International Council for the
Exploration of the Sea

C. M. 1977/M:3
Anadromous and
Catadromous Fish
Committee

Observations on the spawning migration of the eel (*Anguilla anguilla*) west of the European continental shelf

by

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Synopsis: In the Northern Bay of Biscay and West of the Iberian continental shelf five silver eels (Anguilla anguilla L.) have been tagged with ultrasonic transmitters and tracked 13 to 23 hours over a depth of 2oo to 25oo m. Their mean direction from release to the final position of tracking was 288° and significantly farther west than silver eels tracked earlier in the North Sea (341°).possibly 26o° (direction of the Sargasso Sea 25o°). Four of the transmitters were equipped with pressure sensing devices which signalized the depth down to at least 4oo m. Three of these specimens tracked at night during full moon preferred a mean depth of 125, 166 or 215 m. One specimen choose a depth of 1oo m during moonlight and 5o m after the setting of the moon. Major depth changes occurring normally one per hour ranged up to a maximum of 2oo m and showed a maximum of o,6 m/sec; this is very close to the normal horizontal speed. With dawn the eels dived to a depth of 4oo m or more except one specimen. The diving of the eels was recorded to take place generally below the thermocline.

Résumé: Dans la partis septentrionale du Golfe de Gascogne et à l'ouest du plateau continental ibérique cing anguilles argentées (Anguilla anguilla L.) ont été marquées par ultra-sons transmetteurs et poursuites pendant 13 - 23 heures sur 200 à 2500 m de profondeur. Leur moyenne direction de libération jusqu'à la dernière position de la poursuite était 288°. C'était considérablement plus éloigné à l'ouest que celle des anguilles argentées, poursuites autrefois dans la mer du Nord (341°), peut-être 260° (direction de la Mer de Sargasse 250°). Quatre transmetteurs etaient munis de détecteurs de pression qui marquaient une profondeur de 400 m au moins. Trois des spécimens poursuits pendant la nuit, quand la lune était en son plein, préféraient une profondeur moyenne de 125, 166 ou 215 m; un spécimen une profondeur de 100 m pendant clair de lune et de 50 m après la lune s'était couchée. Plus grande changements en profondeur, avant lieu normalement une fois par heure, ont été déterminé jusqu'à une profondeur maximale de 200 m et à une vitesse maximale de 0,6 m/sec; c'est tout près de la normale vitesse horizontale. A la brune, les anguilles, un spéciment excepté, plongeaient jusqu'à 400 m de profondeur ou plus. On a enregistré que les anguilles plongeaient généralement au-dessous de la thermocline.

Introduction

Direct observations on the spawning migration of fishes in the sea by ultrasonic tracking are rare and mainly restricted to investigations in coastal areas. Primary subjects have been salmonid and anguillid fishes. Among these the European eel (Anguilla anguilla L.) has also been studied in shelf areas of open sea conditions (Tesch 1972, 1974, 1977; Westerberg 1975).

The tracks of the experimental eels exhibited a westerly to northerly direction (see also Westin & Nyman 1976); otherwise barriers and coast lines deflected their preferred swimming direction. On the stimulation and on the cues for orientation of the spawning migration several hypotheses have been presented (see also Stasko & Rommel 1974). They are important for further attempts to investigate the dependence of movements from environmental cues in the laboratory. New investigations in this field and on the oceanic ecology of Anguilla spec. are necessary.

Studies of this type have been conducted by the author during the last few years; they were carried out immediately above the continental slope up to a depth of more than 2500 m off the Bay of Biscay and the North West Iberian slope. As the effort especially concerning ship activity and equipment is very great the number of the tracking experiments with essential results is restricted to five. They are presented in this paper and include directional movements as well as depth preferences measured by pressure sensing transmitters.

