

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

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7  
8 Received 25 August 2003 Accepted 13 July 2004

9 *Key words:* circadian rhythm, migration, tracking, activity patterns, geomagnetism

10 **Synopsis**

11 We studied the circadian and monthly activity, the distribution patterns, and orientation to the earth's  
12 magnetic field, of yellow (non-migratory) female eels in a freshwater pond by means of microchips injected  
13 into their muscles. Detectors for microchips mounted in tubes were placed in the pond to detect if eels  
14 orientated themselves with respect to earth's magnetic field. Based on the frequency of tube visits (search  
15 for shelter), the data indicated that the presence of eel in the tubes decreases gradually during the study  
16 period. We saw more activity during the night in the first months. There was a seasonal component in the  
17 orientation mechanism, with a significantly lower preference component in the summer compared to the  
18 fall. A preference for tubes orientated in a south-southwest direction (the direction of the Sargasso Sea) in  
19 fall suggests an orientation to the earth's magnetic field.  
20

21 **Introduction**

22 Anguillid eels have a complicated life cycle,  
23 which takes place partly in freshwater, and  
24 partly in seawater. Little is known about this  
25 cycle, particularly the ecology or behaviour of  
26 the eels during the oceanic phase. Based on the  
27 work of Schmidt who caught leptocephali (the  
28 larvae of the eel) in the ocean, it is assumed that  
29 the spawning grounds of the European eel are  
30 6000 km away in the Sargasso Sea (Schmidt  
31 1923; Miller & McCleave 1994; Fricke & Kaese  
32 1995). Transport of the leptocephali larvae by  
33 the sea currents, towards the coasts of Europe,  
34 probably lasts 1–3 years. It is probably not  
35 purely a passive process (Lecomte-Finiger 1994).  
36 On reaching the coasts of Europe, the larvae  
37 transform into glass eels. They can be observed  
38 in March–April in the North Sea and in July in  
39 the Baltic Sea.

40 When they invade the inland waters they develop  
41 pigmentation (Tesch 1977) and are called yellow eel.  
42 This is the juvenile life phase of feeding and growth.  
43 Gonad differentiation occurs during the time spent  
44 in fresh water. After this growth period, which last  
45 3–12 years in males and 5–35 years in females, the  
46 animals prepare themselves for their return journey  
47 to the ocean. An enlargement of the eyes, a regres-  
48 sion of the digestive tract and a silvering of the body  
49 color characterize this phase. However, little eco-  
50 logical information is available about this fresh-  
51 water phase of several years prior to migration.  
52 Processes like circadian rhythm, annual activity  
53 patterns, hierarchy, foraging area and distribution  
54 patterns of eels in relation to season and age, and  
55 orientation on the earth's magnetic field need to be  
56 elucidated. The presented work mainly concerns the  
57 observation of activity patterns of 40 female eels by  
58 means of microchips on a 0.8 ha pond during the  
59 first 7 months of the 2 year field research period.

	Journal : <b>EBFI</b>	Dispatch : <b>15-9-2004</b>	Pages : <b>8</b>
	PIPS No. : <b>DO00002585</b>	<input type="checkbox"/> LE	<input type="checkbox"/> TYPESET
	MS Code : <b>EBFI2712</b>	<input checked="" type="checkbox"/> CP	<input checked="" type="checkbox"/> DISK

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

79 In order to investigate if eels orientated them-  
 80 selves on the earth's magnetic field, the tubes in the  
 81 pond were positioned in an alternating arrange-  
 82 ment, in the direction of the Sargasso Sea (south-  
 83 south-west), or opposite to it (west-north-west, see  
 84 Figure 2). So, orientation on the earth's magnetic  
 85 field can be investigated depending on the season.

