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Behavioural responses of European silver eels *(Anguilla anguilla)* to the geomagnetic field

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ABSTRACT: Magnetic orientation of European silver eels *(Anguilla anguilla)* was tested in an octagonal tank. Orientation was determined from photo-registrations of eel positions in tests performed alternately in the natural magnetic field and a field with the horizontal component rotated 180°. Tests were performed in LD 11 : 13. At a daytime light intensity of 100 lux the fish were diurnally active, while at 0.10 lux crepuscular or nocturnal activity dominated. The eels probably differed in preferred orientation, largely depending on the clockwise or anti-clockwise swimming of some of the animals. Therefore there was no preferred direction common to all eels. The orientation of single eels differed, however, significantly between the two magnetic fields, suggesting that the eels responded to the geomagnetic field.

INTRODUCTION

Several investigators have tried to test whether the earth's magnetic field may act as an orienting cue in eel migration. However, electrophysiological investigations (McCleave et al., 1971; Rommel & McCleave, 1973; Enger et al., 1976; Berge, 1979; Vriens & Bretschneider, 1979) as well as maze experiments (Branover et al., 1971; Zimmerman & McCleave, 1975) have given contradictory results.

Eel orientation has also been studied in circular tanks. Even in the absence of celestial cues eels seemed able to show directional preferences. American silver eels *(Anguilla rostrata)* were found to orient southwards, appropriate for migration to the presumed spawning place in the Sargasso Sea (Miles, 1968). European silver eels *(Anguilla anguilla)* normally preferred a northerly to westerly direction, while yellow eels oriented along a north-south axis. They also, however, altered their orientation slightly, when the magnetic field direction was changed (Tesch & Lelek, 1973a, b; Tesch, 1974).

The present study was undertaken to examine anew whether silver eels may show directional responses to the geomagnetic field in a tank, with a technique essentially similar to that used by earlier investigators. Some observations on general behaviour of the fish during experiments were also made.

MATERIALS AND METHODS

All 11 silver eels used (length 30–45 cm) were caught in Öresund between Sweden and Denmark in the autumn. In the Uppsala laboratory they were held in a 400-litre tank filled with artificial saltwater (salinity 32–36 ‰) and recirculated through a charcoal filter. The temperature was 8–12 °C and light scheme LD 11 : 13 without twilight. The animals were acclimated for at least 16 days prior to experiments. They were tested within five months after capture in the same salinity, at light-dark rhythm and temperature as in the holding tank. Tests were performed from October to February, during the years 1978 to 1981.

Apparatus

The wooden apparatus consisted of an easily rotatable, octagonal aquarium supported by a frame (Fig. 1). The aquarium interior diameter was 70 cm and each side was provided with holes. Water flowed from the upper holes at a rate of about 1 l/min to a lower located temperation and aeration tank at least 5 m from the aquarium. The water was then pumped back to the testing tank via the lower holes.

