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Microelectronic detection of activity level and magnetic orientation of yellow European eel, *Anguilla anguilla* L., in a pond

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Synopsis

We studied the circadian and monthly activity, the distribution patterns, and orientation to the earth's magnetic field, of yellow (non-migratory) female eels in a freshwater pond by means of microchips injected into their muscles. Detectors for microchips mounted in tubes were placed in the pond to detect if eels oriented themselves with respect to earth's magnetic field. Based on the frequency of tube visits (search for shelter), the data indicated that the presence of eel in the tubes decreases gradually during the study period. We saw more activity during the night in the first months. There was a seasonal component in the orientation mechanism, with a significantly lower preference component in the summer compared to the fall. A preference for tubes oriented in a south-southwest direction (the direction of the Sargasso Sea) in fall suggests an orientation to the earth's magnetic field.

Introduction

Anguillid eels have a complicated life cycle, which takes place partly in freshwater, and partly in seawater. Little is known about this cycle, particularly the ecology or behaviour of the eels during the oceanic phase. Based on the work of Schmidt who caught leptocephali (the larvae of the eel) in the ocean, it is assumed that the spawning grounds of the European eel are 6000 km away in the Sargasso Sea (Schmidt 1923; Miller & McCleave 1994; Fricke & Kaese 1995). Transport of the leptocephali larvae by the sea currents, towards the coasts of Europe, probably lasts 1–3 years. It is probably not purely a passive process (Lecomte-Finiger 1994). On reaching the coasts of Europe, the larvae transform into glass eels. They can be observed in March–April in the North Sea and in July in the Baltic Sea.

When they invade the inland waters they develop pigmentation (Tesch 1977) and are called yellow eel. This is the juvenile life phase of feeding and growth. Gonad differentiation occurs during the time spent in fresh water. After this growth period, which last 3–12 years in males and 5–35 years in females, the animals prepare themselves for their return journey to the ocean. An enlargement of the eyes, a regression of the digestive tract and a silvering of the body color characterize this phase. However, little ecological information is available about this freshwater phase of several years prior to migration. Processes like circadian rhythm, annual activity patterns, hierarchy, foraging area and distribution patterns of eels in relation to season and age, and orientation on the earth's magnetic field need to be elucidated. The present work mainly concerns the observation of activity patterns of 40 female eels by means of microchips on a 0.8 ha pond during the first 7 months of a 2 1/2 year field research period.

The basis for the experimental set up with the tubes with electromagnetic detection is the behavioural response of eels to search for shelter. Probably this behaviour can be explained by the eel's vulnerability to predation in the shallow fresh water. Another possible explanation is that it is a way to protect itself against harmful environmental factors or a way to conserve energy (Edel 1975). The latter factor can be explained because an increase of activity is observed with decreasing shelter availability. This was indicated by Edel (1975) with the term 'negative skiasmokinesis' (skiasma = shelter, shade). Therefore, based on this behaviour, they will visit the tubes with microchip detectors (Figure 1). In this way the frequency of 'tube visit' (search for shelter) and preference position of eels in every tube can easily be measured, not only over the course of one day, but also over the seasons.

In order to investigate if eels orient themselves on the earth's magnetic field, the tubes in the pond were positioned in an alternating arrangement, in the direction of the Sargasso Sea (south–south-west), or opposite to it (west–north-west, see Figure 2). So, orientation on the earth's magnetic field can be investigated depending on the season.

This study will give information about the activity patterns and orientation in relation to the earth's magnetic field of European eel at the end of the fresh water period before the migration period in the ocean starts.

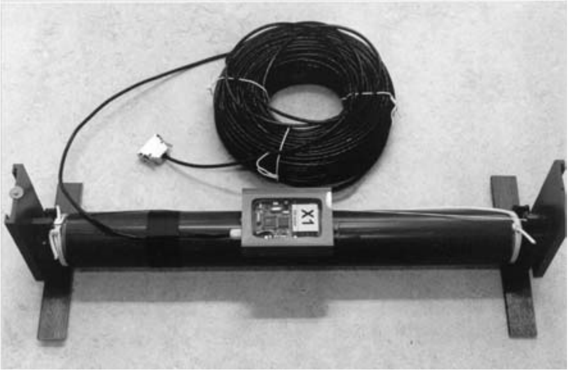

Figure 1. PVC-tube with Trovan detector (Trovan type LID656) in a waterproof box and a detection antenna. The antenna is a solenoid coil of 0.23 mH: 225 windings over a length of 67 cm and with a diameter of 7.5 cm. The coil is placed within the double walled skin of the PVC tube. All 48 detectors are individually linked by a waterproof cable (PUR-CY6x0.25) to 48 serial interfaces (Com ports) of a computer.