86 This study will give information about the  
 87 ecology, activity patterns and orientation in rela-  
 88 tion to the earth's magnetic field of European eel

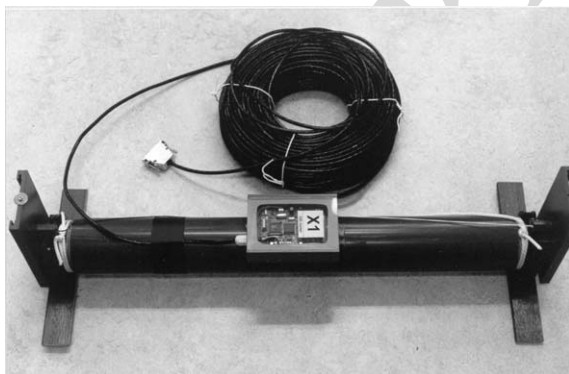


Figure 1. PVC-tube with Trovan detector (Trovan type LID656) in a waterproof box and a detection antenna. The antenna is a solenoid coil of 0.23 mH: 225 windings over a length of 67 cm and with a diameter of 7.5 cm. The coil is placed between the double skin of the PVC tube. All 48 detectors are individually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

at the end of the fresh water period before the  
 migration period in the ocean starts.

## 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 wind-  
 ings 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 indi-  
 vidualy 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 Nether-  
 lands), to the PC network system of the University  
 of Leiden (using PC- Anywhere software).

We placed the tubes with the detectors (Fig-  
 ure 1) in the pond according to a chessboard  
 pattern (Figure 2). Twenty-four tubes were orien-  
 tated in the direction south-south-west at 202.5°  
 (direction of the Sargasso Sea), and 24 tubes were  
 orientated 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  $578 \pm 90$  grams and a mean  
 length of  $64 \pm$  cm. We injected a Trovan ID  
 100 implantable transponder microchip  
 (2.1 × 11.5 mm) in a biocompatible glass encap-  
 sulation in the dorsal muscle 10 cm behind the  
 head of every eel. These transponders are passive  
 transmitters that transmit an ID code when acti-  
 vated 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 indi-  
 cation of the distance that eels migrate can be

136 recorded. In principle, this record is the minimum  
 137 distance an eel has migrated. Every tube has a  
 138 capture device. The computer records directly  
 139 which tube is occupied by which eel. Every  
 140 6 months we captured the eels via the capture  
 141 devices for 'on site' blood sampling. The eels were  
 142 anaesthetised (100 ppm. benzocaine) and released  
 143 again directly after blood sampling. Blood samples  
 144 (1.5 ml) were tested for hormone levels at a later  
 145 stage. This information will be combined with  
 146 maturity and activity measurements in a later  
 147 analysis.

148 We chose the density of eel in the pond (24 kg  
 149 eel 0.8 ha<sup>-1</sup> or 1 eel per 250 m<sup>3</sup>) so that the pond  
 150 can produce enough natural food for growth  
 151 (Klein Breteler *et al.* 1990). We stocked the pond  
 152 with 163 kg of other fish species and fry (Table 1).  
 153 We expected that maturation of the eel would be  
 154 possible during the 2 years following initial  
 155 stocking.

## 156 Calculations and statistics

157 We defined the maximal degree of occupancy  
 158 (100%) as the total number of hours per month  
 159 where all 48 tubes are fully occupied. For instance  
 160 for a month with 31 days the maximal occupancy  
 161 degree is 35 712 h (31 days\*24 h\*48 tubes =  
 162 100%).

163 In order to investigate if eels orientated them-  
 164 selves on the earth's magnetic field, the tubes in the  
 165 pond were positioned in an alternating way, in the  
 166 direction of the Sargasso Sea (south-south-west),  
 167 or opposite to it. For every individual eel, the  
 168 seasonal component in the orientation mechanism  
 169 has been calculated following:

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

		Length	Total kg
Carp	<i>Cyprinus carpio</i>	25–40 cm	50.0
Bream	<i>Abramis brama</i>	> 35 cm	75.0
Roach	<i>Rutilus rutilus</i>	> 15 cm	25.0
Rudd	<i>Scardinius erythrophthalmus</i>	> 13 cm	10.0
Zander	<i>Sander lucioperca</i>	> 45 cm	3.0
Eel	<i>Anguilla anguilla</i> (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: 171  
 1: indicates 100% preference for south-south- 172  
 west tubes, 173  
 0.5: indicates an undirected preference 174  
 0: indicates a 100% preference for west-north- 175  
 west tubes. 176

The summed values of the orientation indices of all 177  
 eels are expressed per month in the orientation- 178  
 coefficient. Our 'between individual months anal- 179  
 ysis' for the preference index did not come up with 180  
 a clear significance below 0.05, but often bordering 181  
 this value. The data however showed a trend with 182  
 higher values in the fall compared to the summer 183  
 months. Therefore we pooled our data over the 184  
 summer period (June, July, August) vs. fall (Sep- 185  
 tember, October, November). 186

