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Orientation mechanisms in migrating European silver eel (*Anguilla anguilla*): temperature and olfaction

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Abstract. The migration pattern of silver eel (*Anguilla anguilla* L.) in the Baltic is well documented from many tagging experiments. This particular investigation differed from previous taggings in that the background of all the eels used was the same. They came from a 1980 stocking programme and had been imported from France as glass eels. When migrating these stocked eels missed the outlet of the Baltic and continued in a southwesterly direction. They were still reported in this southern-most area more than 4 yr later. Indigenous eels turn northwards after passing the south of Sweden and leave the Baltic through the narrow Sound. Since the formerly stocked eels had never been in the Baltic, the absence of an imprinted olfaction cue may explain their orientation failure. Although lacking an imprinted olfaction cue eels were recaptured mainly in a very restricted area in the southwestern Baltic. This reflects another cue, genetic or imprinted during the Atlantic journey. This second cue, temperate, can also serve as the trigger which causes eels to stop migrating and to initiate spawning. The enclosed Baltic acts as a giant trap for eels from the huge stocking programmes undertaken there. As a consequence stocked eels probably contribute little to spawning stocks in the Sargasso Sea which may have contributed to the decrease in abundance of glass eels reported from western Europe in recent decades.

Introduction

European eels (*Anguilla anguilla*) spawn in the Sargasso Sea. Their larvae (Leptocephali) drift across the Atlantic to the coasts of western Europe. The larvae transform into glass eels in coastal waters and gradually become pigmented (elvers). Some elvers stay in salt or brackish water along the coast while others penetrate rivers and streams to complete the growing stage (yellow eel) in fresh water. Finally, they approach maturity and transform into silver eels and start the migration back to the Sargasso Sea to spawn (Tesch 1983).

The Baltic is an important growth area for the European eel. Elvers reach the Danish Straits, the Sound area between Denmark and Sweden and the southern part of the Baltic in late spring. The young eel then proceed northwards more slowly but very little is known about this gradual dispersal (Svärdson 1976).

Exploitation of eel is based on migrating silver eel and commercial fishery takes advantage of the concentrations along the coasts of southeastern Sweden and in the outlets of the Baltic (Fig. 1). Commercial catches of silver eels have decreased considerably since the mid-1960's (Wickström 1986). One explanation is that the annual number of elvers entering the Baltic from the Skagerrak and North Sea has been declining steadily for a long period (Erichsen 1976, Svärdson 1976). As a consequence, stocking programmes have been undertaken since the 1940's in the Baltic to try to strengthen the recruitment of elvers and subsequently improve eel stocks (Leopold 1976, Filuk and Wiktor 1988).

Since the Baltic is the best place for studying European silver eel migration (Tesch 1983), many tagging

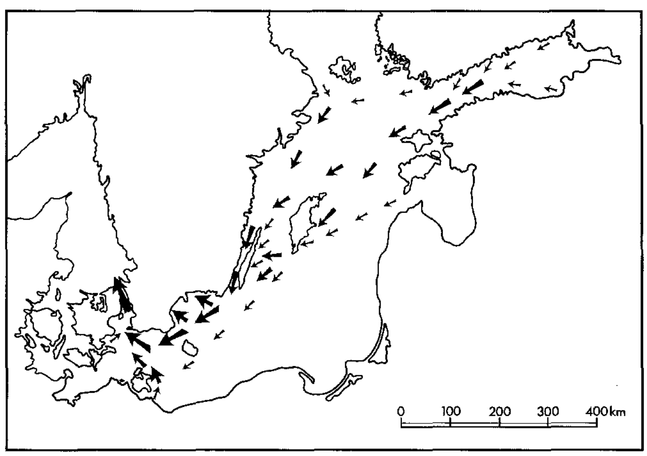

Fig. 1. *Anguilla anguillas.* Silver eel migration in the Baltic as determined by tagging experiments

experiments have been performed over the past 80 yr (Trybom and Schneider 1908, Hessle 1929, Määr 1947, Ask and Erichsen 1976, Westin and Nyman 1979, Karlsson 1984). The investigation reported here differed from previous studies in that the background of all eels tagged was the same since the eels came from a lake stocked with eels originating from France (Wickström 1986).

