with the field vector parallel to, and at right angles to the bodies of *N. norvegicus*. No consistent differences in response were observed. It was noted however, that the antennae and chelae were normally held well out from the body and to the side, which added to the effective width of the animal, and gave it comparable overall length and width.

Mud tank experiments

Burrowing behaviour

The burrows dug by the *N. norvegicus* in the aquarium were in a state of constant modification. Initially, a burrow would consist of one passage with a large entrance hole leading from a scooped-out hollow in the mud, and a smaller vent hole which permitted the passage of a current of water. The vent hole would gradually be enlarged and become another entrance, side branches would be dug, and adjacent burrows would be linked, then expanded and would eventually collapse. The animals usually remained facing outwards at the entrance with their claws just visible.

Response to electric fields

When subjected to electrical stimulation, the *Nephrops norvegicus* emerged from the burrows either backwards (rapidly) from the vent hole (or second entrance), or forwards (slowly) from the main entrance. These two types of reaction corresponded well with the observations made in the open tank. Backward emergence usually carried the animals well clear of their burrows, and the streamlined attitude adopted

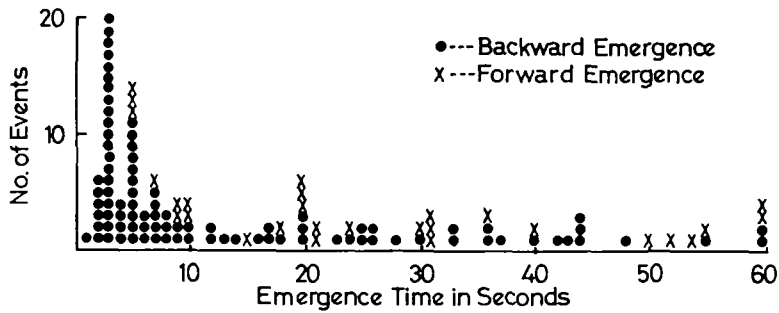


Figure 3. Summary of all tests showing variation in emergence times.

during the backwards movement allowed them to emerge from very narrow vent holes.

Approximately 160 tests were carried out, with various pulse patterns, and the results are summarised in Figure 3, for the tests in which the animals emerged from their burrows. The most commonly recorded emergence time was 3 s. In 48 tests the animal did not emerge but 30 of these were conducted at low frequencies and low field levels, below 5 Hz and 30 V/m. In Figure 4 the measurements of applied electric field strength and emergence time are plotted, showing both backward and forward emergence, for square pulses. No distinction is made between measurements with different pulse widths as this did not seem to be significant in these tests. Similar results (not shown) were obtained for stimulation by exponential pulses and by bursts of 50 Hz a.c. Stimulation by 6 ms exponential pulses required higher field strengths, which corresponds with the open tank observations. Figure 5 shows the relationship between electric field strength and emergence time for backward emergence only, for square pulses and 40 ms exponential pulses. Figure 6 shows the rela-

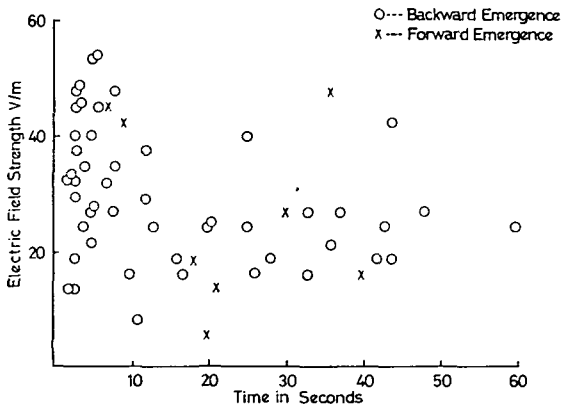


Figure 4. Electric field strength plotted against emergence time for stimulation with square pulses (50 to 200 ms duration) in the frequency range 0.5 to 8 Hz.