We applied a one-way ANOVA, comparing this 187  
 summer period with fall.  $p \leq 0.05$  was considered 188  
 statistically significant. Normality of the data and 189  
 homogeneity of variances were checked by Kol- 190  
 mogorov-Smirnov and  $F_{\max}$  tests. 191

## 192 Results

Immediately after the first 26 eels were released 193  
 in the pond (2 June at 20:00 hours) they search- 194  
 ed for shelter in the tubes. Only 20 min after 195  
 being released, the first eel (code: 0001FC39DB/  
 Saskia) was detected in tube 40 (position E6), a 196  
 southwest orientated tube. Some eels stayed for 197  
 a long time uninterrupted in one tube. For 198  
 example, one eel (code: 0001FCDBB9/Hanneke) 199  
 entered a tube on 17 June and left 2 months 200  
 later on 16 August. Since the total occupancy 201  
 remained at about 12.5% for the first month, we 202  
 decided to increase the number of eels from 26 203  
 to 40. 204  
 205

After releasing the second group of 14 eels (July 206  
 21 at 20:00 h) they did not visit the tubes until the 207  
 next morning. The first eel from the second group 208  
 (code: 0001FCAF0D/Louise) entered at 7:47 h 209  
 tube 34 (D8), a northwest orientated tube that was 210  
 not yet occupied by another eel. Hereafter, in the 211  
 coming hours or days, the eels of the second group 212

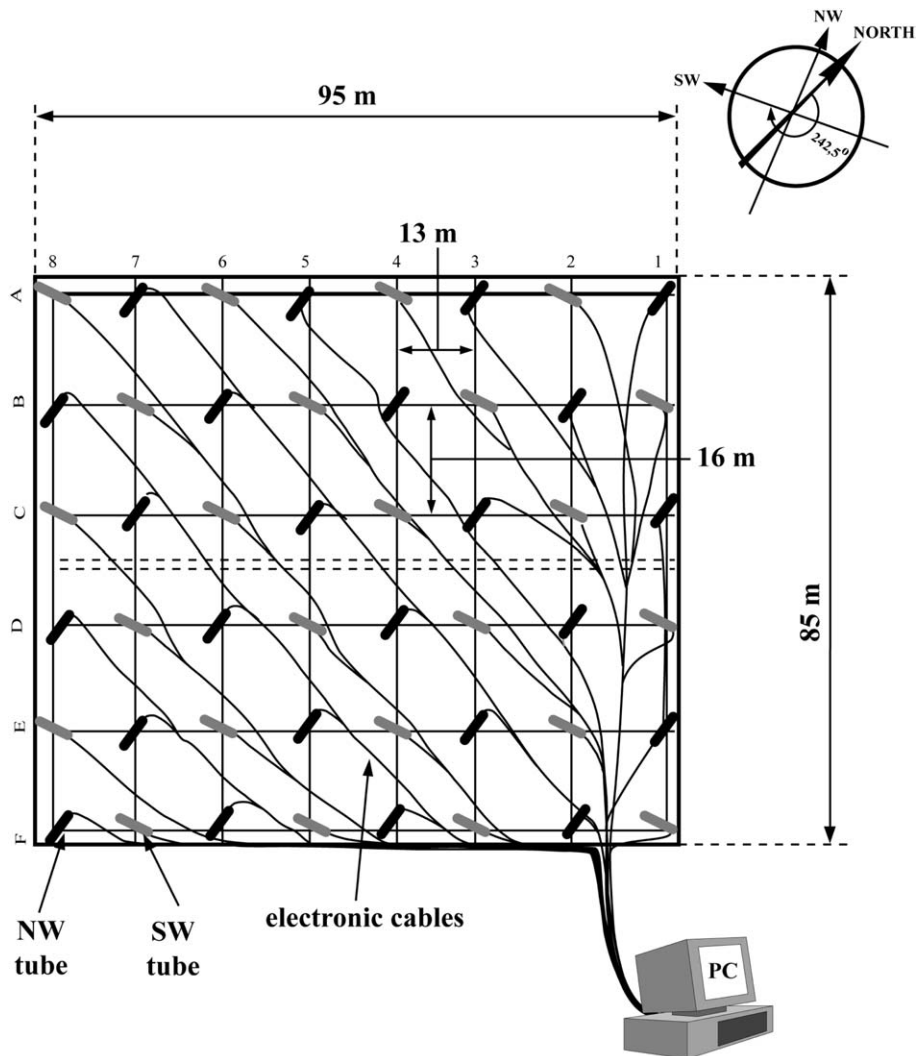


Figure 2. The tubes with the detectors were placed in a pond of 0.8 ha (95 × 85 m) according to a chessboard pattern, 24 tubes were orientated at 202.5° (direction of the Sargasso Sea), and 24 tubes were orientated at 292.5° (opposite direction).