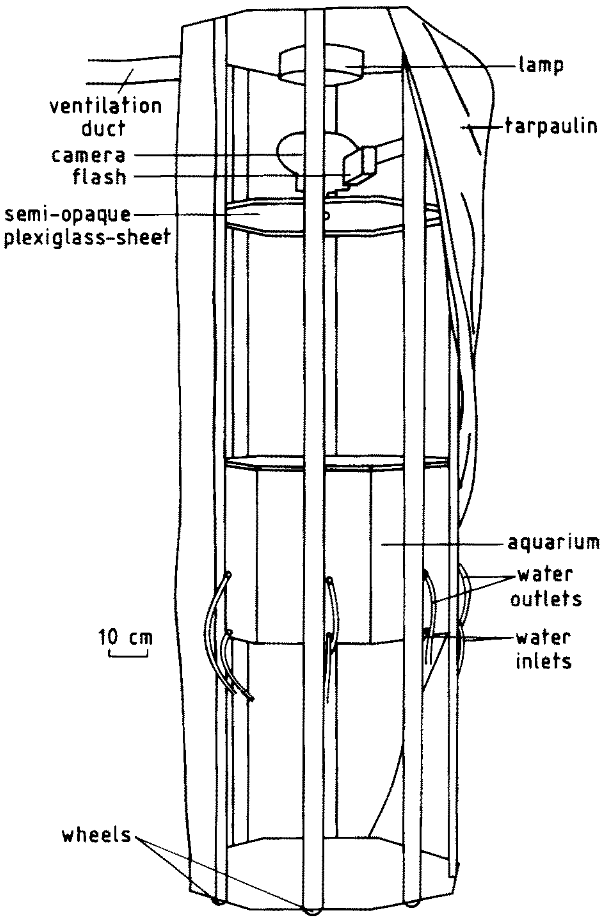

Fig. 1. The apparatus used in orientation experiments. The internal diameter of the octagonal aquarium was 70 cm. During tests the tank was connected via two tubes on each side to an aeration and temperation basin not shown in the figure

Above the aquarium there was a semiopaque plexiglass sheet with a hole in the centre through which the aquarium was photographed with a 16 mm film camera. The camera was connected to a flash with a filter transmitting no light below 600 nm (Kodak Wratten No. 29). An incandescent bulb gave an indirect light in the day time. During experiments the entire apparatus was surrounded by a lightproof tarpaulin and was placed in the centre between a pair of Helmholtz coils in a wooden hut. The coils were wound with copper wire on a wooden frame, placed with their axis in the north-south direction, and connected in series via a constant current rectifier to the mains. When the rectifier was on, the coils produced a horizontal field of 0.30 G opposed to the horizontal part of the earth's magnetic field (approximately 0.15 G at Uppsala). The resulting magnetic field, while equal in strength to the earth's magnetic field, had a horizontal component which was redirected 180° (reversed) compared to the natural magnetic field. The vertical component was left principally unaltered.

Experiments

Each animal was tested in a series of approximately 16 successive experiments, where one test lasted one day and night, with starts and stops during the day. Half of the tests were performed in the natural and half in the reversed magnetic field. To avoid a directional bias caused by the apparatus (Howland, 1973; Wallraff, 1973), the tank was rotated in a pseudorandom manner between experiments; thus each side of the octagonal aquarium was aligned towards the north equally much during tests in both magnetic field conditions. The tests in a series with one animal were performed in random order.

Data analysis

During a test the eel was photographed every 10th minute. The eel's snout and anal fintip position were recorded on a digitizer connected to a microdator. Locomotor activity was measured by counting the number of times an eel had moved more than a certain distance from one photograph to the next. The preferred orientation angle of an eel was estimated in two ways from each photograph. First, from the direction of the center of the aquarium towards the eel's snout, and secondly from the body axis direction of the anal fintip to the snout (Fig. 2). All angles recorded were also doubled to test for a possible bimodal orientation (Batschelet, 1981). As serial registrations on a behavioural parameter in a single test are normally not independent, only one observation per test was used in statistics. This consisted of a circular mean calculated from the maximal 78 registrations of preferred angles from the entire 13 h dark period in one test. Such mean angles were named A_s for snout method and A_b for body axis method. Second order means were then calculated on the basis of these A values for all experiments performed in the same magnetic field with one eel. Such means were tested for divergence from a random distribution according to the Rayleigh test (Batschelet, 1981).

Normally the next step in the analysis would have been a summing over all examined individuals, to obtain a common mean value for the entire population. As will be shown later on, specimens differed in their preferred orientation, so that approach was not suitable. Here instead each individual was used as its own control to compare the preferred direction in both types of magnetic field. This was performed by a

