Eel migration

– results from tagging studies with relevance to management

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To my beloved wife, Frida
The migrations of the freshwater eel are amongst the most remarkable of animal journeys. Although much effort has been devoted to studying the journeys little is actually known, but that little makes an extremely interesting story.

C. Moriarty
Abstract

In response to the drastic decline of the European eel (*Anguilla anguilla* (L.)) fisheries have been reduced and elvers are stocked in areas where natural abundances are low. Are these measures adequate? To answer different aspects of this question, we have analysed more than a century of eel tagging, using both traditional and more novel capture – recapture analyses. Based on these long-term data, we have evaluated the impact of the Swedish eel coastal fisheries using Survival analysis. Our analysis indicates that the fishing mortality just prior the 2009 fishing restrictions were in the order of 10%.

More recent tagging programs have focused on issues related to the fate of stocked fish. If and how they migrate out of the Baltic Sea and further on towards the Atlantic Ocean. Both earlier and our new studies reveal that all eels recaptured on the Swedish East Coast, no matter of their origin, migrate at a reasonable speed and direction towards the outlets of the Baltic Sea. Even though it is sometimes difficult to determine their origin, our analyses indicate that stocked fish were scarce among the recaptures. In an experiment on the Swedish West Coast, we knew the individuals’ origin (stocked or wild) and they had similar migration patterns.

In contrast, silver eel in Lake Mälaren – assumed to have been stocked as elvers or bootlace eels – seemed to have difficulties in finding the outlets. Instead they overwintered and lost weight. However, weight losses are also significant among non-stocked individuals in the Baltic Sea, both if they overwinter and if they appear to be on their way out from the area. It remains an open question whether eels from the Baltic region in general, and whether the overwintered fish in particular, manage to reach the spawning area in the Atlantic Ocean.

Based on current knowledge, I advocate invoking the precautionary approach and to concentrate Swedish eel stockings to the West Coast and allow the young fish to spread out on their own.

Key words

List of papers

This thesis is based on the following papers.

PAPER 1

PAPER 2

PAPER 3

PAPER 4

PAPER 5

PAPER 6
My contributions to the papers are:

**PAPER 1**
Designed the study and conducted the field work. Participated in data processing and writing.

**PAPER 2**
Contributed to the overall study design. Responsible for field work, data processing and most of the writing.

**PAPER 3**
Contributed to study design. Responsible for planning and implementation of the fieldwork. Participated in some of the data processing and analyses. Contributed to the writing.

**PAPER 4**
Contributed to the study design, field work, data analyses and quality control. Participated in the writing.

**PAPER 5**
Contributed to the overall study design. Responsible for field work, data processing and most of the writing.

**PAPER 6**
Contributed to data processing and manuscript writing.
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Historical background

The European eel (*Anguilla anguilla*, (Linneaus 1758)) life cycle is similar to that of the American (*Anguilla rostrata*, Le Sueur 1817)\(^1\). Their spawning areas overlap in the Western Atlantic, North East and North of the West Indies in the well-known Sargasso Sea off Bermuda. The newly hatched eel larvae (*leptocephali*) use the Gulf Stream to reach the mainland coasts where they become glass eels. This metamorphosis takes place after one year for the American eel and probably after 2–3 years for the European eel. They then grow up and become so-called yellow eels for about 5–20 years\(^2\) in fresh or brackish waters before they undergo a second metamorphosis and migrate back to the Sargasso Sea as mature silver eels (e.g. van Ginneken & Maes 2005, Figure 1).

![Life cycle of the European eel](image)

Figure 1. Life cycle of the European eel. Note that spawning and eggs have never been observed in the wild (illustration by Frida Sjöberg, modified after Dekker 2000).

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\(^1\) Le Sueur was first denied the honour of naming the American species. For further reading: Bean, B. A. 1909. The Proper Name of the American Eel *Anguilla rostrata* (Le Sueur). Science, New Series, 29 (752), May 28, 1909, 871–872.

\(^2\) The reason why eels sometimes achieve a much higher age than what is mentioned above is in most cases because they have become trapped in lakes with no outlets, in wells or in mine shafts.
The Norwegian researcher Johan Hjort (Nature 1910) was the first to propose that the breeding grounds of the eel was located somewhere in the central Atlantic, this assumption was, however, based on a quite small sample of larvae. For many years, the Danish biologist Johannes Schmidt and his assistants searched for the larvae by means of trawling and they saw a clear pattern: *leptocephali* larvae increased in number and decreased in size towards a certain area. Finally they pinpointed an actual breeding place based on catches of larvae less than 10 mm (Figure 2). This laborious search took place between 1911 and 1921, i.e. before, during and after the First World War which of course made the work even more tedious (Schmidt 1922). Later expeditions (Schoth & Tesch 1982, Kleckner & McCleave 1988, Munk et al. 2010, Hanel et al. 2014) have corroborated Schmidt’s main conclusions even if a re-examination has shown that some of them are results of distribution of effort (Boëtius & Harding 1985). Hitherto, no one has seen the spawning of either American or European eels in the wild.

Figure 2. Spawning area, based on larvae distribution for American and European eel (dotted for the American and continuous for the European). The innermost curve embrace the breeding areas of both species (from Schmidt 1922).
The spawning grounds of the Japanese eel (*Anguilla japonica* (Temminck & Schlegel 1846)) were not discovered until 1991 (Tsukamoto 1992). Since this discovery intensive investigations have succeeded in collection of both eggs and matured silver eel in the North Equatorial Current about 3,000 km from their growth habitats (Tsukamoto *et al.* 2011). However, for all three anguil-lid species it is still unknown what factors determine the spawning locations but it is hypothesized that the distribution of salinity and temperature with depth plays a major role and that the common condition arises in the so-called subtropical convergence zone (e.g. Kleckner & McCleave 1988, Munk *et al.* 2010, Aoyama *et al.* 2014). It may seem obvious but I think it is worth quoting Kleckner & McCleave’s conclusion; “Intuitively we believe that natural selection would favour strongly the evolution of mechanisms permitting identification by migrating adult *Anguilla* of water masses suitable for larval survival”.

The explanation of why the spawning site in the Atlantic is located at such a long distance (approximately 6–8,000 km) from their nursery areas in Europe and North Africa is believed to be that it originates from the time when continental plates were much closer to each other (Dorit *et al.* 1991). After these land areas during millions of years drifted apart, the migration distance has become increasingly longer for the European eel compared to the American. As a consequence the ancestral eel separated into two species about 10 million years ago (Tsukamoto & Aoyama 1998). During the peak of the latest ice age (around 20–26,000 years before present) the eel larvae could not exploit large territories and seemed to be completely gone from the northern parts of Europe, north of the Gironde basin area. It was only about 11,000 years ago that the eel re-colonized northern Europe. Archaeological findings show that it was probably as late as 6,700 BP when eel again could reach the Baltic region, although it is possible that there were eels even in the Yoldia Sea approximately 2–3,000 years earlier (Kettle *et al.* 2008).

In the Baltic Sea area eels inhabit most lakes, streams and are also found along the coast and in their archipelagos. However, the migration and distribution of young elvers\(^3\) from the North Sea through the sounds into the Baltic Sea is poorly studied. The catches of immigrating eels along the coastal river mouths of Motala ström, Nyköpingsån and farther north at Dal-

\(^3\) Here, elver is a term for a young eel which undergone the metamorphosis from glass eel to a pigmented tiny yellow eel.
älven shows that arriving eels are about 4–7 years old. When they subsequently leave as silver eels, in general after about 10–20 years, they consist almost exclusively of females and the average weight is just over a kilogram in the North and about 0.8 kg in the South. It is unknown what controls the eel’s ability to find their way back to the spawning area in the Atlantic. There are several theories and hypotheses of which most have been well described in Tesch (2003); e.g. olfactory sensory system, magnetic field perception and rheotactic responses to gradients of salinity, currents or temperature.

In the Nordic region tagging experiments on migrating eels were conducted even before J. Schmidt’s discovery of the spawning areas. In 1903, Oscar Nordqvist in Finland and Filip Trybom in Sweden did the first experiments; Nordqvist being a couple of weeks ahead of Trybom. In Finland they used threads of silk in different colours attached through the skin at the back of the eel (Nordqvist 1904). In Sweden, tiny dropped-formed silver plates with individual numbers were attached near the dorsal fin (Trybom 1905).

The objective of these first attempts was to gain general information on the migration direction and routes taken. The first results were relatively sparse with almost no information from the Finnish tagging and just a few Swedish recaptures. It appeared that the migration mainly took place on the Swedish side of the Baltic Sea. Later, more successful experiments in the eastern Baltic showed the eel to migrate out of the Gulf of Finland and along the coast of Estonia and Latvia (Schneider 1918, Mää 1947). Farther south on the eastern coast of the Baltic, the eel fishery use smaller fyke nets and the catches mainly consisted of yellow eels (Nordqvist 1925), possibly indicating that the silver eel migrate further off shore. However, closer to the exit from the Baltic Sea, a more extensive eel fishery – like the one used along the Swedish Baltic coast – took place in German and Danish waters (Martinköwitz 1961, Hoffman et al. 1979). Probably, this description of how the eel fishery catches migrating eels will also apply to the current situation.

The eel is considered a panmictic species, i.e. they mate randomly in the spawning area (Dannewitz et al. 2005, Palm et al. 2009, Als et al. 2011). Offspring from individuals raised in Sweden might end up in a large variety of places from Iceland to North Africa and far into the eastern parts of the Mediterranean, and conversely, the fish reaching Swedish waters could origi-

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4 Age reading is done by counting winter zones on otoliths. Start point is from the glass eel phase, i.e. not birth.
nate from adults grown in any part of this vast area. Another alternative is that all eels could originate from a certain area, e.g. the Mediterranean or the Baltic Sea. However, not taking any risks in management, we must assume that the “local” eel stock is dependent on impacts from elsewhere and consequently the recruitment of eel is dependent on how the stock is managed in different parts of the distribution area. This situation requires co-operation across many national borders and even among continents and there is thus an obvious risk for “the tragedy of the commons” type of problems.

Given the panmixia, one measure to enhance the eel population, is restocking. Eels from areas where they are relatively abundant are caught and stocked where natural recruits are few. Ideas of artificially enhancing the local abundance are not at all new. Ever since the mid-1800s, there have been restocking of young fish from the Atlantic coast to sparsely populated inland waters (Dekker & Beaulaton 2015). The goal has been to increase the yield of local fisheries, and survival during the growth stage of these restocked eels is well documented (Wickström et al. 1996). However, given today’s situation with a general decline of the eel stock all across Europe the question has shifted to whether stocking can increase the abundance of mature fish returning to the Sargasso Sea and in that way contribute to the recovery.

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5 Economic theory by biologist Garrett Hardin (1968) describing how individuals/nations acting independently and rationally according to each’s self-interest, e.g. how shared environmental resources are overused and eventually depleted.

6 Otherwise there might be a risk for loss of genetic variation due to geographically differentiated gene expression (e.g. Pujolar et al. 2006, Als et al. 2011).
The situation of today

In recent decades, eels (*Anguilla* spp.) have declined world-wide and the European eel seems most vulnerable with a recruitment of just 1–10% of former levels (Dekker 2004, Dekker & Casselman 2014, EIFAAC/ICES 2014). There are numerous possible causes of the decline e.g. overfishing, pollution, parasites, migration obstacles, reduced growing areas, turbine mortality and changed oceanic conditions (Dekker 2003). In 2007, the EU issued an eel regulation (EC No 1100/2007) aimed at a recovery of the European eel population. The regulation demands eel management plans from all member states with significant eel stocks. The main objective is that the number of silver eels (spawners) leaving European waters should be at least 40% of what an estimated virgin stock would have produced.

The resulting management plans for many European states are more or less based on restocking to improve the production of spawners. Stocking means that fish are translocated from areas with an assumed local surplus of glass eel, to areas with poor recruitment. However, the ability of stocked eels to migrate back to their spawning area has been questioned ever since Westin’s tagging experiments started (Westin 1990, 1998 and 2003). He claimed that stocking programs just facilitate a fishery but do not increase the eel population, since stocked eels lack behavioural cues making the adult silver eel unable to find the way back to their spawning grounds. The conclusion was based on tagging experiments which showed examples of deviant behaviour compared to earlier taggings. Stocked eels migrated in the wrong direction and with a high degree of overwintering. However, these studies were not conventional and therefore difficult to draw reliable comparisons from. Partly because of geography (since most of the eels were tagged and released at the Island of Gotland which is far from the mainland coast where earlier tagging were conducted), and partly since the experimental design also were different with long distance transports and several weeks of delay before release. All in all, the experiments gave very few recaptured eels compared to what the conventional silver eel tagging in the Baltic Sea area had given over the years (Ask & Erichsen 1976). Given the magnitude of the decrease in recruitment and the lack of knowledge in this field, there is an urgent need to further investigate eel migration towards the spawning area and if the stocking activities support the eel’s recovery as assumed in many of the management plans.
Objective of the thesis

As described above, today’s seriously reduced recruitment to European waters motivated the European Union to introduce a regulation for the stock recovery obliging the member states to produce Eel Management Plans for their respective territories. The unifying link in this thesis is that the selected papers describe subjects and results that could be used in our Swedish eel management, e.g. the impact of the Swedish fishery is assessed. The main aim however, is to investigate whether stocked eels manage to migrate towards the spawning area in the same way as naturally recruited fish do. I will also briefly address the question of what cues, circumstances or characteristics that make them migrate in a certain direction. The tool is silver eel tagging experiments, both historic (started in 1903) and recently conducted, made by myself and colleagues.
Short descriptions of the included papers

In Paper 1 and 2 we describe migration behaviour, routes taken and the physical maturation of Swedish tagged eels both in a freshwater lake and along the Baltic coast.

On a broader geographical scale, eels are traced from the Swedish West Coast on their way to the Atlantic Ocean. This is described in Paper 3 where we used different types of data storage tags attached to eels of a known origin, natural and stocked.

There is a need for evaluation of restocking and we describe the Swedish approach of handling the issue in Paper 4.

Another factor discussed in relation to the decreasing eel population has been effects of parasite infestation. We address this in Paper 5 where data from tagging and counts of the swimbladder nematode Anguillicola crassus are used to describe how the parasite may affect the eel’s spawning migration.

The restoration of the depleted stock of the European eel requires that anthropogenic impacts are quantified. In Paper 6 we assess the impact of the silver eel fishery on the Baltic Coast in Sweden, applying Survival analysis to 60 years of mark-recapture experiments.
Material & Methods

Much of the tagging data used in this thesis was collected long before I started my PhD studies, but I have also collected new types of data in the context of our own tagging programs (Paper 1, Paper 2 and Paper 5). Analysing also the recaptured eel, and not just prior to tagging, we could obtain data on e.g. changes in condition and eye size. Recaptured fish were also thoroughly investigated for the presence of a parasitic swimbladder nematode, and ages were determined from the otoliths (ear stones). These were analysed further since their elemental composition can lead to understandings of the eel’s origin, i.e. fresh or brackish water during the yellow eel stage. For each article, the section Material & Method will describe these methodological steps. Below are a general description of the fishery for silver eel and a review of the tagging methods used to study eel migration. But also the otolith marking method in use to distinguish stocked eel from naturally arrived fish.

Eel fishery and tagging of eels

The main fishery for migrating eel is performed with large so-called pound nets (“bottengarn” in Swedish, Berntsson 1971, Figure 3). These were introduced from Denmark in 1909 and replaced the previously used smaller fyke nets (Svärdson 1976). The pound nets are positioned perpendicular to the shore at strategic locations along the coasts and are most frequent along the south-eastern coast of Sweden and at the outlets of the Baltic Sea. This type of fishery is less abundant north of Stockholm. On the other side of the Baltic Sea some fishery occurs in the Gulf of Finland but has never been as extensive as in the southern Baltic proper. Pound nets are also used in freshwater lakes while in rivers migratory eels are caught in various types of traps. As
mentioned in the *Historical background* above, silver eel tagging started in 1903. In Sweden, the first tags were tiny silver plates, which proved to be very functional. This tag was replaced by the Carlin tag (Carlin 1955, Figure 4), which has become a standard also in the tagging of other fish, e.g. salmonids. It has not been possible to demonstrate any difference in recaptures rates between the two types of tags (Paper 6).

The Institute of Freshwater Research in Drottningholm has over the years received most reports of tagged fish in Sweden. The archive contains thousands of recapture cards, summary reports and various data from recaptures collected since the 1950s. Unfortunately, the different tagging protocols are filed at different places and organizations in the country, but as a foundation for this thesis we located and digitized these protocols which served as a basis for Paper 6.

In Sweden, tagging eel with Carlin tags has become an important part within the EU’s data collection programs (EC No 665/2008)

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7 Previously belonging to the Swedish Board of Fisheries but after 2011 a part of the Swedish University of Agricultural Sciences and the Department of Aquatic resources (SLU Aqua).
However, the Swedish West Coast eel fishery was closed in 2012 and a closure of the East Coast fishery has also been discussed. If so, the Carlin tagging program will no longer be functional since it is based entirely on recaptures from commercial fishing. This situation would require tags of fishery-independent nature. Such tagging methods are not at all new. Telemetry has been used in several studies to track eel over fairly short distances (e.g. Westerberg 1979, Tesch 1989, McCleave & Arnold 1999). Acoustic tags have also been used to determine whether different types of anthropogenic activities affect eel migration ability (Lagenfelt et al. 2006, Westerberg & Lagenfelt 2008). Furthermore, data storage tags have been used to register information on long-term migratory behaviour (e.g. Westerberg et al. 2007, Aarestrup et al. 2009).

**Data storage and acoustic tags**

Data storage and acoustic tags have been used in several papers in this thesis. Below follow a brief description of each tag and in which paper they have been used. The different types of tags are shown in Figure 5.

*Pop off satellite tag (PSAT)*

The PSAT is 12 cm long and a max diameter of 3.3 cm. It is mounted on the eel in front of the dorsal fin and records depth and temperature, at best with a 15 min sampling rate. At a predetermined time, the tag is released from the fish and rises to the surface, where it transmits its position and the stored data to the ARGOS satellites.

*External data storage tags (e-DST)*

The e-DST is 13 cm long, max diameter of 2 cm and was in the present studies adjusted to record depth every 30 s and temperature every 120 s over more than 2 years’ time. The tag is released from the eel at a predetermined time and it floats on the surface or drifts ashore. The recovery of data relies on the tag being found and returned.

*Implantable data storage tags (i-DST)*

The i-DST also stores data (temperature and depth as in e-DST). It is 13.5 cm long and both floats and data storage unit are 1.1 cm in diameter and are set together in a string (see Figure 5). It is implanted in the eel’s body cavity and when the fish dies and disintegrates the tag rises to the surface. The recovery

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*8 Supplied by CEFAS Technology (www.cefastechnology.co.uk)*
of data relies on the tag being found and returned. The main advantage lies in the avoidance of external attachment.

*Acoustic tags* – used in *Paper 3*

The acoustic tag transmits a unique identity coded signal (every 20 to 50 s in this study) that are recorded when a fish passes a special receiver. Such receiver may, for example, be placed at the mouth of straits. Tags were surgically inserted but could also be attached externally like the pop-up tags described above. The type used in *Paper 3* was 1.8 cm long with a diameter of 0.73 cm.

Figure 5. Three types of DST and one acoustic tag.
a) Pop off satellite tag (PSAT) (Photo: Eeliad project)
b) External data storage tags (e-DST)
c) Implantable data storage tags (i-DST)
d) Acoustic tag (Photo: Ingvar Lagenfelt)

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9 Acoustic tags used in 2010 were supplied by Thelma Biotel (www.thelmabiotel.com)
The Swedish approach

The small size of elvers prevents the use of external tags. Instead, elvers used for stocking are held in water with a high dose of strontium (Sr) for 24 hours, which results in the formation of Sr-rich bands in the otoliths. This band can be detected in ground and polished otoliths with Electron Probe Microanalyses (Figure 6). This method allows the identification of stocked eels during their entire lifetime.

![Image of otoliths with Sr-rich bands](image)

Figure 6. Otoliths from eels marked with strontium. Fish released in Sweden are bathed once in water with excess of strontium (Sr) resulting in formation of one Sr-rich band. For elvers stocked in Finland the procedure are repeated giving two bands.

As a result, stocked elvers can be identified in an efficient and reliable way. This issue was raised and the importance stressed already in the early 2000s, both nationally within the former Swedish Board of Fisheries and at the EU level through the ICES eel working group. Thanks to the work by Håkan Wickström and the good co-operation with SSE, Sr-marking is now mandatory when stocking elvers in Sweden. Since 2009, Sr-marking has been performed in both Sweden and Finland, and two years later it was also recommended internationally (EIFAAC/ICES 2011). The method is extensively described and introduced in Paper 4.