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

215 Presence of eel in the tubes, which can be  
216 derived from the total time of eels in the tube,  
217 decreases during the period June–November  
218 1999. The first month there is an increase of the  
219 presence of eel in the tubes, due to the extra 12  
220 eels we put in the pond. In July, 23.8% of the  
221 tubes were occupied but in November only  
222 6.0%. In the event that all the eels would find  
223 shelter in the tubes during the daytime, then  
224 41.7% occupancy should be found. During the

225 analysed period the average occupancy was  
226 13.7%. Figure 3 gives an overview of the sea-  
227 sonal division of eels over the pond. In sum-  
228 mertime (June, July, August) the eels are equally  
229 divided over the pond. In autumn the tubes  
230 along the edge of the pond are more occupied.

231 There was a circadian activity pattern, with  
232 activity during day and night (not depicted)  
233 during the first months with an increased activity  
234 during the night (between 19:00 and 08:00 h). In  
235 July for example during daytime 27% of the  
236 tubes were occupied, while during nighttime only

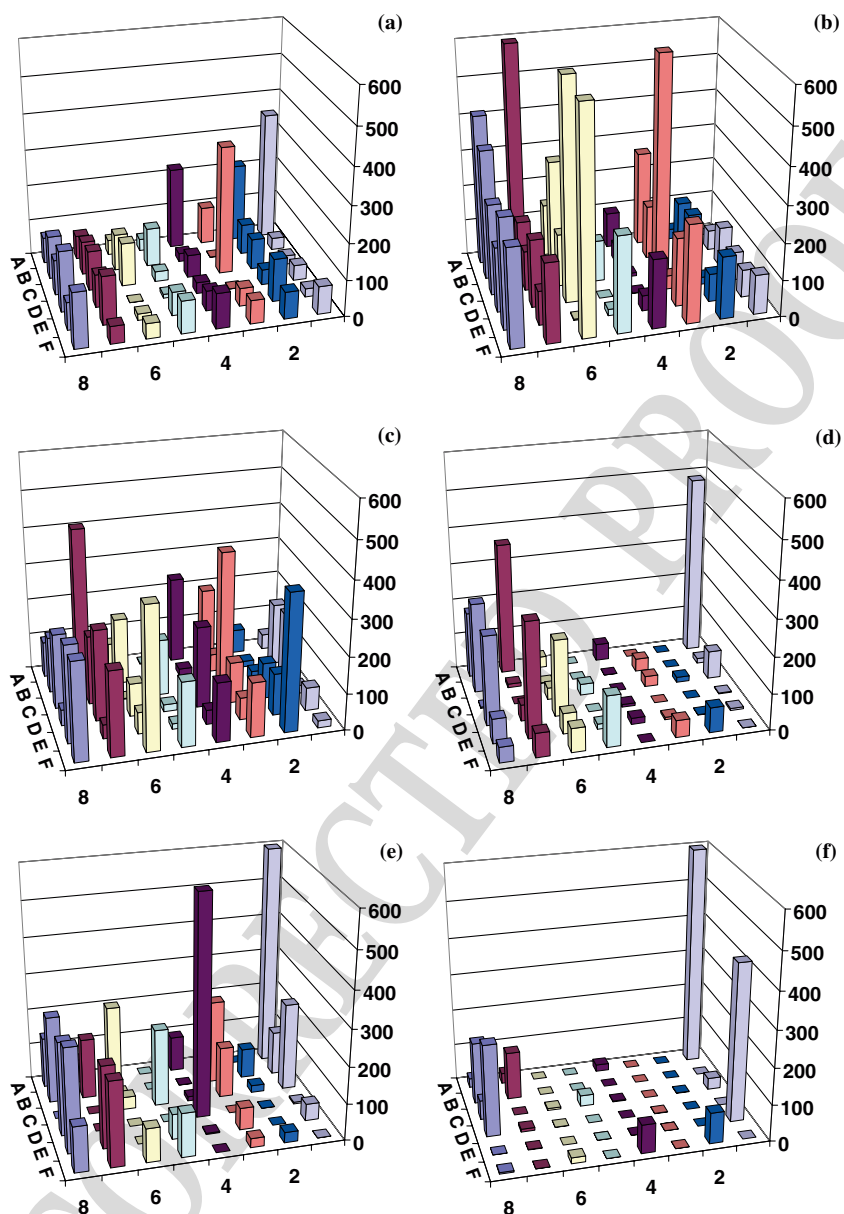


Figure 3. For eel it is observed they are seeking regularly for shelter, so they will visit the tubes with microchip detectors. In this way the frequency and preference position of eels for every tube can easily be measured, not only over a day, but also in relation to season. Y-axis: denotes 'Total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

237 16% were occupied. In November the circadian  
 238 activity pattern was less clear, partly because of  
 239 the low presence of eel in the tubes. During  
 240 winter the water was colder and the eels appar-  
 241 ently preferred to stay in the mud on the bottom  
 242 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  $20 \text{ cm}^{-1}$ . The animal started in the

243  
 244  
 245  
 246  
 247  
 248

249 middle of the left part of the pond (tube C8), swam  
 250 to the south-east (tube F4) returned to the left part  
 251 of the pond (tubes A-F: 8 and 7) and ended in the  
 252 outer south-western part (tube F2) of the pond. In  
 253 principle, because the tubes serve as marking points,  
 254 reflecting the minimal covered distance, the real  
 255 distance, and maximum speed that the eel swam,  
 256 can be much higher. During the period June–  
 257 November 1999 there is an increase in preference for  
 258 the south–south-west (the direction Sargasso Sea)  
 259 orientated tubes. So eels have a preference on the  
 260 earth's-magnetic field for south–south-west ( $202,5^\circ$ )  
 261 orientated tubes. The preference component was 0.4  
 262 in June increasing to 0.68 and 0.67 in September and  
 263 October respectively. Comparing the summer  
 264 months (June, July, August) with fall (September,  