Material and Methods

The experimental animals were silver eels caught in pound or stow nets designed to trap eels on their spawning migration. Eels Nos. 15, 31, 33 (numbering in continuation of earlier experiments) originated from coastal commercial catches of the German Baltic Isle of Fehmarn and Nos. 27 and 32 from Irish Rivers. Shipment to the tracking vessel took place as quickly after the catch as possible, generally within two or three days except No. 27. On board they were gradually adapted to marine salinity ($\approx$33 ‰) within at least six to twelve hours. Residence in this salinity until release (cruise to the tracking area) lasted mostly more than a week. Experiments on these and on eels tracked earlier showed that eels originating from a marine environment and not shipped in freshwater maintained the best condition until release. Size of the experimental eels as well as conditions and area of tracking are summarized in Tab. 1. Anaesthetizing of eels with benzocaine (sewing the pinger in front of the dorsal fin) was similar to earlier experiments (Tesch 1974, 1977).

For all experiments, except No. 15, pressure sensing transmitters of the Electrial Engineering Department, University of New Brunswick, Fredericton, Canada were used (see Stasko & Rommel 1974) (size 84 x 14 mm, 55 dB re μb, 1 m). No. 15 was a 52 dB re 1 μb, 1 m transmitter of Smith Root Electronics (USA). A specimen of this transmitter has proven to resist a water depth of 13o m at a maximum, others less.

Tab. 1 Size of eels, time and area of tracking and weather conditions

Silver eel tracking experiment No.	Length of eel (cm)	Date of tracking	Time of tracking (GMT)	Area of release	Water depth (m)	Weather conditions during tracking
15	82	17.-18. Nov.1973	18.1o-17.2o	Biscay 9onm SW of Brest	2oo - 575	overcast, later clear wind SSE 4
27	1o5	14.-15. Nov.1975	23.25-12.15	43 nm West of Vigo (Spain)	2ooo-22oo	clear, wind from varying directions
31	94	4.-5. Nov.1976	o9.58-11.28	Biscay 1oo nm West of Brest	41o - 15o	overcast, wind westerly 2 - 5
32	97	5.-6. Nov.1976	15.35-12.45	Biscay 1oo nm WSW of Brest	96o - 25oo	overcast, wind westerly 2 - 7
33	89	6.-7. Nov.1976	17.39-1o.2o	Biscay 1oo nm WSW of Brest	145o-2ooo	overcast, wind 5 - 8

A second pinger from the same company connected with a silver eel and released shortly before No. 15 obviously crashed about 3o seconds after release of the experimental fish. No. 15 also finished its transmission suddenly after 23 hours of tracking, indicating a probable defect due to high pressure. The pressure sensing transmitters were examined to resist a water depth of 2ooo m. Their pressure transducer was guaranteed to resist a water depth of 2oo m. Practice showed that measurements of about 4oo m were possible, but this reduced the normal life of the battery from a week to a day because of a too rapid sequence of pulses. - All transmitters were made buoyant by a balsa wood saddle to reduce experimental influence and to improve connection with the fish.

The receiver and hydrophon system was that of Krupp- Atlas Elektronik, Germany, used in earlier experiments (Tesch 1972, 1974, 1977). Pulse counting, which was necessary for the registration of the depth, was occasionally automatically attempted using a Hewlitt Packard recorder, but interfering noise made counting by use of a stop watch more practicable.

The tracking vessel was R. V. "Friedrich Heincke" (total length 38 m) which is of a size sufficient to offer safety under East Atlantic conditions but provides also adequate manœvrebility for the tracking operations. From this vessel hydrographical bottle samples in different depths were also made in the resprective areas to obtain information on the temperature and salinity conditions.

In contrast to earlier studies an exact and detailed determination of the tracking courses was not possible. This depended partly on less exact Decca navigation values in these areas farther distant from Decca transmitters. It also depended on less accurate finding of the eel's position because of the great vertical distance from the eel which together with rough seas made it uncertain whether the ship was vertically above the fish or not. Furthermore, determination of the current (Westerberg 1975; Tesch 1977) in the depth preferred by the eel was impossible. However, tidal currents in such a depth are negligible The same is true with temporal wind generated currents in the depth under consideration. Permanent currents in the preferred layers are comparatively low and on the continental slope change with depth, probably being vertical. Hence the change of horizontal position can be taken as the eel's direction through the water.