Material and methods

In June 1999, we placed 48 PVC tubes, with an inner diameter of 4.3 cm and a length of 80 cm, in a 1.5 m shallow pond of 0.8 ha (95 × 85 m). We mounted detectors for microchip transmitters on the tubes (Figure 1). The detector consists of a printed circuit board (Trovan type LID656) in a waterproof box, and a detection antenna. The antenna is a solenoid coil of 0.23 mH: 225 windings over a length of 67 cm and with a diameter of 7.5 cm. The coil is placed between the double layers of the PVC tube. All 48 detectors are individually linked by a waterproof cable (PUR-CY6x0.25) to 48 serial interfaces (Com ports) of a computer. Special software was developed to record all activities. We connected the registration computer near the pond in Beesd (the Netherlands), to the PC network system of the University of Leiden (using PC- Anywhere software).

We placed the tubes with the detectors (Figure 1) in the pond according to a chessboard pattern (Figure 2). Twenty-four tubes were oriented in the direction south–south-west at 202.5° (direction of the Sargasso Sea), and 24 tubes were oriented in the direction west–north-west at 292.5° (perpendicular to the direction Sargasso Sea, Figure 2).

On 2 June 1999, the pond was stocked with 26 eels. On 21 July 1999 we placed 14 additional eels into the pond. The eels were obtained from a hatchery (Royaal BV) with a mean age of 2 years, a mean weight of 578 ± 90 grams and a mean length of 64± cm. We injected a Trovan ID 100 implantable transponder microchip (2.1 × 11.5 mm) in a biocompatible glass capsule in the dorsal muscle 10 cm behind the head of every eel. These transponders are passive transmitters that transmit an ID code when activated in an electromagnetic field of 128 kHz.

The Trovan-system continuously recorded all eel activity in the pond. These data were translated to migration and distribution patterns of the individual eels in the pond. The precise distance between the various tubes is known, so an indication of the distance that eels migrate can be recorded. In principle, this record is the minimum distance an eel has migrated. Every tube has a capture device. The computer records directly which tube is occupied by which eel. Every 6 months we captured the eels via the capture devices for 'on site' blood sampling. The eels were anaesthetised (100 ppm. benzocaine) and released again directly after blood sampling. Blood samples (1.5 ml) were tested for hormone levels at a later stage. This information will be combined with maturity and activity measurements in a later analysis.

We chose the density of eel in the pond (24 kg eel 0.8 ha^{-1} or 1 eel per 250 m^3) so that the pond can produce enough natural food for growth (Klein Breteler *et al.* 1990). We stocked the pond with 163 kg of other fish species and fry (Table 1). We expected that maturation of the eel would be possible during the 2 years following initial stocking.

Calculations and statistics

We defined the maximal degree of occupancy (100%) as the total number of hours per month where all 48 tubes are fully occupied. For instance for a month with 31 days the maximal occupancy degree is 35 712 h (31 days∗24 h∗48 tubes = 100%).

In order to investigate if eels oriented themselves on the earth's magnetic field, the tubes in the pond were positioned in an alternating way, in the direction of the Sargasso Sea (south–south-west), or opposite to it. For every individual eel, the seasonal component in the orientation mechanism has been calculated following:

Table 1. Fish occupation of the pond in May 1999 at the start of the experiment.

		Length	Total kg
Carp	*Cyprinus carpio*	25–40 cm	50.0
Bream	*Abramis brama*	> 35 cm	75.0
Roach	*Rutilus rutilus*	> 15 cm	25.0
Rudd	*Scardinius erythrophthalmus*	> 13 cm	10.0
Zander	*Sander lucioperca*	> 45 cm	3.0
Eel	*Anguilla anguilla* (our tagged eels)	> 57 cm	22.5
Fry	Unspecified fish brood	< 8 cm	10.0

$$\text{Preference index (per eel)} = \frac{\text{number of hours in south-south-west tubes}}{\text{number of hours in (south–south-west) + west–north-west tubes)}}$$

According to this index:

1: indicates 100% preference for south–south-west tubes,
0.5: indicates an undirected preference
0: indicates a 100% preference for west–north-west tubes.