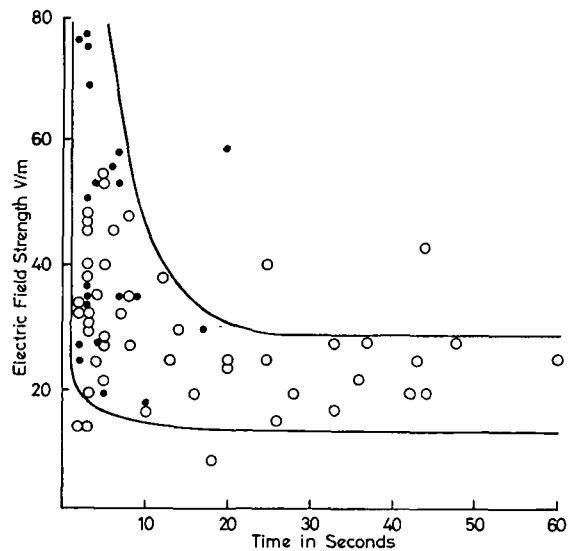


Figure 5. Electric field strength plotted against emergence time for stimulation with square pulses (o) and 40 ms exponential pulses (•) which resulted in backward emergence. An envelope has been sketched enclosing most of the experimental points.

tionship between pulse frequency and emergence time for backward emergence. Fast emergences occurred most frequently in the range 1 to 5 Hz. The higher frequencies are close to the frequency at which tetanus occurs. In Figure 7 the voltage and emergence time are plotted for all the observations made on one animal; a female, carapace length 35 mm. These observations were made with a gap of at least one day between tests. For the colony as a whole, the emergence time did not appear to be related to animal size.

Taxis Experiment

With widely separated electrodes, as described, the voltage was increased from zero and no response was

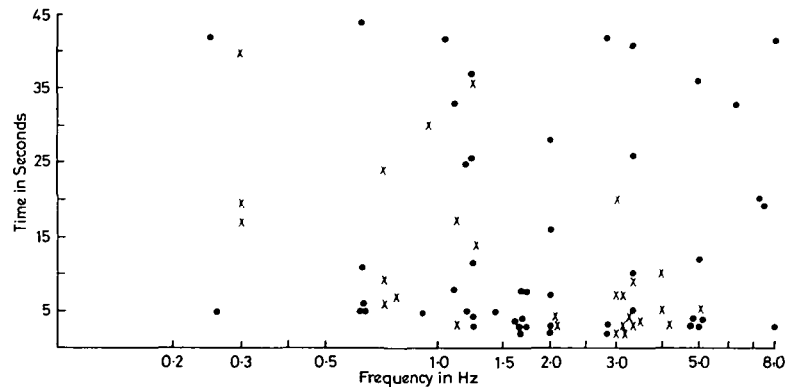


Figure 6. Emergence time plotted against pulse frequency for stimulation with square pulses (•) and exponential pulses (x) which resulted in backward emergence.

seen until 20 V was exceeded. After a lapse of several minutes in each test, a few animals emerged from their burrows, and one or two walked slowly backwards towards the anode, into a region of higher electric field strength. The paths taken corresponded roughly with current flow lines. When the animals touched the anode they appeared to receive a more powerful shock, and swam rapidly backwards away from the electrode. Once an animal had been shocked like this it did not approach the anode again during the 2 day duration of the experiment. The larger animals were more commonly induced to move to the anode than the smaller.

Fields experiments

In the first series of experiments the stimulation applied to occupied burrows was continuous pulsing at frequencies of 2 Hz and above, ie the type of stimulus found effective in the aquarium tests. Pulsed electric fields were applied to about 100 occupied burrows, some of these being repeat tests. The behaviour of the *N. norvegicus* was observed to be significantly different from that seen in the aquarium tests. On 20 occasions an animal emerged from its burrow, sometimes only after the stimulation had been stopped. On only 3 occasions did an animal emerge in less than 5 s, and emergence generally took between 20 and 40 s. The electric field was clearly penetrating the regions around the burrows as the animals were always observed to twitch in response to the pulses. Clouds of mud were frequently observed to come from subsidiary burrow entrances showing that the *N. norvegicus* were moving violently inside the burrow. Two rapid backward emergences

were observed, and all the other animals which emerged did so by walking forwards slowly. Strong tail flicks were produced by 4 animals after emergence, which carried them out of range of the electric field. Those which emerged forwards tended to move straight back into their burrows when the stimulation was stopped, some by using their strong tail flick.

The electric field was non-uniform close to the electrodes (see Figure 1), but in the central zone the field was reasonably uniform. Initially the field set up in this zone was about 40 V/m and in later tests this was reduced to about 20 V/m (low in terms of the aquarium experiments). The applied voltage and pulse frequency were varied throughout the available range without inducing rapid emergence by the use of the strong tail flick.