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10 Scandinavian Silver Eel is an eel farming company in Helsingborg. Here all imported elvers are placed in quarantine where also the marking procedure takes place (www.silvereel.se).
Results and discussion

Recaptures of tagged eel were relatively scarce in the early 1900s, probably because fish tagging were a new phenomenon and the fishers were unaware of the ongoing experiments. In addition, the fishery was not as extensive as it became later. In 1958 Swedish eel landings from the Baltic Sea reached an all-time high of more than 2500 tons of silver eel. This was also reflected in the recapture rate (Figure 7). After this, catches decreased and so did the recapture rates. However, a bit unsynchronized since the intensity of the fishery started to decrease somewhat later, in the early 1970s (Andersson et al. 2012).

Within the Baltic Sea, no recapture of Swedish tagged eel has been made along the eastern Baltic, between Estonia and Poland. This also holds for eels tagged in the Gulf of Finland and for all but one eel tagged in Estonia (Määr 1947). Since there is no major fishing activity in that area it is difficult to determine if silver eel migrate there. However, if migratory eel were passing in any substantial numbers it is not far-fetched to assume that people living in these areas would have found this out and made use of the resource. Fishing is not intensive until we approach the Polish coast towards the border with Germany and further on towards the German region of Rügen. However,
pound nets used in this area presumably catch eel produced in the estuaries and rivers of the southern Baltic. Since recaptures of eel tagged in Finland and the Baltic republics are rare in this region, this gives a hint on the migration routes of fish from the north-eastern part of the Baltic proper (e.g. Määr 1947). So far, based on the tagging from 1903 to present, the most correct map of silver eel migration in the Baltic is still that of Svärdson (1976). However, before our compilation of old tagging data (Sjöberg & Petersson 2005, Paper 6) many of the recaptures made in the Danish Belts had been disregarded. Consequently, a couple of additional migration routes would fit well with current knowledge (Figure 8).

![Figure 8. Arrows in red added to a map made after Svärdson (1976). The compilation of old tagging data show that migration through the Danish Belts are common directional paths for Swedish silver eels.](image)

The systematic compilation of thousands of old recapture reports and the creation of a database allowed integrated analyses for 100+ years of data, enabling a novel type of analysis of mark-recapture data. The conventional analysis counts recaptures in a predefined space or time interval. For the silver eel, the interpretation of recapture counts is complicated by the fact that much of the fishery is concentrated quite near the outlet of the Baltic Sea. A consequence of this is that the recapture likelihood increases in that particular area, while a large share of the silver eel stock emigrates into our coastal waters only there. Conventional mark-release-recapture analysis quantifies...
the mortality exerted on the marked animals, that is: the eels marked before – excluding those late emigrants. Conventional mark-release-recapture-analyses cannot address the fishing impact in the area where eel is most abundant and fishing mortality is at its highest. We approach this problem in a new way, using Survival analysis (Allison 2010). This statistical technique is related to mark-release-recapture but addresses the recapture information from a different viewpoint, focusing on the survival time of the individual eel wherever it occurred. In this way, we characterize the risk or hazard for that eel to be captured along its migration route (i.e. the fishing mortality). This approach produces a more accurate picture of fishing mortality during the migration towards the outlet of the Baltic Sea. The Swedish fishery on the Baltic Sea coast once yielded over 2 000 tons of eel per year, but gradually declined to 300 tons and recent management restrictions have reduced the catch to 200 tons. Our analysis indicates a decreasing fishing mortality over the decades – from 40% in the 1950s to 10% in recent years (Paper 6). The most recent, but preliminary estimate indicates that the fishing mortality is now even lower than before (Willem Dekker pers. comm.).

The new approach, where not only the tag but the intact recaptured fish was returned for analysis, created opportunities to follow tagged eels and how they changed from tagging to recapture concerning e.g. condition and eye size. We showed how the development of the eye seem to be a proceeding process since the eye index increases while eels are actively migrating (Paper 2). We also showed that eel weight decreased with migrated distance and with time between tagging and recapture (Figure 9).

Analyses of recaptures also allowed for the study of infestation from the swimbladder nematode Anguillicola crassus\(^{11}\) and how it could be associated with eel migration behaviour (Paper 5). Both migrated distance and migration time (from tagging and release to recapture) decreased with intensity of parasite infection, but did not correlate with migration speed. This means that less infected eels managed to migrate longer distance before being caught in a pound net (Figure 10). The interpretation was that more severely infected eels swam closer to shore to avoid deeper waters and large dives since these excursions require a well-functioning swimbladder. Parasitized fish were therefore more easily caught in fisheries.

\(^{11}\) By some authors named Anguillicoloides crassus (e.g. Lefevbre et al. 2013)
Figure 9. The tagging in Väddö 2008 shows a weight decrease for each eel between time of tagging until recapture. Eels were tagged 9-10 September 2008.

Figure 10. Relationship between migrated distance from tagging to recapture site and the number of Anguillicola crassus in the swimbladder. Migrated distance decreases with number of A. crassus (n= 190, p < 0.05). Paper 5 was published in J. Fish. Biol. and in that article we used pooled correlation coefficients in order to control for differences between release sites. In this graph I have re-analyzed the data and used a mixed model instead, with sites as random factor and distance as fixed factor. However, the conclusions from the published article were not affected by this new approach.
Analyses of the microchemistry of otoliths can in certain cases show if an eel has been stocked: a glass eel caught in River Severn in England, quarantined in Helsingborg in Sweden and after that released in a freshwater lake, will show a sudden drop in the otolith’s Sr-profile, since the saline Atlantic water is comparatively rich in Sr while freshwaters are Sr poor (Figure 11). In addition, some stocking have been conducted on the coast and therefore these otoliths do not show the same dip in the Sr-profile. However, coastal stocked eel seem to constitute a very small fraction of the coastal population (Clevestam & Wickström 2008, the National eel stocking database (kept at SLU Aqua)).

This information, and data on capture and recapture of tagged individuals, was used to explore migration differences between fish with different recruitment history (Paper 2). A minority of the recaptured eels originated from fish stocked in freshwater. Instead, they were dominated by supposed natural immigrants which had spent most of their lives in brackish waters. However, available data do not confirm any migration differences between stocked eels and naturally arrived fish (Paper 2).
To be confident that we investigated migration pattern of stocked eels, an additional tagging experiment was conducted in Lake Mälaren. This lake has been stocked since the 1960s, first by relocated bootlace\textsuperscript{12} eels from the Swedish West Coast and later also by elvers imported from England or France. Here we immediately observed differences from the parallel coastal studies. A majority of the fish remained in the lake to overwinter, irrespective of eel’s origins (50% stocked as elvers, 50% as relocated bootlace). It is possible, however, that the latter group also contained some natural immigrants. This overwintering behaviour is described in \textbf{Paper 1}, based on data from i-DST tags. Tagged individuals, classified as silver eels, seem to regain the foraging behaviour of yellow eel during summer. As the temperature started to decrease in August, the diving activity changed. The amplitude of the excursions increased which indicates that the eels moved over deeper areas. They showed the migration behaviour of silver eels but appear unable to leave for the Baltic Sea through any of the open outlets and in November, the next dormancy period started (Figure 12).

Despite the eels in our study still seemed to feed, they showed a decreased condition with time (\textbf{Paper 1 and 2}). Thus, from a management point of view, it is questionable to try to produce large fecund females by stocking lakes such as Lake Mälaren. Whether this is because of the lack of imprinting of cues from a self-performed immigration, as Lars Westin suggested in his conclusion from a tagging experiment on the Baltic Sea island of Gotland (Westin 1998, 2003), or if there are other explanations remains an open question. Interestingly, this difficulty in migration was not seen in the stocked eels from the Swedish West Coast (\textbf{Paper 3}).

Work carried out within the EU project EELIAD led to \textbf{Paper 3}. All three types of data storage tags (DST) and the acoustic tags were used (described under Material & Methods). From the start of the EELIAD project, the DST were used off Ireland and France, but when predation revealed to be a big problem (Wahlberg \textit{et al.} 2014) we decided to use some of the expensive tags (between 1000-4000 Euro/each) in our northern waters. Here was the predation pressure assumed to be lower and in addition, the best long track in the EELIAD project available to compare PSAT tagging and internal tagging was released in Sweden; “the Shetland tag” (Westerberg 2013). Initially, the aim was to tag eels caught in the outlet of the Baltic Sea but the experiment was conducted on the Swedish West Coast, where the fishing intensity is much

\textsuperscript{12} Undersized (<100g) yellow eel.
Figure 12. Depth (black) and temperature (red) recorded by three eels during the period between two successive overwintering periods. As the temperature started to decrease in August, the diving activity changed. The amplitude of the excursions increased which indicates that the eels moved over deeper areas. Time scale is the same in the three panels.
lower and fish of known origin (natural immigrants from the River Enning-dalsån and stocked eels from the River Ätran) could be found. The results from these experiments were very successful since relatively many tags with long series of data were received. The eels showed a clear dial vertical migration (Figure 13) which made it possible to estimate the longitude using the time of local noon (Paper 3). Trajectories could be reconstructed and we could produce a map of likely migration routes of individual eel (Figure 14).
There were no statistically significant differences in behaviour regarding route, swimming speed and preferred swimming depth between stocked and naturally recruited eels. These results provide the first empirical evidence of a Scandinavian migration route and contradict the hypothesis that a sequential imprinting of the route during immigration is necessary for adequate orientation or behaviour during the adult spawning migration, at least not outside the Baltic Sea.

As mentioned above, eels stocked in Sweden and Finland have since 2009 been marked with strontium. This provides a tremendous opportunity to discover these eels and detect possible differences in migration patterns (Paper 4). However, these markings were launched rather recently and too few marked eels have been recaptured so far. Thus this information is not present yet and consequently could not be used within the scope of this thesis.
Concluding discussion

Traditionally fishers have used the lunar phase, currents and winds to determine eel migration. However, it is not the same as the eel actually use these abiotic factors to navigate towards the spawning area. In addition, it is not obvious that all, or even the majority, of the silver eel migrates along the coast more or less close to the shores. Eel are regularly caught far away from the coast of the southern Baltic and the North Sea during trawl surveys (Westerberg et al. 2011). In contrast, what we see from recaptures in a single tagging experiment reflects the conditions at a particular time, affected by variation in temperature, wind and current directions during new moon periods that particular season. In longer terms, the total fishery catches also reflect practical possibilities and obstacles where the fishers can set their gear: i.e. deep water, heavily exposed shores, legal restrictions on gear size, etc. (Sjöberg & Peterson 2005). Another parameter affecting the recapture pattern is the willingness to report a recaptured eel, which could vary due to a lower catch, the reward system and local questions like different kinds of anthropogenic activities like discharges from pulp mills, etc. The relations to authorities could also affect the fishers' attitude, both on local, national and international scale. However, the behaviour of fishermen often is a very complex matter (e.g. Pollock et al. 2001) and I have made no attempt to correct for that.

Consequently, a complete understanding of the distribution of migrating eel in the Baltic Sea is not easy to achieve. However, overall and under current conditions, I strongly believe that the use of commercial catches combined with eel tagging has been a very important tool for our understanding of eel migration in the Baltic Sea. Since this thesis is based on several studies, covers a long time period and is based on numerous individuals, the influence of unusual biotic and abiotic conditions should realistically not have had too much impact on the results as a whole, and instead have averaged out.

Eel fishing is nowadays tightly regulated to meet the objectives of the Swedish eel management plan. The coastal fishers who still are allowed to catch eel may do so for only 90 days per year or 60 days in the Sound (strait between Denmark and Sweden). Generally the average age of these fishermen is high and when they quit fishing, according today's regulation, their fishing rights cannot be transferred to anyone else. Thus, the intention seems to be that the fishery should gradually be phased out. This means substantial restrictions in the fishery (Dekker et al. 2011) and decreased catches. The only thing that
can counteract this closure of the eel fishery is that more juvenile eel from the Sargasso Sea reach the European coasts. In fact, according to the recruitment index presented last year from the working group of eel (WGEEL, EIFAAC/ICES 2014) that is what appears to be happening the last few years (Figure 15). It is possible but still unclear whether this increase is a response to executed actions of protection. However, the figures are still far from historical levels and just incoming information tells that glass eel fishing this winter so far indicates a substantially lower number caught in France (UK Newsletter, 2015). The UK has not yet started their fishing season at the time of writing.

![Recruitment index](image)

**Figure 15.** Trend in recruitment of glass eel to the continent. Data from WGEEL 2014. Separate curves are given for the North Sea and elsewhere.

As far as we can see today it is not sure whether the tagging, which requires recaptures in a commercial fishing, is a viable option in future research on eel migration and stockings as a tool in management. The alternative is fishery independent methods (i.e. derived independent of the fishery and the locations of fishing sites). Such data can be obtained by the use of acoustic tags and a system of acoustic receivers in the Baltic outlet straits, or by different types of data storage tags. With these methods it would for the first time
be possible to get information on which eels that actually leave the Baltic Sea. Hitherto, studies have only given information on eels that have failed to escape the fishery or for unknown reasons failed to migrate. We can already conclude that DST has provided unique results (Paper 3) and this strongly motivates us to conduct further studies with data storage tags. However, the relatively large tags had earlier shown to reduce the possible maximum swimming speed and therefore could hinder tagged eel for reaching far enough (Burgerhout et al. 2011) but as the technology advances, the tags become smaller and the opportunity to finally follow eels all the way back to the spawning site should be in the not too distant future.

Should eel stockings continue?

For decades, eel stocking has been the subject for debates. More recently, the question is whether there really exists a surplus of glass eels? If so, there is no doubt that they survive and can produce a substantial number of eels where they are stocked (Wickström 2001). However, stocking in general can have negative impact through predation and competition over resources, e.g. the situation between eel and crayfish (Svärdson 1972). In addition, we have to deal with the question whether stocking actually manages to increase the number of spawners in the Sargasso Sea. Even if tagging on the West Coast showed a common Scandinavian migration route and behaviour for eels of different origin (natural or stocked Paper 3), there are still uncertainties surrounding the issue. Stocking eels in freshwater areas around the Baltic have been shown to result in unexpected migration behaviour which may affect their potential contribution to the spawning biomass (Paper 1, Paper 2, Westin 1998, 2003, Prigge et al. 2013). Furthermore, eel inhabiting freshwater have been shown to be in poorer condition than those grown up in coastal environments (Marohn et al. 2012). However, all these studies had no naturally immigrated controls for comparisons inside respective freshwater.

For eels stocked on the Swedish Baltic coast there is yet no definite answer regarding their navigational ability and therefore stocking on the Baltic coast should be further investigated. Like in Lake Mälaren we could see a weight decrease even among the coastal eels, where the majority were natural immigrants. However, no matters of origin, the coastal eels were all actually migrating (Paper 2). The decrease may not be associated with a migration failure but instead a result of the maturation process as such where e.g. muscle is converted into fat. Future studies should investigate the exact relationship between condition indices and body composition of eels.
We can conclude that it is a great responsibility of those who provide evidence of an existing surplus, to ensure that these abundances are enough to allow for substantial stocking programs in spite of all uncertainties. In times of a strong eel population, stocking is a well-functioning approach to support a profitable fishery. Given today’s critical situation with a risk of extinction, however, it should be considered a secondary option compared to a reduction of the adult mortality.

There are several additional questions that could be raised regarding eel management. For example; should we actively try to prevent eel from migrating upstream if this involves the passing of hydro power plants where the fish would suffer a substantial mortality risk when migrating downstream? Should we actively control populations of predators on eel, such as seals and cormorants? Considering the acute situation of both eel and small scale fishery, the answer is given.

**Where to stock in the future?**

In the current situation, until we know better, I urge to adopt the precautionary approach and the simple solution would then be to only stock on the Swedish West Coast. Here the eel will have a growing environment safe from fisheries and stocked eel have shown the potential to migrate towards their spawning area in the Atlantic. Furthermore, if the risk of limitation of any kind as for example by density dependence, eel stocked in this area may have all opportunity to migrate into west coast rivers (the ones with free passages), into the Baltic and freshwaters like naturally arrived fish. Although we lack knowledge of what cues drive the silver eel migration, a qualified guess would be that this “West Coast strategy” is better adjusted to current and natural circumstances.
Sammanfattning på svenska

Märkning av blankål startade redan sensommaren och tidig höst år 1903 när Filip Trybom och Oscar Nordqvist märkte ål på båda sidor av Ålands hav. Resultaten manade till en fortsättning och sedan dess har dryga 40 000 blankålar märkts i Sverige. Från början var frågeställningen främst att bestämma vandringsmönstret mot lekområdet, som vid den tiden var helt okänt. På senare tid har frågorna ofta varit lokalt förknippade med olika sorts potentiella hinder eller störningar från exempelvis vindkraftsparker, brobyggnationer eller utsläpp från industrier.


Våra egna märkningar har till stor del handlat om frågor som rör skillnader mellan utsatt och naturligt invandrad ål. Resultaten visar att de flesta ålar verkar vandra som förväntat, i god fart mot utloppen av Östersjön, oavsett ursprung. Men det kan ibland vara svårt att särskilja utsatta från naturliga ålar varför viss osäkerhet ändå råder. Vid ett experiment med ål från svenska Västkusten där fiskens ursprung var känd, nämligen naturligt invandrad respektive utsatt ål, fann vi mycket liknande vandringsmönster för de båda grupperna: tydliga vertikala dygnsvandringar och en vandringsriktning längsmed Norska rännan och norr om de brittiska öarna.


I rådande läge med ett akut hot mot ålbeståndet bör utsättning av ål ske på svenska Västkusten där vi kunnat visa att de då verkar bete sig som naturliga ålar. Härifrån har de utsatta ynglen alla möjligheter att vandra vidare till sötare vatten på egen hand.
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Thanks to my wonderful family Frida, Elsa and Charlie. You are my everything.

Niklas

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iDST tag implanted into the abdominal cavity under anaesthesia.
Overwintering dormancy behaviour of the European eel (Anguilla anguilla L.) in a large lake

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Abstract – Overwintering dormancy behaviour was studied in female silver eels in Lake Mälaren in Sweden between 2008 and 2010. Depth choices and movements in relation to temperature were analysed from pressure and temperature records for 13 eels with implanted data storage tags, covering 17 overwintering periods and three intervening summer periods. Dormancy commenced in October–November as temperatures fell below 4–12 °C. Eels tended to remain motionless throughout the winter, with some short periods of activity signalled by small changes in depth distributions. During dormancy, the eel shows a clear avoidance of shallow areas <5 m in favour of the 10–25-m-depth interval. Activity tended to resume 4–6 months later in April–May as temperatures rose above 3–7 °C and ice cover broke, and eels spent more time at shallower depths of <5–10 m. The majority of the eels were assessed as being in the silver eel stage at the time of tagging. During the autumn months, the diving behaviour, with frequent and large vertical excursions and periods at the surface, was similar to that seen in migrating eels in the Baltic and Atlantic Ocean. In spring and summer, the behaviour differed, being dominated by more gradual depth variations, implying that the eels reverted from silver eel migration behaviour to yellow eel foraging behaviour. Body weight declined during dormancy, but other studies of starvation over comparable time periods showed significantly higher average specific weight losses, implying that the Mälaren silver eels must have fed between the end of dormancy and recapture.

Key words: Anguilla anguilla; hibernation; dormancy; data storage tag; annual activity cycle; starvation; growth rate

Introduction

That eels hibernate was used as a defining character by Linneé in Systema Naturae (Linnaeus 1758). It is well known that eel in temperate areas ceases activity in autumn and eventually becomes torpid and buries themselves in the sediment until spring, where its activity increases along with the rise in temperature (e.g., Bertin 1956; Nyman 1972; Walsh et al. 1983). Under these conditions, eels are able to survive to temperatures down to, or below 0 °C.

The terminology used to describe the behaviour of wintering ectotherms is unsettled (Ueltsch 1989). In contrast to hibernating mammals, the body temperature of an ectotherm is unregulated, tracking that of the environment, and they usually retain some responsiveness. In this paper, a state of total motor inactivity will be called ‘torpor’, and we use the term ‘dormancy’ to describe the overwintering behaviour responses of the eel in general, for example timing, habitat choice and cryptic hiding behaviour.

The background to this study is a comprehensive tagging experiment to investigate the migratory success of stocked and naturally recruited eels (Sjöberg in prep). Conventional tagging with Carlin tags was made of presumed migrating eel in Lake Mälaren in eastern Sweden in 2008. Thirty of 290 large eels were in addition fitted with implanted data storage tags (DST) measuring temperature and pressure. Fifteen of the DST-tagged eels were recaptured after

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one or two winter seasons, 10 giving a detailed record of the conditions during one dormancy period and three during two periods.