The summed values of the orientation indices of all eels are expressed per month in the orientation-coefficient. Our 'between individual months analysis' for the preference index did not come up with a clear significance below 0.05, but often bordering this value. The data however showed a trend with higher values in the fall compared to the summer months. Therefore we pooled our data over the summer period (June, July, August) vs. fall (September, October, November).

We applied a one-way ANOVA, comparing this summer period with fall. $p \leq 0.05$ was considered statistically significant. Normality of the data and homogenity of variances were checked by Kolmogorov–Smirnov and $F_{\max}$ tests.

Results

Immediately after the first 26 eels were released in the pond (2 June at 20:00 hours) they searched for shelter in the tubes. Only 20 min after being released, the first eel (code: 0001FC39DB/Saskia) was detected in tube 40 (position E6), a southwest oriented tube. Some eels stayed for a long time uninterrupted in one tube. For example, one eel (code: 0001FCDBB9/Hanneke) entered a tube on 17 June and left 2 months later on 16 August. Since the total occupancy remained at about 12.5% for the first month, we decided to increase the number of eels from 26 to 40.

After releasing the second group of 14 eels (July 21 at 20:00 h) they did not visit the tubes until the next morning. The first eel from the second group (code: 0001FCAF0D/Louise) entered at 7:47 h tube 34 (D8), a northwest oriented tube that was not yet occupied by another eel. Hereafter, in the coming hours or days, the eels of the second group

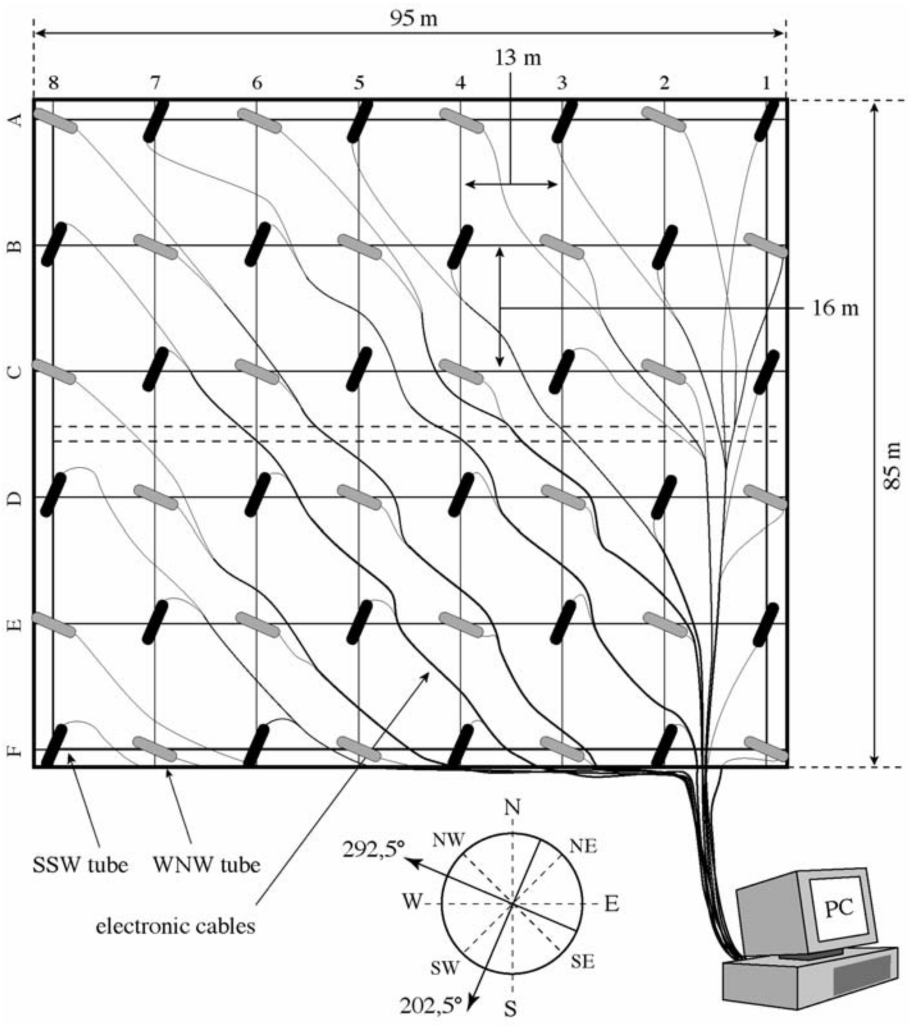

Figure 2. The tubes with the detectors were placed in a pond of 0.8 ha (95 × 85 m) according to a chessboard pattern, 24 tubes were orientated at 202.5° (direction of the Sargasso Sea), and 24 tubes were orientated at 292.5° (opposite direction).

entered tubes that were not yet occupied by other eels of the first or second group.