Results

1. Horizontal movements

The geographical areas of trackings are given in Fig. 1. The single Decca positions and the progress of the eels from release to the end of tracking are illustrated in Fig. 2. During the 13 - to 23-hour-lasting experiments all specimens exhibited progress in a westerly direction with the exception of No. 31 which showed a northerly tendency. Similar directional tendencies are obvious if the courses are divided in vectors and the mean direction for each individual is calculated.

Tab. 2 presents the comparison of the single values, a statistical evaluation and the mean direction. For the single courses Nos. 31, 32, 33 exhibit significant values if the Hodges and Ajne test (Batschelet 1972) is applied. Significance also results if the Rayleigh test (Batschelet 1972) is used on the mean direction from release to end of tracking of the five specimens (error: 2,5 %). Significance is less (error: 1o %) if the test is applied to the mean direction of vectors. This is explicable if the single courses are analysed in more detail. No. 15 for example, during the first third of its tracking exhibited a directed movement to the North; for the rest of the track it was SW. This specimen was released over a depth of 2oo m (Tab. 1), i. e. very near the shore. Later it reached greater depths (up to 575 m). Hence, there is the question as to whether the first part presents a migration on the shelf and the second part an off-shelf migration. On the other hand No. 31, released at 41o m, attained less deep water (finaly 15o m) by its movements in a North-West direction; this specimen changed its direction towards the North during

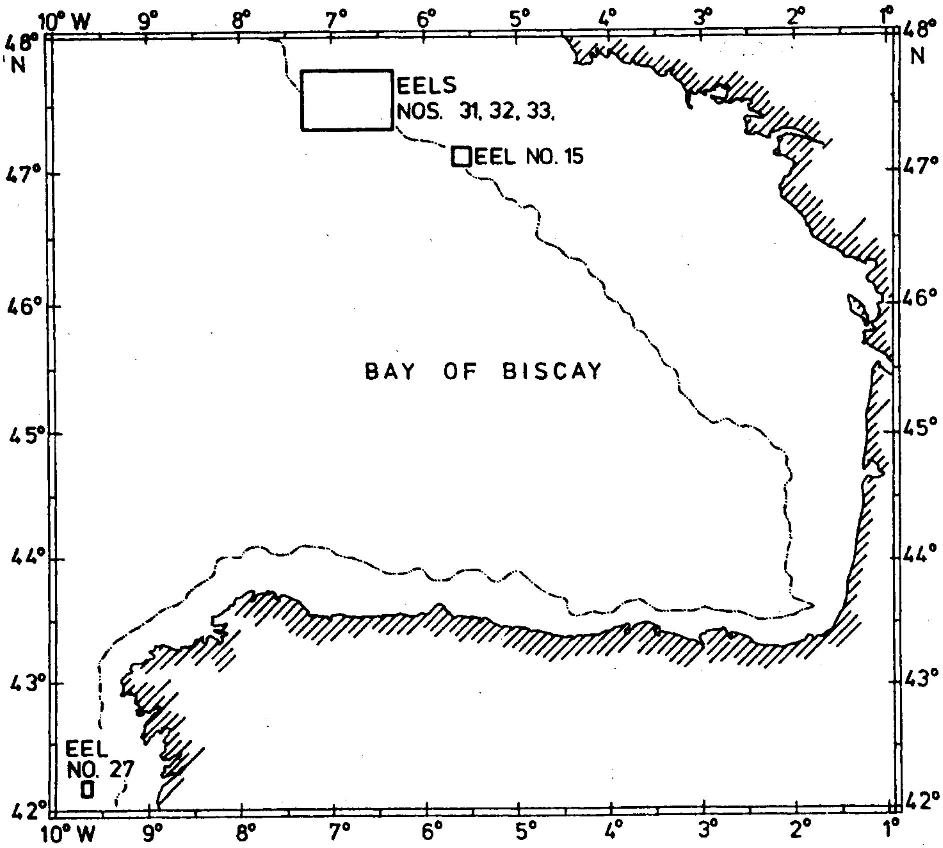

Fig. 1. Areas of trackings in the Bay of Biscay and west of Spain.