Such long-term detailed field data from individual eels are new, and the objective of this study primarily is to describe the environmental conditions and behaviour during dormancy. The question of reversal from silver eel to yellow eel stage was also addressed by looking at the change in behaviour pre- and post-dormancy. As a large proportion of the tagged eels were recovered and measured after recapture, it was possible to look at to what extent silver eels were starving even after having interrupted their migration by overwintering.

Study area
Lake Mälaren is the third largest lake in Sweden, with an area of 1140 km², mean depth of 12.8 m and a maximum depth of 66 m. Approximately 50% of the total lake area has a depth <10 m. Hypsographic data were taken from Sahlberg & Gustavsson (2010). The drainage area is 22,650 km² and includes lake Hjälmaren, which is the fourth largest lake in Sweden.

The lake is connected to the Baltic Sea via several outlets in Stockholm (latitude 59°20’N) and, at high water, at a lock in Södertälje channel (latitude 59°11’N). The geography of the lake is complex, Fig. 1, with subbasins and numerous smaller bays (Kvarnäsv 2001). There are more than 7000 islands larger than 1 ha. From west to east, the lake was divided into a number of sections, Table 1, each covering one or more subbasins. The run-off to and the water level in the lake are regulated and at a maximum during the melting of the snow in the spring. During summer, the run-off to the lake is often less than the evaporation. The run-off gives rise to very low current speeds in the lake. Typically, even narrow channels between the islands have a cross-section of the order of magnitude $10^4$ m², and the mean velocity becomes $<10^{-2}$ m s⁻¹ (Sahlberg & Gustavsson 2010). The instantaneous currents are stronger, highly variable and wind-driven (Liungman 2010). The total lake discharge from the release and during the first dormancy period in this study is shown as Figure S1.

The seasonal thermocline in the lake develops in spring. The depth of the thermocline increases from approximately 5 m in May to 12–15 m in June-August. The lake is dimictic, but the temperature difference between the surface and bottom water is usually <1 degree after the autumn overturning and during the winter period (Kvarnäsv 2001; Sonesten 2013). The oxygen content in the bottom water has a minimum in August before the autumn overturning and varies between basins and years. With the exception of section G, the minimum is typically 3–7 mg l⁻¹ and rarely falls below 2 mg l⁻¹ (Sonester 2013).

The lake is usually covered by ice from the end of December to April. When temperatures rise, the ice melts and vertical mixing leads to a spring overturn of the thermocline. Daily maps of the ice cover are archived at http://www.smhi.se/oceanografi/istjanst/is_prod.php and were used to study the ice conditions during the ending of the dormancy period.

Materials and methods
Eels used in the study
During the autumn of 2008, a total of 290 eels (Anguilla anguilla L.) were caught with pound nets
Tagging details

The fish were tagged externally with a Carlin tag (a 18 × 4 mm plastic plate with a mass 0.12 g that was attached in front of the dorsal fin, cf. McFarlane et al. 1990). Each tag had a unique number and text offering a reward and urging the fisherman to contact the Swedish Board of Fisheries.

Thirty of the largest silver eels (724–963 mm) were implanted with DST. To ensure that the DST tags were noticed by the fishermen, the eels were also tagged externally with a Carlin tag. The DST were supplied by CEFAS Technology Ltd, G5 long life tags (www.cefastechnology.co.uk/), with incompressible floats to make them buoyant (Figure S2). The purpose was to allow recovery of stranded tags from individuals that died by other causes than the fishery. The overall length of the tag was 135 mm and the diameter 11 mm. Detailed specifications of the tag are found in the Supporting information.

Tagging was carried out under anaesthesia using metomidate (1L-1-(1-phenylethyl)-5-(methoxycarboxyl) imidazole hydrochloride) at the concentration 40 mg·l⁻¹ for approximately 6 min. For implantation, the DST was pushed through a small incision into the body cavity that was subsequently closed with a single suture. Surgery took approximately 7 min, with a time to recovery of approximately the same duration. A detailed description of the surgery can be found in Thorstad et al. (2013).

Analysis of recaptured eels

Information about the study was given to eel fishermen associations and in the trade press. Recaptured eels were received from fishermen in Sweden and Denmark. In the laboratory, the eels were measured (eye diameter, total length and weight). As the eels had been frozen before analyses, length and weight were corrected for the shrinkage (Wickström 1986). An eye index was, when possible, measured according to Pankhurst (1982). An eye index was, when possible, measured according to Pankhurst (1982).

Weight change was analysed in terms of the specific growth rate (SGR), defined as

\[ SGR = \frac{(\ln W_{\text{end}} - \ln W_0)}{T} \]

where \( W_{\text{end}} \) is the wet mass after recapture, corrected for the effect of freezing, \( W_0 \) is the wet mass at tagging, and \( T \) is the number of days between tagging and recapture.

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in Lake Mälaren (Stallarholmen, 59.347°N and 17.333°E, Fig. 1). Total length and weight were measured. The minimum length was 625 mm and thus all were female. The fishermen classified the eel as silver eels after examining their external appearance. A digital calliper was used for measuring the eye diameter, and the calculated eye index was then used to determine maturation stage according to Pankhurst (1982). This made it clear that approximately 20% of the DST-tagged eels had an index <6.5 and should have been classified as yellow eels. A pectoral fin index larger than 4.5 indicates an advanced stage of maturation (Durif et al. 2005). Approximately 23% of the eels had a pectoral fin index <4.5. There was no correlation between the two indices \( R^2 = -0.02 \); however, 92% of the eel were in a migratory or pre-migratory stage according to one or the other of the indices.

Tagging was made 3–8 September 2008, and the eels were released the same day as the tagging near the site of capture. The DST tagging was made on the 8 September. Recaptures were expected from pound nets in the Lake or in the Baltic. The morphological measurements are summarised in Table 2.

### Table 2. Mean, range and standard deviation of the length, weight and Pankhurst eye index (Pankhurst 1982) of eels according to the tagging method. The \( P \)-value refers to an unpaired \( t \)-test comparing the average measures of released eels with the eels that were recaptured. The number of eels measured after recapture was 10 for data storage tags (DST)-tagged and 42 for Carlin tagged.

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<td>DST</td>
<td>30</td>
<td>14</td>
<td>0.09</td>
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<tr>
<td>Carlin</td>
<td>260</td>
<td>112</td>
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Westerberg & Sjöberg

In the Lake Malaren experiment, eels captured early were in several cases released again to have a second chance to find the outlet. In 2008 and 2009, a total of 40 of the 107 recaptured eels (37%) were released again one or more times. Of those 4 of 15 (27%) were DST-tagged.

Analysis of DST data

The maximum depth recorded in this study was approximately 60 m, whereas the range of the pressure sensor was 1000 m. This means that the resolution of the swimming depth is relatively low, with a digitization error of ±0.25 m.

A period of torpor was defined as a period of at least 5 days duration where the vertical excursions of the eel were less than the resolution of the DST (see Supporting information for a detailed definition of this).

For each tag data series, all such periods of torpor were identified, and the date, depth and temperature at the start and end of the periods were recorded. The dormancy period was defined as the period between the start of the first and end of the last such torpor period. Between the longer torpor periods, there were in many cases days where the depth range was less than ±0.25 m. To estimate the total time of torpor, all days fulfilling a ±0.25-m criterion were counted for the whole dormancy period in a winter season.

Results

Recaptures

Of the 30 DST-tagged eels released, a total of 15 eels were recaptured, all in fishing gear. Of those, 10 recorded one full overwintering episode, three contained two complete winter seasons, one had pressure failure before the first winter (but yielded temperature data), and one eel was released back without downloading the DST, and after that never was recovered. One eel was captured in Denmark 2009 and could have left Lake Mälaren before the dormancy period. Two tags were detected when slaughtering the eels at a fishmonger, where the eels had been mixed in a holding basin and the capture location could have been either in Lake Mälaren or on the Baltic coast. The maximum recorded depth and the development of temperature during the dormancy period for the eels with unknown dormancy location were the same as for eels that were recaptured in the lake. Thus, the dormancy probably took place in Lake Mälaren also for these eels. Table 3 gives summary data for all recaptured tags. Information about morphometric and maturity data for all DST-tagged eel is found in Table S1. There was no significant difference in the Pankhurst maturity index neither between all DST-tagged and recaptured eels nor between those caught in the lake and possibly recaptured in the Baltic (t-test $P = 0.97$ and $P = 1.0$, respectively, Tables 1 and S1).

In four of the recaptures in 2009–2012, the implanted tag had started expulsion through the abdominal wall. This is a phenomenon often seen in long-term studies (reviewed by Cooke et al. 2011) and seems not necessarily to affect the fitness of the fish seriously (Welch et al. 2007). Inspection of these eels showed no sign of infection around the opening, where part of the tag was outside the eel (Figure S5). Partially extruding tags made snagging possible in gillnets with otherwise too large meshes to capture eels however.

Data were successfully downloaded from 13 DSTs, but in seven cases, tags had experienced pressure sensor failure after varying time periods (Table 3).

Both for DST- and for Carlin-tagged eels, the morphological measurements made in connection with the release did not differ significantly between the tagged and the recovered eels (Table 2). The measurements made on the eels after recapture show no shrinking in length, but a significant weight loss (see below and Supporting information).

Overwintering behaviour

Data storage tags data showed that all the eels exhibited similar behaviour prior to and during overwintering. Activity after release was characterised by large amplitude dives, often to the surface during nighttime, and with shorter periods at the bottom. The diving ceased and the eel stayed in a limited depth interval for 5–6 months, with occasional short and small depth changes. An example is shown in Fig. 2.

A torpor period was defined as periods longer than 5 days without activity resulting in depth changes >0.5 m and the dormancy period as the period between start and end of the first and last torpor periods. Figure S3 shows time lines of dormancy behaviour for the individual eels. During the season 2008–2009, the start of the dormancy period varied from 30 September to 22 November (average 29 October) for the 13 eels with a record of the whole winter period. During 2009, the end of the dormancy period varied between 13 April and 20 May (average 25 April). During 2009–2010, four dormancy periods were recorded. Both the start and end were somewhat later. The start varied between 3 November and 5 December (average 8 November) and the end between 19 April and 14 May (average 27 April).

Ice starts to form in December–January. In 2009, the ice in lake Mälaren started to break up around 10 April and the lake became ice-free on the 13 April.
The ice season was longer in 2010. The ice had started to break up 17 April, and the lake was ice-free 20 April.

The water temperature during the first and last torpor period of the first winter after the release is shown in Fig. 3. The average temperature at the onset of dormancy was 9.1 °C, standard deviation 2.4 °C. The average water temperature at the end of the dormancy period was 5.2 °C, standard deviation 1.4 °C.

The mean dormancy depth chosen by individual eels during the first winter varied between 5 and 31 m. In most cases, the eel stayed within 10 m of the mean dormancy depth. The median of the individual mean depths was 11.4 m. Additional and more detailed data about conditions during the overwintering, including data for the winter 2009–2010, are found in the Supporting information.

**Behaviour before and after dormancy**

The DST depth data were averaged for each month. Figure 4 shows the yearly cycle of the mean monthly depth chosen by the eels.

The three eels that yielded DST data for both temperature and pressure covering 2008–2009 and 2009–2010 provide information not only about pre- and postoverwintering and overwintering periods but also about the active summer season. These eels were all in the silver eel stage (Pankhurst maturity...
Fig. 3. Temperature at start and end of the first and last dormancy period for the individual eels recorded during the winter 2008–2009.

Fig. 4. The monthly average depth occupied by the eels during 2008–2010. Small dots show values for individual eels and the large dots the ensemble average with standard deviation. The bar graph shows the number of eel datasets with data for a given month.
index between 9.5 and 10.3, both at tagging and when measured after recapture). All showed a similar general pattern (Fig. 5). After the activation in April–May, the eels moved into shallower water and there were excursions both up and down, but mainly well below the surface. As the temperature started to decrease in August, the diving activity changed. The amplitude of the excursions increased and frequently reached to the surface. The maximum depth indicates that the eels moved over deeper areas. In November, the next dormancy period started.

Data storage tags versus Carlin-tagged eels

A total of 112 (43.1%) of the 260 eels tagged with a Carlin tag without DST were recaptured. This is close to the 50% recapture rate of the DST-tagged eels (no significant difference, Fisher’s exact test \( P = 0.73 \)). Including cases where the eel was released again, a total of 201 recaptures were recorded of all the tagged eels. The maximum number of times an individual eel was recaptured was 6. In the following discussion, only time and position of the last recapture is included in the reporting.

Most of the recaptures were made in Lake Mälaren. Just 2.7% of the recaptures of all tagged eel were made in the Baltic proper. The longest migration was made by one of the DST-tagged eels, which was recaptured on the Baltic coast of Denmark after 937 km of migration (shortest distance in water). Figure 6 shows the geographical distribution of recaptures. The release was made in sector E, and recaptures were made in all parts of the lake except sector G. Most of the recaptures are from sector C, 60–70 km west from the release point.

Since 2011, the eel fishery yields and effort have been reported for three regions of the lake, corresponding to the sectors A, B+C and D+E+F+G in Fig. 1 and Table 1. This makes it possible to compare the distribution of the recaptures to the fishing effort. The eel fishery in the lake has been stable for many years (measured as number of active fishermen, fishing period and number and position of pound

Fig. 5. Depth (solid) and temperature (dotted) recorded by three eels during the period between two successive overwintering periods. Time scale is the same in the three panels.
 nets). Consequently, the catch data from 2011 onwards are probably representative for the fishing effort during the period 2008–2010, where effort data are lacking. Table 4 shows the relation between fishing effort estimated in this way and the relative distribution of recaptures by region and year of recapture. Approximately 50% of the Carlin-tagged eels were recaptured the year after release. With time, the tagged eels seem to accumulate in the eastern and western end of the lake.

In addition to pound nets, several kinds of gill nets with large mesh sizes are common in the lake. Eels can normally not be caught in such nets, and this part of the fishing effort is thus not included. An eel with an extruding tag can become snagged, however, which probably explains the increasing relative proportion of DST-tagged eel with time (Figure S4).

The average specific weight change of the eels, assessed as SGR, showed high individual variability (Fig. 8). There is a weak trend towards increasing weight loss with time (F-test, P = 0.0044), but there is no significant difference between those tagged with an implanted DST and those with the small external tag only (two-tailed t-test P = 0.48), indicating that implanted DSTs did not have specific effects on growth.

Discussion

Environmental conditions at start and end of dormancy

This study gives detailed information for the entire dormancy periods of 10 eels during one and 3 during two winter seasons. All the eels commenced more or less continuous periods at the bottom when the water temperature was decreasing, but there is a large variation in the temperature where this started. The first period of torpor started at 4.5–12.4 °C in the first year (Fig. 3). In the second year, the range was narrower, from 6.8 to 8.9 °C (Table S3). These temperatures are in the same range as those reported in Nyman (1972) and Walsh et al. (1983), based on laboratory studies, by Hammond & Welsh (2009) in telemetry studies of large yellow American eel, or indirectly from capture data by Vøllestad et al. (1986), showing a cessation of feeding and activity at or below 8 °C. The wider range observed in 2008 could be a residual effect of the tagging, which took place 1–2 months before the start of dormancy. The difference between the means in 2008 and 2009 is not statistically significant however (t-test P = 0.35).

During the first winter season, the end of dormancy and beginning of active movement took place at a lower temperature than that at the start, average 5.1 °C, range 3.3–7.2 °C. In contrast, Nyman (1972) studied the activation process on yellow eel in an aquarium with a range of bottom substrates and found that all eels remained inactive at temperatures

![Fig. 6. Distribution of the final recapture positions of tagged eels (bars) compared to the distribution of fishing effort (circles). The labelling of the sectors is as in Fig. 1.](image-url)
Dormancy in eels

below 8 °C. Silver eel responded less to an increased temperature and instead showed increased activity when temperature was artificially decreased (Westin & Nyman 1979).

Other stimuli than temperature, for example light, may be a factor in the activation. The termination of dormancy coincides with the break-up of the ice both in 2008 and 2009. There evidently is a correlation between heating and the break-up of ice, as well as with water-quality parameters as DO and pH. Without more years of data, this may be coincidental. The eels are probably buried in the sediments in which case they lack information on light and conditions in the water column. The break-up of the ice is accompanied by a sudden change in the noise level in the water, both from the break-up itself and from wave activity. This means that another possibility is that acoustic cues could be involved in the activation.

Depth selected for dormancy

The average depth occupied by different eels during the dormancy period was 13.2 ± 8.9 m during the winter 2008–2009 (N = 13) and 15.2 ± 7.3 m (N = 4) in 2009–2010 (Tables S4 and S5). In most cases, the total change in depth during dormancy was <2 m during the first winter. The depth variation for the four individual eels during the second winter was considerably larger. There was no difference in average depth between the 11 eels that with certainty spent the dormancy in the Lake Mälaren compared to those where the location was unclear.

Assuming that all the dormancy periods took place in the lake, we can compare the overwintering depths with the distribution of bottom depth (Sahlberg & Gustavsson 2010). Approximately 25% of the area of the lake is <5 m deep, but the dormancy depth of only one of 13 eels was in this depth interval during the season 2008–2009 (Fig. 7). The overrepresentation of depths during dormancy deeper than 5 m compared to a random choice is significant (P = 0.29, Fisher’s exact test, H_0 equal distribution). This difference is even more pronounced for 2009–2010.

There is no information about the habitat type at different depths in the lake, so the reason for avoiding shallow depths for dormancy could be a difference in bottom substrate, a strategy to avoid the lowest temperatures just below the ice or mechanical disturbance from ice and wave action. The risk of predation from pikes and cormorants is also a possible factor.

Weight loss during dormancy

Of the DST-tagged eels with at least one dormancy period, 92% were in the premigrant or migrant stages according to their eye or pectoral fin index at tagging. In this stage, they stop feeding (e.g., Pankhurst & Sorensen 1984; Tesch 2003). Dormancy is also characterised by a cessation of feeding for yellow eel even if they are offered food (Nyman 1972). Including the Carlin tagging experiment, a total of 52 eels were weighed after recapture, from 385 to 1478 days after release. This gives a large sample of individual values of the SGR. In all cases but one, Carlin-tagged only, the SGR was negative, indicating weight loss (Fig. 8). In the literature, there are a few comparable long-term starvation studies on large silver eels. Boëtius & Boëtius (1985) starved female silver eels for up to 1000 days at 14 °C and found a SGR value of −8.4*10^{-4} ± 0.8*10^{-4}. Olivereau & Olivereau (1997) starved smaller silver eel over 600 days at seasonally varying temperature. They found an average value of SGR of −6.9*10^{-4} ± 0.5*10^{-4}. Starvation over shorter duration, between 4 and 6 months made with yellow eel, has been reported, for example, by Dave et al. (1975) and Caruso et al. (2010). Mann (1960) measured the weight loss of female silver eels over 4 months in freshwater. Those studies gave values of SGR between −12*10^{-4} and −63*10^{-4}. Figure 8 shows the range of SGR values found in the present study compared to the different literature values. There was no statistical difference in weight loss between the eels with DST implants and those with an external tag only, which indicates that the DST tagging did not prevent feeding or severely disrupt the physiology of the eels. Compared to all the literature values on starvation, the average relative rate of weight loss is significantly lower in the present experiment. The conclusion is that the eels must have been feeding at least during some period before the recapture. There is no correlation between SGR and the Pankhurst index at the time of tagging (adjusted R^2 < 0.05), so this seems to hold also for the silver eels in the study.

Change of behaviour before and after dormancy

There is a clear difference in depth preference between the dormancy period and the active spring and summer seasons, where the eel searches shallower and warmer water (Figs 4 and 5). During this period, the characteristic behaviour is excursions both up and down from a daytime resting level. The eels seldom approached the surface. The likely interpretation is that this is foraging behaviour, corroborating the assumption that the eels start feeding after the dormancy. That silver eels can change back to the yellow eel stage has been observed in other studies (Dollerup & Graver 1985; Acou et al. 2008; Durif et al. 2009).
In Sweden, lakes are an important habitat for eels, but there are few studies of depth preferences in lakes. In a single survey, Yokouchi et al. (2009) studied the distribution of yellow eel in Lough Ennell in the River Shannon system in Ireland and found an increasing catch per unit effort towards the deepest part of the lake (20–25 m). This is contrary to the distribution found in this study during the warm period of the year. The Lough Ennell study was made in August, and no data are presented about the temperature distribution and the variation of bottom substrate. Schulze et al. (2004) found the highest yellow eel abundance above the thermocline in a small German lake, with the highest concentration in the shallowest areas and with a preference for muddy substrate. In Lake Mälaren, it seems that the eel also prefers depths above the thermocline. A reason could be the prevalence of low oxygen levels in the bottom water in the summer. Soft bottom areas are abundant, but as there is no information on the position of the eels, their substrate preferences could not be investigated.