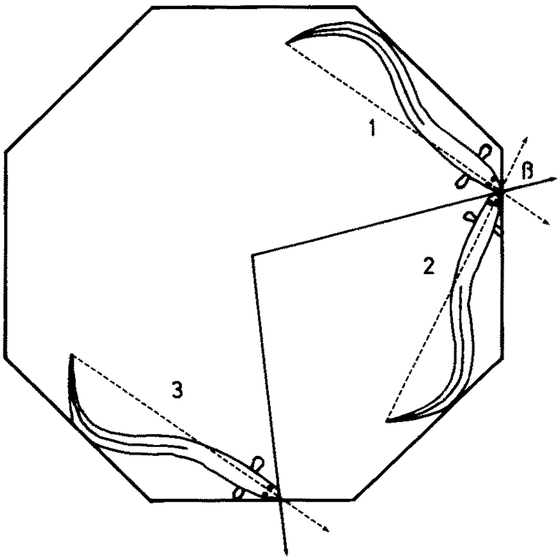

Fig. 2. Scheme showing an eel in three variants of a normal position. Orientation was recorded both as direction from the centre of the aquarium to the eel's snout (full line) and as direction of the eel's body axis (dotted line). The orientation recorded by the two methods will normally differ (β in 2). In (1) and (2) orientation angles recorded for the snout method are similar, but differ for the body axis method, while the opposite is true regarding (1) and (3)

comparison of A values in both magnetic fields in each series by the nonparametric Mardia-Watson-Wheeler test (MWW test). To obtain an estimate of the probability that all tested eels, regarded as a group, changed their preferred direction when the magnetic field regime was altered, the technique was used of summing exact p-values from independent tests (Sokal & Rohlf, 1969). Exact P-values for the MWW tests were obtained from statistical tables, supplemented by values from a χ^2-approximation proposed by Mardia (1967).

Experimental series

Part A. Two eels, Nos 1–2, were tested one at a time. The experiments were performed in a barn situated 20 km north of Uppsala. The barn was completely undisturbed by human activities. Square Helmholtz coils were used, the distance between them was 77 cm and each side measured 140 cm in length. Measurements with a gauss meter in the experimental tank showed that the coils gave a variation in intensity of the reversed field of less than 5 % of the intensity of the natural field. The light intensity during day time was 90–110 lux.

Part B. Four eels, Nos 3–6, were used two at a time. The same coils were utilized as in A. Tests were performed in a suburban garden on the southern outskirts of Uppsala. A transparent plexiglass sheet was fitted at 9 cm above the aquarium bottom, and one eel was placed on each floor.

Part C. Five eels, Nos 7–11, were tested one at a time. Experiments were performed in the same garden as in B. Octagonal Helmholtz coils were utilized, measuring 199 cm in diameter and standing 100 cm apart. When powered the coils gave a magnetic field intensity variation of less than 4 % from natural intensity. The light intensity during the day time was 0.08–0.10 lux.

RESULTS AND DISCUSSION

An eel in the experimental tank normally stayed near the wall both during the day and at night (Fig. 2). Eels tested in a daytime light intensity of 100 lux in A and B, were more active during the light period (Fig. 3). As it seemed probable that the behaviour

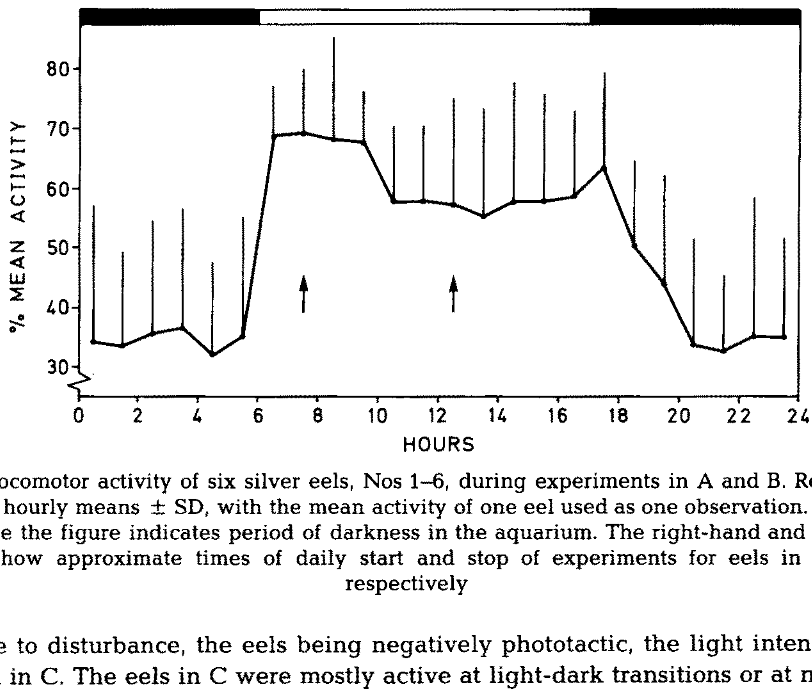

Fig. 3. Locomotor activity of six silver eels, Nos 1–6, during experiments in A and B. Results are given as hourly means ± SD, with the mean activity of one eel used as one observation. The dark bar above the figure indicates period of darkness in the aquarium. The right-hand and left-hand arrows show approximate times of daily start and stop of experiments for eels in A and B respectively