 265 October, November) resulted in a significant higher  
 266 Preference Index during fall ( $p \leq 0.045$ ).

## 267 Discussion

268 The basis for the experimental set up with the tubes  
 269 with electromagnetic detection is the endogenous  
 270 behavioural response of eels to search for shelter.  
 271 The circadian rhythms found in our study indicate  
 272 that the eels are more active during darkness than in  
 273 during day light. This was also observed by Edel  
 274 (1975, 1976) and given the name 'endogenously  
 275 scotokinetic' (scoot = dark). The animals showed  
 276 increased nocturnal activity with crepuscular peaks  
 277 of activity corresponding with transitions from light  
 278 to dark and vice versa (Edel 1976). From literature,  
 279 it is known that activity patterns were also depen-  
 280 dent on the maturational stage of the animals.  
 281 Immature eels were more active nocturnally and  
 282 showed peaks of activity at light-dark transitions.  
 283 This was also observed in this study with yellow eel.  
 284 In contrast, maturing eels were equally active by day  
 285 and by night but remained responsive to light-dark  
 286 transitions (Edel 1976). Hain (1975) reported that  
 287 yellow eels have several 'try outs' or dry runs before  
 288 their final migration to the Sargasso Sea as silver  
 289 eels. A temporary slight maturation of yellow eels  
 290 can possibly cause the observed differences in  
 291 activity patterns during the season, with a decrease  
 292 as the migration season progresses in the fall. When  
 293 the animals become mature they are nocturnal and  
 294 overall activity decreases. Besides a maturing effect,  
 295 the seasonal effect can also be explained by tem-

perature 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). Hiber-  
 nation or metabolic depression has recently also  
 been demonstrated for European eel in a micro-  
 calorimeter 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 Ginne-  
 ken 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 migra-  
 tion 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 ter-  
 ritory or home range, which is defined as the for-  
 aging 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 indi-  
 vidual eel (0001F85D9D/Floortje) swam in Au-  
 gust 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 eels were given the choice  
 between swimming upstream (positive rheotaxis),  
 downstream (negative rheotaxis), and no current  
 (neutral response), the animals displayed in Au-  
 gust 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 dif-  
 ferences in rheotaxis between August and October  
 found by Hain (1975), or the observed differences  
 in the preference component in our study,

346 indicative for a seasonal dependent orientation on  
347 the earth's magnetic field, possibly can be ex-  
348 plained by this theory of migratory 'try outs' of  
349 yellow eel.