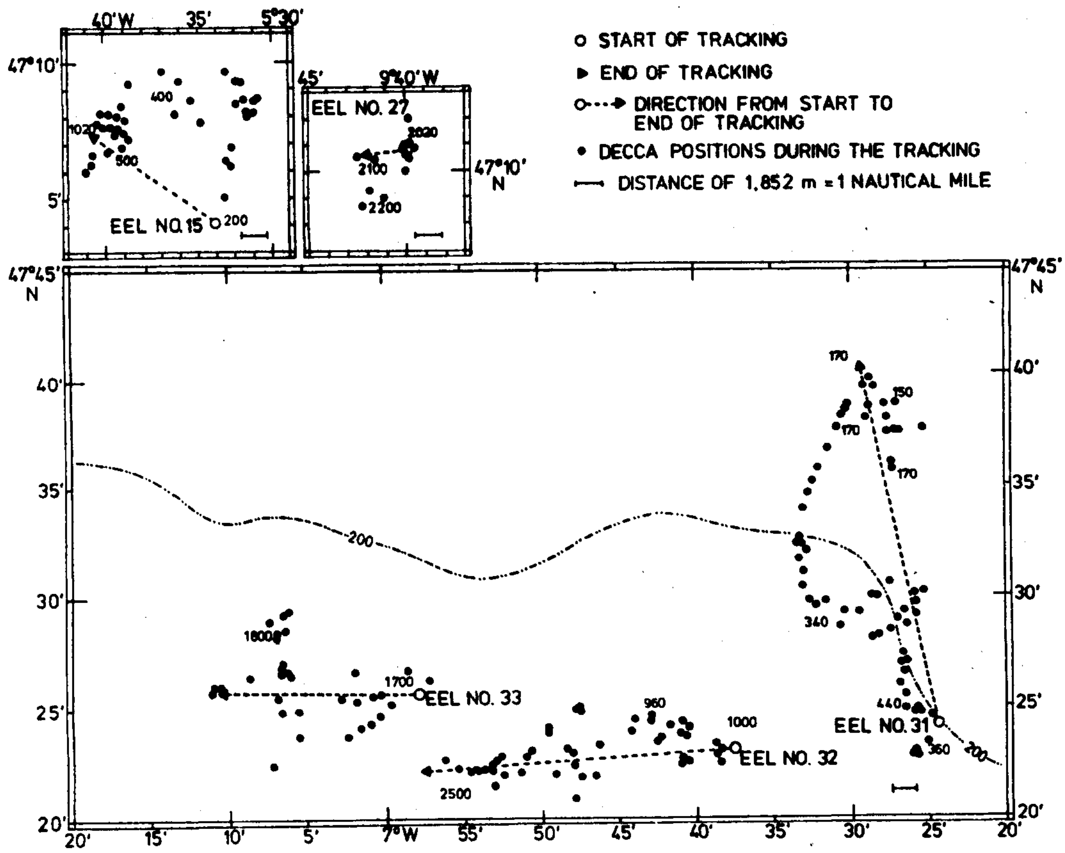

Fig. 2. Tracking positions of five eels on the continental slope of the Bay of Biscay (Nos. 15, 31, 32, 33) and west of Spain (No. 27) with directions from start to end of track and water depths (small numbers).

Tab. 2

Eel No.	Directions from release to end of tracking	Mean direction of different vectors of the course	Hodges and Ajne Test (P)	Speed on a straight line between release and end of tracking (kn)	Mean speed of different vectors (kn)
15	304°	291°	non-significant	0.2	1.3
27	260°	206°	non-significan	0.2	0.8
31	348°	348°	0.01	0.6	2.4
32	265°	267°	0.01	0.6	2.0
33	274°	281°	0.01	0.5	2.1
mean	289°	279°			
Rayleigh-Test					
z	3.6(p=0.025)	2.6(p=0.10)			

the second part of the track sometimes even a little east. For the second part of that experiment one should better consider this eel as migrating on the shelf and axhibiting a directional behaviour described earlier for the shelf migration (Tesch 1974). Nos. 27, 32, 33 were generally observed to make horizontal progress with an increase of water depth (Tab. 1). This corresponds with progress in a westerly direction.

