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Changes in swimming depth and direction of silver eels (*Anguilla anguilla* L.) from the continental shelf to the deep sea

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Abstract

Sixteen silver eels (*Anguilla anguilla* L.) were tagged with pressure-sensing ultrasonic transmitters and tracked for 1 to 152 hours, 12 in the western Mediterranean and 4, treated with pituitary extracts, in the Sargasso Sea. When released on the shelf of the Mediterranean near Gibraltar the eels preferred a course which led them continuously to deeper water. Four specimens released on the Morrocan shelf, reached depths of 350 m, continued to swim north or changed their earlier easterly course towards the north. Three eels in the Sargasso Sea showed progress in a southwesterly direction. No influence of tidal stream on the swimming course and speed is obvious except for one eel, released in the Straits of Gibraltar. In the Mediterranean, the eels exhibited conspicuous daily vertical migration downward during dusk and upward during dawn with a mean swimming depth of 196 m during darkness, 344 m during daylight. Depth preference during night probably varied with the phase of the moon. Maximum swimming depth near Gibraltar as well as in the Sargasso Sea was nearly 700 m. The eels in the Mediterranean swam at a mean speed of $0.3\,m.s^{-1}$ and were slower than most eels tracked in northern waters. Differences in the speed and in the directed swimming in the course of the lunar or the solar day are visible.

Keywords : *Anguilla anguilla*, migration, behaviour, Mediterranean Sea.

Variations de la profondeur et de la direction de nage d'anguilles argentées (Anguilla anguilla *L.*) *quittant le plateau continental vers la mer profonde.*

Résumé

Seize anguilles argentées (*Anguilla anguilla* L.), traitées avec de l'extrait hypophysaire, et sur lesquelles des émetteurs ultrasoniques ont été implantés, sont suivies durant 1 à 152 heures, à raison de 12 animaux dans la Méditerranée occidentale et 4 dans la mer des Sargasses. Libérées sur le plateau continental de la Méditerranée, à proximité de Gibraltar, les anguilles s'orientent préférentiellement vers des profondeurs de plus en plus grandes. Les quatre spécimens libérés sur le plateau continental marocain, et qui atteignent une profondeur de 350 m en nageant vers le Nord ou vers l'Est, s'orientent ensuite vers le Nord. Dans la mer des Sargasses, trois anguilles présentent un déplacement vers le Sud-Ouest. Aucune influence des marées, sur la direction et sur la vitesse de nage, n'est observée, à l'exception du cas d'une anguille libérée dans le détroit de Gibraltar. En Méditerranée, les anguilles présentent des migrations verticales très nettes, dirigées le matin vers les plus grandes profondeurs et le soir vers la surface, avec une profondeur moyenne de nage de 196 m pendant la nuit et de 344 m pendant la journée. La profondeur préférentielle durant la nuit varie probablement avec les phases de la lune. La profondeur maximale atteinte est d'environ 700 m, à proximité de Gibraltar comme dans la mer des Sargasses. En Méditerranée, les anguilles nagent en moyenne à une vitesse de $0{,}3\,m.s^{-1}$, ce qui est inférieur à la plupart des observations concernant des anguilles dans des mers plus nordiques. Des différences quant à la vitesse et à la direction de nage sont visibles au cours du jour solaire et lunaire.

Mots-clés : *Anguilla anguilla*, migration, comportement, Méditerranée.

INTRODUCTION

Silver eels which had been captured during their spawning migration were released and tracked in North Sea and Northeast Atlantic shelf areas. These fish exhibited a preferred northerly swimming direction (*Tesch*, 1974, 1979). Eels released over greater depth showed different directional tendencies. In addition, a dawn downward movement of probably over 400 m was observed (Tesch, 1978 *a*, *b*).

In order to confirm the migratory tendencies on the shelf and off the continental slope a number of tracking experiments were performed between 1979 and 1984 mainly in the Alboran Sea, the westernmost area of the Mediterranean. A few preliminary trackings took place near the spawning grounds of *Anguilla* sp. on eels at an artificially advanced stage of maturity (Tesch, 1983; p. 271). These trials were designed to provide information on hydrographical conditions for spawning. This paper presents the results of studies on the horizontal swimming direction and swimming speed as well as the extent of vertical movements during spawning migration. The speed of vertical movements and its physiological consequences are published elsewhere.

MATERIAL AND METHODS

Geographical location as well as technical and environmental data of trackings between 1979 and 1984 are summarized in *table* 1. The weight of most of the eels was around 1 500 g. They were captured mainly by fyke or poundnets in the brackish Baltic by commercial fishermen. Transportation for most of the distance and most of the eels took place on board the research vessel *Friedrich Heincke* with running sea water or dry by air.

Before being tagged the eels were anaesthesized for 5 to 20 minutes with Benzocaine. The pressure-sensing pingers (*table* 1) produced by VEMCO, Canada, had a weight in water of 14 g (type: V 3 p-3 hi; length 74 mm; width 16 mm), a life of 2-4 days and 58 dB or 19 g (V 3 p-5 hi; length 103 mm; width 16 mm) a life of 8 to 14 days and 59 dB. A frequency of 50 kHz was used. A magnetic switch in some of the pingers allowed activation after the tagging procedure which saved life time. The release after tagging took place about 3 hours later at a minimum, with magnetic switch 5 hours and more which allowed better recovery after anaesthetization. This was found to be necessary in other fish (Gallepp and Magnuson, 1972) to allow for recovery from negative buoyancy caused by the tag. The weight of the tag was probably essentially below maximum which can be compensated for the fish (Stasko and Rommel, 1974; Fried *et al.*, 1976; Summerfelt and Mosier, 1984).

For the tracking experiments in the Sargasso Sea and at the beginning of the trackings in the Alboran Sea, I used a Krupp-Atlas-Electronic receiver (Tesch, 1972) modified for operation in conjunction with a V-10 hydrophon of VEMCO, Canada. This means that a simplified technique with no automatic directional advice as during earlier trackings (Tesch, 1974, 1979) was used. The hydrophone was released by a hoist assembly through a hole of the hull beside the keel about 15 m behind the bow. For the later trackings in the Alboran Sea I used another receiver (VEMCO CR 40) together with the depth decoder VEMCO CI 40. In all cases, the tracking vessel was *RV Friedrich Heincke* (Tesch, 1978 *a*).

