

Silver eel migration behaviour in the Baltic

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Female silver eels (*Anguilla anguilla* L.) were tagged with data storage tags and released in the Baltic Sea at the same time at a single site on the east coast of Sweden. Data on temperature, light, and depth were obtained from six eels, continuous records for 71 d at sea. The swimming behaviour was similar for all fish, almost stereotyped: swimming activity was between dusk and dawn, starting at a light level corresponding to civic twilight and ending in the morning at generally the same light level. During daylight, the eels rested on the seabed at depths of 2–36 m. Swimming depth was typically close to the surface: up to 95% of swimming time was spent within 0.5 m of the surface. Short dives at irregular intervals (some 1–2 h⁻¹) were made down to the thermocline depth, or occasionally, to the seabed. The duration of such dives were typically 5–10 min. Although only a few days at liberty, the eels had migrated a considerable distance between recapture and release sites, indicating a mean rate of travel of ~16 km d⁻¹. The recapture positions suggested unidirectional movements towards the southwestern Baltic Sea, i.e. close to the straits leading to the ocean, supporting a belief that the recorded movements were related to eel spawning migratory behaviour.

Keywords: diurnal behaviour, eel, migration, swimming depth.

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Introduction

The spawning migration of European eel (*Anguilla anguilla* L.), from brackish waters, rivers and streams of Europe, Asia minor and north Africa to the Sargasso Sea, is one of the most impressive feats of animal migration and orientation. The migratory behaviour over short distances has been studied previously, using telemetry tracking (Westerberg, 1979; Tesch, 1989; McCleave and Arnold, 1999), but so far the navigation mechanism has remained unknown. Geomagnetic cues (Tesch *et al.*, 1992a) and selective stream transport (McCleave and Kleckner, 1982) have been proposed. Westin (1998) claimed that imprinting of the transportation route is necessary, and that eels, transported and stocked as glass eels, are unable to fulfil their spawning migration as silver eels.

The purpose of this paper was therefore to present data on the behaviour of eels during the early phase of the spawning run. For this purpose, we use an unique dataset of six silver eels monitored simultaneously during migration from 7 to 23 d at liberty. The most significant findings were the regular diurnal activity, the active swimming very close to the surface at night, and the occasional dives of short duration. Those features were remarkably similar in all eels studied.

Material and methods

Fish tagging

Tagging and release were accomplished on 31 September 2005 in the Kalmar Sound, between Öland and the Swedish mainland (Figure 1). The eels were captured in trapnets just north of the release site on the same day. The fish were tagged without the use of anaesthesia, and the length and weight of the eels was measured, together with the eye diameter and fat content (to assess the degree of silvering; Pankhurst and Lythgoe, 1983). All the eels with data storage tags (DSTs) were female silver eels.

The mean length was 78 ± 7 cm and the mean weight 0.95 ± 0.26 kg, ranging from 0.5 to 1.2 kg.

In all, 16 eels were fitted with Lotek 2410 DSTs (www.lotek.com). This tag has a pressure range equal to 200 m seawater depth with 1% full-scale accuracy and 0.05% full-scale resolution, corresponding to 2 m and 0.1 m, respectively. The final records of pressure were noted from all returned tags when brought from water into the air, and varied in the range -0.2 to -0.4 dbar. Those values were used to correct the swimming depth time-series. The weight in water of the tag is 3 g, <0.6% of the total mean body weight of the eels and well below the 2% deemed a maximum to allow undisturbed behaviour (Jepsen *et al.*, 2002).

The DSTs were programmed to start logging at 00:00 UTC on 1 October, ~5 h after release. Data were recorded on a time-scale of 1 min. The experiment was advertised in the Swedish and Danish fishery media. Fishers who reported recaptures were rewarded for tag and fish, and also had to indicate the date and position of the recapture. Six of the eight returned tags yielded readable data.

The approximate nightly temperature profile along each eel's trajectory was constructed from the depth and temperature values during dives. The time constant of the external temperature sensor of the tag is 3 s. Typically, the vertical velocity during descent and ascent was 0.15 m s^{-1} , which made the temperature–depth measurement relatively imprecise.

The tags were attached externally, anterior to the dorsal fin, using stainless suture. The eels were kept in moist seaweed before tagging, and handled with a wet cloth to avoid injury to the epidermis. The whole handling procedure took ~1 min, and the fish was immediately released into the sea. The release was made together with a total of 60 eels tagged with coded acoustic tags (Vemco V13) in a square array with Vemco V2 data-logging buoys.

