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Influence of geomagnetism and salinity on the directional choice of silver eels (*Anguilla* sp.)

by

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Abstract

The directional preferences of 25 silver European eels, *Anguilla anguilla*, and American eels, *Anguilla rostrata*, have been studied by photographic methods in a circular tank under different conditions of geomagnetic field, in sea water and in fresh water. Movement of eels during recording was quite restricted. Under the influence of a normal geomagnetic field and maintenance in sea water, the eels preferred the directions North and South as partly found in previous investigations. Reduction of the horizontal North component of geomagnetism to about zero resulted in a significant directional choice to the East, by eels in all three samples (eels from the estuary and the Hamburg area of the Elbe River and from Rhode Island) compared with the control. Reversal of the magnetic North component to the South caused no consistent change. In fresh water and under either a reduced or reversed horizontal geomagnetic field the eels exhibited a directional choice to the right of the controls. In all nine examinations under different magnetic conditions in fresh water a directionel preference between 93° and 184° (SE) was found. In four cases this preference was in addition to one in the opposite direction. A discussion is presented which concerns the differences observed in field and in laboratory studies and the possibilities of magnetical or electrical stimulation. An ecological example from the Elbe estuary is given which

demonstrates the combined action of geomagnetism and salinity on migratory orientation of silver eels. From the laboratory experiments it seems obvious that in eels which during their down stream migration reach the North Sea the saline water activates a northward swimming; the directional stimuli are caused by influences of the geomagnetic field.

Introduction

European eels Anguilla anguilla on their spawning migration in the North Sea obviously swim on a compass course which is directed in a northern to northwestern direction (Tesch, 1972, 1974). The mechanism which enables the silver eels to have a constant directional choice is unknown. Silver eels investigated in a circular tank exhibited a similar directional preference, provided the test animals were caught during their migration in the Elbe estuary and transported immediatly in sea water tanks to the laboratory on the Island of Helgoland to be examined a few days after capture (Tesch and Lelek, 1973 a). The results of the laboratory investigations rule out that visual stimuli, olfaction pressure or perception of the stream flow provided cues for the directional constancy.

Branover et al. (1971), Vasilyev and Gleiser (1973) and Vasilyev et al. (1973) observed in glass eels and older juvenile stages of A. anguilla the ability to respond to changes in the magnetic field. The capability to "perceive" the direction of magnetic fields suffered if strong artificial magnetic fields were induced. Other investigations demonstrated that eels can perceive very weak electric fields. It was supposed that magnetohydrodynamical effects which produce electrical fields could be involved (McCleave et al., 1971; Rommel and McCleave, 1973).

Using the method of photographing the directional choice of silver eels in a circular tank, it is also possible to examine the directional behaviour under conditions of a changed geomagnetic field. The results presented here were obtained by this technique and include the use of Helmholtz coils for the generation of artificial magnetic fields.

Material and Methods

Migratory European eels in the so-called silvery stage (body length 3o - 4o cm) were selected from commercial catches in two locations of the River Elbe. Nine males were from fyke-net catches in Hamburg harbour on August 26 and 27, 1973. Examination of these eels took place from August 28 to September 5, 1973. Eleven males were caught at the end of October in the Elbe estuary in the same location (Brunsbüttel as described by Tesch and Lelek (1973 b) by a cutter with a framed gape net (a stow net). They were examined from November 6 to 11, 1973. Five female silver American eels (Anguilla anguilla) about 7o cm long were caught by commercial fisherman near Kingston, Rhode Island (USA), They were flown to Hamburg at the end of October 1973 immediately after capture, and were examined on October 3o and from November 19 to 29,1973.

The eels were maintained in fresh water at 12° to 14°C. Water temperatu[illegible] in the experimental tank was 14° to 15°C. One set of experiments was conducted in fresh water (tap water); another set was performed in sea water transported to Hamburg from the Helgoland area. The salinity was > 3o ‰.

The plastic circular tank (1 m diameter, 5o cm height, water level 35 - 4o cm with a bottom of transparent plexiglas) and the recording camera, as well as all other experimental installation and procedure, were the same as described earlier (Tesch and Lelek, 1973 b). Instead of a metal stand and a plastic cover, fibreglass reinforced polyester tube-like stand was installed underneath the circular tank to eliminate interference with the magnetic field (Fig. 1). During observation periods the eels were kept in total darkness except during photographic recording (every 1o to 3o min) by flash illumination.

The circular tank was framed by two square, wooden Helmholtz coils (Fig. 2) 2 m on a side. The distance between coils was 1.o6 m. Coils each had 25 turns of 4.5 mm copper wire and were connected in series. The current was taken from the mains supply through a rectifier and could be adjusted from 0 to 8 amps. An ammeter indicated the current.