The eels used for the tracking in the Sargasso Sea (*table* 1) at the beginning of January 1979 were injected intramuscularly once a week with 0.5 cm^3 of soluble extracts of crude carp pituitary powder in sterile 0.9% NaCl-solution. This corresponded to 1 mg pituitary powder/100 g body weight. From February 12 to the start of tracking, this took place on board the tracking vessel in a 200-l container with preheated ambient sea water of 17-20°C. The eels attained an estimated gonosomatic index of about 10. Full ripeness is about 30 (Tesch, 1983; p. 54). The ovocytes grew to a diameter of 0.3 mm which is a third of a mature eel egg. Positions where eels were released are listed in *table* 7 with three eels in the northern and one eel in the central spawning area of *Anguilla anguilla*. The positions were determined by satellite fixes, in the Alboran Sea by Decca or terrestrial points. The prevailing weather conditions were moderate to fair, which was one of the reasons for conducting most of the tracking experiments in an area protected from strong westerly winds of the East-Atlantic. Only one eel (2/82) was lost due to stormy weather (*table* 1).

The direction that eels take from one geographical position to the next is calculated. The total track (n positions) is 100% directed if all positions are on a straight line. The percentage of directed swimming (*table* 2) decreases as much as the course deviates from a straight course. It is calculated by dividing the lengths of all vectors by the sum of distances moved from position to position. The depths of the eels are measured about 5 times.h^{-1} (1982), 11 times.h^{-1} (1983), 13 times.h^{-1} (1984). Mean depths are calculated on a time dependent basis.

RESULTS

Mediterranean

Horizontal movements

Figure 1 presents the directional patterns of all the eels tracked in the Alboran Sea except No. 4/84 which after release remained stationary at a water depth of 120 m. All other eels moved and were followed for 7 to 152 hours (*table* 1). The eels were released at a

Table 1. — Length and origin of sels, date and time of trackings, water temperature, reasons for the end of tracking and transmitter type.

No. of tracking experiment	Length of eel (cm)	Location of capture	Date of capture	Date of release	Time of release (CET)	No. of tracking hours	Lunar period at release (*)	Surface water temperature at release (°C)	Reason for the end of tracking	Type of transmitter with pulse width
1/82	about 80	Isle of Fehmarn	before Oct. 23	Nov. 4, 1982	10.32	35.4	II+3[d]	17.6	abandoned because last movements irregular	V 3 P-3 hi, 20 ms
2/82	90	Isle of Fehmarn	before Oct. 23	Nov. 5, 1982	22.46	25.5	II+4[d]	17.6	given up because strong wind impeded navigation	V 3 P-3 hi, 20 ms
3/82	76	Isle of Fehmarn	before Oct. 23	Nov. 8, 1982	13.34	56.3	III+2[d]	16.7	probably battery of transmitter exhausted	V 3 P-3 hi, 20 ms
1/83	95	Isle of Fehmarn	beginning of Nov.	Nov. 19, 1983	7.10	30.8	II−1[d]	19.0	probably battery of transmitter exhausted	V 3 P-3 hi, 20 ms
2/83	87	Isle of Fehmarn	beginning of Nov.	Nov. 20, 1983	15.52	17.6	II	19.5	lost at a depth of 700 m	V 3 P-3 hi, 20 ms
3/83	74	Isle of Fehmarn	beginning of Nov.	Nov. 21, 1983	16.59	10.9	II+1[d]	19.5	lost	V 3 P-3 hi, 20 ms
4/83	85	Isle of Fehmarn	beginning of Nov.	Nov. 22, 1983	12.25	51.5	II+2[d]	18.5	probably battery of transmitter exhausted	V 3 P-3 hi, 20 ms
1/84	about 80	Isle of Fehmarn	beginning of Nov.	Nov. 23, 1984	22.50	7.2	O+1[d]	–	lost because of hydrophone defect	V 3 P-3 hi, 10 ms
2/84	75	Isle of Fehmarn	beginning of Nov.	Nov. 29, 1984	19.30	7.3	I−1[d]	16.8	lost	V 3 P-3 hi, 15 ms
3/84	80	Isle of Fehmarn	beginning of Nov.	Dec. 1, 1984	22.30	20.6	I+1[d]	17.0	lost because of dolphin interference	V 3 P-5 hi, 15 ms
4/84	85	Bristol Channel	mid of Nov.	Dec. 3, 1984	00.46	180.8	I+3[d]	17.0	abandonned because stationary, retrieved after 7 days	V 3 P-5 hi, 15 ms
5/84	79	Isle of Fehmarn	beginning of Nov.	Dec. 4, 1984	00.04	151.9	I+4[d]	18.0	abandoned because shipping time limited	V 3 P-5 hi, 15 ms
1/79	92	Denmark, Baltic Sea	beginning of Dec. 1978	March 4, 1979	00.25	0.7	I−1[d]	19.0	lost	P-101 (Luke *et al.*, 1973)
2/79	85	Baltic Sea	beginning of Dec. 1978	March 8, 1979	11.01	1.8	I+3[d]	19.0	lost	P-101 (Luke *et al.*, 1973)
3/79	78	Baltic Sea	beginning of Dec. 1978	March 11, 1979	13.54	9.9	II−2[d]	22.0	lost	P-101 (Luke *et al.*, 1973)
4/79	92	Baltic Sea	beginning of Dec. 1979	March 15, 1979	13.55	3.7	II+1[d]	25.0	lost (small range of transmitter)	P-101 (Luke *et al.*, 1973)

(*) I = first quarter; II = full moon; III = last quarter; O = new moon.

water depth of 100 to 200 m (*fig.* 2). The three eels released on the Spanish shelf did not make much horizontale progress. They exhibited horizontal progress in an ESE direction (*fig.* 1; *table* 2) at an angle of 108° (mean). A mean easterly direction was shown also by the seven eels tracked on the Moroccan shelf (68°). An explanation for the tendency is provided by *figure* 2 which shows the depth increase when leaving the Moroccan coast eastwards and the eel's progress in water depth from one geographical position to the next. There is a steady increase in water depth during the different trackings, both on the Spanish and on the Moroccan side. The eels gain in water depth is particularly strong between 100 and 280 m (*fig.* 2 *a*) as the gradient is steep. From 280 m on the slope is weaker and the eels' gain in depth is more irregular which is especially true for the eels on the Spanish shelf. Sometimes the depth increase is interrupted by short depth decreases.