350 By using tubes that were laid out following a  
351 chessboard pattern, alternatively in a south-south-  
352 westerly or a west-north-westerly direction (90°  
353 difference), we were able to study the orientation  
354 behaviour of sub-adult eel during the whole season,  
355 which covered a period of 7 months. We have to  
356 admit that our electronic system was not capable of  
357 distinguishing a 180° difference in orientation of the  
358 eels when inside the tubes. In addition, we can not  
359 observe within the same tube whether an animal is  
360 with its head in SSW vs. NNE direction; the same  
361 for the 90° opposite tube: WNW vs. ESE direction.  
362 This is the topic of the so called 'directional ambi-  
363 guity'. We are aware of the limitation of our method  
364 on this point but are strengthened in our opinion  
365 that yellow eels have a preference for SSW tubes  
366 (direction Sargasso Sea) in the fall by the following  
367 two observations. First, Hain (1975) also observed  
368 for yellow eel a strong negative rheotaxis in fall.  
369 Secondly, we observed the same pattern in Prefer-  
370 ence Index (preference SSW tubes in fall) the fol-  
371 lowing two consecutive years (1999 and 2000) in the  
372 same pond with the same experimental set up and  
373 animals. In fall 1999, the Preference Index was sig-  
374 nificantly higher compared to the summer period  
375 ( $p \leq 0.045$ ). Also in fall 2000, a significant higher  
376 Preference Index was observed compared to the  
377 summer period ( $p \leq 0.038$ ) (unpublished results).

378 The possibility exists that homing of eels is based  
379 on olfactory principles. However results in the  
380 Baltic with tagged anosmic eels (the olfactory organ  
381 has been removed) exclude this mechanism. No  
382 difference in orientation was observed with a con-  
383 trol group during a 100–500 km migration  
384 (Karlsson 1984). Another possibility for eel to  
385 determine their global position is by detecting fea-  
386 tures of the earth's magnetic field. Many animals in  
387 nature, like birds (Walcott 1991), honeybees  
388 (Walker & Bitterman 1989), whales (Kirschvink  
389 et al. 1986), dolphins (Walker et al. 1992), logger-  
390 head turtles (Lohmann & Lohmann 1996), and  
391 possibly also fish (Walker 1984) make use of fea-  
392 tures of the earth's magnetic field like the magnetic  
393 field intensity and the magnetic inclination angle. In  
394 fish lateral line organs may be important (Walker  
395 1984). For sockeye salmon (*Oncorhynchus nerka*)

396 fry and smolt it has been demonstrated they use 396  
397 both celestial and magnetic cues as orientation 397  
398 mechanism when migrating to and from nursery 398  
399 lakes, respectively (Quinn 1980; Brannon et al. 399  
400 1981; Quinn and Brannon 1982). The directional 400  
401 preferences were innate and population specific 401  
402 depending on characteristics of the waters the fish 402  
403 grew up. 403

404 In the literature, several field studies with eel 404  
405 support the view that orientation is accomplished 405  
406 through features of the earth magnetic field. In 406  
407 tank experiments, Miles (1968) found that Ameri- 407  
408 can silver eels oriented southwards a direction 408  
409 considered appropriate for the spawning migration 409  
410 to the Sargasso Sea. Telemetric tracking studies 410  
411 with European yellow and silver eels in the German 411  
412 North Sea coast indicated that the yellow eel pre- 412  
413 ferred a north-south axis while silver eels had a 413  
414 tendency towards a north-westerly direction (Tesch 414  
415 1972, 1974). This direction for orientation was 415  
416 considered appropriate for European eels on 416  
417 spawning migration. In addition, strong artificial 417  
418 magnetic fields under laboratory conditions can 418  
419 override the natural directional preference of eels 419  
420 (Branover et al. 1971, Tesch 1974). Finally, strong 420  
421 evidence for orientation of eel on the earth-mag- 421  
422 netic field comes from the observation that mag- 422  
423 netic substances were found in the skull and bones 423  
424 of eels (Hanson et al. 1984). 424