The reactions of non-burrowed *N. norvegicus* were

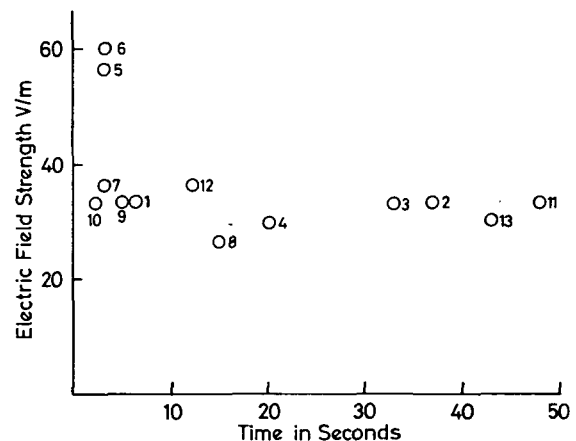


Figure 7. Electric field strength plotted against emergence time for all the observations made on one animal (Female; carapace length 35 mm).

tested in the net cage described above. When subjected to continuous pulsing at 2 Hz the muscles of the tail and chelae were observed to contract in response to the pulses, but only one specimen reacted by using a strong tail flick. Increasing the pulse frequency did not induce the use of the tail flick, and tetanus was produced when the frequency exceeded 10 Hz and the field strength was sufficiently high. Some of the animals used in this experiment were taken to the surface in creels, handled, taken to the bottom, put in the cage and shocked all within the space of 10 min. These animals might have been expected to be in a sensitive condition but nevertheless failed to use the strong tail flick when stimulated.

In the next series of field experiments the stimulation used was 1 second long bursts of 50 Hz d.c. pulses of 4 ms duration at 0.5 Hz, with a peak field in the uniform central zone of 20 V/m. It was anticipated that this stimulus would have a tetanising effect, but that the *N. norvegicus* might take evasive action in the periods between the bursts. Tests were conducted on over 40 burrows, 18 of which were definitely occupied, though not necessarily by *N. norvegicus*. From 12 of these burrows *N. norvegicus* emerged backwards by using the strong tail flick and 6 of the animals did so very soon after the application of the field. The emergence times were estimated at between 1 and 2 s, which implied that the animals escaped after the first or second burst of pulses.

A direct comparison of the intermittent tetanising and continuous non-tetanising types of stimulus was possible with one specimen of *N. norvegicus*. This animal emerged directly on application of the 50 Hz burst stimulus, which was then stopped. The animal returned to its burrow and was then stimulated with 2 Hz, 40 ms duration pulses, and although tail and chelae contractions were observed the animal remained in its burrow. Reapplication of the 50 Hz burst caused immediate emergence.

In the experiments using underwater TV in deeper water the stimulus used was 0.5 Hz bursts of 50 Hz a.c. of constant amplitude, producing a peak field strength in the uniform region of about 10 V/m. It should be noted that the effective pulse width was longer than in the shallower water experiments using divers. Over 30 specimens of *N. norvegicus* were induced to leave their burrows, but due to the nature of this experiment, conducted from a ship swinging at anchor, the recorded events, although providing a range of qualitative information, gave little detailed information on emergence times or electric field strengths at the burrows. However, several emergence times of under 3 s were measured.

The variable amplitude of the stimulus used by the divers on the natural colony appears, in the light of

these results with a constant amplitude stimulus, to have little importance.

Discussion

The reaction mechanism

Although these experiments demonstrated that *N. norvegicus* can be induced to leave their burrows under electrical stimulation, they showed that this was not a direct effect of the electric field but that the stimulus was scaring the animals into escaping from the electric field zone. Pulsed electric fields caused muscular contractions, and if these were sufficiently disturbing *N. norvegicus* took avoiding action either by walking slowly out of the field or by using a strong tail flick to make a rapid escape. This tail flick is the normal escape mechanism used by *N. norvegicus*, and the complex muscular movements used in raising and then tightly closing the tail to produce a strong flick could not be induced by the "blanket" type electric fields necessarily used in these experiments. The severity of the stimulus required to "frighten" *N. norvegicus* into leaving its burrows was markedly different in aquarium and natural conditions; the animals in their natural habitat requiring an intermittent tetanising stimulus to induce them to use their tail flick to escape. Measurements in the open tank indicated that tetanus could be produced at frequencies above 10 Hz by d.c. pulses with a 3 ms time constant and an electric field strength of 30 V/m. Since tetanus is an involuntary response the same behaviour should be found in natural conditions. Aquarium experiments cannot, however, reliably determine the minimum duration of tetanus needed to stimulate the use of the strong tail flick. This information could only be obtained by studying a natural colony.