Material and methods

An eel-free lake, Fardume Träsk, situated on the island of Gotland, was stocked with eels in September 1980. The eels (*Anguilla anguilla* L.) had been imported from France as glass eels in spring 1980 and raised in heated water until liberation (Wickström 1986).

At the lake outlet, a fixed wire-trap was built. In 1984 and 1986, only males were tagged using Floy-tags and released at the other side of the trap into the small stream which emptied into the Baltic. In 1987 and 1988 females dominated, and the type of tag used was mostly the Carlin-tag (Table 1). As controls, native silver eels from Faludden on the southeastern coast of Gotland and 100 km distant from Lake Fardume Träsk were bought from a local fisherman for tagging in 1987 and 1988 (Table 2). In 1987 the control group was tagged and released 1 km south of the trapping area together with eels originating and transported from Lake Fardume Träsk (Tables 1 and 2).

In 1988 a second control group originating from south Gotland was tagged, transported and released in the small stream from Lake Fardume Träsk (Table 2). At the same time and at the same spot silver eels from Lake Fardume were released (Table 1). One month later a third control group originating from the same fisherman was tagged and released together with silver eels from Lake Fardume Träsk. The release point in this case was also 1 km south of the area where the control group was caught at south Gotland (Tables 1 and 2).

Results

Altogether 605 (452 males and 153 females) tagged silver eels (*Anguilla anguilla*) originating from the Lake Fardume stocking programme were released on 20 occassions. The recapture total of males was 11 (2.4%) and of females 12 (7.8%). The males were all reported from the Danish islands, eight of them concentrated in a rather restricted area around Møn, Lolland and Falster. Three of these were caught by the same fisherman on the same day at the same locality. Another was the first ever to be caught beyond the passage of the Belt or Sound areas off Ebeltoft in the Kattegat (Ask and Erichsen 1976). The 12 females were also recaptured from the SW Baltic (Fig. 2).

The three control groups consisted of 70 females with nine (12.9%) recaptures reported – but this time in areas where migrating eels are mainly expected according to earlier investigations (Fig. 3). A comparison of the two groups shows that the migrating eels from Lake Fardume Träsk miss the entrance to the Sound area and continue in a more southwesterly direction instead of turning north as do natural silver eels. In silver eel taggings along the Swedish Baltic coast a reported recapture rate of at least 30% is normal (Erichsen 1976, Karlsson 1984). In the present experiment only 3.6% of the stocked eel were reported as recaptured.

Table 1. *Anguilla anguilla*. Silver eels from Lake Fardume Träsk tagged and released. Values in parenthesis denote months between release ans recapture For locations see Fig. 2

Date	*n*	Sex	Tag	Recaptures	
Release point outlet Lake Fardume Träsk					
1984					
June 14	12	♂	Floy	21 (4)	
20	12	♂	Floy	26 (53)	
30	11	♂	Floy	42 (6)	
July 22	45	♂	Floy	53 (28)	61 (5)
				81 (5)	84 (27)
26	16	♂	Floy	118 (48)	
27	34	♂	Floy		
29	26	♂	Floy		
Aug. 02	11	♂	Floy		
05	22	♂	Floy		
Sep. 26	22	♂	Floy	240 (11)	
27	18	♂	Floy		
28	17	♂	Floy		
Oct. 01	52	♂	Floy		
1986					
May 27	77	♂	Floy	406 (7)	446 (5)
July 21	9	♂	Floy		
1987					
June 12	57	♂	Carlin		
12	56	♀	Carlin	798 (29)	
1988					
Sep. 15	23	♀	Carlin	182 (7)	
16	16	♀	Carlin	166 (1)	170 (3)
				193 (14)	198 (13)
Release point Faludden					
1987					
Aug. 28	7	♂	Floy		
28	17	♀	Floy	547 (15)	
28	16	♀	Carlin	664 (2)	667 (2)
				668 (2)	
1988					
Oct. 15	4	♂	Carlin		
15	25	♀	Carlin	775 (5)	771 (11)
Total	605	♂ 452		23 (♂ 11)	
		♀ 153		(♀ 12)	

Table 2. *Anguilla anguilla*. Control groups, tagged and released silver eels from the south coast of Gotland (Faludden). Values in parenthesis denote months between release and recapture. For locations see Fig. 3