The switch to a higher frequency of large vertical excursions and movement close to or at the surface is similar to those seen for migrating silver eel in the Baltic (Westerberg et al. 2007). This possibly means that the eel resumes silver eel behaviour while searching for the outlet of the lake, albeit mostly without success.

**Perspectives**

Both yellow and silver eels are physiologically able to swim and be active during the whole winter (Westin & Nyman 1979; Westerberg et al. 2014). The likely explanation is that dormancy is a strategy to exploit the depressive effect of cold on the metabolic rate to save energy in a period of low-food availability (Walsh et al. 1983; Storey & Storey 2011).
A question raised by this study is why eels with external characteristics similar to migrating eels remain in and overwinter in the lake? Even though a larger proportion of eels were recaptured near the outlet than would have been expected from fishing pressure alone (Fig. 6 and Table 4), conspicuously many eels moved in opposite direction to the outlet. Evidently, the complex geography and the very low through flow in Lake Mälaren during the migration period preceding the start of dormancy (Figure S1) could make orientation difficult. This is in contrast to rivers and small lakes with a distinct flow directed towards the outlet (Haro 2003). In the latter cases, eels move more or less actively with the current (e.g., Völlestad et al. 1986; Behrmann-Godel & Eckmann 2003). It is desirable to make further studies on the migration behaviour in large lakes using telemetry tracking or other methods with a possibility to follow the position of the eels in sufficient detail.

An alternative explanation to the lack of escape from the lake is that the eels used in this study were predominantly of stocked origin and therefore lacked a necessary imprinting of the migration route (Westin 1998, 2003). This aspect is presently analysed and will be discussed elsewhere.

The focus of the present study is the dormancy period, but the DST data cover one to two whole years. The similarity of the results from the groups with implanted tags and those with only a small external tag suggests that implanted DST tags have a potential for long-term studies of eel behaviour. The rational for fitting the tags with floats was to make them buoyant so that they could be recovered if they became separated from the eel. In ocean migration studies, such tags have been recovered on shores and have provided useful information (Westerberg et al. 2014), but no floating tags were returned in the present study. This means that a smaller tag could be used which allows studies of yellow eel over extended periods and possibly reduces the problem with extrusion. A depth sensor more adapted to the depth in the lake should also allow a more detailed analysis of the behaviour. Future long-term studies should address several questions raised by the results of this study, such as, the behaviour in relation to final preferred temperature and the SGR of yellow and silver eel, respectively.

Acknowledgements

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The institutional and national guides for the care and use of laboratory animals were followed under permission from Centrala försöksdjursnämnden dnr 349-2008.

References


Supporting Information

Additional Supporting Information may be found in the online version of this article:
Figure S1. Discharge for Lake Mälaren.
Figure S2. Implant data storage tag.
Figure S3. Time line of periods of torpor longer than 5 days recorded during 2008–2009.
Figure S4. Recaptures of eels by year shown as percentage of all recaptures of Carlin tagged and DST tagged eels respectively.
Figure S5. Example of a DST tag where part of the floats has been extruded and where the eel was recaptured in a gillnet.
Table S1. Data for all eels tagged with data storage tags.
Table S2. Environmental conditions during the first and last torpor period longer than 5 days for all eels with data from the 2008–2009 winter period.
Table S3. Same as Table S2, but for the 2009 2010 winter period.
Table S4. Time weighted mean depth of dormancy periods for eels during the 2008–2009 period.
Table S5. As Table S4, but for the period 2009 2010.
Overwintering dormancy behaviour of the European eel (*Anguilla anguilla* L) in a large lake

Supporting information

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Study area and material and methods

Figure S1. Discharge for Lake Mälaren. Data from http://vattenweb.smhi.se/station/#516

**Specifications of the DST tag**

The overall length of the tag was 135 mm and the diameter 11 mm. The buoyancy corresponds to an upward force of approximately 1 g. They were programmed to record depth data every 30 seconds and temperature data every 120 seconds. The depth range, 1000 m, was intended for oceanic migration. The depth accuracy is 1 % of the total range, 10 m, and the resolution 0.3 m. Temperature range is -2 to 40 °C with ± 0.1 °C accuracy and 0.03°C resolution.

All tags showed an initial zero-point offset and a slow drift. The initial offset was read from the pressure reading at approximately 20 °C in air before the release. Correcting for this offset improved the accuracy to the order of magnitude of 1 m. The drift was estimated from the uncorrected values during long periods where the eel was assumed to be in torpor at the bottom. This drift was interpreted as a drift in offset rather than as a change in sensitivity and added to the initial zero offset correction.
For all tags the drift consistently increased the apparent pressure reading (mean 0.01392 m/day, standard deviation 0.00494. Maximum was 0.0245 and minimum 0.0067 m/day). A probable cause for the drift is that the urethane rubber covering of the pressure sensor in the tag slowly absorbed water, swelled and gradually increased the pressure on the sensor.

A period of torpor was defined as a period of at least 5 days duration where the vertical excursions of the eel were less than or equal to ± one least significant bit in the ADC conversion (corresponding to 0.5 m). This is the noise level expected from the digitization error alone. Additional pressure variations caused by changes in water level or atmospheric pressure (approximate amplitude 0.3 and 0.5 m respectively) were not accounted for so this definition of torpor is conservative.

Figure S2. Implanted data storage tag. The purpose of the floats is to make the tag buoyant so that it could be recovered after detachment from the eel and subsequent stranding on the coastline.
Morphological measurements

Table S1. Data for all eels tagged with data storage tags. The handling time is the total time under anaesthesia that was used to surgically implant the DST tag. Days of data shows the total period with pressure and temperature record from the eel at liberty. The pectoral fin index is as defined by Durif et al. (2005).

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Results

Figure S3. Time line of periods of torpor longer than 5 days recorded during 2008 to 2009. Each horizontal line corresponds to one individual eel (A03082 at the bottom to A03463 at the top, see Table 3).
Table S2. Environmental conditions during the first and last torpor period longer than 5 days for all eels with data from the 2008-2009 winter period.

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<td>10.25</td>
<td>-0.17</td>
<td>07/05/2009</td>
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<td>-0.14</td>
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<td>-0.20</td>
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<tr>
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<td>-0.11</td>
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</tr>
<tr>
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<td>23/10/2008</td>
<td>10.42</td>
<td>-0.13</td>
<td>20/05/2009</td>
<td>7.11</td>
<td>-0.04</td>
</tr>
<tr>
<td>A03452</td>
<td>26/11/2008</td>
<td>4.45</td>
<td>-0.10</td>
<td>26/04/2009</td>
<td>4.14</td>
<td>0.06</td>
</tr>
<tr>
<td>A03455</td>
<td>02/11/2008</td>
<td>7.76</td>
<td>-0.17</td>
<td>20/04/2009</td>
<td>5.36</td>
<td>0.09</td>
</tr>
<tr>
<td>A03459</td>
<td>28/10/2008</td>
<td>9.49</td>
<td>-0.16</td>
<td>14/04/2009</td>
<td>3.33</td>
<td>0.02</td>
</tr>
<tr>
<td>A03461</td>
<td>22/11/2008</td>
<td>5.45</td>
<td>-0.16</td>
<td>13/04/2009</td>
<td>4.35</td>
<td>0.08</td>
</tr>
<tr>
<td>A03463</td>
<td>30/09/2008</td>
<td>12.39</td>
<td>-0.25</td>
<td>25/04/2009</td>
<td>7.16</td>
<td>0.31</td>
</tr>
<tr>
<td>Mean</td>
<td>29/10/2008</td>
<td>9.10</td>
<td>-0.15</td>
<td>25/04/2009</td>
<td>5.15</td>
<td>0.08</td>
</tr>
</tbody>
</table>

| SD (days) | 17 | 2.39 | 0.05 | 12 | 1.42 | 0.13 |

Table S3. Same as Table S2, but for the 2009-2010 winter period.

<table>
<thead>
<tr>
<th>Tag #</th>
<th>start of first immobile period</th>
<th>temp at start</th>
<th>gradient grad/day</th>
<th>end of last immobile period</th>
<th>temp at end</th>
<th>gradient grad/day</th>
</tr>
</thead>
<tbody>
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<td>14/05/2010</td>
<td>8.15</td>
<td>0.13</td>
</tr>
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<td>-0.13</td>
<td>21/04/2010</td>
<td>2.76</td>
<td>0.05</td>
</tr>
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<td>-0.09</td>
<td>19/04/2010</td>
<td>2.64</td>
<td>0.01</td>
</tr>
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<td>-0.17</td>
<td>25/04/2010</td>
<td>3.69</td>
<td>0.08</td>
</tr>
<tr>
<td>Mean</td>
<td>08/11/2009</td>
<td>7.91</td>
<td>-0.11</td>
<td>27/04/2010</td>
<td>4.31</td>
<td>0.07</td>
</tr>
<tr>
<td>SD (days)</td>
<td>18</td>
<td>0.91</td>
<td>0.05</td>
<td>11</td>
<td>2.60</td>
<td>0.05</td>
</tr>
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</table>
Table S4. Time weighted mean depth of dormancy periods for eels during the 2008-2009 period.

<table>
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<th>Mean depth (m)</th>
<th>Max</th>
<th>Min</th>
</tr>
</thead>
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<td>12.1</td>
<td>10.5</td>
</tr>
<tr>
<td>A03084</td>
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</tr>
<tr>
<td>A03087</td>
<td>13.9</td>
<td>16.1</td>
<td>13.0</td>
</tr>
<tr>
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<td>7.9</td>
<td>8.5</td>
<td>7.6</td>
</tr>
<tr>
<td>A03092</td>
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<td>6.9</td>
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<td>6.9</td>
<td>8.1</td>
<td>5.8</td>
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</tr>
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<td>16.2</td>
<td>16.9</td>
<td>16.0</td>
</tr>
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<td>17.7</td>
<td>19.1</td>
<td>17.7</td>
</tr>
<tr>
<td>A03455</td>
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<td>13.3</td>
<td>10.8</td>
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<td>21.3</td>
<td>21.6</td>
<td>21.0</td>
</tr>
<tr>
<td>A03461</td>
<td>5.3</td>
<td>6.2</td>
<td>3.9</td>
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<tr>
<td>A03463</td>
<td>4.9</td>
<td>5.5</td>
<td>4.3</td>
</tr>
<tr>
<td>Mean</td>
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<td></td>
<td></td>
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<tr>
<td>SD (days)</td>
<td>8.9</td>
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<td></td>
</tr>
</tbody>
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Table S5. As Table S4, but for the period 2009-2010.

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<th>Mean depth (m)</th>
<th>Max</th>
<th>Min</th>
</tr>
</thead>
<tbody>
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<td>6.7</td>
<td>11.8</td>
<td>1.4</td>
</tr>
<tr>
<td>A03443</td>
<td>20.5</td>
<td>30.3</td>
<td>12.0</td>
</tr>
<tr>
<td>A03451</td>
<td>22.1</td>
<td>34.2</td>
<td>17.6</td>
</tr>
<tr>
<td>A03459</td>
<td>11.6</td>
<td>11.9</td>
<td>10.5</td>
</tr>
<tr>
<td>Mean</td>
<td>15.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SD (days)</td>
<td>7.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure S4. Recaptures of eels by year shown as percentage of all recaptures of Carlin tagged and DST tagged eels respectively. The DST tagged recaptures have been separated into whether part of the tag was extruded or not at recapture.

Figure S5. Example of a DST tag where part of the floats has been extruded and where the eel was recaptured in a gillnet.
On top a tagged silver eel released near Kråkelund in 2006.

Underneath shows two eels from the Lake Mälaren tagging. Above, a silver eel caught two years after release, still inside Lake Mälaren. The other eel is A799 (see more details in paper 2, figure 4).
Eels (Anguilla spp.) are in decline worldwide and the signs of a reduced recruitment have been observed in continental Europe ever since the early 1970s. In order to protect and recover the European eel stock, EU (the European Union) decided in 2007 to establish a recovery plan, aiming at protection and restoration. Stocking is, together with reduced fisheries and higher survival when passing hydro-electrical power plants, a measure accepted by the EU, and is today used by many European countries, according to their management plans. In the early 20th century eel stocking programs started in Sweden and in other countries around the Baltic Sea, and in Sweden the responsible authorities encouraged stocking activities already at the end of 19th century.

In this study, tagging experiments were conducted to follow eel migration from Lake Mälaren and at four sites along the Swedish east coast in the Baltic Sea. Recaptured tagged eels were retrieved from fishermen, allowing for the opportunity to investigate origin by otolith microchemistry and to discover morphological differences after tagging. Several changes took place; e.g. eye index increased while weight and condition decreased with migrated distance and time until recapture.

A majority of the tagged eels in Lake Mälaren did not migrate out through any of the outlets in the eastern part of the lake, irrespective of their origin. Most of them were caught in the opposite direction and continued to be caught in the lake 1-3 years after tagging, with significant weight losses. Overwintering is suggested to be a poorly chosen option, but it is uncertain whether this is a natural behaviour or a result of translocation and restocking.

For coastal eels, origin had no effect on the migration behaviour; a majority of the tagged eels migrated towards the outlet of the Baltic Sea. Interestingly, a minority of the recaptured eels originated from stocked fish. Instead, they were dominated by natural immigrants who had spent most of their lives in brackish waters.

**KEY WORDS** Anguilla anguilla, silver eel, Carlin tagging, stocking, otolith microchemistry, strontium
Stocking eels have been questioned by several researchers. Westin (2003) claimed that stocking programs just facilitate a fishery but do not increase the eel population since stocked eels lack behavioural cues making the adult silver eel unable to find the way back to their spawning grounds. The conclusion was based on tagging experiments which showed examples of deviant behaviour compared to earlier tagging. Stocked eels migrated in the wrong direction and with a high degree of overwintering (Westin 1990, 1998). However, the generality of these studies could be questioned. Particularly because of the geography since most of the eels were tagged and released at the Island of Gotland which is far from the mainland coast where earlier tagging were conducted, and partly since the experimental design also were different with long distance transports and several weeks of delay before release. All in all, the Gotland tagging gave very few recaptures in the sea compared to the conventional silver eel tagging in the Baltic Sea area gave over the years (Ask & Erichsen 1976). More recent experiments in a German river near the Baltic coast showed former stocked eels to have an initial delay to their migration and that recaptured eels decrease in body length and weight, which was attributed to the stocked origin (Prigge et al. 2013). The study, however, had no naturally immigrated controls for comparisons.

Since time immemorial humans have moved fish in general and perhaps eels in particular (Dekker & Beaulaton 2015). The economical value in combination with the fact that eel is a hardy species makes them suitable for stocking purposes. In Sweden the authority encouraged stocking activities already at the end of 19th century (Trybom 1893), and in the early 20th century eel stocking programs started in Sweden and other countries around the Baltic Sea (Sjöberg & Petersson 2005). Large amounts of eels have been stocked in freshwaters of Poland and Germany, and since 1910s more than a billion of small eels have been stocked in the Baltic Sea drainage area (Sjöberg & Peterson 2005, Dekker & Beaulaton 2015). Nowadays the eels stocked in Sweden are imported from England or France as glass eels. Before, also large quantities were translocated nationally as medium sized yellow eels (bootlace), for example from the Swedish West Coast to inland lakes (Holmgren & Wickström 1988).

For these reasons it is important:
• To furthermore investigate if stocked eels do migrate in the same way as natural ones and to determine where stockings are effective in increasing the spawning stock.
• To investigate how morphological characteristics, origin (stocked/natural) and growing area (coastal/lake) affect migration patterns.
• To examine how morphological characters change after tagging and during the migration as a way to predict/assess the chance of successful migration.

Based on an applied study on the outcome from stocking (Sjöberg et al. 2008), silver eels were caught in the autumn, both along the East Coast and in Lake Mälaren. They were tagged and released in direct connection to where they were fished. Life history (stocked or natural) was unknown beforehand but in contrast to earlier tagging experiments the recaptured eels were brought back from the fishery and analysed to determine the eel’s origin and to derive measurements of physical changes after migration (eye size, length and weight). From these parameters eye and condition index were estimated and together with length and weight correlated to the eel’s origin and migration behaviour.

Material and methods
STUDY AREA AND FISHERIES

The Baltic Sea is a 377 000 km² brackish sea in northern Europe, which drains through several narrow and shallow straits in the southwest via the Kattegat/Skagerrak into the North Sea and the Atlantic Ocean. The average depth of the Baltic is 62 m, with a maximum of 459 m. Most of the East Coast of Sweden is dominated by rocky shores and archipelagos, but towards the south there are more open and sandy shores. The salinity of surface waters varies from 1-5‰ in the north to 10-15‰ in the southern parts. Approximately 500 km³ of freshwater enters the Baltic annually and on average about the same amount of sea water comes in through the straits in the south (Elmgren & Hill 1997).

Lake Mälaren is the third largest lake in Sweden (1140 km²) and drains into the Baltic Sea via two sluices and one rapid in Stockholm city centre (latitude 59°20’N) and one sluice in Södertälje (latitude 59°11’N) 35 km south west of Stockholm. It is a shallow nutrient rich lake with an average depth of 13 meters. Maximum depth is 64 m and the lake spans 120 km from west to east near the outlet connection to the Baltic Sea. For the geographical distribution of the fishery and for a more detailed description of the lake, see Westerberg & Sjöberg (2014).

Eel occurs in many different coastal and inland habitats all over the Baltic area. Stock densities vary naturally as well as due to human activities (e.g. construction of migration obstacles and stockings of young eel). North of the release site Väddö (Figure 1),
the stock densities rapidly decline. Based on the onset of maturation to silver eel stage (starting from north in summertime and continuing during autumn further south) it is possible to judge when eels start to migrate toward the Baltic Sea outlet. An extensive fishing occurs from about 200 km north of Stockholm along the east coast of Sweden and at Danish coasts and in the straits between Denmark-Germany and Denmark-Sweden (the Öresund strait). Fishing gear used are large pound nets (Berntsson 1971). It is generally believed that the pound net fishery targets silver eel derived from all over the Baltic area and old tag experiments showed that the general direction from the eastern parts of the Baltic (Finland, Estonia and Latvia) was to migrate westerly across the Baltic towards the outlet straits (Määr 1947). Outside the Baltic outlet, north of the Öresund strait there is no fishery for silver eel.

**TAGGING AND RELEASE**

During the autumn of 2006 and 2008 silver eels (n=1197) were caught with pound nets at four different locations along the Swedish Baltic Sea coast and in Lake Mälaren (Figure 1, Table 1). Eels were classified as migrants after examining their external appearance. Length and weight were measured and the maturity of each eel was judged from the ratio between eye-area and body length (Pankhurst 1982) as

\[
EI = \frac{25\pi}{8TL} \left( (A + B)^2_R + (A + B)^2_L \right)
\]

where A and B are the horizontal and vertical eye diameters respectively, TL is the total length, and R and L are right and left eyes respectively. Pankhurst (1982) classified eels with an eye index larger than 6.5 as silver eels.

The condition index was calculated according to Fulton (1904) as

\[
CI = \frac{W}{L^3}
\]

where W=the weight of the fish, and L is the total length.

The eels were tagged with a Carlin dangler (a 18×4 mm plastic plate, cf. Carlin 1955, McFarlane et al. 1990) that was attached in front of the dorsal fin (Figure 1). As the Carlin tags were small, it was assumed that their influence on the large A. anguilla used was minimal (Jepsen et al. 2002). The fish were released at the site where they were captured. Each tag had a unique number and information about what to do with a recaptured eel (freeze the fish and contact the Swedish Board of Fisheries for further details, reward etc.). Information about the study was given to eel fishermen associations and in the trade press.

**RECAPTURES**

Eels were recaptured by Swedish and Danish fishermen and sent to the Institute of Freshwater Research. Measures were taken of eye diameter, total length and weight. Since the eels had been frozen before analyses, length and weight were corrected for shrinkage (Wickström 1986). Ear stones (otoliths) were used for aging and prepared for otolith microchemical analyses. The fat content was measured by the EC-method (Anon 1998), i.e. a solvent extraction-gravi-metric method. An eye index was used to decide
maturation stage according to Pankhurst (1982). The condition index was calculated according to Fulton (1904) and age readings were done by counting winter zones in the sagittae otolith (Svedäng et al. 1998). Prevalence and intensity of the infestation of the parasitic nematode Anguillicola crassus were determined according to methods described in Wickström et al. (1998). Migrated distance from place of release to recapture was measured as the shortest route in open water (ArcGis version 9.3). The migration speed was derived as the distance covered in km day⁻¹. In the Lake Mälaren experiment, eels captured were mainly, especially the first year, released again to have a second chance to find the outlet. After two winter seasons eels still caught were collected for dissection procedures as described above.