The total intensity of the geomagnetic field (F) in Hamburg is about o.48 Gauss, the horizontal intensity (H) o.18 Gauss and the inclination (I) 68^{o}. In the circular tank in the basement laboratory of the Biologische Anstalt Helgoland in Hamburg (BAH) the north component of the horizontal field (X) measured by means of a Foerster Sonde was o.18 Gauss. The east component (Y) amounted to $<$- o.o1 Gauss. Compensation

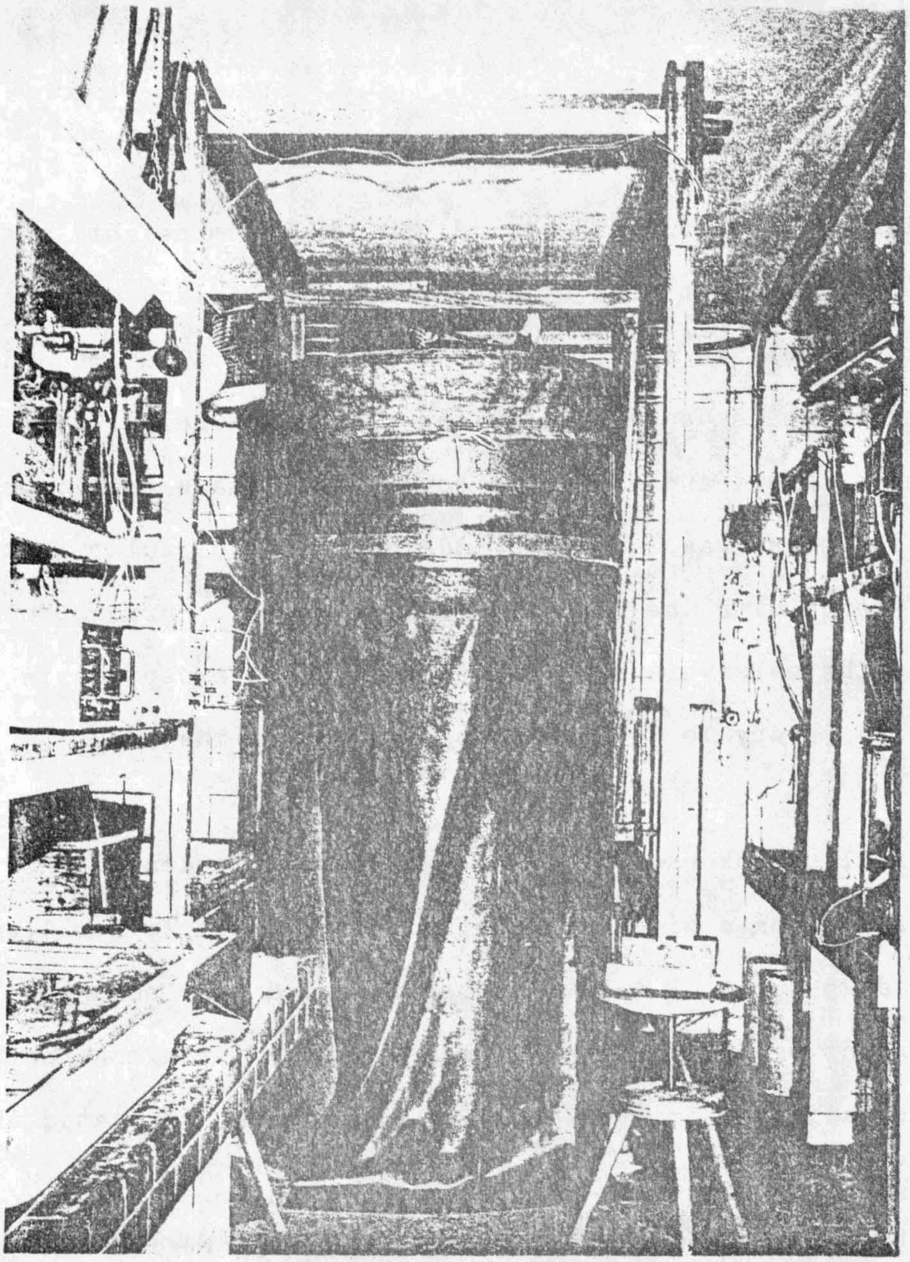

Fig. 1 The experimental arrangement. In the center is the fibreglas reinforced polyester stand with the circular tank on top of it, on the left and right sides parts of the Helmholtz coils, on the left margin outside of the coils the power supply and timing apparatus for the camera.