Date	*n*	Sex	Tag	Recaptures	
Release point outlet Lake Fardume Träsk					
1988					
Sep. 16	24	♀	Carlin	♀ 720 (1)	♀ 726 (1)
				♀ 730 (1)	♀ 741 (1)
				♀ 743 (1)	
Release point Faludden					
1987					
Aug. 28	19	♀	Carlin	♀ 679 (1)	♀ 694 (3)
1988					
Oct. 15	27	♀	Carlin	♀ 886 (1)	♀ 863 (1)
Total	70	♀		♀♀	

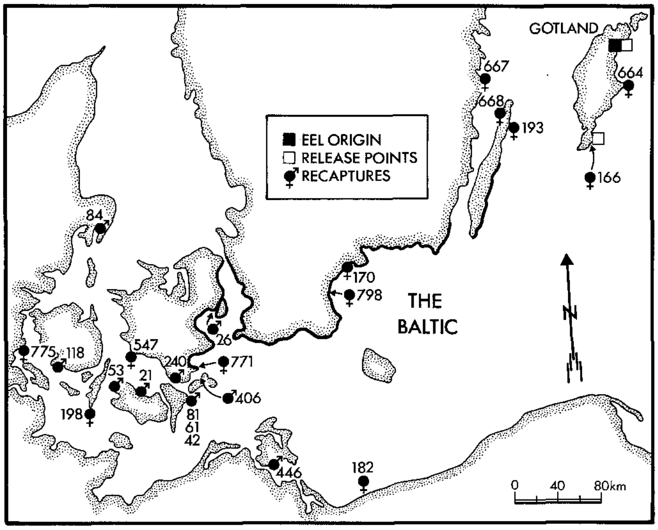

Fig. 2. *Anguilla anguilla.* Origin, release points and recaptures in silver eel tagging experiments from Lake Fardume Träsk, Gotland. Dark coastline indicates main recapture area in earlier tagging investigations

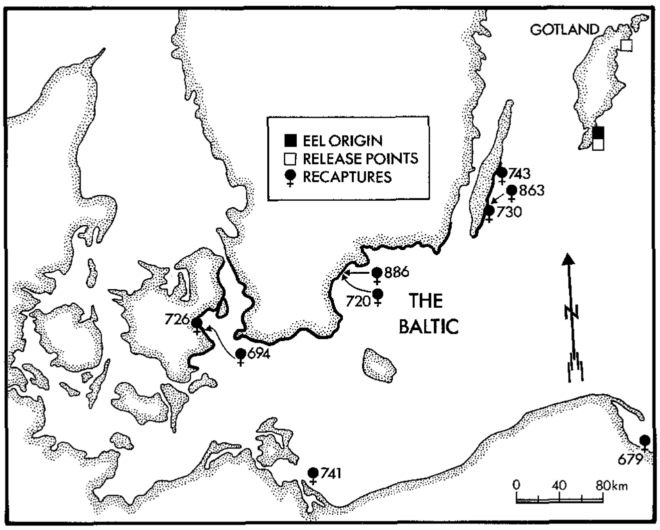

Fig. 3. *Anguilla anguilla.* Release points and recaptures of control groups of Silver eels orginating from the south coast of Gotland. Dark coastline indicates main recapture area in earlier tagging investigations

Statistical testing by Z-test, a normal deviate test for differences between proportions of total (male + female) tagged and recaptured silver eels from Fardume vs recaptures from control groups during the migrating season indicated significant differences ($p = 0.001$). A significant difference was also found when females tagged from lake Fardume were compared to the all-female control groups ($p = 0.016$).

It is difficult to compare recapture rates between eels from Lake Fardume and controls since the latter migrated directly towards the Baltic outlet and passed out to the North Sea (mean 1 mo) while recaptures for the former group are still being reported 53 mo later. Therefore, only recaptures from the first 6 mo have been used in the Z-test.

The mean elapsed time between release and recapture was 13 mo for eels originating from Lake Fardume Träsk and 1 mo for controls, a highly significant difference ($p = 0.0001$), based on a permutation test.