The results on the speed (Tab. 2) are not very reliable. For Nos. 31 to 33 it is evident that the speed within different vectors of the tracks cannot present the true values, which are much influenced by the scattering of the positions. On the other hand, the speed on a straight line between release and end of tracking is too low; silver eels are found to move with a speed of about 1 kn (Tesch 1972, 1974, 1977). Within sections Nos. 15 and 27 showed a speed of that order. Hence the scattering of position in both these cases seemed to me minimal and therefore according to Fig. 2 the directionality of No. 27 small.

2. Vertical movement

Fig. 3 presents the depth preference pattern of the whole track of No. 27. Details of the other eels' depth patterns are similar. For convenience they are compressed, and together with No. 27 are exhibited in graphs of hourly mean depth preferences (Figs. 4 and 5). No. 27 was tracked during the lunar period of the first quarter to full moon with a moon mostly completely visible until setting. After this eel was released at midnight, it

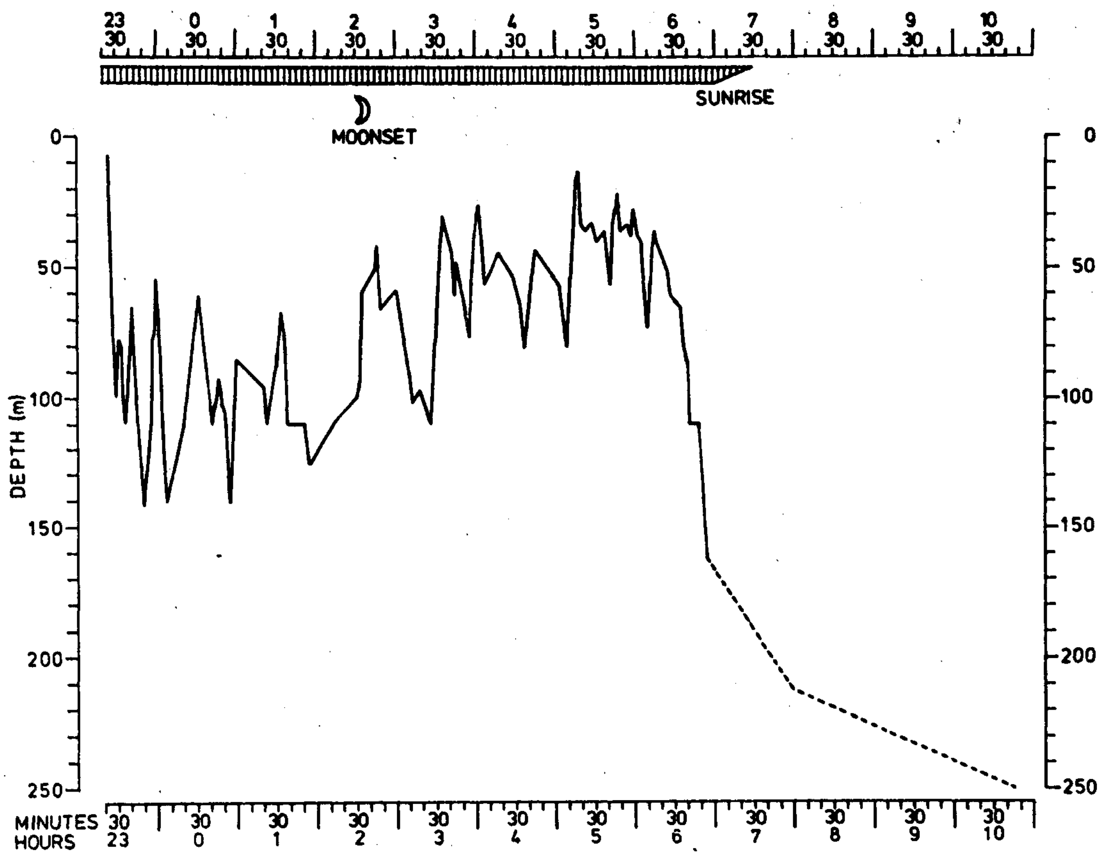

Fig. 3. Example of vertical movement pattern from release to end of tracking (eel No. 27; Nov. 14-15, 1975, GMT) with sunrise and moonset. Dashed line: no continuous and accarate recording.