The difference in the response of *N. norvegicus* in aquarium and natural conditions was not unexpected, since aquarium conditions are unavoidably artificial. The tests carried out underwater in the net cage showed that the sensitivity of *N. norvegicus* was not suddenly increased by the experience of being caught and handled. The greater reactivity of the aquarium animals may therefore have developed over a longer period of time in captivity during which they had been exposed to a variety of stimuli.

The principal physical differences between the aquarium and natural conditions during tests were the water pressure and light intensity. No abnormal behaviour was observed which could be directly related to the difference in depth, but it was noted that increasing the light intensity tended to inhibit the response of *N. norvegicus* to electrical stimulation.

Mud-Tank observations

The data presented on experiments in the aquarium mud tank was mostly obtained at frequencies below 8 Hz, but tests with intermittent 50 Hz stimulation produced very similar information. Examination of Figures 4 and 5 suggests that a fast response, causing the immediate use of the rapid tail flick, becomes highly probable if the electric field strength exceeds 30 V/m. There is considerable scatter in the experimental points in Figures 4 and 5. This is to be expected because of the variations in the size and shape of the burrows and in the size of the animals, which directly affects the time taken by them to escape from their burrows. Further, the electric field in the burrows, which are below the level of the electrodes, will be distorted and weaker than the measured value.

Figure 6 suggests that there is a slight frequency dependence in the emergence time. The minimum values have a broad peak running from 1 to 5 Hz. With continuous pulsing this result appears realistic in that at frequencies below 1 Hz the effective stimulus is weak and at higher frequencies tetanus tends to appear making it difficult for the animal to move.

In Figure 7 the behaviour of one animal, which was typical of the group, is shown. The experimental points were obtained over a period of several weeks and there is no evidence of learning in the results. Successive tests gave no indication that the animal was reacting more or less strongly to the stimulus. Evidence of learning was seen in the taxis experiment in which the *N. norvegicus*, at least for one or two days, avoided the electrodes which they had initially been induced to approach and touch. Higman (1956) has observed a taxis response in *P. duorarum* Burkenroad in a d.c. electric field, at a level which induced the use of the tail flick escape mechanism.

The lack of dependence of the emergence time on the animal size is noteworthy in view of the observations made in the open tank which established that larger animals responded at lower field strengths than smaller animals. This effect may simply be due to the greater difficulty the large animals experience in forcing their way out of the burrows.

Practical applications

The observed reactions of *N. norvegicus* to pulsed electric fields suggest that it may be possible to use this behaviour as an aid to capture by trawls. An electrode array could be rigged on a trawl so that it was towed in contact with the bottom in front of the footrope. *N. norvegicus* forced from their burrows by pulsed electric fields would then be caught in the

trawl. For this to be effective however, the emergence time is critically important and ideally should be very short. The most frequent emergence time recorded in the aquarium experiments was 3 s (Fig. 3) which in practice would require either slow towing or the electrode array to be slung far in front of the footrope of the trawl. For example, at 3 knots, the rear of the electrode array would have to be 4.5 m ahead of the footrope to maximise the probability of an emergence in front of the footrope. The evidence obtained in natural conditions however, though limited, suggests that emergence times can be shorter than 3 s. With the use of a periodic "tetanising" type of stimulus of shorter duration than 1 s, and if the *N. norvegicus* escapes after the first burst of pulses, the minimum emergence time is likely to be about 1 s after application of the field.

The use of pulsed electric fields in highly conducting sea water requires very high instantaneous power levels, and in order to minimise the cost, bulk and power consumption of underwater pulse generating equipment, a stimulus with low power requirements should be used. In practical terms this means that an effective stimulus with the lowest possible pulse amplitude, duration and frequency is required. It has been shown that pulse amplitude and duration are interdependent (below approximately 40 ms duration) so that short pulses require to be of greater amplitude than long pulses to produce a reaction. The selection of pulse duration and amplitude is then influenced by technical factors such as the resistance presented by the electrodes, the detailed design of the pulse generator, etc. The experiment on the field colony showed that 1 second long bursts of 50 Hz d.c. pulses of 4 ms duration at 0.5 Hz repetition frequency, with a peak amplitude of 20 V/m at the burrow constituted an effective stimulus. The observations on tetanus suggest that any pulse frequency greater than 10 Hz should be an equally effective stimulus. If this is the case and a lower frequency than 50 Hz can be used, then the power requirements will be reduced. Experiments are in progress using a beam trawl fitted with electrodes to fish for *N. norvegicus*. A beam trawl was chosen for these pilot experiments as it provided a rigid geometry to support the electrode array and pulse generator.

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