Discussion

The outcome of the tagging experiments of silver eels (*Anguilla anguilla*) from a stocking programme differs in every aspect, both from earlier investigations which have been performed repeatedly since the beginning of the century, and from the control groups. The Fardume eels have a much lower recapture rate, migrate to the wrong area and miss the outlet from the Baltic through the Sound, being caught in this "wrong" area much too late in the season and where they are still recaptured up to 4 yr after release.

An explanation for this is that the Fardume eels do not follow the migration route of native eels and, therefore, seldom approach the coasts where silver eels are normally caught and where gear is set out to trap them. Native eels will have travelled through the area on a previous occasion as elvers or yellow eels. The Fardume eels originated in France and were transported to Fardume after cultivation. The Baltic is therefore, an unknown area for them. They seem to lack an imprinted directional cue.

The capacity of eels to orientate, and their consequent migration has been attributed to many mechanisms (Tesch 1983). The majority of investigations on the orientation of eels were performed in the Baltic. During the last decade a number of conventional eel tagging experiments have been reported (Karlsson 1984, Karlsson et al. 1988) and many tracking studies have also been carried out in the southern Baltic, both with intact (Tesch 1979, Westerberg 1979, Tesch et al. 1989) and anosmic eels (Tesch et al. 1989).

In a tagging investigation using eels with inhibited visual, magnetic and olfactory sense, the anosmic group behaved differently from the control and other experimental groups. The anosmic group was clearly slower compared to the control group and was the only one which missed the Sound area on reaching the Swedish south coast (Karlsson unpublished). In tracking studies in the central Baltic (Tesch et al. 1989) anosmic eels were compared with intact eels with regard to migration. The anosmic eels showed irregular swimming behaviour, their average speed was approximately half that of normal eels and they displayed no common direction. The swimming depth and diurnal patterns of the eels were however the same as for normal eels.

Eels (anosmic and untreated) originating from the Masurian lakes in Poland were used in a tagging experiment off the Polish coast (Karlsson et al. 1988) to study eel migration in the southeastern Baltic and to check the earlier tagging experiment near the Swedish coast which had indicated that anosmic eels differed from controls. The results showed a surprisingly low recapture rate, about 10%, with most of the eels being recaptured in a westerly direction from the release point. A few were taken from the Sound area, but the majority were from the Danish islands further south to west. No clear differences were found between normal and anosmic eels, and anosmic eels reached the western Baltic at about the same time as the control eels. This was in contrast to earlier results from experiments near the Swedish coast (Karlsson et al. 1988).

An interesting point arising from the investigation off the Polish coast concerns the origin of the silver eels tagged and released. These were caught in traps at outlets when migrating from the Masurian lakes in Poland. Since the 1940's these lakes have been heavily stocked with elvers (Ciepielewski 1976, Leopold 1976) imported from western Europe (Filuk and Wiktor 1988).

The natural eel stock has practically ceased to exist in this area (Filuk 1984). Thus the material from the Masurian lakes was dominated by formerly stocked eels. It is therefore not a coincidence that this tagging experiment (Karlsson et al. 1988) agreed in every aspect with my investigation of the eels from Lake Fardume Träsk.

One aim of the investigation off the Polish coast was to test differences between anosmic and control eels. Since the orientation of the anosmic eels was not influenced to any measurable degree compared to controls the investigation proved instead that anosmic eels migrate in the same way as formerly stocked eels.

The nose is probably the most sensitive sense organ in eels, and for at least part of its spawning migration it may play an important role (Tesch et al. 1989). There is experimental evidence which shows that silver eels can discriminate water of increased salinity by their sense of smell (Tesch, 1974; Hain, 1975). The olfactory sense of sexually immature eels is also known to be incredibly acute (Teichmann 1959).

Whether olfaction alone can lead migrating eels out of the Baltic is uncertain and difficult to prove but it does not seem to be the only orientation cue which leads migrating eels back to the spawning areas. In both my own and the Polish investigation (Karlsson et al. 1988) the eels gathered in a restricted area within the Baltic. They seemed to respond in a precise way to a second mechanism which may, initially, direct eels relying only on this mechanism off course. An example is the release from Faludden 870828 (Table 1) where, after only 2 mo three females were reported from a northerly or northwesterly direction. In earlier studies along the Swedish east coast, eels were only seldom found to migrate to the north (Ask and Erichsen 1976). A fourth female from the same release was reported 15 mo later from the Danish islands in the southern Baltic. Another example of how this second cue works is the report from the Danish fisherman who on the same day and at the same locality caught three of my tagged eels released on different occasions 5 to 6 mo earlier.