The four eels which reached the Moroccan shelf at a depth of about 350 m changed to a northern course or kept to a northern course if it had been northern on the shelf. The mean direction of the four eels when leaving the shelf at that water depth was 16°. The

Table 2. — Mean values of horizontal and vertical swimming of releases in the Alboran Sea (in brackets: minimum and maximum values). Percentage directed = directed section. 100/total distance swum; directed section $= \sum_{k=1}^{n} . V_k$; V_k = Vector of angle and distance between two stations.

Eel No.	Horizontal: Direction on the shelf (°)	% directed	Direction off the shelf (°)	% directed	Total distance (nm)	Mean speed ($m.s^{-1}$)	Vertical: Mean depth at daylight (m)	Mean depth at night (m)	Mean water depth (m)
1/82	121	43			18.8	0.28	296 (181-361)	154 (44-273)	279 (120-355)
2/82	108	32			10.8	0.23	215 (167-231)	121 (3-219)	218 (110-265)
3/82	357	41	12	42	35.3	0.32	258 (131-302) (*)	147 (0-479)	314 (62-560)
1/83	27	96	27	64	28.3	0.47	420 (314-491) (*)	84 (2-304)	411 (106-600)
2/83	–	–	268	17	13.7	0.42	623 (448-694) (*)	267 (61-504)	802 (700-820)
3/83	98	75			7.4	0.35	110 (0-198)	189 (64-337)	252 (140-340)
4/83	93	42	13	50	34.9	0.35	212 (157-450) (*)	118 (9-288)	341 (165-420)
1/84	95	47			4.1	0.36	–	120 (0-251)	213 (186-250)
2/84	47	47			6.4	0.45	–	154 (0-280)	202 (82-280)
3/84	63	35			14.5	0.37	349 (227-370)	164 (203-342)	273 (100-350)
5/84	92	62	16	56	69.5	0.24	405 (206-618)	278 (0-491)	618 (100-920)

(*) Except for the first hours after release.

northern course of three of these eels was not continous (*fig.* 1). It was interrupted from time to time by back and forth or zigzag swimming, twice each for eel Nos. 3/82 and 1/83. Eel No. 5/84 which had been followed for more than 6 days showed during its northern course 4 to 5 such interruptions, two additional ones from the time of release to the beginning of the northern course (*fig.* 3).

Those interruptions of the track 5/84 mostly occur at night which produced the following differences of the track between day and night: (1) a consistently straighter daylight course (days 1 to 6, $p = 1\%$, using a two-tailed Mann Whitney-U-test; (2) a faster speed during daylight (day $= 0.14 m.s^{-1}$; night $= 0.11 m.s^{-1}$); (3) a clear correlation swimming speed, constellation and phases of the moon (nadir $= 0.14 m.s^{-1}$ zenith $= 0.09 m.s^{-1}$); (4) a more easterly and northerly progress. In contrast to these observations, eel No. 3/82 which was observed before new moon (moon at its zenith during daylight) swam twice as fast at night and progressed to a lesser extend towards easterly and northerly directions at daylight. There is good correlation between swimming speed, constellation and phases of the moon (*fig.* 4). Other eels for with we have sufficient data exhibited speeds over the ground with show some relationship between speed over ground and phase of the moon (*fig.* 5). Speeds were higher at its nadir than at its zenith.

As concerns the average speed of all the eels released in the Mediterranean, it is computed to be $0.3 m.s^{-1}$ (about 0.3 fish length $.s^{-1}$) and therefore comparatively low. During the first night after the release of No. 5/85, its speed was $0.40 m.s^{-1}$ and during the following daylight period this decreased strongly to $0.16 m.s^{-1}$. The other three eels, tracked for a comparatively long period of time, from release to dusk exhibited a speed of 0.41 (3/82), 0.47 (1/83) and $0.35 m.s^{-1}$ (4/83) and therefore at the start did not swim that much faster comparing their mean speed during the whole track (*table* 2).

Vertical movements

A summary of the depths during day (344 m) and night (196 m) exhibited by the 11 eels is provided by *table* 2. It shows that the mean depths of the single eels during daylight (110-623 m) are considerably deeper than during the night (84-278 m), with a maximum depth of 694 at daylight and 504 m at night. The considerable differences between eels have several reasons, *e. g*, lowering effect by the eel's swimming in a diminished depth immediately after release or by swimming on the shelf (depth of 80 to 200 m) only (*e. g. fig.* 6 and 7).

A typical diel vertical movement pattern during one of the experiments is shown in *figure* 6 with the strongest movements at dusk and dawn. *Figure* 7 shows also very clearly the very different day and night preferences. The vertical movement pattern of the four eels which left the Moroccan shelf (*fig.* 1) is shown in *table* 5 in two-hourly means averaged for the whole track of each eel. They are essentially similar.

When the average day and night depth levels of eel No. 5/84 are compared from the first to the 7th day of the track (*fig.* 7), a continuous increase to full moon and a following decrease can be observed. A similar decrease in depth with decreasing moon is also shown for eel No. 4/83 (*fig.* 6) when comparing the first and second night of tracking with the second and the third night after full moon.

An attempt has been made to analyse the long track of No. 5/84 with reference to the influence of the moonsets and -rises on its depth preference (*fig.* 7). Unfortunately, for an essential part of the track the moon was above the horizon only at night