**PRESENTATION OF THE CHARACTERISTICS**

Table 4-7 describes four different characteristics (EI (eye index), CI (condition index), weight and length) in relation to time until recapture (Time) and migrated distance (Distance). We present results for these characteristics taken at tagging (Tag) and as a change from tagging until recapture. The Change is calculated as

\[
\text{Change} = \frac{(Tag - Rec)}{Tag}
\]

where Rec is the corresponding measurement taken after the recaptured eel have been collected from the fisher. Tag shows characteristics of recaptured eels as they were at the time of tagging. A difference for Tag indicates a predetermined difference and not influenced by e.g. the migration or tagging procedure. A difference for Change describes if the eels have changed individually during migration from tagging until recapture.

The calculations are presented with or without overwintered eels and the tagging inside Lake Mälaren (Table 4-7). This is to better understand the quite complex relationship that shows in the material of tagged eels.

**ANALYSIS OF SR/CA DATA FROM OTOLITHS**

The strontium (Sr) levels in the otoliths were determined with analysis made at Lund Nuclear Microprobe Laboratory, using particle induced X-ray emission spectrometry (μPIXE, Malmqvist et al. 1993).

Recaptured eels were divided into three different groups according to their origin and habitat preference based on the strontium level. The interpretation of data was based on a reference material of known origin (Tzeng et al. 1997). The decision that eels were of stocked origin was made according to Clevestam & Wickström (2008). Analysing Sr/Ca ratios with PIXE as in this case gives slightly higher values than from a electron microprobe (EMP), but the form of the transects are the same (Campana et al. 1997).

**EXAMPLES OF THE THREE TYPES ARE SHOWN IN FIGURE 2 A-D;**

- **SFW** – Stocked in fresh water. Eels have been stocked into freshwater at a small size, stayed there (Figure 2a) or migrated out to the coast later on (Figure 2b).
- **BW** – Brackish water. After arriving to Baltic Sea waters the eels have stayed in coastal areas (Figure 2c). In this group there are supposed to be a large majority of natural immigrants but there may also be some stocked eel, the ones stocked on the coast which we were not able to distinguish from the natural recruits.
- **BW & FW** – Brackish and Freshwater. After living their first years in a brackish environment they have migrated or been translocated into a freshwater lake (Figure 2d).

**STATISTICAL ANALYSIS**

Differences between means have been analysed using t-test (two samples) of least-square means from mixed linear models. If the data was not normally distributed, normality was achieved using log-transformation prior to analyses. In one-way models with heterogeneous variance multiplicity adjustments were done using Dunnett’s T3 method (Dunnett 1980), which is based on the studentized maximum modulus. The dependence of several variables on independent variables was analysed with mixed model covariance analyses; first release site and independent variable and the interaction was used, release site and interaction being random effects and the independent variable fixed effect. If the interaction was not significant it was removed from the model and analyses were run once more, with release site as random effect and the independent variable as fixed effect. The estimate of the slope from that model was used to illustrate the relation between dependent and independent variables. The dependence of binary responses (leaving or not leaving a lake) on various predictors (independent variables) was analysed using logistic regression. In order to compensate for over-dispersion the dispersion parameter was estimated by the Pearson χ² statistic divided by its degrees of freedom. All values are given as mean ± standard deviation, if not otherwise stated. Two-way frequency tables were analysed using Pearson’s χ²-test with Yate’s correction for continuity. For statistical analyses SAS statistical software is used.
Figure 2 a-d. Examples of strontium (Sr) level in the otoliths of recaptured eels representing: a. & b. stocked in freshwater (SFW), c. brackish water (BW), d. change between brackish- and freshwater (BW&FW). The central peaks of high Sr represents the larvae/glass eel stages before arriving at the European coasts. From these central parts Sr-levels are shown towards both edges, which represents the time of recapture. In each figure the analysed otolith is shown as a PIXE-map. In b. also the corresponding microscopic image is inserted.
Results

GENERAL CHARACTERISTICS

Out of 1197 *A. anguilla* tagged and released, 413 (34.5%) were reported recaptured (Table 2). For the taggings made on the coast the overall direction of movement was towards the outlet straits (Figure 3), as expected for silver eels on their way to spawning grounds. The fish were all caught along the Swedish and Danish shores, and none was recaptured in the Kattegat or Skagerrak as there are no fisheries for migrating eels north of the Öresund strait. Eels tagged at Marsö and Borgholm located near and inside Kalmar strait moved slower than eels from other coastal sites (Table 3).

A majority of the recaptures were made the same autumn the eels were tagged. However, some overwintering also occurred, especially in the Lake Mälaren where recaptured eels were found up till 4 years after release (Figure 4). The release site in Lake Mälaren was in the eastern half of the lake, but eels were recaptured predominately further inside the lake and in the opposite direction of the outlet (Figure 4).

When reports of tagged eels started to drop in from the western part of the lake, fishermen were asked to re-release the eels for the chance to investigate the continuation of their migration. As can be seen in Table 2 eels were re-released (denoted with r) the first three years, some were collected/killed (k) and 19 eels were recaptured more than two times. One eel was caught six times and after the last time collected for dissection procedures. Two eels were first captured about 40 kilometres westerly in the lake. After one and two overwintering seasons they were caught out on the coast 528 and 214 km from the release site respectively (Figure 4, ID A839 and A799). A839 lost 31% in weight after one year from tagging and was either naturally immigrated or stocked as a bootlace (type Figure 2d). A799 was of stocked origin (type Figure 2a) and had lost 17% of

![Figure 3. Map of the study area and site of the recaptures (filled circles) from the coastal taggings.](image-url)

Only one eel was caught north of the release site (north of Väddö) and that eel was released and caught again 4 months later but this time in the Sound between Denmark and Sweden.
In Lake Mälaren 58 eels were recaptured year 1 (2008). 13 of them were recaptured again (r13). 4 eels of the 58 were killed (k4) and sampled. The second year (2009) 54 other eels were recaptured. In addition, 27 were recaptured for more than one time (first years recaptures included, which means that when an eel recaptured and released in 2008 (from the 58) was recaptured again in 2009 the eel was included among those 27). This second year 17 eels were killed and collected for dissection. Third year (2010), 8 new eels were recaptured (never caught in year 1 or 2). 9 eels, already caught for one or several times in year 1, 2 (not 3 since all 17 were killed) were caught again and 17 eels were killed. Year four, four new eels were recaptured and killed and year five, one new eel was caught and brought in to lab.

Table 2. Number of eels used in the tagging experiment (Ntag). Number of eels recaptured for each year after release where the first (Nrec Year 1) is the same autumn when tagged and released.

<table>
<thead>
<tr>
<th>Year</th>
<th>Place</th>
<th>Ntag</th>
<th>Nrec Year 1</th>
<th>Nrec Year 2</th>
<th>Nrec Year 3</th>
<th>Nrec Year 4</th>
<th>Nrec Year 5</th>
<th>Nrec (%)</th>
</tr>
</thead>
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<td>Väddö</td>
<td>219</td>
<td>57</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>58 (20)</td>
</tr>
<tr>
<td>2008</td>
<td>Väddö</td>
<td>200</td>
<td>23</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>11 (5.5)</td>
</tr>
<tr>
<td>2008*</td>
<td>Mälaren</td>
<td>290</td>
<td>58 (r13, k4)</td>
<td>54 (r27, k17)</td>
<td>8 (r9, k17)</td>
<td>4 (r0, k4)</td>
<td>1 (r0, k1)</td>
<td>125 (43.1)</td>
</tr>
<tr>
<td>2006</td>
<td>Mårösö</td>
<td>208</td>
<td>209</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>110 (52.4)</td>
</tr>
<tr>
<td>2006</td>
<td>Borgholm</td>
<td>60</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>21 (33)</td>
</tr>
<tr>
<td>2006</td>
<td>Hanö</td>
<td>220</td>
<td>67</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>67 (30.5)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>1197</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>413 (34.5)</td>
</tr>
</tbody>
</table>

r=re-recaptured, k=killed

* In Lake Mälaren 58 eels were recaptured year 1 (2008). 13 of them were recaptured again (r13). 4 eels of the 58 were killed (k4) and sampled. The second year (2009) 54 other eels were recaptured. In addition, 27 were recaptured for more than one time first years recaptures included, which means that when an eel recaptured and released in 2008 (from the 58) was recaptured again in 2009 the eel was included among those 27. This second year 17 eels were killed and collected for dissection. Third year (2010), 8 new eels were recaptured (never caught in year 1 or 2). 9 eels, already caught for one or several times in year 1, 2 (not 3 since all 17 were killed) were caught again and 17 eels were killed. Year four, four new eels were recaptured and killed and year five, one new eel was caught and brought in to lab.

Table 3. Recaptured eels (Nrec) and measurements after recapture. Mean ±s.D for age, fat (F), Total length (LT), Total weight (MT), Eye index (EI), Condition index (CI), Migrated distance (MD) and Migration speed (MS) only from first year of migration. In addition, the different origins and/or grown up habitats based on otolith analyses; Brackish water (BW), stocked in freshwater SFW and mix in between (BW-FW). Note the number of eels analyzed for each site is within parenthesis (n) since not all recaptures were able to be collected and analyzed.

<table>
<thead>
<tr>
<th>Year</th>
<th>Place</th>
<th>Nrec</th>
<th>Age (years)</th>
<th>F (%)</th>
<th>LT (mm)</th>
<th>MT (g)</th>
<th>EI (n)</th>
<th>CI (n)</th>
<th>MD (km)</th>
<th>MS (km/d)</th>
<th>BW (%)</th>
<th>SFW (%)</th>
<th>BW-FW (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>Väddö</td>
<td>58</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td>Väddö</td>
<td>33</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
<tr>
<td>2008*</td>
<td>Mälaren</td>
<td>125</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>Mårösö</td>
<td>109</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>Borgholm</td>
<td>60</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>Hanö</td>
<td>67</td>
<td>17.3 ±2.0 (31)</td>
<td>28.4 ±2.9 (26) ++</td>
<td>763 ±58 (36)</td>
<td>787 ±223 (37)</td>
<td>8.3 ±1.4 (35)</td>
<td>0.18 ±0.02 (56)</td>
<td>85 ±129 (58)</td>
<td>12.7 ±4.8 (57)</td>
<td>92 (45)</td>
<td>8 (4)</td>
<td></td>
</tr>
</tbody>
</table>

++ based on earlier samples from 2005. *Values used are from last recapture when eels were recaptured more than once.

Figure 4. Map of the release site and positions of the recaptures in Lake Mälaren. The smaller map in the right corner shows recaptures outside the lake, along the coast and in the Danish straits.
### Table 4. Eye measurements versus time – and distance from tagging until recapture for all six tag experiments.
The first variable in the top row is the predictor (independent variable) and the second is the response variable. The release site is a random class variable in all cases. EI-tag is the measurements of the eye index taken at tagging. EI-change is the individual change from tagging to recapture, calculated as (EI-tag - EI-rec/EI-tag) where EI-rec is the corresponding measure at recapture. Eye measurement was not taken from Borgholm 2006 during the tagging procedure. Since overwintering did affect the level of significance there is one line showing result with them excluded concerning recaptured eels.

<table>
<thead>
<tr>
<th>Statistics presented</th>
<th>CI-tag vs Time</th>
<th>CI-tag vs Distance</th>
<th>Distance vs CI-change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>slope p-value</td>
<td>0.11</td>
<td>-0.24</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.71</td>
<td>0.040</td>
</tr>
<tr>
<td>Overwintering eels excluded</td>
<td>slope p-value</td>
<td>0.000005</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.99</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Lake Mälaren excluded</td>
<td>slope p-value</td>
<td>0.0002</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.19</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

### Table 5. Condition index versus time – and distance from tagging until recapture for all six tag experiments. The first variable in the top row is the predictor (independent variable) and the second is the response variable. The release site is a random class variable in all cases. CI-tag is the measurements of the condition index taken at tagging. CI-change is the individual change from tagging to recapture, calculated as (CI-tag - CI-rec/CI-tag) where CI-rec is the corresponding measure after recapture. Since overwintering did affect the level of significance there is one line showing result with them excluded concerning recaptured eels.

<table>
<thead>
<tr>
<th>Statistics presented</th>
<th>Weight-tag vs Time</th>
<th>Weight-tag vs Distance</th>
<th>Distance vs Weight-change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>slope p-value</td>
<td>-0.000003</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.46</td>
<td>273</td>
</tr>
<tr>
<td>Overwintering eels excluded</td>
<td>slope p-value</td>
<td>-0.000005</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.27</td>
<td>0.041</td>
</tr>
<tr>
<td>Lake Mälaren excluded</td>
<td>slope p-value</td>
<td>0.000004</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.68</td>
<td>0.0007</td>
</tr>
<tr>
<td>Lake Mälaren only</td>
<td>slope p-value</td>
<td>-0.000004</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.56</td>
<td>0.0009</td>
</tr>
</tbody>
</table>

### Table 6. Weight versus time – and distance from tagging until recapture for all six tag experiments. The first variable in the top row is the predictor (independent variable) and the second is the response variable. The release site is a random class variable in all cases. Weight-tag is the measurements of the condition index taken at tagging. Weight-change is the individual change from tagging to recapture, calculated as (Weight-tag - Weight-rec/Weight-tag) where Weight-rec is the corresponding measure after recapture. Since overwintering did affect the level of significance there is one line showing result with them excluded concerning recaptured eels.

<table>
<thead>
<tr>
<th>Statistics presented</th>
<th>Length-tag vs Time</th>
<th>Length-tag vs Distance</th>
<th>Distance vs Length-change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>slope p-value</td>
<td>-0.000007</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.49</td>
<td>0.0063</td>
</tr>
<tr>
<td>Overwintering eels excluded</td>
<td>slope p-value</td>
<td>-0.000001</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.52</td>
<td>0.045</td>
</tr>
<tr>
<td>Lake Mälaren excluded</td>
<td>slope p-value</td>
<td>0.000028</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.56</td>
<td>0.0007</td>
</tr>
<tr>
<td>Lake Mälaren only</td>
<td>slope p-value</td>
<td>-0.000030</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.12</td>
<td>0.010</td>
</tr>
</tbody>
</table>
its body weight at the time of recapture, almost two years after tagging.

Overwintering was also seen in some of the eels tagged at the northernmost area (Väddö), located reasonably close to Lake Mälaren. One eel from the tagging in 2006 and 10 eels in 2008 overwintered (Table 2). One of the overwintered eels (2008) was caught 26 km north of the release site in July and then again caught 4 months later. This time around 800 km further south near the Danish island Mön with a 19% decrease in body weight (origin unknown).

Results from the coastal tagging show that fat content was positively correlated to eel length (p=0.022, slope=0.0052, t=2.31, n=218) and weight (p=0.0054, slope=0.0023, t=2.81, n=218). Fat content did not correlate to migrated distance, condition index or time until recapture (p>0.15 in all cases, place of release included as random factor). In Lake Mälaren the recaptures were not measured for fat content (numbers in Table 3 are from a reference material).

Concerning the parasitic nematode Anguillicola, there were no differences between infected and non-infected eels due to size or condition (p>0.12 in all cases, place of release was included as random factor). Among the infected fish, there was no correlation between the intensity (number of worms per eel) and size or condition. (p>0.33 in all cases, place of release included as random factor).

Figure 5. Predicted probability for eels tagged in Lake Mälaren to migrate out of the lake; two predictors were used in the logistic regression: condition index (Wald $\chi^2=6.42$, p=0.0113) and eye index (Wald $\chi^2=1.87$, p=0.172). Eels with higher condition index have an increased possibility to reach the coastal areas. The dotted lines indicate the condition index needed for 50% probability of leaving the lake according the logistic regression model.

THE DEVELOPMENT OF EELS DURING MIGRATION

Eye index

There was no correlation between either time until recapture and migrated distance with eye size measured at tagging (Table 4, EI-tag vs Time and EI-tag vs Distance). Eyes of recaptured eels had increased in size with migrated distance and also with time to recapture but only if overwintered eels were excluded (Table 4, EI-change vs Time and EI-change vs Distance).

Condition index

The condition index decreased while migrating (Table 5, CI-change vs Time). It also decreased with migrated distance if overwintered eels or eels from Lake Mälaren (Stallarholmen) are excluded (Table 5, CI-change vs Distance). That is because overwintered eels had totally stopped their movement/migrated distance.

In Lake Mälaren just a few eels were recaptured towards the outlet or outside the lake (Figure 4). Nevertheless, a logistic regression using eye index and condition index at time of tagging showed that the probability for leaving the lake increased with higher condition index (Figure 5). Based on this analysis we estimated that eels from Lake Mälaren had a 50% probability to leave the lake when the condition index was 0.265, but at average condition index (0.20, see Table 1) the probability of leaving the lake was just 5% during the study period (2008–2012; no recaptures in 2013 and 2014).

Weight and length

Weight decreased with distance migrated (except for Lake Mälaren) and time until recapture (Table 6, weight-change vs distance/time). In Lake Mälaren most of the eels were caught inside the lake and consequently had not migrated any significant distance when recaptured, resulting in non-significant relationship between weight-change vs distance (Table 6).

Not surprisingly, there is no change in length while migrating. But notable, smaller eels seem to reach longer distances before being recaptured (Table 6 and 7, Length/weight-tag vs Distance).
In total, 32 eels were dissected including analysing the otoliths (age reading and Sr-level). Half of them seem to have been stocked as imported elvers (type as in Figure 2a) and the remaining had the type described in Figure 2d, which is either stocked as translocated bootlace from the Swedish West Coast or had immigrated naturally. There were no differences between these two groups concerning eye index, length, weight or condition index (0.32 < p < 0.60 n=32). The infestation rate of the parasitic nematode *Anguillicola crassus* (infesting the swimbladder) was about 70% and both groups were about the same age, 17.4 for translocated/natural and 17.2 for stocked (conf. limits 16.3-18.4 and 16.1-18.3 respectively). Out of those 32 dissected fish there were just four which were recaptured outside the lake, three from the type translocated/natural and one stocked as elver. This is too few individuals for statistical analysis.

**Overwintering**

The condition index and weight decreased after tagging (i.e. during migration) and this result became even stronger when overwintered eels were included (Table 5 and 6). In contrast the eye index increase, but this was only significant when overwintered fish were excluded (Table 4). In Lake Mälaren 67 of the 125 recaptured eels overwintered one or several seasons (Table 2). The eye index did not change after tagging for Lake Mälaren eels (Table 4). The weight loss was 11.5% on average and the decrease is significantly correlated with time after tagging (Figure 6). One could expect overwintered eels to gain weight during summer and autumn. However, there was no seasonal difference between eels recaptured in spring compared with those caught later in the season (Figure 6; p=0.27 n=12 (springtime) and n=35 (summer and autumn combined).

In addition, overwintering was substantial from the coastal tagging at Väddö in 2008. Ten out of 33 recaptures were made the following autumn, in 2009 (missing data from one of the recaptures). These overwintered eels showed similar results as those in Lake Mälaren. They also lost weight (on average 10.5%) and the weight loss increased significantly over time (Figure 7). In addition, the condition index
was lower at time of tagging (CI-tag) for eels recaptured after long time (p<0.05, slope=-2.10, t=-2.05, n=33), indicating that eel which later on will overwinter already from start had lower condition index. The increasing eye size seemed to be triggered by the migration distance but ceased if the fish overwintered (Table 4). Consequently, the overwintered eels did not differ from not overwintering eels in terms of their eye size (p=0.79 n=9 (overwintering) and n=24 (not overwintering)).

The origin of the overwintered fish from Lake Mälaren was evenly distributed between the two groups viewed in Figure 2a and 2d (14 stocked as elvers and 13 translocated/natural). There were more recaptures from the stocked than translocated/natural in 2010 (9 to 6) which was the last year of recaptures. However, the overall distribution between years for overwintered eels was not significantly different (χ²-test, p=0.34, n=27), presumably since the number of eels/recaptures per year was low.

Among the 213 coastal recaptures 8 of the 11 overwintered eels were analysed according to origin by otolith chemistry. Six had grown up in brackish water (type as in Figure 2c), one had been stocked as an elver in freshwater (Figure 2b), and the last one stocked as a boylace or is a natural immigrant to freshwater (Figure 2d).