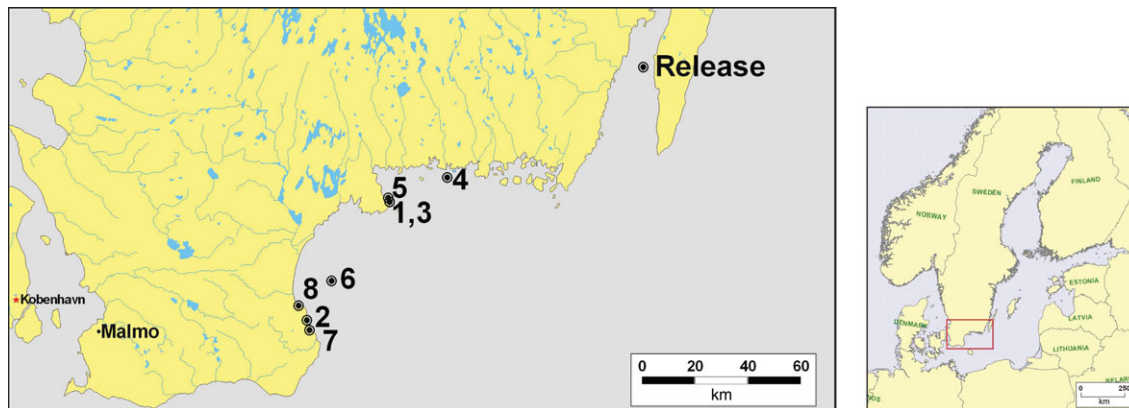


Figure 1. Release and recapture points for the DST-tagged eels in this study. The rectangle in the overview corresponds to the area of the main map.

Data analysis

The duration of vertical activity was easily obtained by simple visual inspection of the depth time-series. The onset and termination of vertical activity was therefore determined for all returned fish, and its mean duration was calculated per day, using data from all active eels on each day.

To analyse diving behaviour, a dive was defined as the period when the eel changed from swimming depths <1 m below the surface to greater depths for more than 2 min. A deep exploratory dive was defined as a dive when the maximum recorded depth exceeded 4 m. Diurnal patterns in dives were studied for each eel by calculating the frequency of dives per hour for all those active nights that included continuous, unbroken time-series.

For each eel, the total recorded active period was calculated. The shortest water route from the release point to the place of recapture gives the minimum distance of horizontal movement. Using those parameter values, the minimum mean horizontal swimming speed was obtained.

Results

Following release during daylight, most of the acoustically tagged eels remained at the bottom inside the array until dusk the same day. Active migration started around 20:30 local time (18:30 UTC). It was hence assumed that DST-tagged eels behaved in a similar way.

In all, eight (50%) of the DST-tagged eels were recaptured. Downloading the data was not possible from two of the tags that had been frozen after capture. All recaptures were made south of the release site. Table 1 summarizes the recapture data and Figure 1 shows the sites of recapture. Two recaptures were made in bottom-set gillnets for cod, which seldom capture eels, but where the external tag possibly became entangled. The other recaptures were reported from eel trapnets, the main gear used in the Baltic to fish migrating silver eels.

Activity patterns and diving behaviour

All eels showed a specific diurnal activity pattern: passively resting on the sea floor during daylight, then swimming at or just beneath the surface at night. Figure 2 shows an overview of the vertical activity pattern in all time-series. In one case (eel 8, 7 October 2005), the fish remained active for the whole day, but stayed close to the thermocline during daylight, i.e. fairly deep. Eels 1 and 6 remained at the bottom for one or several full days before resuming their migration.

The onset and the termination of swimming activity were clear. The average time of initiation and termination of activity, respectively, corresponded to the times of civic twilight (Figure 3).

On average the eels spent >55% of the active swimming time <1 m from the surface. The maximum time close to the surface was seen in eel 6, which spent up to 90% of its active time in

Table 1. Summary of data for the recaptured eels.