was due to disturbance, the eels being negatively phototactic, the light intensity was lowered in C. The eels in C were mostly active at light-dark transitions or at night.

The diurnal activity of the eels in parts A and B was surprising in the light of results from other studies, where the animals have been almost exclusively nocturnally active (Bohun & Winn, 1966; Edel, 1975, 1976, 1979). Edel (1975, 1979) concluded that silver eels both with and without shelter show a nocturnal activity pattern, though less pronounced in the latter case. At least in an early report (Edel, 1975) the eels used by him were not fully transformed from the yellow to the silver phase. The eels may thus have had the weaker yellow eel sensitivity to light (Bräutigaum, 1961a, b; Tesch, 1977), while the animals in the present study exhibited a more typical silver eel response, being more disturbed by a high light intensity.

As orientation to the magnetic field may have occurred, though the Rayleigh test was not significant, here mostly results will be dealt with from MWW tests. Summed probabilities for MWW tests in A showed that there was a significant difference in preferred orientation between magnetic field regimes (snout $P = 0.004$ and body axis $P = 0.07$) as indicated by Fig. 4 and Table 1. In B, two eels were tested at the same time.

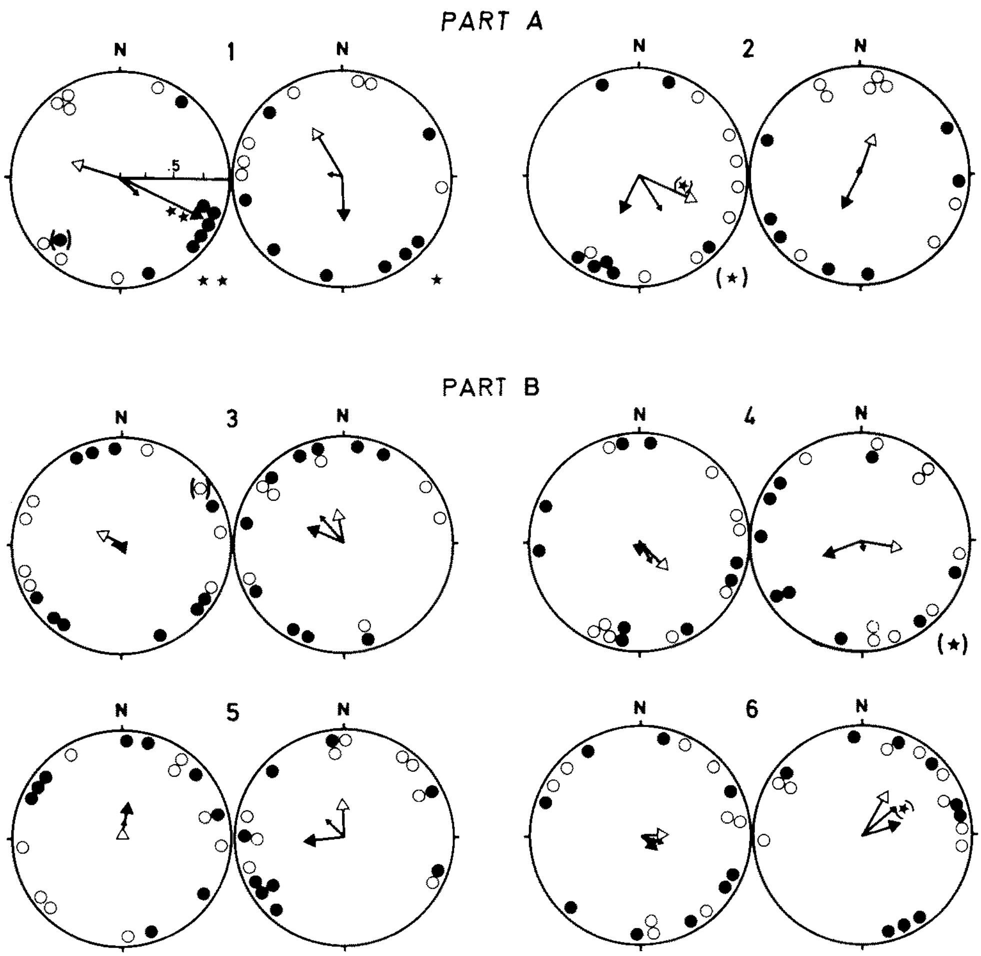

Fig. 4. Directions chosen by silver eels in parts A and B. Eel numbers are given above each pair of diagrams. The left-hand one shows orientation according to the snout method and the right-hand according to the body axis concept. North is upward as shown by the N above each diagram. In diagrams each dot indicates the circular mean orientation during one night. Tests with the degree of concentration, r, lower than 0.03 are excluded from statistics, yet shown in brackets. Arrows are mean vectors. Small arrow-heads indicate means for the total series. Larger arrow-heads and dots which are filled indicate natural magnetic field tests, similar unfilled symbols represent reversed magnetic field. The result of a Rayleigh test is shown beside each mean vector. Significance levels according to a Mardia-Watson-Wheeler (MWW) test are stated below to the right of each diagram. Significance levels are: $p > 0.10$, not shown; $0.10 >= p > 0.05$, (*); $0.05 >= p > 0.01$, *; $0.01 >= p > 0.001$, **; $0.001 >= p$, ***