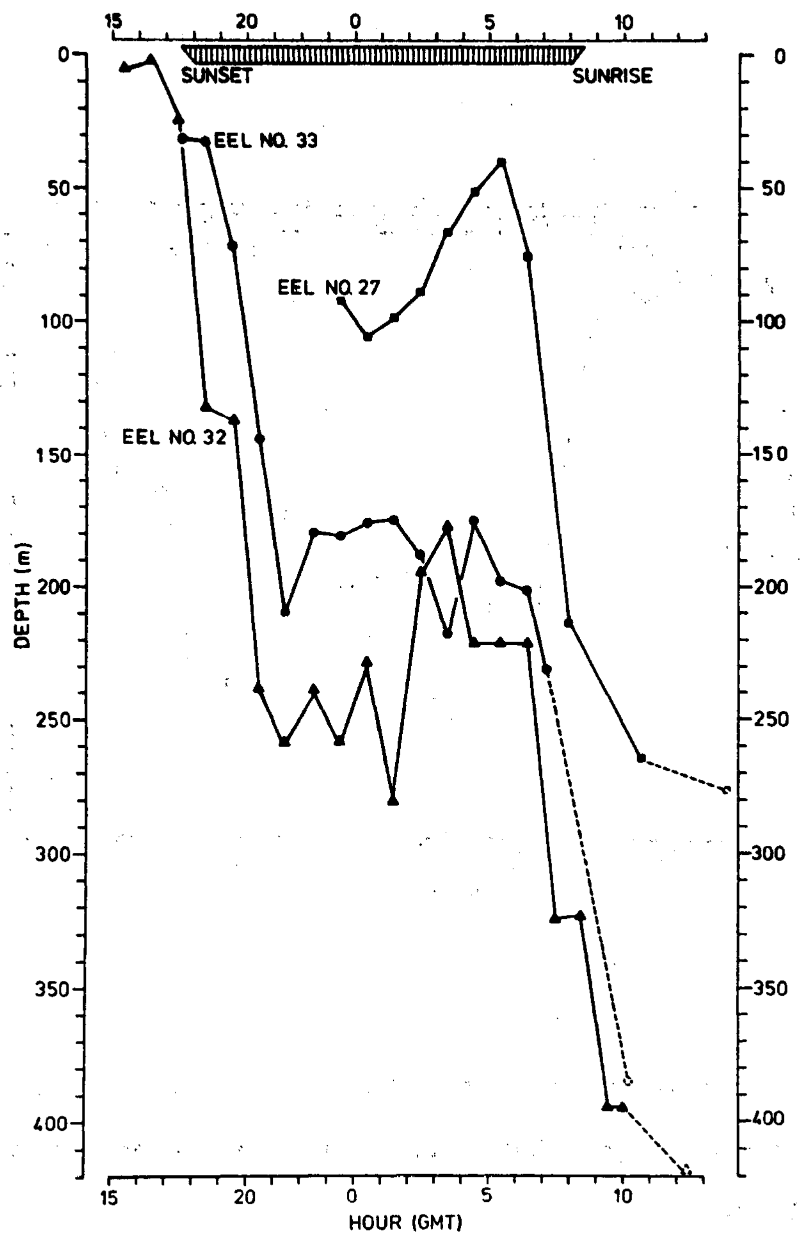

Fig. 4. Hoarly mean swimming depth of eels (Nos. 27, 32, and 33) in relation to sunrise and sunset. Dashed line: no continuous and accurate recording.