Eel	Length (m)	Weight (kg)	Recapture date	Days at liberty	Gear	Data	Distance in water (km)	Total swimming time (h)	Rate (m s^{-1})	Rate (BL s^{-1})
1	0.69	0.9	11 October	11	Poundnet	Yes	130	103	0.35	0.51
2	0.77	1	12 October	12	Poundnet	Yes	170	132	0.36	0.47
3	0.72	0.75	10 October	10	Poundnet	Yes	130	107	0.34	0.47
4	0.85	1.25	6 October	6	Gillnet	No	110			
5	0.78	0.78	8 October	8	Poundnet	First day missing	130	86	0.42	0.54
6	0.81	1.2	24 October	24	Gillnet	Yes	155	146	0.29	0.36
7	0.84	1.13	2 November	33	Poundnet	No	170			
8	0.64	0.48	11 October	11	Poundnet	Yes	170	142	0.33	0.52

All eels were released on 31 September 2005. Minimum mean swimming velocity assuming a straight trajectory (BL, body length).

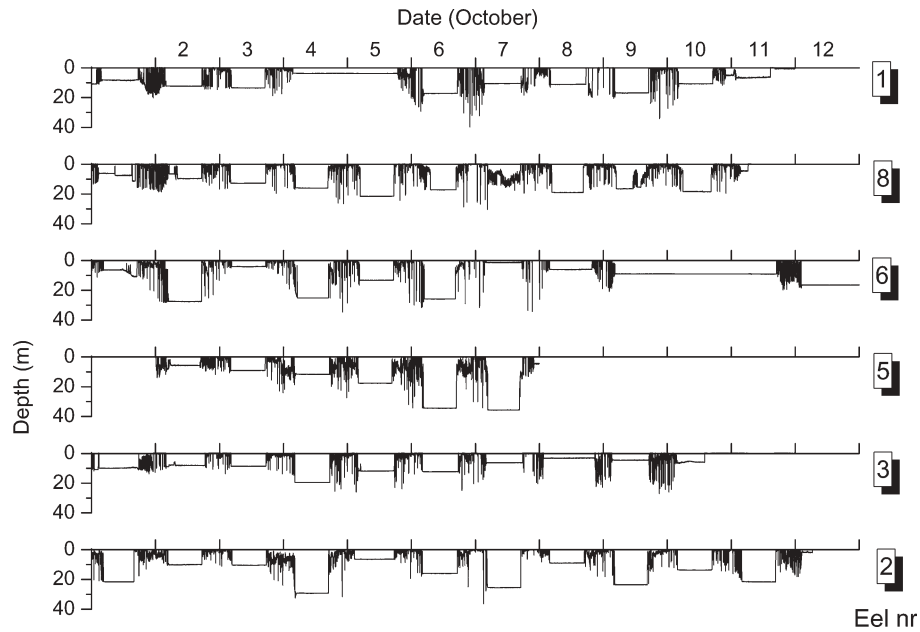


Figure 2. Swimming depth time-series of all eels shown on a common time-scale.

water < 1 m deep. Sporadic dives were a common feature for all eels, taking place between long periods of swimming close to the surface. Figure 4 shows an example of dives, which usually consisted of a single, monotonic movement down, then swimming upwards again. The duration of the dives was proportional to the maximum depth, 3–5 min for a 10 m dive, and without prolonged periods at mid-depth. The periods close to the surface could be quite long, up to 2 h deviating < 0.5 m from zero depth. The time and the maximum depth of all deep exploratory dives were compiled, and the total number per night between 1 and 12 October is shown in Figure 5. The average number of

deep dives ranged between 10 and 25 per night, but there was no clear trend in this behaviour during the study period.

The mean number of deep dives per hour for the whole 12-d period is shown in Figure 6. The number of deep dives was equally distributed between hours during the active swimming period at night, although there was some indication of a greater diving frequency in the early and late phase of the active period, compared with the middle of the night.

Swimming distances, velocity, and reconstructed trajectories

The results of this analysis are shown in Table 1. The eels swam between 130 and 170 km during their periods at liberty, assuming a straight trajectory. Estimates of minimum mean swimming velocity gave similar values for all eels.