Discussion

MATURATION PROCESS

In the Baltic Sea it is possible to follow the eel during such a long time and for a long distance since the fishery is situated all the way along the coastline. This in turn allows researchers to study migration behaviour, routes taken and effects on physiological characteristics and possible changes during this first step of the journey back to the spawning grounds. This study shows how the development of the eel seems to be a continuous process and therefore also a response to the new environment, i.e. not only a preparation before leaving which has been stated earlier (Hain 1975). On the coast eye size increases while eels are actively migrating. It seems to be the migration as such which causes increased eye index, since when the overwintered eels are included in the analysis this increase had stopped and the same holds for the delayed eels from Lake Mälaren (Table 4). However, this is not consistent with earlier findings showing eye diameter to increase during migration in just freshwater (Palstra & Thillart 2010). But notable, eye size was relatively large from start in the lake (Table 1), but these eels were also older (Table 3) and age-dependent maturation has been suggested as a key factor for successful maturation (Palstra &Thillart 2010). We can conclude that even if the eels in Lake Mälaren still continue some of their migrating activity (Westerberg & Sjöberg 2014) these unsuccessful eels had ceased the silvering process and this also seems to apply to the overwintered eels on the coast.

An eye size index is used to distinguish between silver eels and stationary yellow eels (Pankhurst 1982). However, in this study the eye size indices of eels from the lake and at the coast indicate that it might be difficult to separate eels based on this metric. Apparently there were not any clear limits in size; there seems to be eels with relatively small eyes that still migrate with good speed towards the Baltic outlet while others do not, even though they to the exterior look like silver eels, and there is no correlation between eye index at tagging and migrated distance (Table 4, EI-tag vs Distance). Thus, eye and also the condition index will just give guidance but are still a preferably indicator compared to subjective alternatives like color shifts (silverness) and more or less developed neuromasts (lateral line system). Unfortunately, measurements of pectoral fins were not included in our dissection procedures at this time and by that no calculation of the more recent silver index according to Durif could be made (Durif et al. 2005).

EEL-SIZE AND CATCHABILITY

Our results indicate that smaller eels are recaptured after longer migrated distance (Table 6 and 7). The amount of observed variance explained is low. This is, however, an interesting result if the fact that in the Swedish fishery eels are smaller towards the outlet of the Baltic Sea is regarded. The generally accepted explanation is that larger and older eels are coming from north and waters with relatively low productivity, whereas the eels from the southern and more productive water are smaller. This is consistent with the result from the southernmost place (Hanö in Table 3). However, based on the correlation between length/weight and migrated distance it seems that the migration behaviour could be connected to size of the eel. Are larger eels migrating closer to the shore? This explanation is comparable with the one that eels more infested by parasites were more easily caught (Sjöberg et al. 2009). However, there is no correlation between eel size and prevalence or infestation of the swimbladder nematode Anguillicola crassus. In addition, there is no indication that fishermen release smaller eels of some reason and furthermore, most eels are larger than the minimum according to the legislation and smaller eels maintain
the same market value per kilogram. We suggest the explanation that the equipment used in the silver eel fishery, the large pound nets, are size selective and more easily trap larger eels.

**ORIGIN**

The otolith chemistry data indicated that an overwhelming majority of the recaptured eels had inhabited brackish waters and that only 10% derived from freshwater. Such a low contribution from freshwater areas has also been noted by Tsukamoto *et al.* (1998) who concluded that eels are facultative catadromous. In addition, the low proportion of freshwater eels found in this study may mirror a situation with relatively low natural immigration, enough habitats in estuaries and effective migration barriers excluding eels from many heavily modified freshwater areas.

Earlier investigations show that the share of stocked eels in the outlet Öresund strait are around 20–30% (Limburg *et al.* 2003, Clevestam & Wickström 2008), compared to 10% in this study. This difference could be partly explained by a general decrease in stocking activity, but also by how the stocked eels are distributed. When taking samples in the outlet straits it is reasonable to believe that the majority part derives from freshwater areas of Poland and Germany since they stand for most of stocking in the Baltic Sea drainage area (Westerberg & Wickström 2015).

Unfortunately, we cannot distinguish the fraction of eels stocked at the coast among the recaptures since they have a similar otolith microchemical signature as natural recruits (see Figure 2c). However, coastal stocked eel seem to constitute a very small fraction of the coastal population (Clevestam & Wickström 2008, National eel stocking database [kept at SLU Aqua]). In the future all stocked eels (coastal or freshwater) will be possible to distinguish from natural immigrants because since 2009 all Swedish and Finnish elvers are chemically marked before release (Wickström & Sjöberg 2013). Moreover, it is highly desirable to have all stocked eels marked in a similar way and with opportunity to distinguish also national origin, not just in the Baltic but in all countries using the European eel for stocking purposes. This will be a good way to evaluate the stocking programs and also to provide better knowledge for future eel management plans.

**OVERWINTERING**

Westin (1998) showed that many stocked eels from Gotland overwintered and a similar effect was indicated in our study. One explanation for such behaviour might be that eels delayed their migration and stayed another winter as a strategy to increase energy for the consuming journey (Svedäng & Wickström 1997) but our study actually showed an opposite effect. Even if a true starvation gives greater weight loss and the eels in Lake Mälaren seem to feed after waking up from dormancy (Westerberg & Sjöberg 2014), this weight decrease is substantial and many of the eels were caught late in the following seasons which should have enabled them to regain weight. In other words, they did not seem to recover body mass.

The same results could be seen in 16 recaptured eels from a German tag experiment (Prigge *et al.* 2013) which also found a decrease in body length. However, the length decrease in that study was most likely an effect of freezing shrinkage. However, our study did compensate for that and found no such connection (Table 7).

One obvious question is whether the difficulty to find the outlet from Lake Mälaren reflects the normal situation before 1960s–1970s when the stocking programs started and the fishery became more intense (Rundberg 1968). There are indications that this is the case, as because there has been no extensive eel fishery in or near the outlet of the lake, at least not in modern times. The fishery is instead located westerly from the release site and the recaptures in Lake Mälaren do quite well reflect the geographic distribution of the large pound nets inside the lake (Westerberg & Sjöberg 2014). Furthermore, it seems to be a random autumn wandering where eels are recaptured several kilometres in the wrong direction than toward the exit, several years after release. On the other hand, higher condition increases chance to reach out of the lake. This suggests that it is not a coincidence which eels eventually succeed to fulfill their spawning migration. Consequently, eels with higher condition index would be the ones most advanced in their metamorphosis (from physical aspect not covered in this study) and therefore has some sort of advantage in finding the exit. A possible interpretation is that eels in Lake Mälaren are not allowed to mature enough to really decide to leave because of the extensive fishing. Instead the eel get caught, often several times, which may interfere with physical development and the ability to migrate, resulting in a decreased condition and a potential hindering of the metamorphic mechanism.

An initial delay among migrating eels has also been identified and discussed earlier (Crook *et al.* 2014, Westerberg *et al.* 2014). One complicating matter is that eel having spent all their lives at the coast – which means they most likely are of natural origin – also chose to overwinter (Våddö in 2008). Overwintering has previously been shown to increase with latitude for site of release (more frequent up
north) and is 2.2% based on total amount of earlier taggings made in the Baltic Sea (Sjöberg & Petersson 2005). The variable and lack of clear cut salinity gradients in the Baltic, especially up north, may complicate the migration and result in overwintering, since salinity seems to be a factor for the positive rheotaxis of migration of silver eels (Hain 1975). In addition, the further from the Baltic outlet the migration begins the greater risk that the eels experience a multitude of disturbances hindering a continued migration. In our experiments the handling procedure (fishing and tagging) is a distraction in itself. Other anthropogenic stressors and obstacles such as electric cables, sound and light from bridges and wind mills, different discharges as cooling water or effluents from paper mills could all end up in undesirable overwintering. Consequently these disturbances increase with migrated distance, i.e. with latitude of release site, regardless of origin.

The condition index seems to play a central role for eel migration behaviour. In Lake Mälaren eels with higher condition had a higher probability of migrating (Figure 5), and eels from the northern release site Väddö (who had a lower condition from start) more often chose to stay another winter with further decreased condition). Altogether, higher condition seems to trigger or being a prerequisite for a more targeted migration without overwintering.

**Conclusions**

This study provides a deeper understanding concerning migration of stocked eels and show there are large concerns, in terms of the ability of eels to find their way out of a lake, as well as the conceivable delays of this migration.

There is a risk associated with judging stocked eels potential migration success based on just tagging result, because this method gives an artificial view of the migration behaviour not telling the fact of unaffected eel migration behaviour. However, the majority of silver eel taggings in the Baltic Sea have resulted in recaptured eels in expected direction and with expected speed. In addition, a study on the Swedish West Coast gave substantial migratory behavioral information using data storage tags in spite of relatively rough handling procedures (Westerberg et al. 2014). It still remains to repeat the same investigation with eels from the Baltic Sea, where eels of known origin are traced long distances, especially since large amounts of former stocked eels nowadays are trapped in lakes and transported around hydro-power plants and released on the East Coast, without monitoring.

It is obvious that eels from Lake Mälaren have huge problem finding the outlet. Once they found their way out they have lost a lot of weight. Therefore it seems to be an unsafe choice to use Lake Mälaren for stocking purposes. Future studies will tell if it is feasible to use trap and transport to bypass the problem or if the eel at reduced fishing pressure may have the chance to increase their condition and migrate out by themselves. Perhaps the weight decrease may not be associated with a migration failure but instead be a result of the maturation process where e.g. muscle is converted into fat. The exact relationship between condition indices and body composition of eels should also be further investigated.

The proportion of natural to stocked eel is unknown and the need to answer the question is becoming outdated since the translocation of west coast eel has stopped (and time will tell). In the present situation, where the focus is to support the eel stock rather than fishery, the advice and conclusion is that west coast eel have a better opportunity to increase the eel population by determining their growing areas themselves. If stocking imported elvers it seems preferably to stock them at the West Coast where they have the opportunity to migrate to inland waters and the Baltic Sea if needed.

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INTRODUCTION

The dramatic decrease in recruitment of the European eel, *Anguilla anguilla* L., during the last 30 yr (Dekker 1998, 2008, ICES 2011a) has motivated the European Union (EU) to introduce a regulation establishing measures for the recovery of the stock (Council Regulation No. 1100/2007). This regulation requires the member states to prepare eel management plans (EMPs) for all eel habitats. The objective of each EMP as stated in Article 2 of the regulation is to reduce anthropogenic mortalities 'so as to permit with high probability the escapement to the sea of at least 40% of the biomass of silver eel relative to the best estimate of escapement that would have existed if no anthropogenic influences would have impacted...

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**ABSTRACT:** One objection to the stocking of translocated eels as a management measure for the European eel, *Anguilla anguilla* L., is that these eels may lack the ability to find their way back to the spawning area in the Sargasso Sea because the translocation will confuse their imprinted navigation. We undertook a series of tagging experiments using satellite tags, data storage tags and acoustic tags to test the hypothesis that eels translocated 1200 km from the UK to Sweden differed in their ability to migrate compared to naturally recruited eels. Eels to be tagged were caught in 2 locations, one with a record of eel stocking for more than 20 yr and with a series of barriers to upstream migration and another in a river with only natural immigration and without barriers to upstream migration. In the first year, the naturally recruited and stocked eels were released in a fjord where the initial escapement behaviour could be monitored by acoustic tagging in addition to using archival tags to track the subsequent marine migration. In the second year, eels were tagged with archival or satellite tags and released on the open coast, and only their marine migration was investigated. Eels were tracked more than 2000 km along a route that, after leaving the Skagerrak, followed the Norwegian Trench to the Norwegian Sea, turned south and west along the Faroe-Shetland channel before emerging into the Atlantic Ocean, and then continued west. There were no statistically significant differences in estuarine or oceanic behaviour regarding route, swimming speed and preferred swimming depth between stocked and naturally recruited eels. These results provide the first empirical evidence of a Nordic migration route and do not support the hypothesis that a sequential imprinting of the route during immigration is necessary for adequate orientation or behaviour during the adult spawning migration.

**KEY WORDS:** Eel management plan · *Anguilla anguilla* · Translocation · North Atlantic · Electronic tags
INTRODUCTION

The dramatic decrease in recruitment of the European eel Anguilla anguilla L. during the last 30 yr (Dekker 1998, 2008, ICES 2011a) has motivated the European Union (EU) to introduce a regulation establishing measures for the recovery of the stock (Council Regulation No. 1100/2007). This regulation requires the member states to prepare eel management plans (EMPs) for all eel habitats. The objective of each EMP as stated in Article 2 of the regulation is to reduce anthropogenic mortalities ‘so as to permit with high probability the escapement to the sea of at least 40% of the biomass of silver eel relative to the best estimate of escapement that would have existed if no anthropogenic influences would have impacted...”
the stock’. The regulation lists some possible management measures that could be used in an EMP, including the trapping and transport (hereafter termed ‘stocking’) of surplus glass eels from one EU country to another.

Stocking has taken place for more than a century with the goal of increasing the yield of local fisheries. As such, several studies document the survival of stocked eels during their growth stage (Wickström et al. 1996, Huertas & Cerdà 2006) and the effects of stocking on the output of the fishery (EIFAC 1982, Rosell et al. 2005). In general, stocking has a beneficial effect on fishery yields, and it seems reasonable to conclude that stocking, in combination with greater control of fishing activity, could lead to higher silver eel escapement values.

In previous years, stocking has been considered problematic on several accounts, e.g. risk of spreading of disease and loss of genetic variation because of geographically differentiated gene expression (Pujo lar et al. 2006, Als et al. 2011). Crucially, the ability of stocked eels to migrate back to their natal spawning area has been questioned, primarily based on a series of tagging experiments in the Baltic that aimed to examine the effect of stocking on migration success (Westin 1990, 1998, 2003). These studies concluded that stocked eels lacked the orientation mechanism necessary to locate the outlet to the Baltic Sea and, consequently, that their contribution to recruitment is null. More recent experiments in a German river at the Baltic coast have shown that stocked eels also have an initial delay to their migration, which was attributed to their stocked origin (Prigge et al. 2013). The underlying assumption of these studies is that larval eels imprint the migration route from the Sargasso Sea to their growth habitat, possibly using a magnetic map (Svedäng & Gipperth 2012), and then retrace this route when returning to spawn as adults. Eels that either do not have the full route imprinted on them or have a different route imprinted than the one they should take are assumed to have no value to the spawning stock. To date, however, no studies have been undertaken to examine this hypothesis.

Despite the criticism and uncertainty, stocking has become a major, if not the primary, measure in many national EMPs because it allows compliance with eel regulation targets without severe cuts in fishing effort or changes in catchment management. The advice from ICES is that ‘When stocking to maximize output from the limited supply of glass eel currently available, an estimation of the prospective net benefit to silver eel escapement, to the extent possible, should be made prior to translocation for stocking’ (ICES 2011b, p. 3). In Sweden in particular, stocking of glass eels (typically from the River Severn in England) has been used for many years in many rivers to help increase fisheries yield, and stocking efforts are well documented in a national database. Consequently, it is possible to identify rivers that are populated with predominantly stocked or naturally recruited eels and, therefore, to test the hypothesis that translocated and stocked eels differ from naturally recruited eels in their ability to navigate and migrate. Here, we describe the results of a 2 yr telemetry study of the marine migratory behaviour of eels originating from stocked and unstocked rivers and present the evidence for differences in migration route and speed between them. Additional tables (S1–S5) and a figure (S1) that are related to material, methods and acoustic tagging data are provided in the Supplement at www.int-res.com/articles/suppl/m496p145_supp.pdf

MATERIALS AND METHODS

Origin of eels

Stocking is widespread and not always well documented. The tendency for eels to disperse and the long period of time between stocking and subsequent silver eel escapement makes it almost impossible to find with certainty silver eels that are of stocked or naturally recruited origin. However, all eel stocking that has been undertaken in Sweden using government funding or as part of a license condition for a hydroelectric power plant is registered in a central database, thus providing a guide to those rivers likely to be dominated by stocked eels. We selected silver eels from 2 locations in that database, the River Enningdal and the River Ätran (Fig. 1). The Enningdal represented a river that in all likelihood contained only eels that were naturally recruited. This is because the river has no barriers to upstream migration, and there are no records of stocking into this river. In addition, the commercial eel fishery in this area is limited, making unreported, illegal stocking very unlikely (P. O. Wahrnberg pers. comm.). The risk of contamination by stocked eels at this locality was therefore considered extremely low. Eels from this river were captured in a silver eel trap in the commercial fishery in Kynne älv in the River Enningdal drainage area. In contrast, the River Ätran has been heavily stocked since 1983 as a compensation
for the removal of eel ladders at hydroelectric dams. The capture site was at the outlet from Lake Fegen, upstream of 7 dams, where since 1990 all officially recorded stocking has been made using from 2000 to 10 000 imported and quarantined glass eels per year from the River Severn in England (Thörne & Carlsson 2004). However, approximately 6000 bootlace eels, caught somewhere on the Swedish west coast (i.e. stocked origin but short transfer), were stocked in Lake Fegen in 1988 and 1989 (Thörne & Carlsson 2004), and some private and unrecorded stocking of approximately 200 bootlace eels, also caught on the Swedish west coast, is known to have taken place in a lake connected to Lake Fegen each year since 2000 (I. Alenäs pers. comm.). Thus, while there was a possibility that a minority of eels in the River Åtran would originate from Skagerrak or Kattegatt, all eels captured in this river were of stocked origin, and the majority were translocated as glass eels. Eels from this river were caught in a Wolf trap in Mölneby, near the outlet of Lake Fegen, approximately 80 km from the river mouth.

To validate the origin of eels in these rivers, 10 reference eels from each capture location were sacrificed, and their otoliths were removed. Age readings were undertaken by counting winter zones in the otoliths (Svedäng et al. 1998). The ages varied between 15 and 21 yr for the Enningdal eels and between 15 and 22 yr for the Åtran eels. The strontium:calcium ratio of one of the otoliths from each eel was analysed using particle-induced X-ray emission spectrometry (µPIXE, Malmqvist et al. 1993) at the Lund Nuclear Microprobe Laboratory. The analysis showed that all 10 of the individuals from Enningdal
had spent time in salt and brackish water as juveniles (i.e. were of naturally recruited origin), while 8 of the Åtran eels had been transferred directly to freshwater as glass eels (i.e. were of stocked origin). By back-calculating from the ages of the sampled eels, the corresponding period of stocking was found to have been between 1988 and 1997, during which time 80 000 glass eels and 8000 bootlace eels (equivalent to approximately 18 000 glass eels if the mortality until the age of stocking is taken into account, Dekker 2012) were stocked. The expected proportion of eels stocked as glass eels was therefore 82%, which agrees with the analysis of the otoliths.

### Eel tagging and release

Captured eels (minimum 75 cm) that were classified as silver eels were sorted and accumulated up to 3 wk prior to tagging in each of the 2 study systems. From these, a subset of 99 silver eels was selected to be tagged during the 2 yr of the experiment (Table 1). All eels were large females. The overall means and standard deviations of length were 881 ± 55 mm for River Enningdal eels and 940 ± 80 mm for Enningdal eels (2-way ANOVA, site effect, $F_{1,95} = 18.6, p < 0.05$, Table S1 in the Supplement at www.int-res.com/articles/suppl/m496p145_suppl.pdf). However, the average length or weight of tagged eels did not differ significantly between the capture sites within each year (2-way ANOVA, year × site interaction, $F_{1,95} = 3.7$ for length and $F_{1,95} = 1.01$ for weight, $p > 0.05$ in both cases, Table S1 in the Supplement). The maturity of each eel was judged by 2 indices, the ratio between eye area and body length (BL) (Pankhurst 1982) and the ratio between the length of the pectoral fin and BL (Durif et al. 2005). According to those indices, all eels were in the silver eel stage. The mean Pankhurst index of the Enningdal and Åtran eels did not differ significantly within each year (2-way ANOVA, year × site interaction, $F_{1,95} = 0.456, p > 0.05$), while the fin index was significantly higher in 2010 for the Enningdal eels but lower in 2011 (2-way ANOVA, year × site interaction, $F_{1,95} = 5.3, p < 0.05$, Table S1 in the Supplement).

Each year, equal numbers of eels from each river were tagged with internal or external electronic tags (Table 1). Four types of tags were used in the experiments. Pop-up satellite tags (PSATs, X-tags) were supplied by Microwave Telemetry (www.microwave telemetry.com); these tags transmit depth and temperature data with, at best, a 15 min sampling rate. Data storage tags (DSTs, G5 long-life tags) were supplied by CEFAS Technology (www.cefastechology.co.uk) and have incompressible floats to make them buoyant. They were configured for either internal implantation (i-DSTs) or external attachment (e-DSTs) and were programmed to record depth data every 30 s and temperature data every 120 s. Acoustic tags used in 2010 were supplied by Thelma Biotel (www.thelma biotel.com) and transmitted a signal every 20 to 50 s. Further details of tag type and specifications are given in Table S3 in the Supplement.