To recapitulate, at the beginning the eels can be found in any part of the Baltic proper, but they have in common that they gather in the most soutwesterly part of the Baltic in late autumn/winter and are still reported there up to 4 yr later.

It is generally held that the European eel derives from a single panmictic population in the Sargasso Sea (Williams 1975) implying that the orientation ability does not have a genetic origin. The second cue may have been imprinted during the larval or Leptocephalus stage during the Atlantic journey. It is likely, however, that it is of genetic origin because it functions in the same way independent of locality.

In an investigation of diel activity of yellow and silver eels it was shown that their behaviour is different in one respect. When temperature decreased, the level of activity in yellow eels also decreased in contrast to silver eels where the activity immediately increased. This was interpreted as an avoidance reaction (Westin and Nyman 1979). When trying to avoid colder water during the migrating season eels are ultimately pushed to the least cold area of the Baltic, the most southwesterly area, and the outlet to the north is missed. Since one cue is absent in formerly stocked eels, the gradual cooling down of the Baltic from north to south, therefore, also explain the delayed migration. However, a new question now arises. What happens to the eels after this point? There have been only two earlier reports of macrophthalmous eels (partial spawning dress) in the Baltic (Svärdson 1949, Rasmussen 1951), but today such eels are by no means unusual in catches from south Gotland (Westin unpublished). Perhaps the eels wander to and fro during the year?

Temperature as a second orientation cue offers at least one more advantage with regard to the oceanic part of the migration – it can terminate migration. A persistent oceanic front, located in the North Atlantic Subtropical Convergence at about 24° to 29° N, has abrupt horizontal temperature and salinity changes in the upper 150 to 250 m (Voorhis 1969). The highest concentrations of newly hatched larvae were found in and to the south of the Atlantic front over a large area along the east-west axis. This suggests that the front acts as the northern boundary of the spawning area and provides a signal to terminate migration and commence spawning (McCleave et al. 1987).

Vertical excursions are reported during tracking studies of American and European eels both in shelf areas and also in the deep sea (Stasko and Rommel 1974, Tesch 1979, 1986, Westerberg 1979, 1984). In this way a migrating eel may sense the temperature gradients since vertical stratification over a few tens of metres may reflect mean horizontal conditions over a few tens of kilometres (Westerberg 1984). Similar vertical enhancement of horizontal gradients may well occur with odorants (Døving et al. 1985). According to data collected over many years salinities and temperatures in the Baltic show well developed gradients from north to south and east to west (Bock 1971, Lenz 1971).

It is abvious that the eels in my investigation encountered difficulties when trying to find the way out of the Baltic. After leaving the Baltic very little is known about the further migration of natural eels. Ask and Erichsen (1976) concluded that out of 8302 recaptured eels, none had been reported from areas north of the Belt or the Sound.

One male silver eel from Lake Fardume Träsk was recaptured after the extreme period of 27 mo, and was also the first Baltic eel recaptured byond the Belt or Sound, being caught 65 km north of this area (Ebeltoft vig.). This indicates that difficulties in orientation still exist compared with "wild" eels which obviously never approach the coast and thus are never captured after passing the Danish Straits.

From a commercial standpoint, it is a good investment to stock eels in lakes and harvest at the outlet. The enormous stocking programme suggested for the Baltic (Svärdson 1976) to improve the eel stocks could, however, prove a failure because the direction of the stocked eels when migrating is difficult to predict since they do not reach the coast in the expected areas. The Baltic is a very enclosed area and seems, according to this investigation to act as a trap for eels from stocking programmes. As a consequence, it may not contribute much to the spawning stock in the Sargasso Sea. If this is a problem common to other enclosed areas (i.e. the Mediterranean), this could, in conjunction with the heavy exploitation of the European eel contribute to the reported decrease in glass eel abundance in the north Atlantic (Erichsen 1976, Svärdson 1976, Moriarty 1986).

The sex ratio is also of interest in this context since remote areas like the Baltic are almost exclusively populated by females (Svärdson 1976).

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