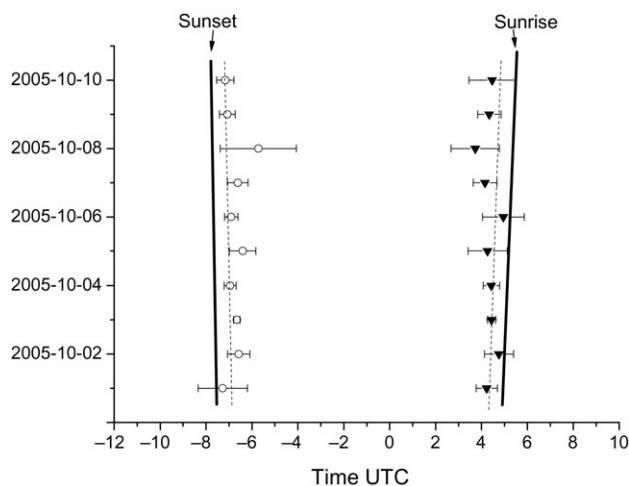


Figure 3. Average time of onset of activity (circles) and termination (inverted triangles) for the six eels on a given date. The solid lines show the time of sunset and sunrise corrected for date and approximate longitude of the eels. The error bars show the 95% confidence intervals, and dashed lines the time of start and end of civic twilight.

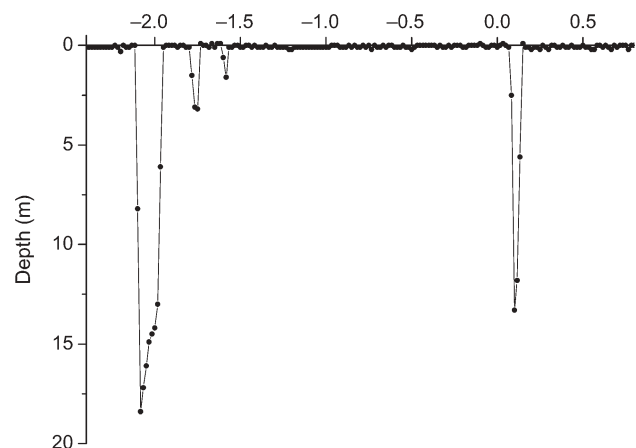


Figure 4. Examples of exploratory dives of eel 1 around midnight 9–10 October. The horizontal scale shows hours, with zero at midnight UTC. The dots show the measuring points at 1 min intervals.

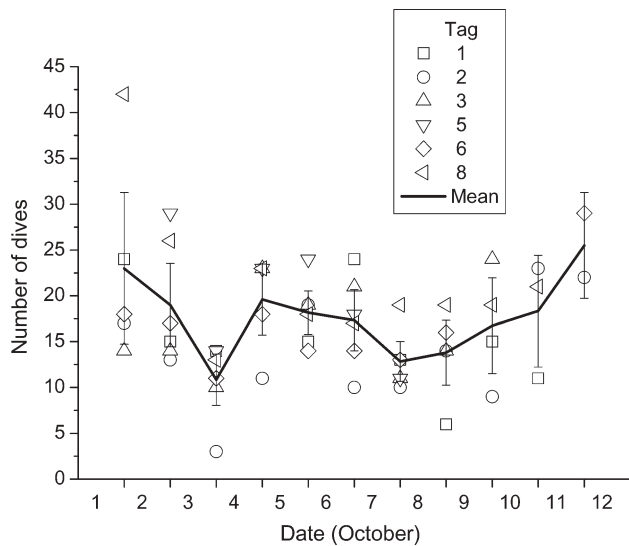


Figure 5. The number of deep exploratory dives during the nightly activity period of individual eels and averaged for all the eels (solid line). The error bars show the 90% confidence interval of the average.

The maximum vertical velocity recorded was $0.2\text{--}0.3\text{ m s}^{-1}$. There was no clear difference in the maximum rate of ascent and descent. The 99% percentile may be used as an estimate of the characteristic vertical velocity during dives. Table 2 lists the statistics of vertical velocity for each recaptured eel.

Light measurements can in principle be used to estimate the daily position of the eel. The precision of the positions obtained was, however, poor, and the latitude estimates were not useful for reconstructing the trajectories of the eels. One reason for the uncertainty is the specific behaviour around dawn and dusk, when the eel usually made large excursions up and down between the bottom and surface. This caused large disturbances in the light record during the most sensitive period for determining the time of sunrise or sunset.