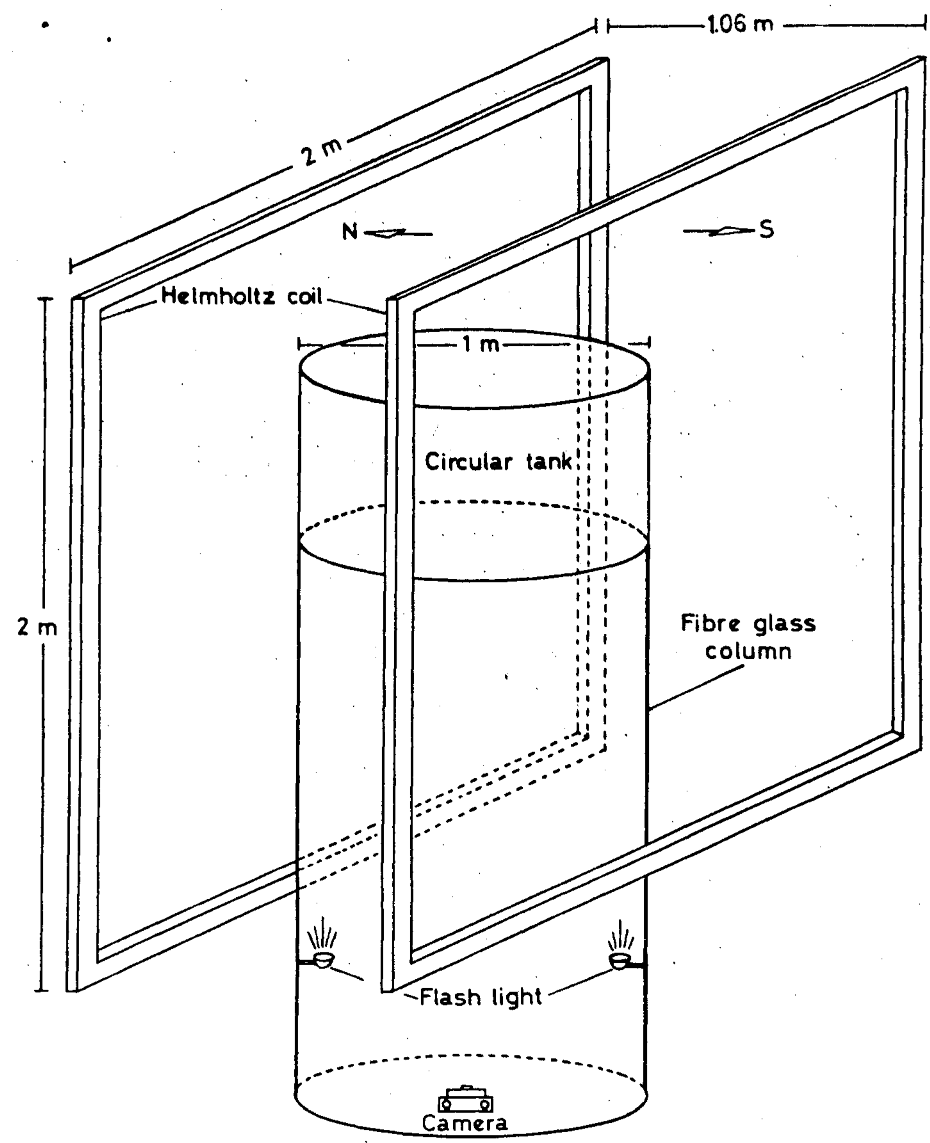

Fig. 2 Coil arrangement around the circular tank and dimensions.

of X by current flow through the Helmholtz coils to a value of about zero was effected by a current of o.8 A; reversal of X (geographic North to South) was attained at 1.7A. If, at compensation of X to zero in the centre of the bottom of the circular tank, a value of o.ooo Gauss was measured, at some peripheral points of the tank X amounted to a value not higher than o.oo5 Gauss.

Examination of the directional position of the eels took place with X compensated to zero, with X reversed from North to South, and with normal X relationships in the BAH laboratory as a control. Each examination last 17 to 22 hours (in two cases 4.5 or 12 hours) including the night period. As in earlier experiments (Tesch and Lelek, 1973 b) day and night results were compared and no difference was found, if there was sufficient material for a comparison.

The mean angle (direction), the concentration, and the angular deviation were calculated (Batschelet, 1965). The statistical treatment of the results was performed as proposed by Batschelet (1965): a χ^2 test to determine if a non-uniform circular distribution was present (see also Tesch and Lelek, 1973 a,b); the Rayleigh test (critical test value) to determine if the concentration around a preferred direction is significant; a non-parametric two-sample test (also a χ^2 test) to determine if the preferred direction of two samples are significantly different provided the angular deviation of the two samples is comparable in size. A difficulty arose since many of the circular distributions resulted in a bimodal distribution, as found earlier (Tesch and Lelek, 1973 a). For this reason, in all cases in which a bimodal distribution was found, the calculation of the mean angle was performed by the method of "doubling the angle" (Batschelet, 1965). The Rayleigh test was also performed by this method and two sample tests between bimodal distribution samples. A bimodal calculation was conducted in each sample which exhibited no significance by unimodal treatment through the Rayleigh test. Smoothing of the circular distribution rendered no better test results, but smoothed graphical illustration (Fig. 4 and 5) presents the differences more clearly. The procedure for smoothing the single directional frequences (fm) was a follows:

$$fm = \frac{fm - 1 + 2\,fm + fm + 1}{4}$$

Results

A summary of the circular distributions exhibited by the different experiments is given in Table 1. Table 2 presents the mean angles and their level of significance, and Table 3 the mathematical-statistical treatment of the differences. The preferred directions of all silver eels treated in sea water or in fresh water deviated to the right (increase of t e azimuth angle between 5° and $11o^{\circ}$) if the North geomagnetism (X) was compensated to zero (Fig. 3). Fig. 4 presents an example of these differences by means of a circular distribution graph. Reversal of the North magnetism (X) from North to South resulted in no consistent change of the azimuth angle, although in fresh water an increase occurred in all three cases. The most striking findings were the differences between the directional behaviour in sea water and fresh water (Fig.3). In sea water both the controls and the eels under a reversed magnetic field (X) travelled north- or southward. If the field was compensated to zero they pointed in an easterly direction. In fresh water the preferred direction was turned right, i. e. southeast under all three experimental conditions or, to a lesser degree, in the opposite direction. The general impression is that either compensation of the North magnetism to zero or change from sea to fresh water altered the directional choice from a northern or southern direction to an eastern or, to a lesser degree to a western direction.