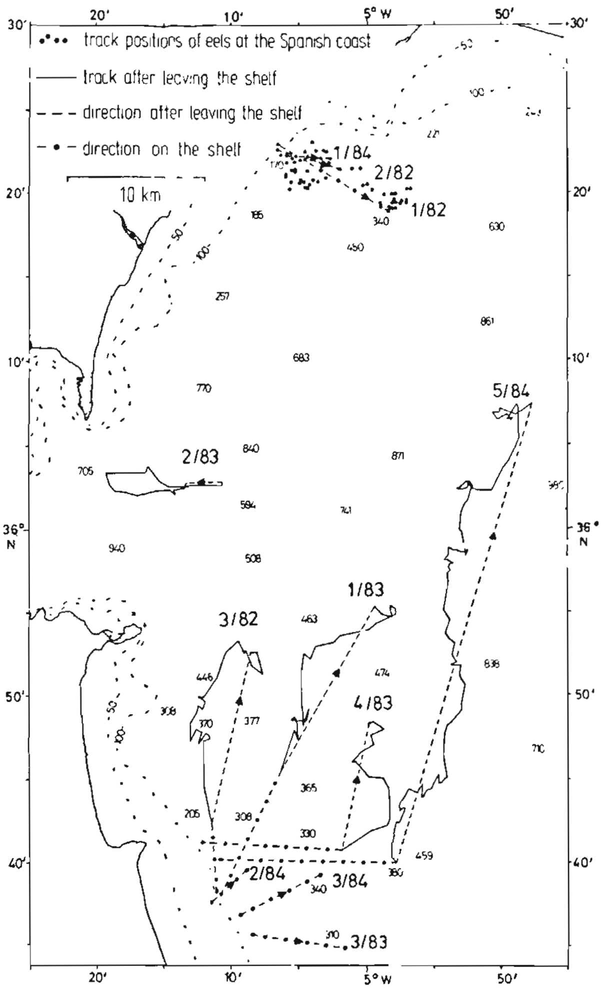

Figure 1. — A map of the western Mediterranean (Alboran Sea) displaying schematically the directional swimming patterns of eleven tracked eels. Spanish shelf: dots indicate tracking positions of eels No. 1/82, 2/82, 1/84; dotted-and-dashed lines indicate the directions taken from release to end of tracking. Track near Gibraltar (2/83): continuous line indicates the tracking course; dashed line direction from release to end of tracking. Moroccan shelf: Eels No. 3/83, 2/84, 3/84; dotted-and-dashed lines show directions of tracks from release to the position at a depth of about 350 m, continuous lines the tracking courses in deeper water, dashed lines the direction from the position at a depth of about 350 to end of tracking. Small numbers indicate water depth (m).

time. But in the morning hours of the first four days, during darkness (at moonset) a decrease in the eels depth can be observed which is especially visible for the first, third and fourth night in *figure* 7. One calculation shows that at night the eel was 268 m deep before moonset and 231 m after moonset, a difference in favour of influence by the moon. *Figure* 6 shows the time of the moon above the horizon for eel No. 4/83 which was tracked for 2 to 4 days after full moon. At the beginning of the second night, before moonrise, a distinct smaller depth tendency is obvious although during the first night it was not. Perhaps full adaptation of the eel 6 hours after release had not been established.

Hydrographical conditions

Hydrographical conditions during tracking on the basis of vertical temperature distributions (*fig.* 8) are shown by the example of the vertical residence of eel No. 4/83 (*fig.* 6). No preferences for special temperature layers are visible. During the track of eel No. 5/84 (*fig.* 6*a*), the stratification was similar and the thermocline around 73 m. The eel remained below the thermocline except for once on the second day and once on the 6th day. Contrarily, eel No. 1/83 stayed at night above the thermocline, 89 m (*table* 2), for the first part of the night mainly at 60 m. Crossing of the thermocline during the night took place five times which included a maximum of 160 m. The thermocline was similar to that shown in *figure* 8. On the second day eel No. 1/83 swam like the other eels, in the thick layer of 13°C, also reaching down to the bottom. During the track of eel No. 3/82 there was a strong thermocline at 150 m changing later to 180 m and finally to 80 m. The eel to some extent preferred 80 to 100 m during daylight but obviously showed no coincidence between its depth preference and this change of the thermocline.

With respect to influence of the tides *figure* 3 presents the time of hight and low tide at Gibraltar along the track. Although the tidal stream in the area of investigation is much lower than at Gibraltar there could be an influence. But the zig-zag and back and forth swimming occurs during both HW and LW and suggests no influence. I have also compared the progress of eel No. 5/84 both to the east and to the north on and off the shelf respectively (*table* 3). There is no consistent difference of progress between HW to LW and LW to HW. On the shelf where the tidal influence is generally much stronger than in deep water the difference between the two phases is even zero. *Table* 4 presents the speed of this and the other three eels, which reached deeper water during different phases of the tide. No consistent difference exists and especially for No. 5/84, the longest track, the difference is very small. Similarly, the depth preference of these eels, computed for different phases of the tide, show no conformity. An influence of the tide on the migration therefore cannot be demonstrated.

An exception is provided by eel No. 2/83 which was released in the Straits of Gibraltar immediately before its entrance into the Mediterranean Sea (*fig.* 1). A strong indication of tidal influence is the change of direction (*table* 2: percentage directed = 17%) by about 180° which corresponds to the directional changes of tides in the Straits of Gibraltar.

Sargasso Sea

As the results obtained from the experiments in the Sargasso Sea are rather preliminary they are reported