Presence of eel in the tubes, which can be derived from the total time of eels in the tube, decreased during the period June–November 1999. After the first month there is an increase of the presence of eel in the tubes, due to the extra 12 eels we put in the pond. In July, 23.8% of the tubes were occupied but in November only 6.0%. In the event that all the eels would find shelter in the tubes during the daytime, then 41.7% occupancy should be found. During the analysed period the average occupancy was 13.7%. Figure 3 gives an overview of the seasonal division of eels over the pond. In summertime (June, July, August) the eels are equally divided over the pond. In autumn the tubes along the edge of the pond are more occupied.

There was a circadian activity pattern, with activity during day and night (not depicted) during the first months with an increased activity during the night (between 19:00 and 08:00 h). In July for example during daytime 27% of the tubes were occupied, while during nighttime only 16% were occupied. In November the circadian activity pattern was less clear, partly because of

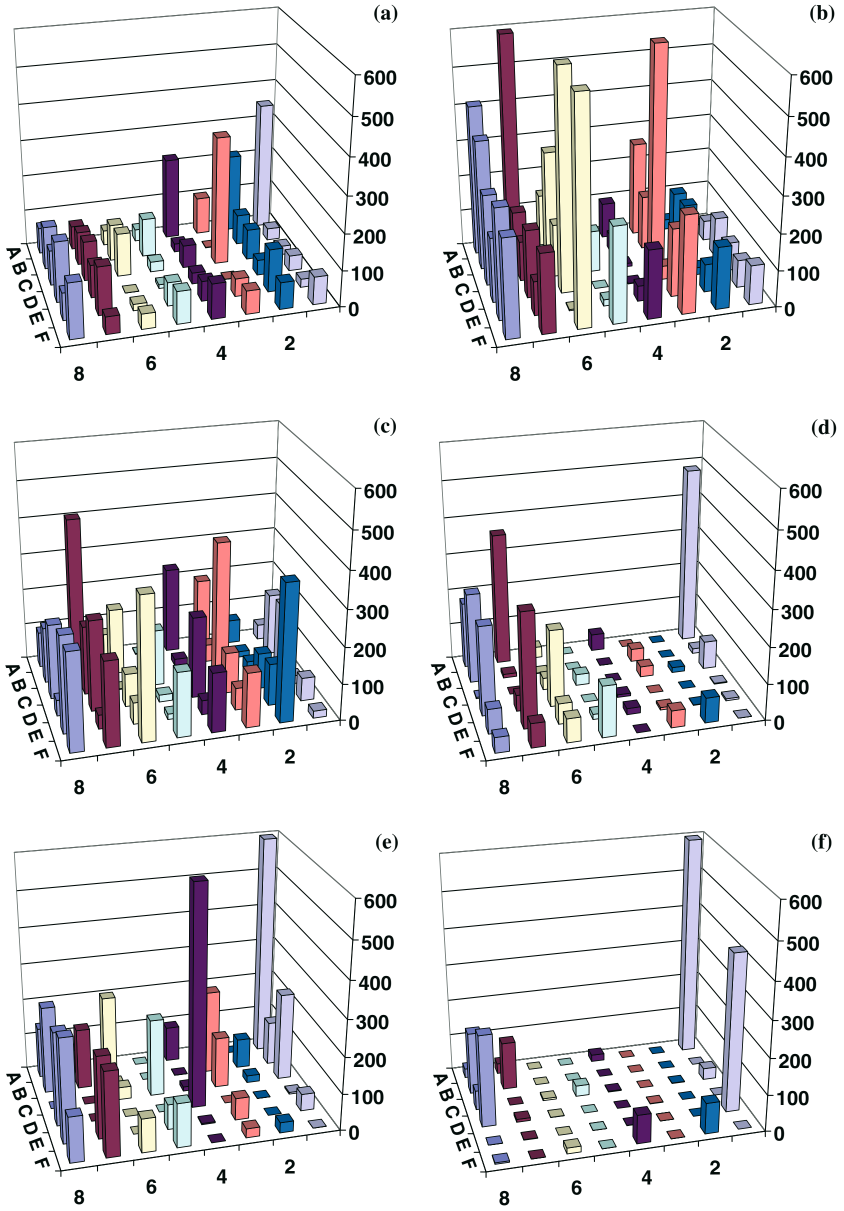

Figure 3. For eel it is observed they are seeking regularly for shelter, so they will visit the tubes with microchip detectors. In this way the frequency and preference position of eels for every tube can easily be measured, not only over a day, but also in relation to season. Y-axis: denotes 'Total time of eels in the tubes per month' in [hours]. a: June, b: July, c: August, d: September, e: October, f: November in 1999.

the low presence of eel in the tubes. During winter the water was colder and the eels apparently preferred to stay in the mud on the bottom of the pond.

As an example, we described the activity pattern for one eel (0001F85D9D/Floortje) for August 1999. In this month we registered, based on our detection method with tubes, that this eel swam at least 609 m between the tubes with a minimum average speed of 20 cm $^{-1}$. The animal started in the middle of the left part of the pond (tube C8), swam to the south-east (tube F4) returned to the left part of the pond (tubes A-F: 8 and 7) and ended in the outer south-western part (tube F2) of the pond. In principle, because the tubes serve as marking points, reflecting the minimal covered distance, the real distance, and maximum speed that the eel swam, can be much higher. During the period June–November 1999 there is an increase in preference for the south–south-west (the direction Sargasso Sea) oriented tubes. So eels have a preference on the earth's-magnetic field for south–south-west (202,5°) oriented tubes. The preference component was 0.4 in June increasing to 0.68 and 0.67 in September and October respectively. Comparing the summer months (June, July, August) with fall (September, October, November) resulted in a significant higher Preference Index during fall ($p \leq 0.045$).