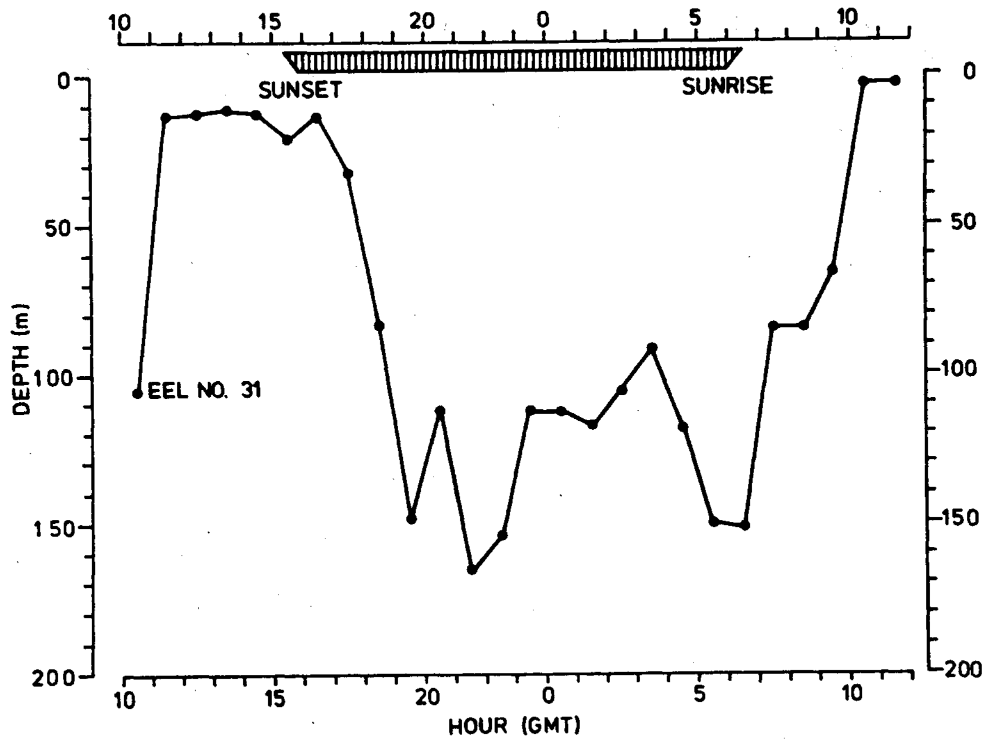

Fig. 5. Hourly mean swimming depth of eel No. 31 in relation to sunrise and sunset. Dahed line: no continuous and accurate recording.

chose a depth of about 1oo m although changing from time to time between about 6o and 14o m. After setting of the moon it changed to a preferred depth of about 5o m with a minimum of 18 and a maximum of 11o m.

Common in all four eels with pressure sensing devices and more pronounced in No. 31 (Fig. 5) than in No. 27 was a deep diving immediately after release. Nos. 31 and 32 were released during daylight and following the first deep diving swam at comparatively shallow levels (Fig. 4, preferably 2 to 2o m); No. 31 made one excursion per hour to about 4o m. About one hour after sunset they exhibited deeper preferences (Figs. 4, 5), similar to the other two specimens released at night. Preferred (mean) depths at night of Nos. 31, 32 and 33 were 125, 215 and 166 m, respectively, and therefore deeper than No. 27. Lunar period during all three experiments was nearly full moon, i. e. throughout the night the moon was above the horizon but most of the time was covered with clouds (Tab. 1). Single excursions down to a maximum of nearly 3oo m were observed; the most shallow records were generally 8o m, although No. 31 twice swam to 2o or 3o m. Major depth changes normally occurred once per hours or less, for No. 31 more often. The depth changes of Nos. 31 to 33 were greater than in No. 27 and attained maxima of 2oo m. Maximal diving and emerging speed were o,3 to o,6 m per sec. but normally less. Thus the eels must occasionally have swum more than one knot in a vertical direction and hence at a similar speed as during horizontal movement. The real mean swimming speed must therefore be higher than measured by the horizontal progress.

In the morning hours with the slightest appearance of dawn all specimens except No. 31 exhibited a strong downward trend (Figs. 3 and 4). The continous increase of the pulse frequency of the pinger was measured for No. 32 down to a depth of 400 m. During full daylight the pulse frequency could no longer be measured because of too rapid speeds. Later evaluation by means of a tape recorder and time-lens reading revealed a depth of more than 1000 m. But as the pinger continued at the high speed pulse frequency and showed no variation, a defect of the pressure transducer could have occurred. The transducers of the other pingers showed a similar questionable function when the daylight increased. Hence the question of the exact depth during daytime could not be resolved satiffactorily.