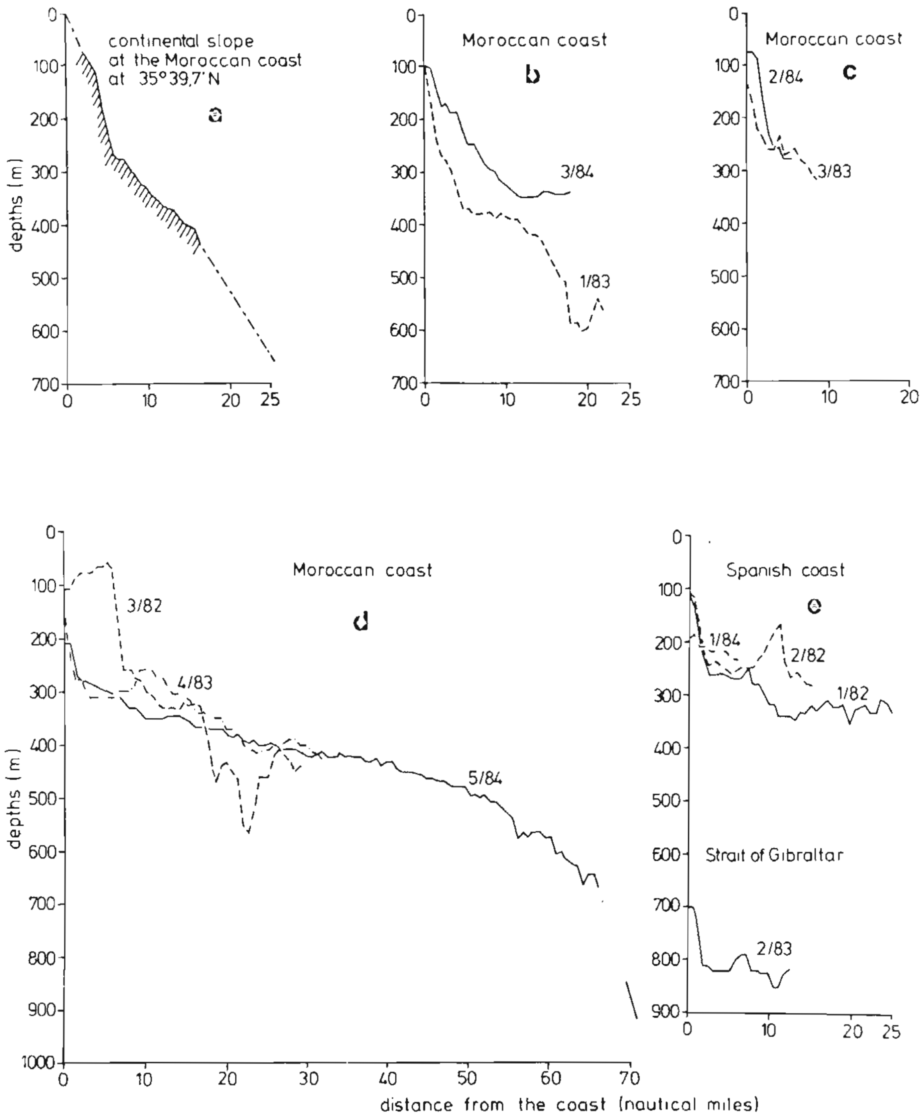

Figure 2. – Tracking of offshore migration of silver eels in the Alboran Sea. (*a*) Shelf depth profile (easterly direction); (*b-e*) increase in swimming depth tracked in relation to offshore positions (separately for all individual eels studied in this area).

here very briefly. The horizontal progress of the four specimens is summarized in *table* 6. Direction and distance travelled by eels No. 2/79 and 4/79 between satellite fixes are probably essentially in accordance with direction and distance from release to end of tracking. No. 3/79 provided five additional satellite fixes during the 10 hours in which it was tracked. This showed a rather strong zig-zag or forth and back swimming. For No. 1/79, no second satellite fix was available and therefore no measure of the horizontal progress. The mean direction of the three other eels was WSW (237°). The horizontal swimming speed of No. 2/79 was $0.8\,m.s^{-1}$. No. 4 swam $0.1\,m.s^{-1}$, No. 3/79 exhibited $0.5\,m.s^{-1}$.

The vertical preferences have been illustrated by Tesch *et al.* (1979). Compared with the Mediterranean trackings no clear pattern of preference could be shown. The short duration of the single tracks are very likely the reason. Maximum swimming depths (670 m) were as in the Mediterranean Sea.

DISCUSSION

Horizontal orientation

The eels released on the shelf of the Alboran Sea showed without exception the tendency to reach greater bathymetric depths. In the present case, it is SE or NE, a direction which during earlier studies in benthic shelf areas had not been observed. In the southwestern Baltic (Tesch, 1979), the North Sea (Tesch, 1974) and on the East Atlantic shelf (Tesch,

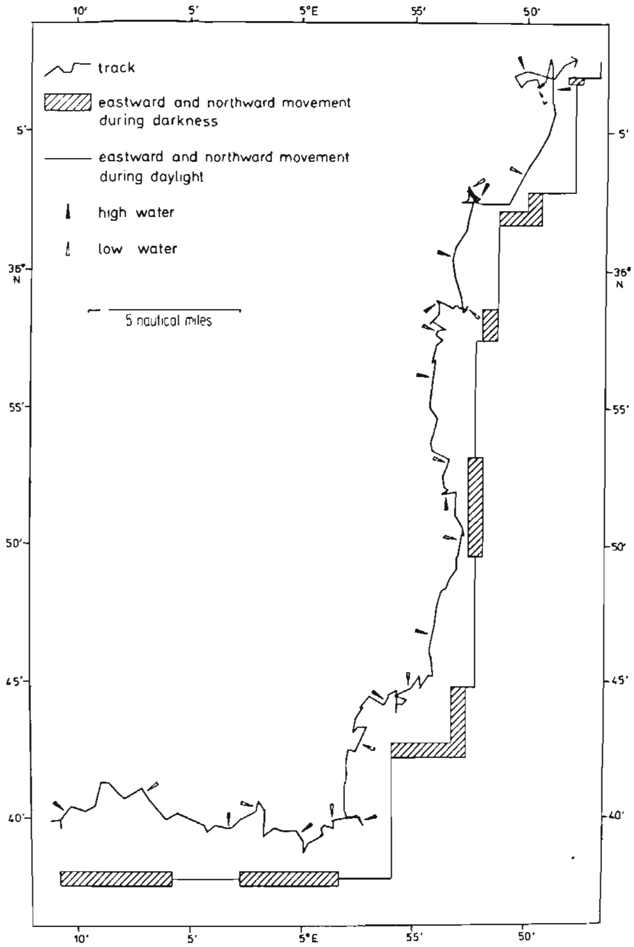

Figure 3. — Directional movement of migrating silver eels in the area northeast of the Moroccan coast (see *fig.* 1) in relation to tidal and diurnal cycles. Results of tracking of eel No. 5/84.

1979) it was N to W. During this study, the eels, when attaining deeper water, changed course also to the North. The previous direction (E) was probably an orientation for deeper water and therefore, as categorized earlier (Tesch, 1980*a*), a "shoreline orientation". Information as to the direction in which a slope is inclined is perhaps available to the eel on or near the bottom only. There is evidence that all the eels dived several times to the bottom especially when they were migrating on the shelf. But also at great depths, some contacts to the bottom have been observed. These contacts occurred during daylight but at comparatively low depths also at night.

The sensitivity of the eel to hydrostatic pressure which is necessary to detect the direction of the slope no matter if the swimbladder is involved or not could be sufficient, as reviewed for other fish species by Tesch (1980) and Smith (1985). An orientation on the direction of the slope of all the eels seems therefore possible, provided stability of the direction by perhaps an inert guidance for some hours is included (perhaps 3 hours: Harden-Jones, 1982). A compass course guided by other cues but initiated by the direction of the slope seems possible as well.