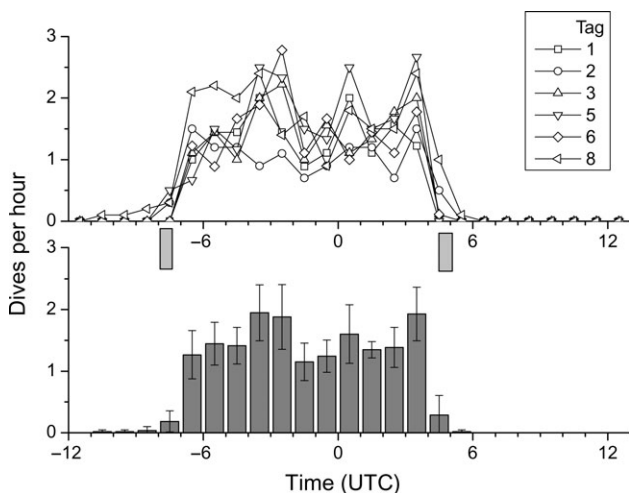


Figure 6. Diving activity pattern of individual eels averaged for all full nights of activity. The upper panel is an average for individual eels, and the lower panel the mean activity of all eels. Error bars show the 95% confidence interval.

Table 2. Statistics of mean instantaneous vertical velocity, averaged over a 60 s sampling interval, calculated for a total of ~ 70 h for each eel.

Eel	Mean absolute velocity (m s^{-1})	s.d.	Minimum (m s^{-1})	Maximum (m s^{-1})	99% percentile of absolute velocity (m s^{-1})
1	0.021	0.0343	-0.29	0.19	0.14
2	0.016	0.0240	-0.22	0.19	0.12
3	0.019	0.0320	-0.28	0.23	0.15
5	0.027	0.0312	-0.22	0.25	0.13
6	0.018	0.0356	-0.28	0.30	0.18
8	0.020	0.0339	-0.25	0.23	0.16

An alternative way to reconstruct an eel's trajectory is to use the accurately known time of activity each night combined with the observed depth at the place where the eel spent the intervening daylight periods. If the mean swimming speed at night is assumed to be equal to that for the whole track, then the length of the successive nightly movement may be calculated. The observed mean swimming speeds when active (Table 1) are similar to the instantaneous velocities seen in telemetry tracks of eels in the Baltic (Tesch *et al.* 1992b), so this assumption is clearly realistic.

The bathymetry of the area is uncomplicated, with essentially a gradual depth increase with distance from the coast. The depth relative to mean water level was taken from Swedish navigational charts. As there are small water level variations and no tide in the Baltic, depth and distance can be used to define a single most probable position for most cases. Figure 7 shows the individual tracks constructed in this way. The eels seem mostly to follow the coastline, but at some distance offshore. The median depth where the eels stopped during daylight was 12 m.

Discussion

The main findings of this study were the strict diurnal rhythm in swimming activity, i.e. resting during daylight, the start and cessation of the migratory (swimming) period at civic twilight, the fact that the eels mostly swam very close to the surface, and the ubiquitous exploratory dives. These results are also supported by observations from telemetry experiments, though recorded from fewer eels and with shorter durations.

Several factors support an assumption that the behavioural pattern observed in this study is indeed representative for return-migrating silver eels in the Baltic. The observed behaviour was similar both within and between eels. Additionally, many observations fitted earlier data well. The migration rate of $10\text{--}20\text{ km d}^{-1}$ observed in this study falls within the range found from earlier conventional tagging experiments (Trybom and Schneider, 1908; Martinkowitz, 1961; Sjöberg and Petterson, 2005), and the average swimming speed of 0.5 body lengths s^{-1} is similar to what has been observed in telemetry tracking in the Baltic (Westerberg, 1979; Tesch *et al.*, 1992b). However, some behavioural variation was observed, because eel 6 rested three times at the bottom for a period of 2–3 d.

The resting periods on the seafloor by daylight have been observed previously (Westerberg, 1979). The regularity of onset and ending of activity was striking in the present data. The direct light measurements from the DST were of little help in understanding the cue for this behaviour, because the threshold