Eels were tagged under anaesthesia using metomidate (d1-1-(1-phenylethyl)-5-(metoxycarbonyl) imidazole hydrochloride) at a concentration of 40 mg l⁻¹ for approximately 6 min. For implantation, the i-DSTs and acoustic tags were pushed through a small incision in the body cavity that was subsequently closed with independent single sutures (Thorstad et al. 2013). All external tags were attached in front of the dorsal fin using a 3-point attachment. Surgery took approximately 7 min, with time to recovery of approximately the same duration. Eels were released in the evening of the day they were tagged. A detailed description of the surgery and tagging methods can be found in Thorstad et al. (2013) and Økland et al. (2013).

Eels from both rivers were tagged with internal or external electronic tags, as detailed in Table 1, and released on consecutive days in October, near the time of peak silver eel escapement in this part of Sweden. In 2010, the release was made innermost of the southernmost branch of the Gullmaren fjord, and in 2011, the release was made off the coast at Marstrand (Fig. 1). The first experiment in 2010 was designed to enable assessment of both the downfjord and oceanic migration, and hence eels were double-tagged with i-DSTs and with identification-coded acoustic tags, making it possible to follow their
progress in the fjord using hydrophone arrays and to trace the oceanic migration using the data recovered from the DSTs. The second experiment was designed to enable further assessment of the oceanic migrations, and so approximately half of the eels from each river were tagged with satellite tags and half were tagged with e-DSTs to increase data recovery. The number and type of tags at the different release sites by year are shown in Table 1. Tagged eels were released from the shore after sundown.

The data from the PSATs were transmitted to the Argos system and decoded by Microwave Telemetry. Recovery of data from e- and i-DSTs depended on retrieval of tags that drifted to the shore. Tags were recovered from the shorelines of western Scotland and as far as northern Norway, and a reward was paid to the finder.

Acoustic tracking

The Gullmaren fjord is approximately 25 km long and 1 to 3 km wide, with a U-shaped cross-section and 100 to 120 m maximum depth, except at the threshold to the Skagerrak, where the threshold depth is 20 to 40 m. Five Vemco VR2W or VR2 receivers were deployed at 3 transects downstream of the release location (Fig. 1). The receivers were anchored with a subsurface buoy approximately 1 m above the seabed and, for retrieval, with a 60 m rope stretched along the bottom to a second anchor. The depth of the receiver varied from 10 to 40 m in different localities. The innermost single receiver was placed 5 km from the release point, where the distance to the opposite shore was 0.35 km, deemed enough to cover the section by 1 hydrophone (Transect 1). At the next 2 sections (Transects 2 and 3), 2 receivers, one on each side of the fjord, were moored 1.3 and 1.2 km apart, respectively. The number of receivers available did not allow for a closer spacing. A range test made at transect 3 with a control tag gave a minimum range of 250 m with 100% detection probability. The maximum range varied greatly with direction and depth from the receiver because of the strong stratification and complicated bathymetry in this area. As a result, the acoustic reception of each transect did not completely cross the fjord, allowing some potential passages to go undetected (DG Pincock unpubl. data, www.vemco.com/pdf/line_performance.pdf, accessed 5 Jan 2014). All receivers were deployed 2 wk before eels were released, and all were successfully retrieved on 13 or 14 December 2010.

Analysing oceanic migrations

The trajectories of PSAT- and e-DST-tagged eels were reconstructed by first estimating the longitude at an interval of approximately 7 d or every 100 to 150 km. Longitude was calculated by using the diurnal swimming depth changes of the eel as a proxy for sunset and sunrise; this provides an estimate of the time of local noon and thereby the longitude (Nielsen et al. 2006). All the eels displayed this diurnal cycle, and there is strong justification to believe that the depth changes are cued to dawn and dusk (Westerberg et al. 2007). Fig. 2 gives an example of the diurnal depth change for 2 PSATs during the days preceding their pop-up. Linear regression of the longitude estimates for the dates preceding pop-up with the longitude of the transmitted first position provided validation of this technique (transmitted longitude = 1.015 × calculated longitude, $F_{1,7} = 195$, $p < 0.001$). However,
because of variation in vertical migration behaviour from day to day and between eels, some longitude estimates were obvious outliers. To minimize this effect, we used estimates of longitude only for those periods when the timing of vertical migration behaviour showed low variability from day to day.

The time series of longitude estimates were then used as a starting point for further reconstruction of the trajectories of the eels. In the first step, position estimates were refined by comparing eel maximum daily depths with the bathymetry of the general area. This was particularly effective in the narrow Norwegian Trench south and west of Norway.

In a final refinement, we used specific hydrographic features that could be identified in most records and that were used as checkpoints. One point is where the swimming depth exceeded 450 m simultaneously with a longitude estimate less than 6° E, which means that the eel must have reached the open Norwegian Sea at approximately 62° N, since the maximum depth in the Norwegian Trench is less than 350 m along the west coast of Norway. Another unique point is where there was a sudden change in environmental temperature from less than 2°C to more than 7°C at depths greater than approximately 500 m, clearly indicating when the eel passes the Iceland-Scotland ridge, separating the cold Norwegian Sea deep water from the warmer Atlantic water south of the ridge.

Three milestones were defined in the marine migration. The first was the release date. The second was the beginning of active oceanic migration, defined as the day when the maximum depth reached by the eel exceeded 100 m, which corresponds to the entrance to the Norwegian Trench in the Skagerrak (see Fig. 1). The third milestone was the end position of the track, taken as the position of first transmission of a PSAT or the pop-up position of the DST. The former has a least-squares position error of less than 1.5 km, while the latter was found by comparing the temperature recorded by the DST with satellite measurements of sea surface temperature (SST) for the current date. This provided a relatively narrow latitude estimate which was combined with the estimate of longitude at the end of the track. The position error depends mostly on the uncertainty of the longitude estimate and is on the order of 100 km. To test for effects of longitude, origin and moon phase on habitat selection (either mean depth during the day or night or the difference between them), we used a generalised linear mixed model analysis using the glmm function of the nlme library (Pinheiro et al. 2012). Year, day of the year and eel ID were included in the model as random factors. The relationship between temperature experience (mean temperature during the day or night) was explored in the same way.

RESULTS

Fjord behaviour

All but one of the eels tagged with acoustic transmitters were detected after release by at least one of the receivers at one transect (total detections 2128, median 38 detections per eel). Several tags were undetected at Transect 1 or 2 but were recorded at Transect 3 near the fjord threshold (Table S4 in the Supplement). The most likely reason that eels were not detected was that the eel was too far from the receiver for the tag signal to be successfully detected. More detections were made during the time of the new moon than during the full moon (Fig. 3), although this difference was not statistically significant. Not all of the tags were detected at the final transect; the number of individuals detected at the end of the fjord decreased to 17 from 25 at the 2 inner transects. The total period of time that the eels stayed in the fjord varied. The first eel to leave the fjord was registered at the exit of the fjord after 7 d, while the last to leave was recorded at the outer transect after 52 d.

We used the differences in time between the last recording of a tag at each transect to determine the transit time of individual eels in each group (Table 2).

![Fig. 3. Number of individual eels registered per 5 d period at the different transects. Symbols show the phases of the moon (arrow indicates the release date). Transect numbers as in Fig. 1](image-url)
Table 2. Mean ± SD and number of observations (n) of the transit time in days between the release point and the last record of the acoustic tag at Transect 1 (T1) and between different pairs of transects. A Kolmogorov-Smirnov test showed no significant deviation from normality for the data in each transect interval and river group (0.17 < p < 0.95); hence, a heterogeneous t-test of the difference between the mean transit time of the River Enningdal and Åtran groups has been calculated for each inter-transect comparison.

<table>
<thead>
<tr>
<th>Interval</th>
<th>Enningdal Mean ± SD</th>
<th>Åtran Mean ± SD</th>
<th>t-test t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release to T1</td>
<td>12.67 ± 9.18</td>
<td>12.86 ± 15.9</td>
<td>-0.04</td>
<td>19.5</td>
<td>0.97</td>
</tr>
<tr>
<td>T1 to T2</td>
<td>6.39 ± 8.02</td>
<td>12.12 ± 17.84</td>
<td>-0.96</td>
<td>14.3</td>
<td>0.35</td>
</tr>
<tr>
<td>T2 to T3</td>
<td>9.75 ± 14.44</td>
<td>4.3 ± 5.26</td>
<td>1.05</td>
<td>10.55</td>
<td>0.32</td>
</tr>
<tr>
<td>T1 to T3</td>
<td>15.26 ± 13.31</td>
<td>14.58 ± 16.81</td>
<td>0.08</td>
<td>6.85</td>
<td>0.94</td>
</tr>
</tbody>
</table>

The time from release to the first transect was similar between eels of different origin, at approximately 13 d. Eels from the River Åtran took, on average, ~12 d to pass from Transect 1 to Transect 2, almost double that of the Enningdal eels (6.4 d). However, this difference was reversed in the remaining portion of the journey, where Åtran eels took only 4.3 d between transects in comparison to 9.75 d for the Enningdal eels. None of these transit times were significantly different.

From the innermost acoustic line, the mean swimming velocity of each eel can be calculated over the 11 and 7.5 km intervals between successive transects. The individual values varied between 0.2 and 42 km d\(^{-1}\) and will have done so partly because of real differences in swimming velocity, straightness of trajectory or periods of rest at the bottom during day-time. For example, 4 eels (3 from Enningdal and 1 from Åtran) completed the migration between the inner and outer transects in less than 2 d, indicating more or less continuous swimming. Conversely, 3 eels took more than 40 d, which likely indicates periods of rest between bouts of active migration. In 6 cases, the eels covered the distance between the first and middle transect or from the middle to the second transect in the same night (Tables S4 & S5 in the Supplement). If we assume that this represents continuous swimming on a relatively straight course along the fjord, the mean swimming velocity over ground can be calculated. The speed of those eels varied between 30 and 42 km d\(^{-1}\) or 0.34 to 0.53 BL s\(^{-1}\); however, sample size was insufficient to make a comparison between the groups.

**Oceanic migration**

Of the 99 eels tagged with DSTs or PSATs, data were recovered from 24 tags. Three PSATs and 3 e-DSTs surfaced after less than 7 d and provided no useful data on migration. The reason for the premature release of these tags is unclear and could have been because of entanglement in fishing gear or eels being preyed on by seals or other predators. One e-DST had a malfunctioning pressure sensor and gave
no usable data. The salient results for the comparison between stocked and naturally recruited eels are the remaining 17 tracks with durations between 1.5 and 5 mo (Table 3). There was no significant difference in eel length, weight or silvering index between the eels that carried tags that were recovered and those that did not (heterogeneous t-tests, p > 0.05 in all cases, Table S2 in the Supplement), and hence the tags recovered from Åtran eels were from slightly smaller eels than those originating from Enningdal eels (Table S2). Of the returned tags, 11 were attached to eels that originated from the River Åtran (6 e-DSTs and 5 PSATs), and 6 were from the River Enningdal (2 e-DSTs, 1 i-DST and 3 PSATs). These tags yielded, in total, 1227 d of data for eels caught in the River Åtran and 606 d for eels caught in the River Enningdal.

The reconstructed trajectories for those 17 eels are shown in Fig. 4. All eels followed essentially the same route through the Skagerrak and along the Norwegian west coast. The main guide for the eels appeared to be the Norwegian Trench, where the depth is greater than 200 m and up to 700 m in the Skagerrak south of Norway. In the Norwegian Sea, the trajectories became more dispersed, but except for one Enningdal eel that migrated to the northeast, the overall result was that the eels turned southwest and followed the continental shelf, past the Iceland-Scotland ridge into the Rockall Channel west of Scotland.

The reconstructed trajectories were used to calculate the average migration speed. In the first stage of the migration, from the coast to the start of active oceanic migration (depth >100 m), there was often a period where the eels spent time at the seabed in shallow water. This varied between 1 and 32 d for the Åtran eels, mean 12 d (Table 4), and 7 to 38 d for the Enningdal eels, mean 25 d (heterogeneous 2-sample t-test, $t_9 = 2.5$, $p < 0.05$). In the second stage, from the start of the oceanic migration to the time when the tag was released from the eel, the mean (± SD) migration speed was 21.6 km d$^{-1}$ (± 8.1 km d$^{-1}$, range 12.2 to 51 km d$^{-1}$), with no significant difference in

![Fig. 4. Trajectories of eels from the rivers Åtran (dashed lines) and Enningdal (solid lines). The Iceland-Faroe and Wyville-Thompson (W-T) ridges are the 2 parts of the Scotland-Iceland ridge](image-url)
Table 4. Summary of ocean migration behaviour of naturally recruited (Enningdal) eels (n = 6) and stocked (Åtran) eels (n = 11, except as noted) calculated from the point where the maximum swimming depth exceeded 100 m in the Skagerrak (i.e. Skagerrak entrance, row 1). Values for speed and duration of migration are calculated as average ± SD values for individuals, while values for depth and temperature are calculated at each estimated location for eels in the 2 experimental groups. ns: not significant at the 5% level

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Enningdal</th>
<th>Åtran</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to Skagerrak entrance (d)</td>
<td>25.33 ± 10.54</td>
<td>12.45 ± 9.05</td>
<td>2.6</td>
<td>9.1</td>
<td>0.03</td>
</tr>
<tr>
<td>Speed to Norwegian Sea (km d⁻¹)</td>
<td>26.28 ± 5.40</td>
<td>25.64 ± 14.08</td>
<td>0.11</td>
<td>9.95</td>
<td>ns</td>
</tr>
<tr>
<td>BL s⁻¹ to Norwegian Sea</td>
<td>0.31 ± 0.08</td>
<td>0.33 ± 0.19</td>
<td>0.3</td>
<td>9.6</td>
<td>ns</td>
</tr>
<tr>
<td>Speed to end of track (km d⁻¹)</td>
<td>26.52 ± 8.53</td>
<td>18.89 ± 6.80</td>
<td>1.8</td>
<td>8.6</td>
<td>ns</td>
</tr>
<tr>
<td>BL s⁻¹ to end of track</td>
<td>0.32 ± 0.11</td>
<td>0.25 ± 0.09</td>
<td>1.3</td>
<td>8.7</td>
<td>ns</td>
</tr>
<tr>
<td>Daytime depth (m)</td>
<td>285.9 ± 95.83</td>
<td>281.549 ± 108.1</td>
<td>0.23</td>
<td>72</td>
<td>ns</td>
</tr>
<tr>
<td>Nighttime depth (m)</td>
<td>109.9 ± 72.6</td>
<td>127.8 ± 76.2</td>
<td>1.3</td>
<td>67.2</td>
<td>ns</td>
</tr>
<tr>
<td>Daytime temperature (°C)</td>
<td>6.66 ± 2.44</td>
<td>6.97 ± 1.86</td>
<td>0.7</td>
<td>50.7</td>
<td>ns</td>
</tr>
<tr>
<td>Nighttime temperature (°C)</td>
<td>8.82 ± 1.33</td>
<td>9.12 ± 0.06</td>
<td>1.2</td>
<td>52</td>
<td>ns</td>
</tr>
</tbody>
</table>

the migration speed of stocked or naturally recruited eels (t-test, t₈,₉ = 1.9, p > 0.05, Table 4) or in BL s⁻¹ (t-test, t₈,₇ = 1.4, p > 0.05, Table 4). However, because the total length of the trajectories varied considerably, it is more appropriate to make comparisons between the groups over a standardised distance. Most tracks (n = 14) covered the approximately 900 km distance between the 100 m contour in the Skagerrak and the entry to the Norwegian Sea, with an average speed of 25.9 km d⁻¹ (±10.9 km d⁻¹).

Again, there was no difference in swimming speed between stocked or naturally recruited eels (t-test, t₈,₆ = 1.9, p > 0.05, Table 4) or in BL s⁻¹ (t-test, t₈,₆ = 0.3, p > 0.05).

During migration, all the eels showed a continuous diurnal depth cycle, with a deeper swimming level during the daylight period (282.7 ± 104.6 m) and shallower swimming level during the night (123 ± 75.4 m). The shift between deep and shallow residence depths was essentially synchronous between eels in the same area and likely cued by the daylight variation. Fig. 5 gives an example of the simultaneous record of swimming depth of 2 eels in approximately the same area of the Norwegian Sea, one (#111814) of stocked origin from the River Åtran and the other (#111816) of naturally recruited origin from the River Enningdal.

the stocked and naturally recruited groups was assessed using a linear mixed model. Longitude proved to be a highly significant (p < 0.01, Table 5) predictor of daytime vertical position and vertical range; as

Table 5. Effect of environment (longitude and moon phase) and origin on the habitat selection of eels during their oceanic migration. Values in the table provide the significance (probability of effect, p) of each factor in a generalized linear mixed model, with interactions between different factors. Year, day of year and eel ID were included in the model as random factors

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Longitude</th>
<th>Moon phase</th>
<th>Origin</th>
<th>Longitude × origin</th>
<th>Moon phase × origin</th>
<th>Longitude × moon phase × origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean depth (m) during day</td>
<td>&lt;0.05</td>
<td>0.80</td>
<td>0.27</td>
<td>0.69</td>
<td>0.72</td>
<td>0.89</td>
</tr>
<tr>
<td>Mean depth (m) during night</td>
<td>0.63</td>
<td>0.58</td>
<td>0.31</td>
<td>0.61</td>
<td>0.72</td>
<td>0.82</td>
</tr>
<tr>
<td>Depth range (m)</td>
<td>&lt;0.05</td>
<td>0.68</td>
<td>0.90</td>
<td>0.35</td>
<td>0.98</td>
<td>0.81</td>
</tr>
<tr>
<td>Mean temperature (°C) during day</td>
<td>0.84</td>
<td>0.89</td>
<td>0.44</td>
<td>0.22</td>
<td>0.80</td>
<td>0.63</td>
</tr>
<tr>
<td>Mean temperature (°C) during night</td>
<td>0.69</td>
<td>0.45</td>
<td>0.10</td>
<td>0.09</td>
<td>0.39</td>
<td>0.32</td>
</tr>
</tbody>
</table>
eels travelled towards the Sargasso Sea, they occupied deeper water during the day and therefore moved over a larger depth range (linear regression:

\[
day \text{ depth} = -16.4 \times \text{longitude} + 358.4, \quad F_{1,135} = 224.7, \quad p < 0.01 \text{ and depth range } = -8.17 \times \text{longitude} + 197.4, \quad F_{1,135} = 74, \quad p < 0.01.
\]

Eel origin, moon phase or the interaction between eel origin and longitude, or any of the random effects in the model (year of tagging, day of year or eel ID), were not significant in any of the models (p > 0.05, Table 5). Surprisingly, longitude was not a significant predictor of temperature experience (Table 5).

**DISCUSSION**

We used several different methods of telemetry to determine the movements and migrations of European eels of different origin. The results from our analysis of the initial behaviour in the fjord, at-sea migration and vertical movements do not suggest that the navigation of naturally recruited eels versus those of probable stocked origin is significantly different. Our experiments were conducted in separate years, and while there were some small differences in BL and weight between the experimental groups overall (but not within each year), the migration speed, timing of migration and migration route taken as well as vertical behaviour were not different between experimental groups.

**Migration speeds**

During the initial period after release in the fjord, there were no statistically significant differences in delay before arrival at the first acoustic transect or in average time to departure from the fjord between the stocked eels from the River Åtran and the naturally recruited eels from the River Enningdal. Unfortunately, we were not able to set up the acoustic array in the fjord to enable 100% detection of tags as they passed down the fjord, so not all eels were detected at each acoustic transect, and we were not able to confirm the departure of all eels from both experimental groups. However, the experimental setup in the fjord is similar to that used by Aarestrup et al. (2008, 2010) to study down-river migration of eels in the Randers fjord in Denmark and by Davidsen et al. (2011) in the Alta fjord in northern Norway. Just as for our results, these studies showed that there was a low average speed and large spread of out-migration delay but with some eels finding their way to the sea very rapidly. The maximum continuous speed we recorded over a single night (~42 km d\(^{-1}\), Table S5) was similar to the maximum speed found in previous eel tagging experiments in the Baltic (Sjöberg & Petersson 2005).

Stocked eels navigated from the coast to the onset of oceanic migration at the entrance to the Skagerrak more quickly than naturally recruited eels. However, in the subsequent offshore migration during several months and, for some eels, over a distance of more than 2000 km, the swimming speed (expressed either as speed over ground or in BL s\(^{-1}\)) of both stocked and naturally recruited eels was not significantly different. Both groups achieved an average speed over ground of approximately 25 km d\(^{-1}\) (corresponding to ~0.3 BL s\(^{-1}\)), with this average reaching up to 51 km d\(^{-1}\) over the section between the Skagerrak and the Norwegian Sea in one case. The average speed is greater than that reported in previous studies of oceanic eel migration (Aarestrup et al. 2009) and may reflect the greater spatial accuracy with which we reconstructed the migration route. These data also suggest that the swimming ability of eels was not significantly compromised by the tag or the tagging procedure (Methling et al. 2011) and, as suggested in previous studies, provides optimism that tracking the full journey to the Sargasso Sea will be possible with further improvements in tag technology.