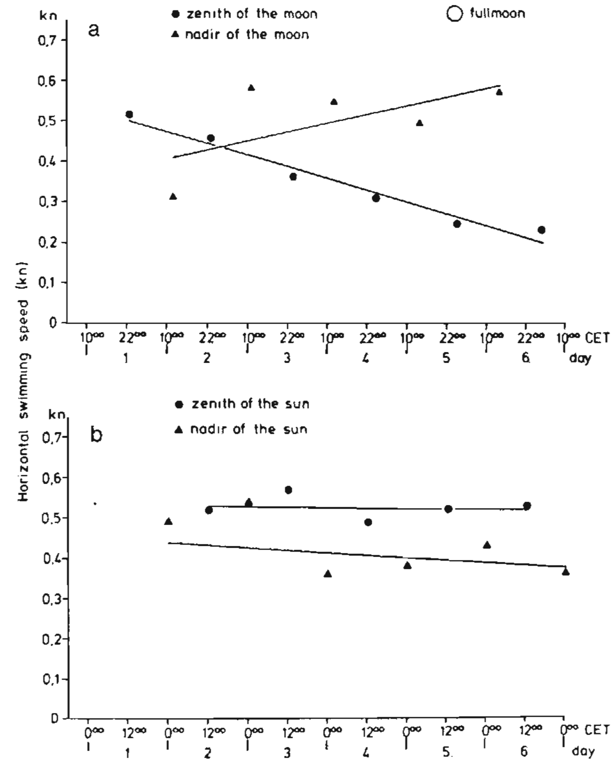

Figure 4. — The swimming speed of eel No. 5/84 calculated on the basis of time and distance between stations *a*) relative to the phase of the moon, 1.5 hours±moon at zenith and nadir and *b*) day and night. The data are for the track off the shelf.

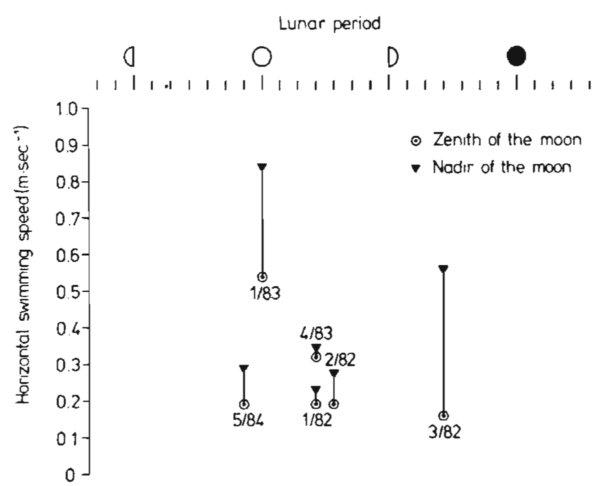

Figure 5. — Swimming speed of eels in the Alboran Sea tracked for longer than one day in relation to the time of the moon at its zenith (±1.5 hours) and at its nadir (±1.5 hours).

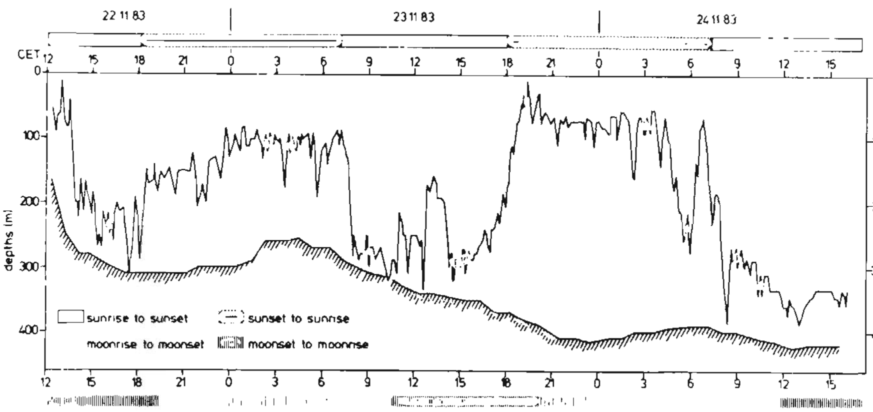

Figure 6. – Swimming depths of eel No. 4/83 released two days after full moon on the shelf of the Moroccan Alboran Sea with rise and set of sun and moon and water depths (hatched line).

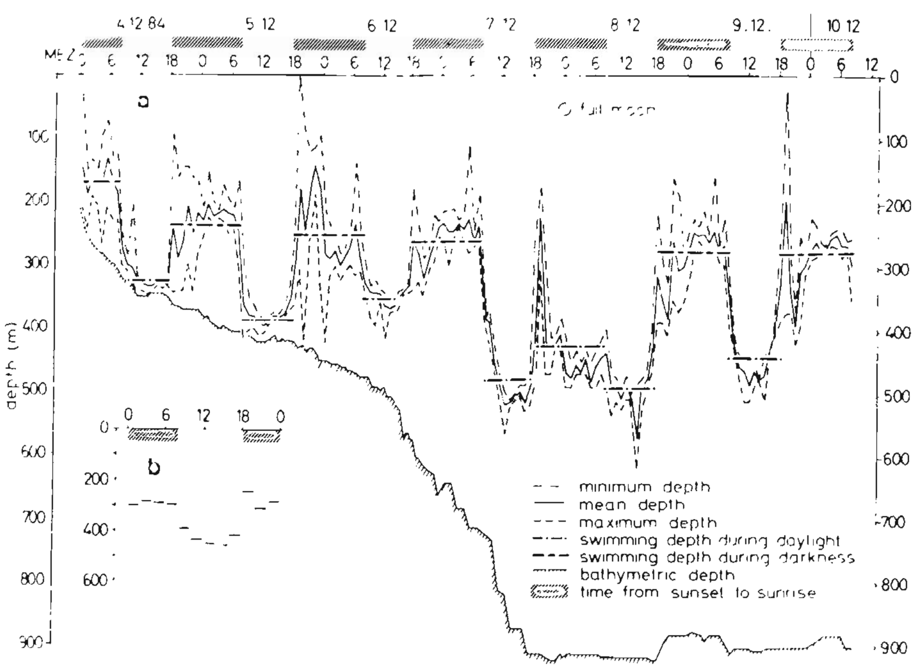

Figure 7. – (*a*) Mean hourly and day and night mean depths of eel No. 5/84 with maximum and minimum bathymetric depths (hatched line) and time of full moon; (*b*) Mean two-hourly depths averaged for the whole track.