Tab. 1 Silver eels (A. anguilla and A. rostrata) recorded on film in their compass-direction sections under different conditions in the circular tank

Locality of capture	Salinity during observation	North component of the geomagnetic field	Number recorded pointing into different compass direction sections									Number of individuals
			N	NE	E	SE	S	SW	W	NW	total	
Elbe near Hamburg	seawater	normal (control)	102	111	81	71	106	113	68	86	738	9
Elbe near Hamburg	seawater	compensated to zero	84	96	95	104	111	82	81	80	733	9
" " "	"	reversed to South	95	85	61	77	87	78	60	105	648	9
" " "	freshwater	normal (control)	107	98	95	122	88	90	72	83	755	9
" " "	"	compensated to zero	93	87	71	110	96	87	58	63	665	9
" " "	"	reversed to South	24	21	21	48	32	19	28	30	223	9
Elbe estuary	seawater	normal (control)	132	110	110	104	127	127	99	137	946	11
" "	"	compensated to zero	96	100	72	104	71	81	84	80	688	11
" "	"	reversed to South	99	82	62	86	85	118	72	75	679	11
" "	freshwater	normal (control)	69	77	63	103	99	72	88	97	668	11
" "	"	compensated to zero	74	70	119	108	108	106	68	74	727	11
" "	"	reversed to South	103	72	93	107	126	115	78	78	772	11
Rhode Island, USA	seawater	normal (control)	45	54	49	43	68	60	40	51	410	3
" " "	"	compensated to zero	45	48	52	48	47	34	37	47	358	3
" " "	"	reversed to South	39	53	49	47	57	57	38	62	402	3
" " "	freshwater	normal (control)	22	35	43	37	34	21	18	15	225	3
" " "	"	compensated to zero	60	43	47	67	44	46	36	45	388	3
" " "	"	reversed to South	41	43	38	52	59	55	45	75	408	3

Tab. 2 Silver eels (A. anguilla and A. rostrata) mean directions and examination of significance

Locality of capture	Salinity during observation	North component of the geomagnetic field	mean direction calculated unimodal	z-value of Rayleigh-Test calculated unimodal	Error P	mean direction calculated bimodal	z-value of Rayleigh-Test calculated bimodal	Error P	X^2	Error P smaller than
Elbe near Hamburg	seawater	normal(control)	11,5°	o,o4	>5 %	24,4°	1o,8	<1 %	24,6	o,1%
" " "	"	compensated to zero	134,3°	57,2	<1 %				1o,5	3o%
" " "	"	reversed to South	337,1°	1,9	>5 %	12,3°	6,9	<1 %	2o,9	1%
" " "	freshwater	normal(control)	93,o°	4,2	<5 %	164,4°	1,4	>5 %	17,2	2,5%
" " "	"	compensated to zero	128,o°	5,2	<1 %				26,5	o,1%
" " "	"	reversed to South	159,7°	1,9	>5 %	14o,2°	6,7	<1 %	22,1	1%
Elbe estuary	seawater	normal(control)	3o3,8°	o,9	>5 %	2,3°	2,7	<5 %	11,9	3o%
" "	"	compensated to zero	78,2°	15,9	<1 %				12,9	1o%
" "	"	reversed to South	214,8°	1,7	>5 %	19,o°	5,9	<1 %	24,7	o,1%
" "	freshwater	normal(control)	2o9,2°	1,8	>5 %	144,2°	4,3	<5 %	19,5	1%
" "	"	compensated to zero	149,4°	13,o	<1 %	115,1°	o,1	>5 %	34,5	o,1%
" "	"	reversed to South	184,o°	7,1	<1 %				27,6	o,1%
Rhode Island, USA	seawater	normal(control)	182,4°	1,1	>5 %	3o,7°	2,4	>5 %	11,8	3o%
" " "	"	compensated to zero	74,3°	2,o	>5 %	141,5°	o,5	>5 %	5,8	7o%
" " "	"	reversed to South	193,3°	o,3	>5 %	3,1°	o,2	>5 %	1o,5	3o%
" " "	freshwater	normal(control)	1o9,3°	12,7	<1 %				26,5	o,1%
" " "	"	compensated to zero	356,2°	1,5	>5 %	156,2°	2,5	>5 %	14,5	5%
" " "	"	reversed to South	252,3°	2,7	>5 %	15o,2°	2,8	>5 %	2o,1	1 %

Tab. 3 Silver eels (A. anguilla and A. rostrata) mean compass directions under different conditions compared by a nonparametric two-sample test (X^2).