It proved difficult to distinguish between eels on different floors and records from many photographs had to be discarded. Only eel No. 4 showed a low probability for a differing orientation in a MWW test employing the body axis method. Evidently the technique in B was not appropriate, so no great importance should be attached to these results. In part C, combined MWW tests showed significance for body axis method ($P = 0.04$),

Table 1. Mardia-Watson-Wheelers test on differences in orientation of silver eels in magnetic fields of opposite directions. Single angles indicate a test for unimodal orientation and double angles an analysis of bimodal orientation. Significance levels as in Fig. 4

Part	Eel No	P-values Single angles Snout	P-values Single angles Body axis	P-values Double angles Snout	P-values Double angles Body axis
A	1	0.004 **	0.05 *	0.30	0.43
	2	0.10 (*)	0.29	0.95	0.45
	Σ	0.004 **	0.07 (*)	0.64	0.51
B	3	0.48	0.91	0.58	0.50
	4	0.99	0.09 (*)	0.12	0.81
	5	0.64	0.25	0.36	0.85
	6	0.85	0.97	0.55	0.99
	Σ	0.95	0.46	0.38	0.98
C	7	0.07 (*)	0.10 (*)	0.08 (*)	0.33
	8	0.37	0.41	0.41	0.80
	9	0.10 (*)	0.04 *	0.80	0.51
	10	0.80	0.04 *	0.41	0.32
	11	0.77	0.90	0.48	0.05 *
	Σ	0.24	0.04 *	0.40	0.27

though eel No. 11 did not contribute to the significance but instead oriented bimodally significant according to the body axis method (Fig. 5, Table 1).

Totally in A, B and C four and five eels showed $p <= 0.10$ in MWW tests according to snout and body axis concept respectively. As these specimens were the main contributors to the overall significance, it was decided to make a comparison of the preferred directions of these eels. The preferred orientation differed between animals in three out of four cases (Fig. 6). In the fourth case, body axis natural field, the reason for the absence of significance was mostly a low degree of concentration, as measured by the mean vector, for eel No. 10 in particular.