Table 3. – Progress to the East on the shelf and to the North in water deeper than 350 m of eel No. 5/84 relative to the time from high water (HW) to low water (LW) and low water to high water at Gibraltar.

Direction	To the East			Mean	To the North									Mean
HW to LW (nm)	12.3	3.4	5.4	7.0	12.2	0.5	9.5	3.3	8.0	0	9.6	0	2.2	5.0
LW to HW (nm)	11.0	6.7	3.2	7.0	3.8	10.0	9.0	10.0	3.0	5.7	0	14.0	2.1	6.4

No conclusive knowledge is available on the sensory mechanism of the eel and other fish which could provide cues for a compass course (Karlsson, 1985). Such a menotactic course is obvious from the four eels after leaving the shelf of the Alboran Sea. A northern compass course has been found also in eels tracked in northern European shelf areas (Tesch, 1974, 1978 and 1979), and compass orientation by geomagnetism has to be seriously considered (for review *see* Smith, 1985).

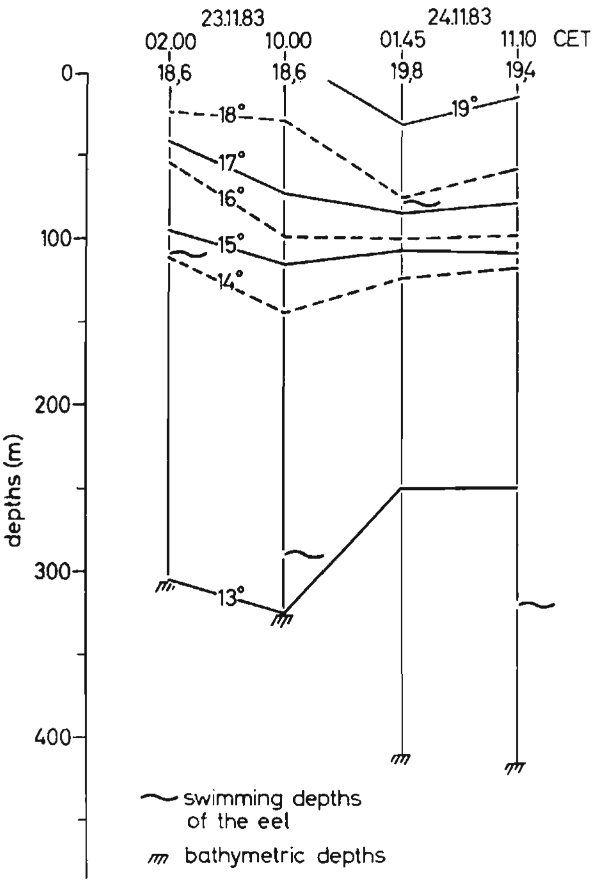

Figure 8. — Isotherms obtained by XBT during the tracking of eel No. 4/83 and depth preferences of this eel.

Table 4. — Speed of the four eels ($n.s^{-1}$) during different phases of the tide which attained water of the Alboran Sea deeper than 350 m. Dates obtained immediately after release for the first three eels are not included.

Eel No.	3/82	1/83	4/83	5/84
HW+6 hours	0.48	0.77	0.67	0.45
LW+6 hours	0.64	0.73	0.58	0.48
HW±3 hours	0.37	0.90	0.78	0.43
LW±3 hours	0.56	0.78	0.63	0.48

An alternative to compass mechanisms would be the use of tidal current transport as shown for the plaice by Harden Jones *et al.* (1979) and proposed on the basis of a computer simulation model for the eel (Arnold and Cook, 1984). There may be weak tidal currents in the main area of tracking and there are strong ones in the Straits of Gibraltar. Eel No. 2/83 was perhaps strongly influenced. But the other eels did not reach this area of strong currents. The high and low water distribution on the track of eel No. 5/84 (*fig.* 3) and in addition neither horizontal speed nor depth preference during different tides have shown any tendency related to tidal currents. Such relationship is also seriously complicated by the diurnal vertical migration.

A second alternative would be residual currents which in the neighbourhood of the Straits of Gibraltar could be of sufficient permanent strength for an eastward transport on the shelf and a westward transport off the shelf. Against this assumption are the very irregular stops and the forth and back swimmings during the whole track of eel No. 5/84. A strong eastward surface current (70 cm.s^{-1}), not much deeper than 100 m and a very weak undercurrent (3 cm.s^{-1}) reaching as far as the bottom which is going west and contributing to the outflow of the Mediterranean (Lacombe *et al.*, 1964; Lacombe and Richez, 1982) reaches to the tracking area. The upper current, coming from the Atlantic is rather shallow for the eels and obviously joins the Spanish and not the Morrocan shelf (Cheney, 1978) where most of these eels were tracked. The undercurrent is probably too slow to be essential for the eel. It is possible that the slight eastward tendencies of the tracks of eels No. 1/83 and 5/84 (*fig.* 1) are the result of the beginning east current. In addition, the movement of the eels released at the Spanish coast showed a tendency more to the east than to the southeast which is the direction to deeper water and therefore perhaps an influence of the mentioned inflowing Atlantic water is possible.

The northern course of the eels after having left the shelf has also been found in Northeast Atlantic shelf areas on both in the North Sea and in the southern Baltic (Tesch, 1974, 1978, 1979). A question arises from the fact that the four eels swimming over

Table 5. — Two-hourly depths of the four eels leaving the shelf and averaged for the whole tracks. First hours of adaption on the shelf are omitted. In brackets: Only one depth registered. No. 5/85 is graphically shown in fig. 6 *b*.