In controls, North component of geomagnetic field normal

	Controls		Comparisons			Experimental:		
Location of capture	Salinity during observation	uni- or bi-modal character of distribution	bi- or uni-modal calculation	X^2 test	error P smaller than	uni- or bi-modal character of distribution	Salinity during observation	North component of geomagnetic field
Elbe near Hamburg	sea water	bi	bi	1o.2	2.5%	uni	sea water	compensated to zero
" " "	" "	bi	bi	1o.3	2.5%	bi	" "	reserved to South
" " "	" "	bi	bi	1o.8	2.5%	uni	fresh water	normal (control)
" " "	fresh water	uni	uni	4.7	7o.o%	uni	" "	copensated to zero
" " "	" "	uni	bi	7.3	1o.o%	bi	" "	reserved to South
Elbe estuary	sea water	bi	uni	15.8	5.o%	uni	sea water	compensated to zero
" "	" "	bi	uni	11.4	3o.o%	bi	" "	reserved to South
" "	" "	bi	bi	4.4	3o.o%	bi	" "	reserved to South
" "	" "	bi	uni	17.3	2.5%	uni	fresh water	normal (control)
" "	fresh water	bi	uni	28.o	o.1%	uni	" "	compensated to zero
" "	" "	bi	bi	8.o	5.o%	uni	" "	reserved to South
" "	" "	bi	uni	21.1	2.5%	uni	" "	reserved to South
Rhode Island, USA	sea water	bi	bi	3.7	3o.o%	uni	sea water	compensated to zero
" " "	" "	bi	uni	8.2	5o.o%	uni	" "	compensated to zero
" " "	" "	bi	bi	2.5	5o.o%	-	" "	reserved to South
" " "	" "	bi	bi	2.6	5o.o%	uni	fresh water	normal(control)
" " "	" "	bi	uni	18.6	1.o%	uni	" "	normal(control)