No. 31 showed a quite different behaviour compared with these three eels. With increasing light in the morning it emerged to lower depths and remained immediately below the surface until 11 h GMT (Fig. 5), when this experiment was stopped. The special behaviour of this eel concerning vertical preferences in addition to abnormal frequent depth changes during the night was in accordance with abnormal horizontal movement far North.

3. Hydrographical donditions

The hydrographical conditions during the investigation on this part of the continental slope showed no special features which could explain the depth preferences. The salinity over a depth of 2ooo m varied between the surface and a depth of 475 m from 35.439 ‰ to 35.521 ‰ ; also nearer to the shelf (4oo m deep) neither a major change with depth nora salinocline occurred (surface: 35.4o4 ‰ ; 3oo m : 35.536 ‰).

The temperature generally decreased slightly over all depths. At 2ooo m with a surface temperature of 12.67° C a weak thermocline between 75 and 1oo m was present; at 475 m the temperature was 1o.88° C. Eels Nos. 32 and 33 examined over this depth swam almost exclusively below the thermocline. At night only No. 31 could have chosen a warm water layer near the shelf at a depth of 125 m (12.27° C); at 1oo m the temperature was 11.98° C (bottom at 15o m: 12.24° C; surface 13.34° C). But this specimen very likely exhibited abnormal behaviour. No. 27 was investigated under conditions which showed at a depth of 185o m a surface temperature of 17.o3° C, a thermocline between 75 m (15.o5° C) and 1oo m (12.96° C) and 12.32° C at 5oo m. Hence it swam during moonlight below the thermocline and after setting of the moon above the thermocline. All these observations show that the silver eel is more sensitive to light than to temperature during its oceanic migration.

The considerable deep diving of the eels with increasing light shows these fishes to be extremely sensitive to light. Probably vertical migration takes place each dawn and dusk over a range of several hundred metres. This is supported by the results of Reinsch (1968) who found silver eels in the stomachs of bottom or near bottom dwelling fishes caught at a depth of over 7oo m. Vertical migration of the silver eels seems to be of a similar character as in eel larvae caught in areas not distant from the tracking positions (Tesch unpublished). The diving tendency of a silver eel during daylight also became evident by the tracking results of Westerberg (1975). He found that the eel was inactive at the bottom during daylight. Thus it retired from the light until stopped by the bottom (depth 4o - 5o m). In the probably comparatively clear water conditions during experiment in the Baltic light at the bottom was still too strong and hence, activity reduced.

That warm water bodies could act as a stimulus for orientation (Westin & Nyman 1977) is unlikely. The deep diving of the eels during the day and partly also during the night carried them away from warm water layers. An exception is perhaps No. 31, but this specimen did not give a good example concerning horizontal or vertical movement.

No. 32, which was released during daylight,, showed a preference for small depths during the first day although deep diving during the second day was observed. Probably a certain time of adaptation to the deep sea conditons is necessary and/or recreation from experimental treatment on board is necessary to exhibit normal behaviour; for No. 31 this perhaps never occurred during the experiment.

Discussion

The mean horizontal direction from release until the end of tracking of the five specimens investigated was 288°. Silver eels tracked in the North Sea with free choise of all directions exhibited a mean of 341° (Tesch 1974). As the concentration of both these samples is similar (k = 3.1 and 3.4, respectively), the parametric two-sample test of Watson and Williams (1956) can be applied. The calculation results in a significance which is slightly above the 5 % level. As mentioned above it is doubtful whether eel No. 31 moved off the shelf, and for No. 15 only the last part of its track is a migration off the shelf. A corrected value for No. 15 (243°) leads to a significance (error: 2.5 %) of the difference between shelf and slope tracks. If in addition No. 31 is omitted the mean direction during off shelf migration is 26o°. The direction from Cape Finisterre to the Sargasso Sea is between 25o° and 255° and hence the mean direction of the eels on the continental slope is nearly in accordance with the course to be expected for the final migration. If it is accepted that the direction changes immediately on the continental slope light or pressure could be the releaser for the change.

The results give further evidence that a compass course perhaps dependent on the geomagnetic field must be involved (Tesch 1975). In the preferred great depths light sources as a directional cue become more unlikely and also for the orientation on currents producing electrial potentials (Stasko & Rommel 1974; Westerberg 1975) no indications are present.

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