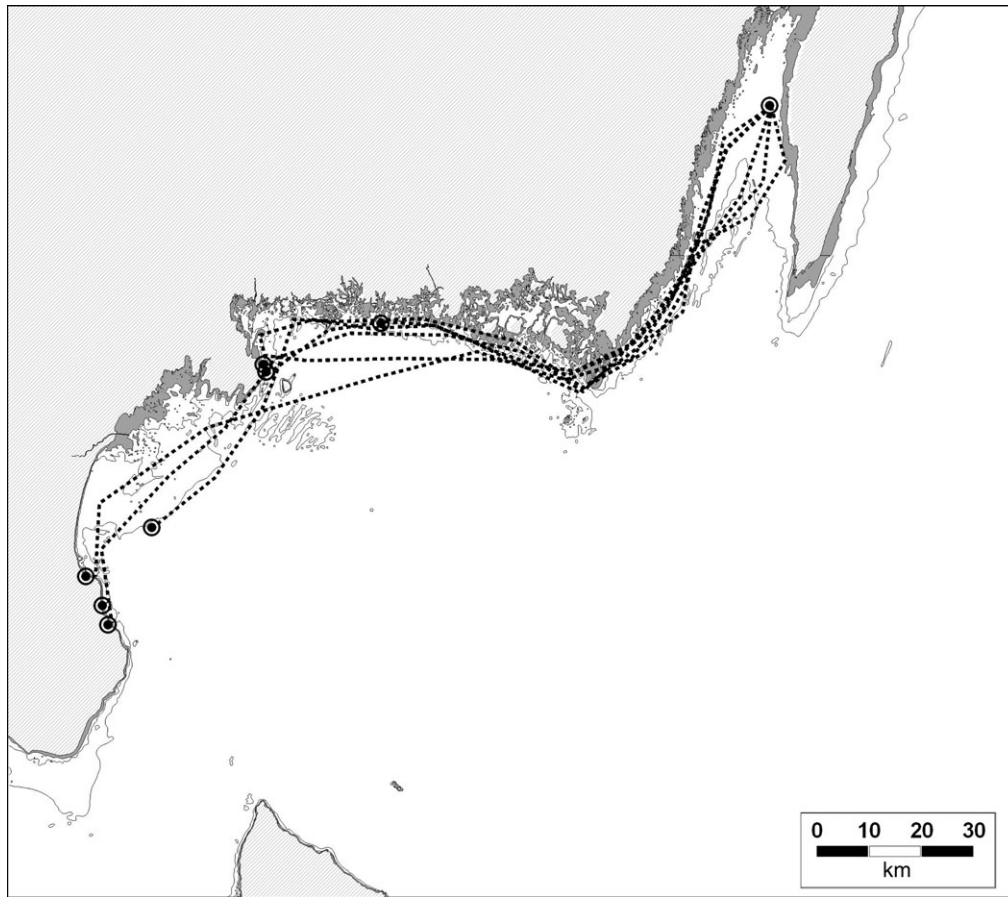


Figure 7. Individual trajectories of the six eels reconstructed from daily distance and the bottom depth at rest. The 0–6 m depth interval is shaded grey, and the 10 m and 20 m isobaths are shown.

light level for the onset of activity seems to be below the resolution of the sensor, and the measurements often were disturbed when the eel was buried in the sediment, or made rapid vertical movements up and down. However, the close relationship with time of local civic twilight (Figure 3) suggests that the cue for activity was light rather than a circadian rhythm.

The moon was in the first quarter during the experimental period. On 1 October, 4% of the moon surface was lit, and it became visible at 02:00 UTC, ~2 h before sunrise. On 11 October, 58% of the moon was lit and visible until 21:00 UTC in the evening, or 4 h after sunset. No aspect of the diving behaviour observed in this study, however, seems to be related to moon phase.

One eel continued migrating also during daylight for a single day. Such continuous migration is the most common behaviour seen in telemetry experiments in the open sea (Tesch, 1989) and has also been observed in the Baltic (Tesch *et al.*, 1992b). A hypothesis is that migration is continuous in deeper sea areas and that the diurnal activity found in this study only takes place in shallow seas.

The prolonged periods of swimming very close to the surface has to our knowledge never been reported before. The actual distances below the water surface were not fully resolved by the DST, but seem to have been just a matter of a few centimetres. The reason for this behaviour is unknown. As a speculation, it might be related to the navigating ability of eels. If eels use celestial cues, migration obviously has to be close to the surface to spot

the celestial objects. Another interpretation is a connection to one of the mechanisms that has been proposed as a basis for magnetic orientation. The “radical pair mechanism” depends on magnetic effects in the retina (Wiltschko and Wiltschko, 2006) and cannot work in total darkness. Starlight is sufficient, however.

The reasons for the sporadic dives are unclear. Some dives probably went right to the seabed and could be a way for the eel to sound depth. The most dives seem, however, to turn at some intermediate depth. The possibility that the dives are a way of saving energy by alternating glides and powered movement up again, which is known in birds and elasmobranchs (Weihs, 1973) has been tested and disproved earlier (Westerberg, 1984). Eels swim actively both down and up.

Acknowledgements

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