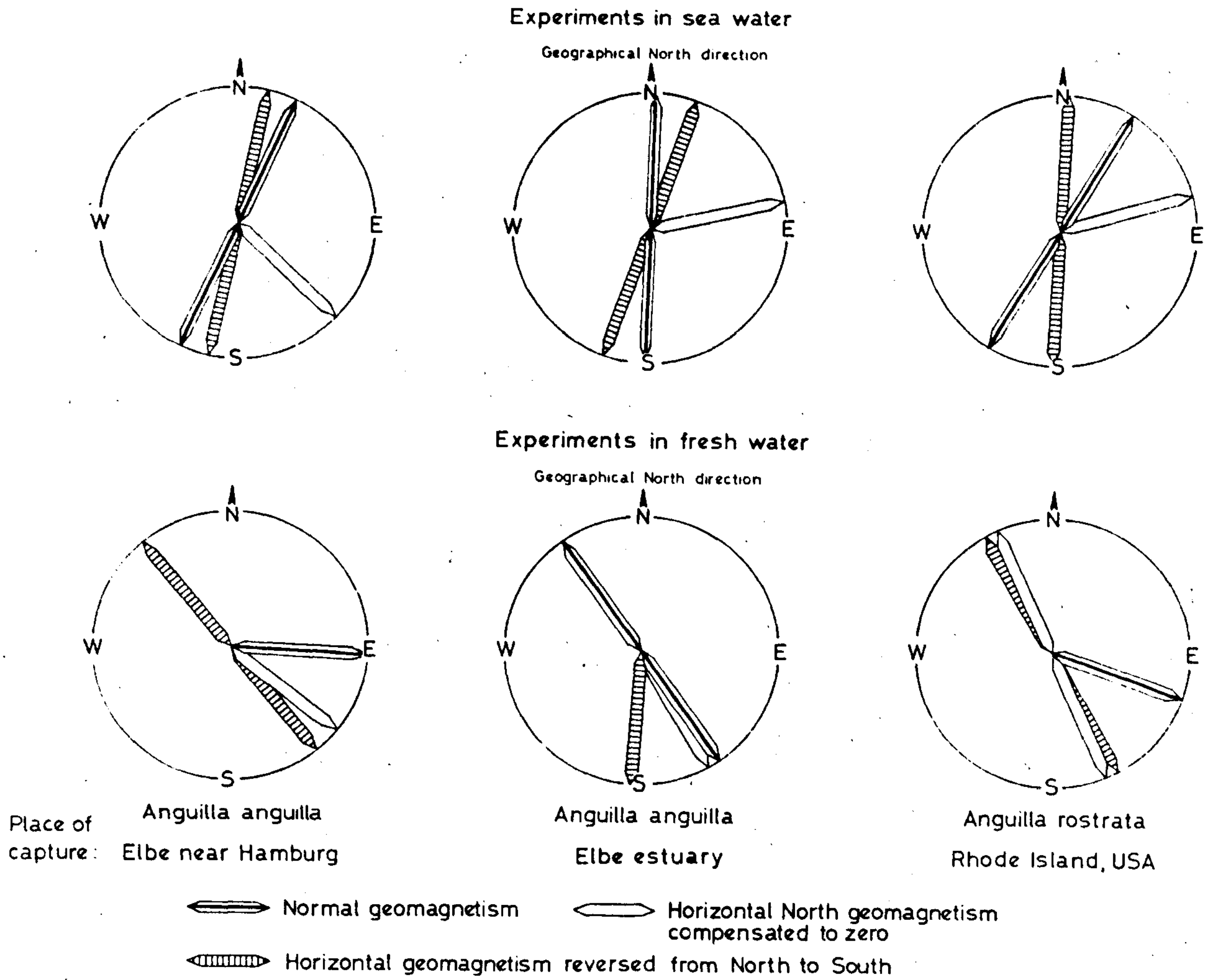

Fig. 3 Mean directional preferences of <u>Anguilla anguilla</u> and <u>Anguilla rostrata</u> examined under different conditions, of the geomagnetic field, in sea water and in fresh water and from different locations.

The Rayleigh test indicated significance for all results obtained from A. anguilla, except the controls of the Elbe estuary, if the highest values are always taken whether from unimodal or bimodal treatment (Tab. 2). Also the x^2 test (test of fit) exhibited high significance for most values, or in two cases, slightly below the 9o % level. Generally not significant are the Rayleigh test values observed in A. rostrata which is probably due to the small samples and number of observations. The x^2 test was more useful. A comparison of the differences between experimental groups on the basis of the x^2 test is presented by Table 3. In A. anguilla the striking differences between sea and fresh water treated animals mentioned is accentuated by significant x^2 values (both samples 2.5 % error). The same is true if the values from eels under compensated conditions and controls are compared (2.5 % and 5 % error).

Although on the basis of the comparatively small sample size of A. rostrata directional concentrations of the circular distributions and their differences are mostly uncertain, a representation of the distribution graphically on the basis of a linear distribution seems to deliver clear results (Fig. 5). It becomes evident from the graph that eels in a compensated field exhibit a completely different (i.e. shifted by 9o^{o}) directional behaviour compared with controls. This is in agreement with the results on A. anguilla (e. g. Fig. 4).

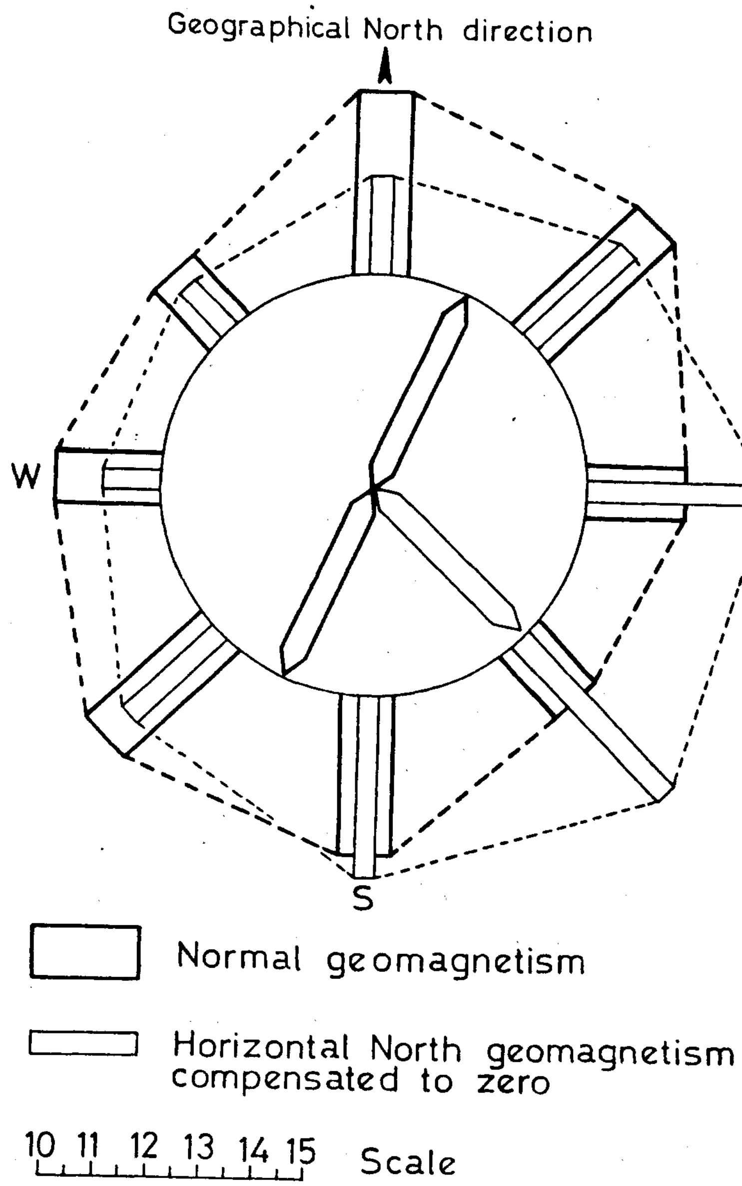

Fig. 4 Directional choice (in percent) of <u>Anguilla anguilla</u>, from the Elbe river at Hamburg examined in sea water, presented by a (smoothed) circular frequency distribution graph., with normal geomagnetic conditions (controls) and with North component of the horizontal geomagnetic field compensated to zero.