425 In conclusion, using this elegant method with 425  
426 tubes positioned according to a chessboard pattern 426  
427 in a pond, we demonstrated that the preferred ori- 427  
428 entation along the earth's-magnetic field of yellow 428  
429 eel, during sheltering in the tube, is season-depen- 429  
430 dent. Advantages of this method are no handling 430  
431 stress of the animals, measurement of the position 431  
432 preference of a whole population, and the fact that 432  
433 the animals were in their natural environment. 433

#### Acknowledgments 434

435 We thank Lex Raat, Organization for Improve- 435  
436 ment of Inland Fisheries, Nieuwegein, the Neth- 436  
437 erlands, for supporting this project and providing 437  
438 the pond, Frans Jacques for technical assistance 438  
439 and pond management, and Royaal BV for provid- 439  
440 ing 48 female eels. Technical assistance was 440  
441 provided by Rob van der Linden, Rinus van der 441  
442 Heijmans, Ab Gluvers, Jeroen Mesman, Frits van 442

443 Tol and Gerard Kostense. Technical detection  
444 equipment on the pond was subsidized by a grant  
445 of 'het Leids Universitair Fonds' (LUF, grant no.  
446 312/15-6-98/X,vT) and the GRATAMA-founda-  
447 tion (Harlingen, grant no. 9815). The eel migration  
448 project at the University Leiden is supported by a  
449 grant of the Technology Foundation (STW),  
450 which is subsidized by the Netherlands Organiza-  
451 tion for Scientific Research (NWO), STW-project  
452 no. LBI66.4199. The field experiment was also  
453 supported by the EU EELREP project no. Q5RS-  
454 2001-01836.

## 455 References

456 Brannon, E.L., T.P. Quinn, G.L. Luchetti & B.D. Ross. 1981.  
457 Compass orientation of sockeye salmon fry from a complex  
458 river system. *Can. J. Zool.* 59: 1548–1553.  
459 Branover, G.G., A.S. Vasil'yev, S.I. Gleyzer & A.B. Tsinober.  
460 1971. A study of the behavior of the eel in natural and arti-  
461 ficial magnetic fields and an analysis of its reception mecha-  
462 nism. *J. Ichthyol.* 11: 608–614.  
463 Edel, R.K. 1975. The effect of shelter availability on the  
464 activity of male silver eels. *Helgoländer Meeresun.* 27: 164–  
465 174.  
466 Edel, R.K. 1976. Activity rhythms of maturing American eels  
467 (*Anguilla rostrata*). *Ma. Biol.* 36: 283–289.  
468 Ford, T.E. & E. Mercer. 1986. Density, size distribution and  
469 home range of American eels, *Anguilla rostrata*, in a Mas-  
470 sachusetts salt march. *Environ. Biol. Fish.* 17: 309–314.  
471 Fricke, H. & R. Kaese. 1995. Tracking of artificially matured  
472 eels (*Anguilla anguilla*) in the Sargasso Sea and the problem  
473 of the Eel's Spawning Site. *Naturwissenschaften* 82: 32–36.  
474 Gunning, G.E. & C.R. Shoop. 1962. Restricted movements of  
475 the American eel, *Anguilla rostrata* (Le Sueuer), in freshwater  
476 streams with comment on growth rate. *Tulane Stud. Zool.* 9:  
477 265–272.  
478 Hain, J.H.W. 1975. The behavior of migratory eels, *Anguilla*  
479 *rostrata*, in response to current, salinity and lunar period.  
480 *Helgoländer Meeresun.* 27: 211–233.  
481 Hanson, M., L. Karlsson & H. Westerberg. 1984. Magnetic  
482 material in European eel (*Anguilla anguilla* L.). *Comp. Bio-*  
483 *chem. Physio.* 77A: 221–224.  
484 Karlsson, L. 1984. Migration of European silver eels, *Anguilla*  
485 *anguilla*. PhD. Thesis, Uppsala University, Uppsala, 745 pp.  
486 Kirschvink, J.L., A.E. Dizon & J.A. Westphal. 1986. Evidence  
487 from strandings for geomagnetic sensitivity in cetaceans. *J.*  
488 *Exp. Biol.* 120: 1–24.  
489 Klein Breteler J.G.P., W. Dekker & E.H.R.R. Lammens. 1990.  
490 Growth and production of yellow eels and glass eels in  
491 ponds. *Int. Rev. ges. Hydrobiol.* 75: 189–205.