To examine whether individual peculiarities in behaviour in the tank might act upon the difference in orientation, A_b values were diminished by A_s angles for all tests with each eel (explained by Fig. 2). The resulting angles had a circular distribution with a mean vector significant at $p < 0.05$ for all eels tested according to the Rayleigh test, indicating a relationship between the snout and the body axis concept. The mean angles varied from 329.7° to 54.2° and the mean vector 95 % confidence interval did not include the 0°-point for four eels. Three of them, Nos 1, 3 and 7, deviated clockwise and one, No. 6, anti-clockwise. An inspection of the films showed that these eels relatively consistently swam clockwise or anti-clockwise throughout the test series, while the behaviour of the others was more varied. The type of swimming, whether clockwise or anti-clockwise, may have caused the difference in preferred direction between eels. A comparison of eels Nos 1 and 7 (Fig. 6), which both swam clockwise to a comparable degree and oriented significantly to the geomagnetic field according to MWW tests, showed, however, that a difference in preferred directions probably occurred also in this case (natural field snout $p < 0.05$, body axis $p = 0.10$; rotated field snout $p > 0.10$ and

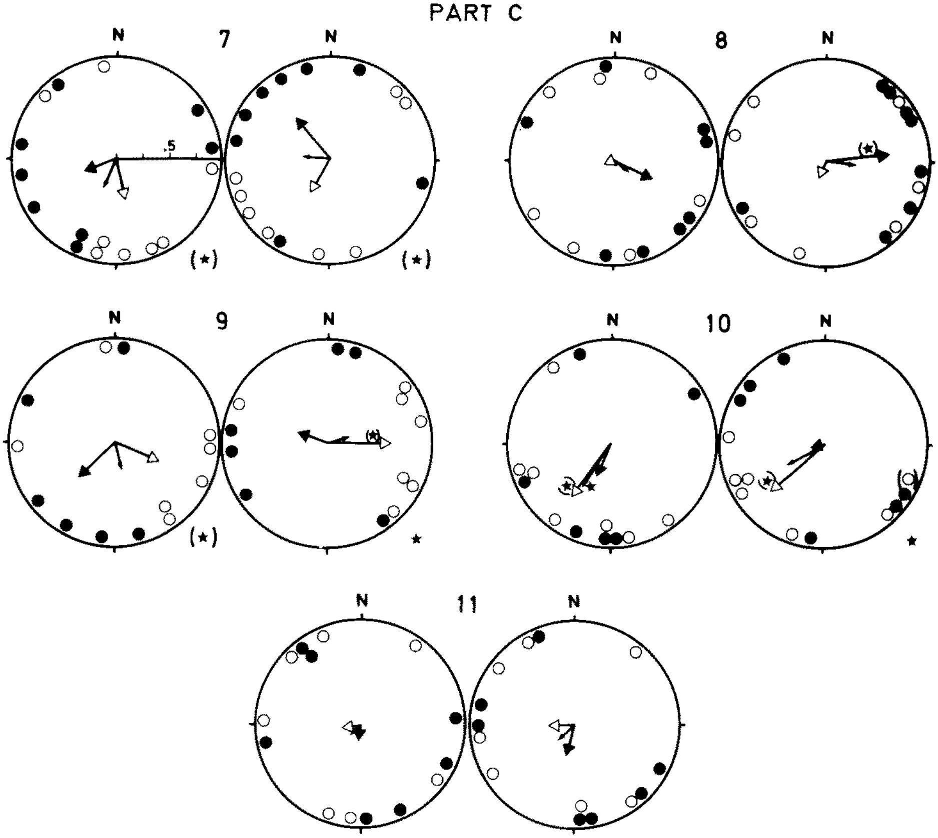

Fig. 5. Directions chosen by silver eels in part C. (Explanations as in Fig. 4)

body axis $p < 0.05$). As only two individuals can be compared in this aspect, this difference may depend on individual variation.

The eels reacted to the geomagnetic field, as the individuals changed their preferred direction when the magnetic field regime was altered. The basis for this conclusion is that the experiments with differing magnetic field direction were performed in random order. No type of non-magnetic phenomenon should be able to cause significance under these circumstances.