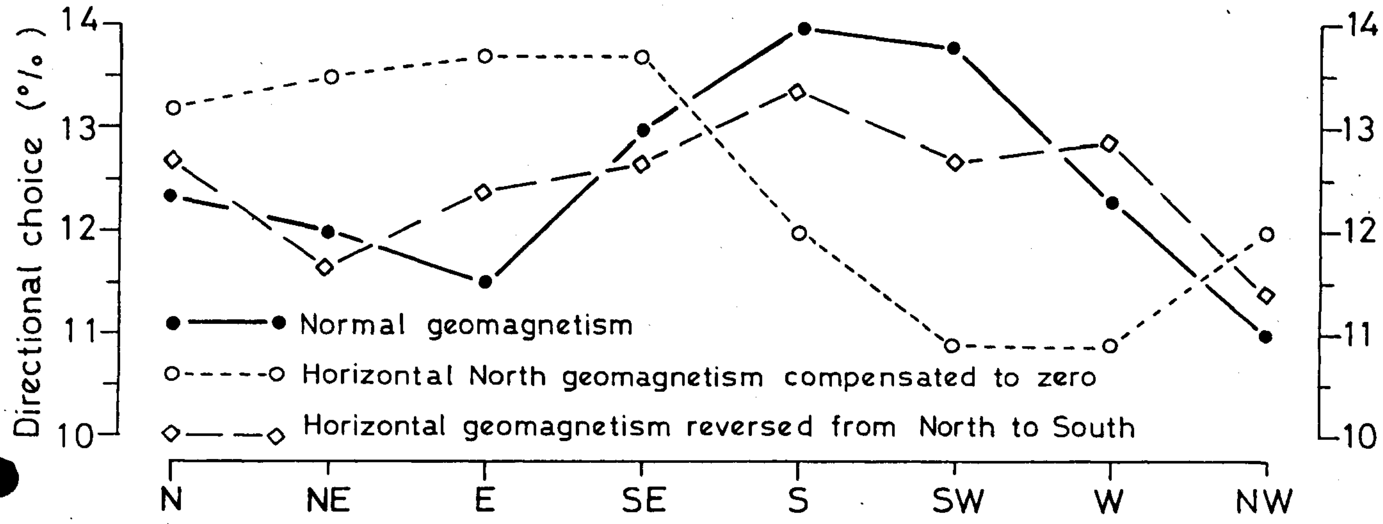

Fig. 5 Directional choice of Anguilla rostrata, examined in sea water, presented by a (smoothed) linear frequency distribution graph, with normal geomagnetic conditions, (controls) with the North component compensated to zero, and with the North component reversed to South.

Although in a small experimental tank like the one used effects such as generation of electric currents by means of the fish's movement through the geomagnetic field seems to be unlikely, some observations on change of position at shorter intervals than those mentioned (1o to 3o min) between the photographic recordings have been made. I took a picture of the eels position every 6 seconds so that nine comparisons of succeeding photos were possible. Out of 77 eel positions 41 (53 %) exhibited no positional change, others changes only slightly. It follows that movement is rare.

Discussion

These investigations have shown that the directional position of silver eels depends on the geomagnetical field. This is evident from the significant differences between the directional choice under a compensated horizontal North magnetism (X) and the controls of Anguilla anguilla in sea water, as well as from similar changes of direction in all three samples of Anguilla sp.. In fresh water the changes were not as clear as in sea water but the directional choice of A. anguilla in fresh water was significantly different from that in sea water. The same was probable in A. rostrata. The preferred direction in sea water was northern and in fresh water eastern to southeastern.(in one case also in the opposite direction). Reversal of the north component of the geomagnetic field (X) to geographic south caused no consistent angular changes.

A directional preference of North or South, as in the controls, was also found during earlier investigations (Tesch and Lelek, 1973) in eels examined in 1971 under normal conditions of geomagnetic field. This was especially true for yellow (stationary) eels as well as for silver eels which obviously were not completely ready for the spawning migration. Undisturbed migratory eels in 1971 preferred a North-West direction (321^{o}) with a high level of significance (Rayleigh test: $z = 14.1$; $p < 1$ %). The silver eels from the Elbe estuary in the present investigations were caught in 1973 at nearly the same place but were not as undisturbed as the 1971 specimens. After capture they were transported and maintained in fresh water and they had to endure a longer delay before examination. This may be the reason why the circular distribution is more bimodal than in 1971, but it is not bimodal enough for a high level of signifance. In addition, the number of measurements was not as great as 1971. The unimodal calculation of the mean direction results in a north-western direction ($3o3^{o}$; Rayleigh test: $z = o.9$; no significance) as in 1971.