Labar, G.W. 1982. Local movements and home-range size of  
492 radio-equipped American eels (*Anguilla rostrata*) from lake  
493 Champlain, with notes on population estimation. p. 72. In:  
494 K. H. Loftus (ed.) *Proceedings of the North American Eel*  
495 *Conference*, Ontario Ministry of Natural Resources, Ontario  
496 *Fisheries Technical Report Series 4*. Toronto, Ontario.  
497  
Lecomte-Finiger, R. 1994. The early life of the European eel.  
498 *Nature* 370: 424.  
499  
Lohmann, K.J. & C.M.F. Lohman. 1996. Detection of mag-  
500 netic field intensity by sea turtles. *Nature* 380: 59–61.  
501  
Miles, S.G. 1968. Laboratory experiments on the orientation of  
502 the adult American eel, *Anguilla rostrata*. *J. Fish. Res. Board*  
503 *Can.* 25: 2143–2155.  
504  
Miller, M. & J.D. McCleave. 1994. Species assemblages of le-  
505ptocephali in the Subtropical Convergence Zone of the Sarg-  
506 gasso Sea. *J. Mar. Res.* 52: 743–772.  
507  
Quinn, T.P. 1980. Evidence for celestial and magnetic compass  
508 orientation in lake migrating sockeye salmon fry. *J. Comp.*  
509 *Physiol.* 137: 243–248.  
510  
Quinn, T.P. & E.L. Brannon. 1982. The use of celestial and  
511 magnetic cues by orienting sockeye salmon smolts. *J. Comp.*  
512 *Physiol.* 147: 547–552.  
513  
Schmidt, J. 1923. Breeding places and migration of the eel.  
514 *Nature* 111: 51–54.  
515  
Tesch, F.W. 1972. Versuche zur telemetrischen Verfolgung der  
516 Laichwanderung von Aalem (*Anguilla anguilla*) in der  
517 Nordsee. *Helgoländer Meeresun.* 23: 165–183.  
518  
Tesch, F.W. 1974. Influence of geomagnetism and salinity on  
519 the directional choice of eels. *Helgoländer Meeresun.* 27:  
520 211–233.  
521  
Tesch, F.W. 1977. The eel. *Biology and Management of An-*  
522 *guilled eels*, Chapman & Hall, London. 434 pp.  
523  
Ultsch, G.R. 1989. Ecology and physiology of hibernation and  
524 overwintering among freshwater turtles and snakes. *Biol.*  
525 *Rev.* 64: 435–516.  
526  
Van Ginneken, V.J.T., M. Onderwater, O. Lamua Olivar &  
527 G.E.E.J.M. van den Thillart. 2001. Metabolic depression and  
528 investigation of glucose/ethanol conversion in the European  
529 eel (*Anguilla anguilla* Linnaeus 1758) during anaerobiosis.  
530 *Thermochim. Acta* 373: 23–30.  
531  
Walcott, C. 1991. Magnetic maps in pigeons. pp. 38–51. In: P.  
532 Berthold (ed.) *Orientation in Birds*. Birhauser, Boston.  
533  
Walker, M.M. 1984. Learned magnetic field discrimination in  
534 yellowfin tuna. *Thunnus albacares*. *J. Comp. Physiol.* 155:  
535 673–679.  
536  
Walker, M.M. & M.E. Bitterman. 1989. Honeybees can be  
537 trained to respond to very small changes in geomagnetic field  
538 intensity. *J. Exp. Biol.* 145: 489–494.  
539  
Walker, M.M., J.L. Kirschvink, G. Ahmed & A.E. Dizon.  
540 1992. Evidence that fin whales respond to the geomagnetic  
541 field during migration. *J. Exp. Biol.* 171: 67–78.  
542  
Walsh, P.J., G.D. Foster. & T.W. Moon. 1983. The effects of  
543 temperature in metabolism of the American eel (*Anguilla*  
544 *rostrata*, Le Sueuer) compensation in the summer and torpor  
545 in the winter. *Physiol. Zool.* 56: 532–540.  
546  
547