Discussion

The basis for the experimental set up with the tubes with electromagnetic detection is the endogenous behavioural response of eels to search for shelter. The circadian rhythms found in our study indicate that the eels are more active during darkness than during day light. This was also observed by Edel (1975, 1976) and given the name 'endogenously scotokinesis' (scoot = dark). The animals showed increased nocturnal activity with crepuscular peaks of activity corresponding with transitions from light to dark and vice versa (Edel 1976). From literature, it is known that activity patterns were also dependent on the maturational stage of the animals. Immature eels were more nocturnally active and showed peaks of activity at light-dark transitions. This was also observed in this study with yellow eel. In contrast, maturing eels were equally active by day and by night but remained responsive to light-dark transitions (Edel 1976). Hain (1975) reported that yellow eels have several 'try outs' or dry runs before their final migration to the Sargasso Sea as silver eels. A temporary slight maturation of yellow eels can possibly cause the observed differences in activity patterns during the season, with a decrease as the migration season progresses in the fall. When the animals become mature they are nocturnal and overall activity decreases. Besides a maturing effect, the seasonal effect can also be explained by temperature changes. In November the tubes are less occupied. Probably the eels hibernate and burrow themselves in the mud in order to reduce the contact with the environment (Walsh et al. 1983). Hibernation or metabolic depression has recently also been demonstrated for European eel in a microcalorimeter under conditions of anoxia. The eel (mass: 125 g) reduced its metabolic rate to 30% of the standard metabolic rate (SMR) while no lactate-ethanol conversion has been observed (van Ginneken et al. 2001). This may be an important survival strategy to save energy stores and diminish end-product accumulation (Ultsch 1989).

The eels we released on the pond were the first year yellow (non-migratory). For yellow eels it is known that they have a very low drive for migration or long distance journeys. This is interesting because Gunning & Shoop (1962) found their territory is restricted to 61 linear meter or less. Research with tagged American eel, *Anguilla rostrata*, shows that their daily activity pattern restricts itself to an area of 30–133 m. Their territory or home range, which is defined as the foraging area of an eel which it daily occupies, restricts itself to 0.2–2.2 ha (Labar 1982, Ford & Mercer 1986). In our study, the route the individual eel (0001F85D9D/Floortje) swam in August covered nearly the whole pond of 0.8 ha.