The question now arises why, under the condition of the North geomagnetism (X) compensated to zero, the circular distribution is not uniform. We still always find an orientation to the east. This may be due to the fact that the horizontal magnetic field (H) also exhibits an easterly component ($Y <- o.o1$ Gauss), which after compensation of magnetic North supplies enough stimulation for further directional orientation. This would imply a very high sensitivity. Only compensation of Y to zero or reversal to the West can resolve this problem. Birds (Erithacus rubecula) have been shown to be disoriented if placed in rooms of a total intensity (F) less than o.3o Gauss, but adaptation to a weakend geomagnetic field was possible (Wiltschko, 1968). It also was found, that not only the horizontal component of the earth's field (X) but also the vertical component (V) was necessary for a directional orientation. Without V the robins had a bimodal directional choice. They measure the inclination (J) of the geomagnetic field lines (Wiltschko, 1972; Wiltschko and Wiltschko, 1972). In the eels a bimodal circular distribution was found only if F was normal and it became unimodal if the horizontal field (H) was weakend by reduction of X. An answer to the question of whether V is important for the orientation of eels only can be given, if results of experimental reduction of V are at hand. From the results presented it seems likely that a mechanism other than that evident from the birds is involved.

A directional choice dependent on geomagnetism was also found in juvenile eels (A. anguilla)by a quite different technique: the labyrinth method (Branover et al., 1971; Vasilyev et al., 1973). These as well as our own results imply that direct stimulation by magnetism is involved: the labyrinth examination, by the fact that strong magnetic fields rendered the eels incapable of orientation by means of magnetism; in the circular tank investigations, by the fact that only rare movement of the test animals in the tank was exhibited which means that hardly any induction and perception of electrical currents by the eels' movements through the earth magnetic field could occur. Electrical currents generated by water movement and their perception, as presumed by McCleave et al. (1971), can definitely be excluded. Tesch (1974) considers such a mechanism of orientation to be too complicated.

Ecologically very important is the influence of salinity on the directional behaviour of the eels, as evidenced by examination either in pure fresh water or in pure sea water. The degree of salinity is obviously of minor importance. The earlier investigations have shown that brackish water (one part sea water, two parts fresh water) induces a North or South preference of the silver eels (Tesch and Lelek, 1973b). The importance of salinity on the behaviour of juvenile eels under the influence of magnetic fields is also demonstrated by experiments of Vasilyev and Gleiser (1973). They found that increased salinity also augmented the effectivness of the magnetical field. The authors attribute these results to the increase in hydrodynamical effects (see discussion above) by augmentation of salinity.

The combined dependence of orientation on geomagnetism and salinity can explain many ecological problems in the eels migratory behaviour. One of these is the phenomenon that silver eels during their spawning migration approaching the Elbe estuary travel along the north bank of the Elbe.

During their migration in fresh water it is known that they drift in the central parts of the river in the main stream. However,when they contact the brackish water of the River Elbe they are only caught near the North bank, as evidenced by the strong concentration of cutters fishing with framed gape nets each migratory season at this special location. The salinity there is about 2 ‰ (Kühl and Mann, 1953). It is interesting that at this same location during their migration from the North Sea into the Elbe the elvers are caught in the highest concentrations (1971 Tesch). Probably, with a critical low salinity a change in orientation and behaviour of the elvers at this location occurs. From an ecological point of view, the salinity acts as releaser in the silver eel which produces activity and a swimming in the direction of magnetical lines, i. e. in the Elbe estuary and in the North Sea, northward, as demonstrated by results of telemetric ultrasonic tracking (Tesch, 1972, 1974) and conventional tagging and recapture (Lühmann and Mann, 1958).

Summary

1. A modified arrangement has been used for the photographic recording of the directional choice of silver eels (Anguilla anguilla and Anguilla rostrata) in a circular tank and under the magnetic action of a Helmholtz coil.

2. The movement of the eels in the experimental tank was very restricted as obvious by photographs taken every 6 sec.

3. Nine male specimens from the Elbe River near Hamburg, 11 male specimens from the Elbe estuary and 3 to 5 female specimens from Rhode Island USA, were examined for 17 to 22 hours, either in sea water or in fresh water, and yielded 225 to 946 photos for each examination.

4. In sea water eels of all three samples changed their preferred direction from north or south to east, when the normal horizontal north (X) component of the geomagnetic field was compensated to zero. (The east component (Y) remained unchanged (< -0.01 Gauss) during all observations). In fresh water, eels also preferred more easterly directions in the compensated field, but to a lesser degree.

5. Reversal of the horizontal North component (X) of the magnetic earth field to the South caused no consistent change in eels examined in sea water compared with the controls. In fresh water a slight but consistant dewiation to the right was observed.

6. Sea and fresh water controls including A. rostrata showed a significant directional difference; sea water specimens choose North or South; fresh water specimens selected East to Southeast.

7. Because of the very small sample of A. rostrata, differences in this species and compared with A. anguilla were mostly not significant. But in all cases the same tendencies as in the European eels have been observed.

8. The question of whether selection of swimming course is affected by the earth magnetic field itself or by magnetohydrodynamically produced electricity is discussed. Mechanisms of orientation under the influence of geomagnetism seems to be different from that observed in birds.

9. An ecological example from the Elbe estuary is given which demonstrate the combined action of geomagnetism and salinity on migratory orientation of silver eels. It is evident that the salinity necessary to release northward swimming is comparatively low; this was also obvious from the results of earlier laboratory investigations (Tesch and Lelek, 1973 b)

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