Eel No.	Time ±1 hour											
	1^{00}	3^{00}	5^{00}	7^{00}	9^{00}	11^{00}	13^{00}	15^{00}	17^{00}	19^{00}	21^{00}	23^{00}
3/82	176	103	74	119	211	254	289	274	217	121	246	(397)
1/83	59	82	100	126	362	438	462	–	231	119	59	48
4/83	86	99	142	144	288	303	292	307	248	134	110	113
5/84	298	282	288	294	387	432	447	454	414	283	309	282

daylight

Tableau 6. — First and final positions, direction and distance between these positions of eels tracked in the Sargasso Sea.

Eel No.	Position of release	Position at end of tracking	From release to end of tracking	
			direction (°)	distance (nm)
1/79	32°05′N 61°38′W	?	?	?
2/79	32°07.8′N 65°03.2′W	32°05.0′N 65°05.0′W	208	3.2
3/79	26°04.8′N 58°34.6′W	26°03.6′N 58°35.7′W	219	1.6
4/79	31°41.2′N 63°07.9′W	31°41.3′N 63°08.4′W	283	0.4

more than 350 m bathymetric depths in the Alboran Sea did not change to a westerly direction. Eel No. 5/84 went as far north as to exceed the central entrance of the Straits of Gibraltar. The only movement which is imaginable in favour for an exit to the Mediterranean outlet is a turning westward at the beginning of the northern slope, a movement which is similarly shown by the eels of the Southern Baltic (Marinköwitz, 1961; Tesch, 1979). But this last mentioned area is a shallow shelf sea. The only observation available from the Mediterranean Sea is provided by J. Schmidt (1912). He wrote: in the Strait of Messina "the silver eels taken here are always migrating in the direction from south to north". The tendency of a northward migration seems therefore not only restricted to eels originating from and migrating in northern waters. From the present results it is also likely that the stimulus to swim in the direction to the Sargasso Sea is not provided when the water depth exceeds 350 m. It must be deeper or some other stimulus of the deep sea is necessary to induce the directional change.

The movements west off the shelf of four eels moving under bathymetric depth conditions mostly more than 1 000 m, exhibited 261° from release to end of tracking (Tesch, 1978 *a*, *b*). Although the direction of the three half ripe Sargasso Sea eels of this study may have a low confidence level they may here be combined with the previous results of directional preferences of four eels in deep sea areas: seven eels exhibit a mean of 250.3° (Rayleigh test: $z=5.6$; $p=1\%$). The direction is congruent with the direction from the central Bay of Biscay, the area of the highest glass eel catches in Europe to the central spawning area. We found the highest small larvae concentration 1979 in a direction of 252° (Schoth and Tesch, 1982) and 1981 in 247° (Tesch, 1982; Schoth and Tesch, 1984) from the central Bay of Biscay.

Whether the eel prefers depths determined by an isolumen is doubtful. Following the calculation of Carey and Robinson (1981) and assuming the comparatively weak attenuation coefficient of Jerlov (1976) for the Mediterranean of $k=0.035$ and taking the depth of 200 m of eel No. 5/84 shown during its first nights of tracking with nearly full moon a light intensity less than $I=2.7\,10^{-4}\,\mu W.cm^{-2}$ has to be expected. Van Veen and Anderson (1982) determined the threshold light intensity for synchronization of yellow eels and estimated an intensity of $6\,10^{-2}$ with a wave length of 548 nm and $2\,10^{-2}\,\mu W.cm^{-2}$ with white light. With this light intensity the yellow eels could not perceive the moon light in the Mediterranean although silver eels which are probably more sensitive perhaps could; deep sea fish are sensitive to a light intensity of $3\,10^{-10}\,\mu W.cm^{-2}$. But it seems impossible that the silver eel can sense the moon light in a depth of 425 m which was the mean depth of No. 5/84 in the full moon night. It is also not possible that the light intensity of the full moon is so much stronger during full moon than 2 or 3 days before full moon as to produce a 200 deeper depth preference of the eel. It should also be mentioned that the sky during full moon was mostly overcast and the light intensity therefore less. A response of the eels' depth preference depending proportional on the light intensity of the moon is therefore unlikely although in shallower depths a depth increase with moonrise and a decrease with moonset was observed (*see* also Tesch, 1978 *b*).

A deeper occurrence during full moon is also likely for the eel larvae (Kracht, 1982) and this is interesting as the older larvae perform very similar diel vertical migration as the adults (Tesch, 1980 *b*; Tesch *et al.*, 1986). The eel larvae during day light occurred in depth between 250 and 600 m but during darkness (*see* also Kracht, 1982) mainly in 50 to 120 m. The larvae at night are therefore shallower than the adults, possibly a requirement for a sufficient nutrition, not actual for the adults.

The question if the moonlight and its intensity is involved arises also when the speed of the silver eels is considered. They seem to swim more slowly with the moon phase progressing to full moon but at the same time during the moon at nadir swim fast, which excludes a direct influence of the moonlight. A relationship between the periods of the lunar month and silver eel activity is also shown by the catches during the silver eel runs (review: Tesch, 1983, p. 187). Whether the speed of migration is concerned becomes obvious by recaptures of tagged silver eels in the Baltic (Lindroth, 1979). During the time of full moon the silver eels travelled shorter distances than after that period. Here perhaps a direct relationship between depth preference and speed is provided. During full moon the eels more frequently and longer could rest on the bottom, which mainly has been observed during periods of daylight (Westerberg, 1975).

As a whole the present results have provided additional indices that not the moonlight directly or an "isolumen" are responsible for differential behaviour of the eel during different mooon-phases and -periods. It is possible that the timing of the different behavioural diel and lunar responses takes place by light. This seems clear for the dusk and dawn vertical migrations which are in accordance with the resident light. The frequent upward movements could provide information on the present light conditions which seems necessary especially for the moonlight which probably does not penetrate as deep as the normal depth of residence of the eel.

Sargasso Sea

The study with hormon treated eels in the Sargasso Sea was very preliminary in two respects. (1) The eels became not fully mature during the necessarily predetermined time of the cruise. They therefore could not exhibit spawning behaviour. Hence the tracking experiments took place with eels on their migration to the spawning grounds and not on movements at the spawning grounds. The advantage of this development is that three additional data of directional preference from Europe to the Sargasso Sea spawning grounds are available although the data on horizontal positions are very restricted. (2) The length of tracking time was insufficient and did not provide complete diel depth preference patterns. Further studies are therefore necessary.

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