There is no indication of which of the two orientation measures was best to evaluate orientation. In part A the snout method gave the highest significance and in part C only the body axis method provided significant results. An animal in the experimental tank often swam and lay with its hindquarters in close contact with the wall (Fig. 2) owing to the strong thigmotactic tendencies of eels (Tesch, 1977). Evidently an eel's "real" orientation direction to a compass cue may be different from the preferred direction, recorded by any of the two methods, due to the thigmotaxi. Presumably also the orientation strength will be affected. It is not stated whether eels preferentially swam along the walls in earlier tank studies (Miles, 1968; Tesch & Lelek, 1973a, b; Tesch, 1974). There several fish were used simultaneously and as the individuals were probably not distinguishable, no individual characteristics in swimming directions could be detected. In the present experiments the differing swimming direction combined with thigmotaxis may explain a substantial part of the variation in preferred directions. On the other hand, the difference in preferred directions between eel Nos 1 and 7 may be associated with other factors not necessarily connected to the thigmotactic behaviour. Moreover the fact that eel No. 10 oriented significantly differently in both the magnetic fields, though the mean vectors differed by only a few degrees, suggests that orienting

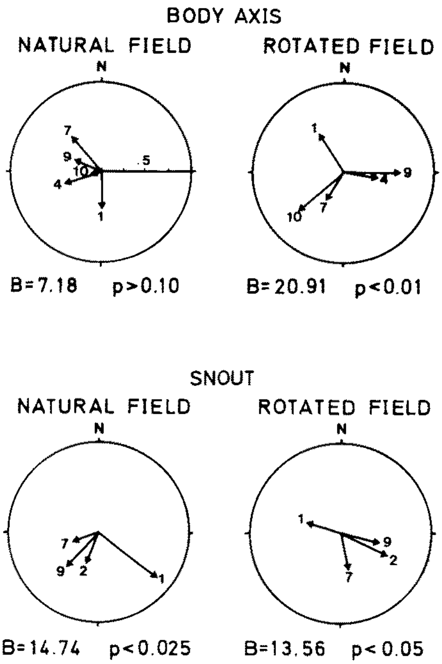

Fig. 6. Mean vectors for individual eels in A, B and C showing p < = 0.10 according to a MWW test for differing orientation in experiments performed in natural and reversed field. Eel numbers are given at the tip of each arrow. The result of a multi MWW test for difference in orientation between eels is given below each diagram

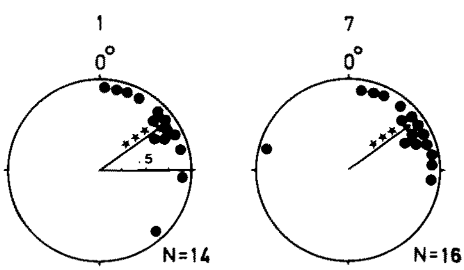

Fig. 7. Consistency in swimming behaviour of two silver eels, Nos 1 and 7, during experiments. Dots are mean angles for single experiments according to the body axis method, A_b, subtracted by mean angles recorded for the snout method, A_s (explained by Fig. 2). Arrows are mean vectors. (Other explanations as in Fig. 4)

factors other than the magnetic field may be available to animals in the tests. The fact that the experimental eels were held in captivity at least 16 days and at most 5 months before tests, may perhaps also influence their preferred orientation.

On the basis of his tank experiments and tracking studies in coastal areas, Tesch (1980) suggested that European silver eels use the earth's magnetic field as a cue to migrate in a westerly to northerly direction when in the sea on the continental shelf. The present results do not give any substantial basis for assessment of the role magnetic stimuli may have under in-situ conditions. However, if eels show directional responses in behavioural experiments of the present type, it seems natural to assume that the animals also may use magnetic directive information during the migration. The perception method for the geomagnetic field is unknown, but silver eels contain magnetic material in association with bone (Hanson et al., 1984). Magnetic crystals are used by some bacteria for magnetoreception and may also be used by higher animals for this purpose (Kirschwink & Gould, 1981).

In conclusion, the present form of tank technique may be used to detect the presence of orientation, in form of directional responses, to the geomagnetic field. As eels will differ in orientation due to differences in general behaviour in the tank, such as swimming direction, the method is not entirely suitable for assessment of whether eels possess a magnetic compass comparable to that of some passerine birds (Wiltschko & Wiltschko, 1976). An exception would be if the difference in orientation due to the thigmotactic behaviour was small and a large number of animals were tested. However, a more functional development of the technique will require recording of orientation more directly, in an environment better adapted to the eel's natural behaviour.

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