It is remarkable, that in our study a seasonal component has been observed in the orientation mechanism of yellow eel. A seasonal component was also observed in yellow eel in the study of Hain (1975). When these eels were given the choice between swimming upstream (positive rheotaxis), downstream (negative rheotaxis), and no current (neutral response), the animals displayed in August an equal response for all choices. But two months later in October during the migratory season, a strong negative rheotaxis was observed (Hain 1975). The author explains this result with the suggestion that yellow eels have several 'try outs' or 'dry runs' several years prior to their final return journey as silver animals to the Sargasso Sea. After each 'false start' or 'trial run' the migratory characteristics will again decrease, either totally or to a large degree, until the next migratory season (Hain 1975). The observed differences in rheotaxis between August and October found by Hain (1975), or the observed differences in the preference component in our study, are indicative for a seasonal dependent orientation on the earth's magnetic field. This can possibly be explained by this theory of migratory 'try outs' of yellow eel.

By using tubes that were laid out following a chessboard pattern, alternatively in a south–south-westerly or a west–north-westerly direction (90° difference), we were able to study the orientation behaviour of sub-adult eel during the whole season, which covered a period of 7 months. We have to admit that our electronic system was not capable of distinguishing a 180° difference in orientation of the eels when inside the tubes. In addition, we can not observe within the same tube whether an animal is with its head in SSW vs. NNE direction; the same for the 90° opposite tube: WNW vs. ESE direction. This is the topic of the so called 'directional ambiguity'. We are aware of the limitation of our method on this point but are strengthened in our opinion that yellow eels have a preference for SSW tubes (direction Sargasso Sea) in the fall by the following two observations. First, Hain (1975) also observed for yellow eel a strong negative rheotaxis in fall. Secondly, we observed the same pattern in Preference Index (preference SSW tubes in fall) the following two consecutive years (1999 and 2000) in the same pond with the same experimental set up and animals. In fall 1999, the Preference Index was significantly higher compared to the summer period ($p \leq 0.045$). Also in fall 2000, a significant higher Preference Index was observed compared to the summer period ($p \leq 0.038$) (unpublished results).

The possibility exists that homing of eels is based on olfactory principles. However results in the Baltic with tagged anosmic eels (the olfactory organ has been removed) exclude this mechanism. No difference in orientation was observed with a control group during a 100–500 km migration (Karlsson 1984). Another possibility for eel to determine their global position is by detecting features of the earth's magnetic field. Many animals in nature, like birds (Walcott 1991), honeybees (Walker & Bitterman 1989), whales (Kirschvink et al. 1986), dolphins (Walker et al. 1992), loggerhead turtles (Lohmann & Lohmann 1996), and possibly also fish (Walker 1984) make use of features of the earth's magnetic field like the magnetic field intensity and the magnetic inclination angle. In fish lateral line organs may be important (Walker 1984). For sockeye salmon (*Oncorhynchus nerka*) fry and smolt it has been demonstrated they use both celestial and magnetic cues as orientation mechanism when migrating to and from nursery lakes (Quinn 1980; Brannon et al. 1981; Quinn and Brannon 1982). The directional preferences were innate and population specific depending on characteristics of the waters where the fish grew up.

In the literature, several field studies with eel support the view that orientation is accomplished through features of the earth magnetic field. In tank experiments, Miles (1968) found that American silver eels oriented southwards a direction considered appropriate for the spawning migration to the Sargasso Sea. Telemetric tracking studies with European yellow and silver eels in the German North Sea coast indicated that the yellow eel preferred a north-south axis while silver eels had a tendency towards a north-westerly direction (Tesch 1972, 1974). This direction for orientation was considered appropriate for European eels on spawning migration. In addition, strong artificial magnetic fields under laboratory conditions can override the natural directional preference of eels (Branover et al. 1971, Tesch 1974). Finally, strong evidence for orientation of eel on the earth-magnetic field comes from the observation that magnetic substances were found in the skull and bones of eels (Hanson et al. 1984).

In conclusion, using this elegant method with tubes positioned according to a chessboard pattern in a pond, we demonstrated that the preferred orientation along the earth's-magnetic field of yellow eel, during sheltering in the tube, is season-dependent. Advantages of this method are no handling stress of the animals, measurement of the position preference of a large group, and the fact that the animals were in their natural environment.

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