**Migration route**

Eels from both experimental groups took the same route along the Norwegian Trench into the Norwegian Sea before turning southwest somewhere north of 62° N once they reached the Norwegian Sea. A single eel from the River Enningdal continued north in the Norwegian Sea until the tag popped off. However, several other eels meandered in the Norwegian Sea before turning south and west towards the Atlantic. All eels showed a daily maximum depth which excludes any alternative, shorter route across the North Sea or south of the Shetland Islands. This ‘Nordic’ migration route resolves many decades of speculation about the route that eels take once they leave the Baltic (Westerberg 2013) and is corroborated by observations of by-catch of silver eels in bottom trawl surveys in the North Sea and the Baltic during groundfish and shrimp surveys in the autumn (e.g. Norwegian Pandalus Survey, North Sea International Bottom Trawl Survey and Baltic International Trawl Survey). These results suggest that eels, whether stocked or naturally recruited, are not
dependent on an imprinted route, at least for the section of the route east of where the eel reaches the continental shelf. Which navigational cues are used is unknown, but orientation seems to be map-independent.

To describe the geographic migrations of tagged eels, it was necessary for us to develop a technique of geolocation based on eel behaviour and the primary hydrographic signals that the tag datasets provided because no other existing geolocation technique, e.g. light-based or SST-based (Nielsen et al. 2006), was suitable. Although our geolocation technique allowed us to reconstruct the migrations of eels in unprecedented detail, the reconstruction of the migrations is in some ways coarse and lacks finer details. For example, there are probably several unrecorded meanderings, especially in the Norwegian Sea and in the deep part of the Norwegian Trench south of Norway. Further development of our technique, using state-space models (Patterson et al. 2008) or more complex water column profile matching techniques, will enable these finer-scale details to be resolved.

**Vertical movements and activity**

The behaviour of the eels varied over the course of the lunar and diel cycles and over the period of their oceanic migration. In the fjord, the activity of the eels varied with the lunar phase, with a peak in activity around the fourth quarter of the moon (Fig. 3). The effect of the lunar cycle on silver eels as they move downstream to the sea during autumn is well known both from laboratory studies and in the fishery (e.g. Boëtius 1967 and Lindroth 1979). No effect of the moon was found in the behaviour of the eels once they left the fjord, however.

During the ocean phase of migration, eels showed a large-amplitude diurnal change in swimming depth that has been described in previous studies of European eels (e.g. Tesch 1978, Aarestrup et al. 2009) as well as, more recently, other Anguilla species (Jellyman & Tsukamoto 2010, Béguer-Pon et al. 2012, Schabetsberger et al. 2013). There was no significant difference in the depths that eels occupied during the day or night, or in the depth range, between stocked or naturally recruited eels, i.e. the diel behaviour did not differ between groups. The large dusk ascent and large dawn descent were clearly cued to changes in light level between day and night, which supports a hypothesis of predator avoidance during the day (Schabetsberger et al. 2013). Furthermore, daytime swimming depth and depth range were significantly influenced by longitude, suggesting that there are environmental factors that influence these aspects of eel habitat occupation that are associated with the westward migration. However, since the occupied temperatures of eels of stocked or natural origin were not influenced by longitude, this remains an open question.

**Effect of eel origin on migration**

We could not be sure that the individuals that we tagged were definitely of stocked or natural origin since the only current method to achieve this is by otolith microchemistry, which requires sacrifice of the eel. The results of our otolith reference assessment confirmed that 100% of eels caught in the Enningdal at the same time and in the same place as our first tagged group were natural recruits and that 80% of the eels caught in the Åtran were stocked as glass eels. However, the number of tags recovered from presumed stocked and presumed natural recruits was only a small proportion of those tagged (25%) and, in principle, the recovered sample could be highly skewed, such that all tags recovered from River Åtran eels were eels originally stocked from the Swedish coast. However, 70% of the PSATs attached to presumed stocked eels were recovered and returned long tracks, which means that at least some (and probably the majority) of these must have been stocked as translocated glass eels.

Despite this slight uncertainty, and although there were small differences in the overall average BL and weight between stocked and naturally recruited groups, we believe that the strength of this study is that there is a comparison between groups with a well-known immigration history. The only other study fulfilling this is the tagging studies with Carlin or Floy tags conducted by Westin in the Baltic (Westin 1998, 2003). Based on a larger spread of tag recaptures and a high degree of overwintering in stocked eels, he concluded that there was a clear behaviour difference in the ability to orientate and that this was caused by a lack of imprinted learning of the route in stocked eels. In the context of our results, we found no difference in behaviour between naturally recruited and stocked eels, which does not support the hypothesis that a sequential imprinting of the route during the immigration is necessary for adequate orientation during the spawning migration. The argument that stocked glass eels are unable to navigate is not supported, therefore, at least outside the Baltic basin. It remains to be investigated if there
is a special requirement of early imprinting to negotiate the navigation difficulties of finding the Baltic outlet or if the results reported by Westin simply reflect a requirement for a period of feeding in the marine environment to increase fat content before the marine migration (Svedång & Wickström 1997, Limburg et al. 2003).

Further work and implications for management

Our results provide, in considerable detail, the longest distances that any eel has been tracked and account for approximately one-third of the total distance from the Skagerrak to the Sargasso Sea. However, our results do not prove that translocated glass eels contribute to the spawning population because none of the tracked eels, stocked or naturally recruited, could be followed to reach the Sargasso Sea and, furthermore, the relatively low sample size did not enable us to assess relative survival rates of stocked versus naturally recruited eels. Nonetheless, the results obtained from the tagging methods used here are encouraging. Smaller DSTs and satellite tags are becoming available, and there should be a realistic chance to cover the whole spawning migration. This potentially allows comparison of the survival and migration success between both stocked and unstocked eels and eels coming from different parts of the distribution range.

In conclusion, the lack of any difference in migration behaviour, either from the fjord or at sea, in terms of migration route, swimming speeds or vertical migration is the strongest indication yet that stocked glass eels have navigational and behavioural abilities similar to those of naturally recruited eels. This provides evidence in support of stocking as a measure to recover the stock of European eels within the framework of the EU’s EMPs. Evidently, there are also relevant concerns about the use of stocking as a management measure. In the present situation, with a dramatic decline of recruitment, stocking merely to compensate for fishery or other anthropogenic mortality is futile.

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**Behaviour of stocked and naturally recruited European eels during migration**

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**Supplement.** Supplementary material to the 'Materials and methods' section and additional data for the result of the acoustic tag experiment in the fjord

**MORPHOLOGY OF TAGGED AND RECOVERED EELS**

Table S1. Length (mm) and weight (g) of the tagged European eels at the 2 capture sites, the River Ätran (n = 49, presumed of stocked origin) and the River Enningdal (n = 50, presumed of naturally recruited origin). Values are means ± SD. Comparisons between sites and years were conducted by 2-way ANOVA. *p < 0.05, ***p < 0.001. NS: not significant. The Pankhurst and fin maturity index are explained in the 'Materials and methods' section of the main text

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Year</th>
<th>Enningdal</th>
<th>Ätran</th>
<th>Significant difference?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average of body length</td>
<td>2010</td>
<td>924.3 ± 66.4</td>
<td>891.6 ± 48.8</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>955.4 ± 91.1</td>
<td>869.8 ± 59.5</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>939.5 ± 80.2</td>
<td>880.7 ± 55.0</td>
<td>***</td>
</tr>
<tr>
<td>Average of body weight</td>
<td>2010</td>
<td>1565.0 ± 352.2</td>
<td>1371.2 ± 247</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>1617.6 ± 377.3</td>
<td>1300.0 ± 216.9</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>1590.8 ± 361.8</td>
<td>1335.6 ± 232.8</td>
<td>***</td>
</tr>
<tr>
<td>Average of Pankhurst index</td>
<td>2010</td>
<td>9.3 ± 1.1</td>
<td>10.5 ± 1.3</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>9.5 ± 1.5</td>
<td>10.3 ± 1.5</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>9.4 ± 1.3</td>
<td>10.4 ± 1.4</td>
<td>***</td>
</tr>
<tr>
<td>Average of fin index</td>
<td>2010</td>
<td>5.0 ± 0.4</td>
<td>4.9 ± 0.4</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>4.9 ± 0.4</td>
<td>5.1 ± 0.3</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Overall</td>
<td>4.9 ± 0.4</td>
<td>5.0 ± 0.3</td>
<td>NS</td>
</tr>
</tbody>
</table>
Table S2. $t$-test of difference between morphological measures of released eels and eels where the time series data were recovered and analyzed. Values are means ± SD. There was no difference in size between the eels tagged and the eels from which tags were recovered. Significance as in Table S1

<table>
<thead>
<tr>
<th>Enningdal</th>
<th>Åtran</th>
<th>Between sites</th>
<th>From release</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>t   df</td>
<td>p</td>
</tr>
<tr>
<td>Average of body length</td>
<td>974.8 ± 51.7</td>
<td>890.9 ± 54.8</td>
<td>3.1</td>
</tr>
<tr>
<td>Average of body weight</td>
<td>1,920.5 ± 259.5</td>
<td>1,382.4 ± 169.9</td>
<td>4.5</td>
</tr>
<tr>
<td>Average of Pankhurst index</td>
<td>10.22 ± 1.24</td>
<td>10.47 ± 1.35</td>
<td>0.38</td>
</tr>
<tr>
<td>Average of fin index</td>
<td>5.06 ± 0.43</td>
<td>4.99 ± 0.21</td>
<td>0.38</td>
</tr>
</tbody>
</table>

TAGS USED IN THE STUDY

Table S3. Specifications for the 4 tag types used. A negative value of the weight in water means that the tag is buoyant. (i-DST = implanted data storage tag, e-DST = externally attached data storage tag, PSAT = externally attached pop-up satellite tag)

<table>
<thead>
<tr>
<th>Tag specification</th>
<th>implanted-DST</th>
<th>external-DST</th>
<th>PSAT</th>
<th>acoustic ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manufacturer</td>
<td>CEFAS Technology, G5</td>
<td>CEFAS Technology, G5</td>
<td>Microwave Telemetry, X-tag</td>
<td>THELMA Biotel</td>
</tr>
<tr>
<td>Total length (mm)</td>
<td>135 (incl. floats)</td>
<td>130 (incl. float)</td>
<td>120 (excl. antenna)</td>
<td>18</td>
</tr>
<tr>
<td>Max diameter (mm)</td>
<td>11</td>
<td>20</td>
<td>33</td>
<td>7.3</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>10</td>
<td>35</td>
<td>45</td>
<td>1.9</td>
</tr>
<tr>
<td>Weight in water (g)</td>
<td>−0.9</td>
<td>−4.7</td>
<td>−2.5</td>
<td>1.2</td>
</tr>
<tr>
<td>Power output (dB re 1 µPa at 1 m)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>139</td>
</tr>
<tr>
<td>Battery life (days)</td>
<td>730</td>
<td>730</td>
<td>300</td>
<td>250</td>
</tr>
<tr>
<td>Depth range (m)</td>
<td>0 to 1000</td>
<td>0 to 1000</td>
<td>0 to 1200</td>
<td>–</td>
</tr>
<tr>
<td>Depth resolution (m)</td>
<td>&lt; 0.3</td>
<td>&lt; 0.3</td>
<td>0.5 to 5</td>
<td>–</td>
</tr>
<tr>
<td>Depth accuracy (m)</td>
<td>± 10</td>
<td>± 10</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Temperature range (°C)</td>
<td>−2 to 40</td>
<td>−2 to 40</td>
<td>−4 to 40</td>
<td>–</td>
</tr>
<tr>
<td>Temperature resolution (°C)</td>
<td>0.03</td>
<td>0.03</td>
<td>0.16 to 0.23</td>
<td>–</td>
</tr>
<tr>
<td>Temperature accuracy (°C)</td>
<td>± 0.1</td>
<td>± 0.1</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Sampling/transmission interval (sec)</td>
<td>30 (depth), 300 (temp)</td>
<td>30 (depth), 300 (temp)</td>
<td>900s or longer</td>
<td>20 to 50</td>
</tr>
</tbody>
</table>
Fig. S1. Three types of tags used in the experiment. From top to bottom: satellite tag, external data storage tag and implanted data storage tag (note the flexible construction to follow the movement of the eel). Scale in cm at the bottom of the picture

ADDITIONAL DATA FOR FJORD TRACKING EXPERIMENT

Table S4. Date (dd/mm/yy, hh:mm) and time for the last record of each individual acoustic ID tags at the 3 transects in the Gullmaren fjord

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>Transect 1</th>
<th>Transect 2</th>
<th>Transect 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>401</td>
<td>19/10/10 18:52</td>
<td>Enningdal</td>
<td>03/11/10 0:56</td>
</tr>
<tr>
<td>402</td>
<td>14/11/10 16:57</td>
<td>15/11/10 16:33</td>
<td>16/11/10 19:13</td>
</tr>
<tr>
<td>403</td>
<td>27/10//10 18:35</td>
<td>01/11/10 22:29</td>
<td></td>
</tr>
<tr>
<td>404</td>
<td>05/11/10 22:45</td>
<td>06/11/10 6:36</td>
<td>06/11/10 16:27</td>
</tr>
<tr>
<td>405</td>
<td>05/11/10 12:06</td>
<td>05/11/10 16:24</td>
<td></td>
</tr>
<tr>
<td>406</td>
<td>24/10/10 23:57</td>
<td>29/10/10 16:00</td>
<td></td>
</tr>
<tr>
<td>407</td>
<td>16/10/10 22:04</td>
<td>06/11/10 20:47</td>
<td></td>
</tr>
<tr>
<td>408</td>
<td>13/10/10 19:31</td>
<td>09/11/10 19:58</td>
<td></td>
</tr>
<tr>
<td>409</td>
<td>04/11/10 23:41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>410</td>
<td>19/10/10 21:26</td>
<td>2110/10 23:46</td>
<td>30/11/10 20:39</td>
</tr>
<tr>
<td>411</td>
<td>31/10/10 1:51</td>
<td>06/11/10 1:27</td>
<td>07/11/10 3:09</td>
</tr>
<tr>
<td>412</td>
<td>19/10/10 22:26</td>
<td>31/10/10 20:07</td>
<td>01/11/10 18:37</td>
</tr>
<tr>
<td>413</td>
<td>29/10/10 6:10</td>
<td>29/10/10 22:45</td>
<td>30/10/10 6:22</td>
</tr>
<tr>
<td>414</td>
<td>19/10/10 20:25</td>
<td>24/10/10 22:51</td>
<td>08/11/10 17:03</td>
</tr>
<tr>
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<td>03/11/10 21:25</td>
<td></td>
</tr>
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<td>06/11/10 22:11</td>
<td></td>
</tr>
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<td>417</td>
<td>12/12/10 19:22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>418</td>
<td>15/10/10 16:51</td>
<td>04/12/10 9:02</td>
<td></td>
</tr>
<tr>
<td>419</td>
<td>01/11/10 16:42</td>
<td>02/11/10 3:16</td>
<td></td>
</tr>
<tr>
<td>420</td>
<td>31/10/10 22:00</td>
<td>02/11/10 23:59</td>
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</tr>
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Table S4. Date (dd/mm/yy, hh:mm) and time for the last record of each individual acoustic ID tags at the 3 transects in the Gullmaren fjord

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<tr>
<th>Transect</th>
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<th>Time 1</th>
<th>Date 2</th>
<th>Time 2</th>
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<td>401</td>
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</tr>
<tr>
<td></td>
<td>402</td>
<td>14/11/10</td>
<td>16:57</td>
<td>15/11/10</td>
<td>16:33</td>
</tr>
<tr>
<td></td>
<td>403</td>
<td>27/10/10</td>
<td>18:35</td>
<td>01/1/10</td>
<td>22:29</td>
</tr>
<tr>
<td></td>
<td>404</td>
<td>05/11/10</td>
<td>22:45</td>
<td>06/11/10</td>
<td>6:36</td>
</tr>
<tr>
<td></td>
<td>405</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>406</td>
<td>05/11/10</td>
<td>12:06</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>407</td>
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<td>23:57</td>
<td>29/10/10</td>
<td>16:00</td>
</tr>
<tr>
<td></td>
<td>408</td>
<td>16/10/10</td>
<td>22:04</td>
<td>06/11/10</td>
<td>20:47</td>
</tr>
<tr>
<td></td>
<td>409</td>
<td>13/10/10</td>
<td>19:31</td>
<td>09/11/10</td>
<td>19:58</td>
</tr>
<tr>
<td></td>
<td>410</td>
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<td>23:41</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>411</td>
<td>19/10/10</td>
<td>21:26</td>
<td>2110/10</td>
<td>23:46</td>
</tr>
<tr>
<td></td>
<td>412</td>
<td>31/10/10</td>
<td>1:51</td>
<td>06/11/10</td>
<td>1:27</td>
</tr>
<tr>
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<td>31/10/10</td>
<td>20:07</td>
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<td>20:25</td>
<td>24/10/10</td>
<td>22:51</td>
</tr>
<tr>
<td></td>
<td>416</td>
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<tr>
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<td>15/10/10</td>
<td>16:51</td>
<td>04/12/10</td>
<td>9:02</td>
</tr>
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<td></td>
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<td>01/11/10</td>
<td>16:42</td>
<td>02/11/10</td>
<td>3:16</td>
</tr>
<tr>
<td></td>
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<td>02/11/10</td>
<td>23:59</td>
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<td>21:26</td>
<td>29/10/10</td>
<td>1:40</td>
</tr>
<tr>
<td></td>
<td>423</td>
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<td>19:47</td>
<td>02/12/10</td>
<td>4:34</td>
</tr>
<tr>
<td></td>
<td>424</td>
<td>28/10/10</td>
<td>19:26</td>
<td>29/10/10</td>
<td>23:09</td>
</tr>
<tr>
<td></td>
<td>425</td>
<td>14/10/10</td>
<td>19:31</td>
<td>17/10/10</td>
<td>0:13</td>
</tr>
<tr>
<td></td>
<td>426</td>
<td></td>
<td></td>
<td>03/12/10</td>
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</tr>
<tr>
<td></td>
<td>427</td>
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<td>1:30</td>
<td>19/10/10</td>
<td>21:08</td>
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<tr>
<td></td>
<td>428</td>
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<td>21:05</td>
<td>30/10/10</td>
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<tr>
<td></td>
<td>429</td>
<td>20/10/10</td>
<td>2:33</td>
<td>23/10/10</td>
<td>1:52</td>
</tr>
<tr>
<td></td>
<td>430</td>
<td>03/11/10</td>
<td>17:55</td>
<td>04/11/10</td>
<td>19:09</td>
</tr>
</tbody>
</table>

Table S5. Speed of eels leaving one transect and reaching the next during the same night

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>km d⁻¹</th>
<th>BL (mm)</th>
<th>BL s⁻¹</th>
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<tr>
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<td>30.50</td>
<td>896</td>
<td>0.39</td>
</tr>
<tr>
<td>404</td>
<td>37.49</td>
<td>938</td>
<td>0.46</td>
</tr>
<tr>
<td>406</td>
<td>42.18</td>
<td>922</td>
<td>0.53</td>
</tr>
<tr>
<td>414</td>
<td>24.58</td>
<td>779</td>
<td>0.37</td>
</tr>
<tr>
<td>417</td>
<td>37.26</td>
<td>880</td>
<td>0.49</td>
</tr>
<tr>
<td>420</td>
<td>26.11</td>
<td>891</td>
<td>0.34</td>
</tr>
<tr>
<td>Mean</td>
<td>33.02</td>
<td>884</td>
<td>0.43</td>
</tr>
</tbody>
</table>
Release of eels marked with $\text{SrCl}_2$ and $\text{BaCl}_2$. Photo: Håkan Wickström
Traceability of stocked eels – the Swedish approach

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Abstract – Stocking of eels is one of the management measures in the eel regulation (EC No 1100/2007) to recover the stock. The Swedish Eel Management Plan doubles the numbers stocked to 2.5 million eels per year. Whether stocked eels contribute to the spawning stock or not has been questioned: stocked eels might not migrate as successful as wild recruited eels. The EIFAAC/ICES Working Group on Eel (2011) recommended ‘that all stocked eel should be marked and thereby separable from wild eel in subsequent sampling’. Since 2009, eels stocked in Sweden have been bathed in a strontium (Sr) solution, which gives a detectable mark in their otoliths. So far, 5.5 million eels have been marked in Sweden; Finland imports eels for stocking via Sweden, and these 0.6 million eels were marked by two Sr rings. We present results on marking success and recapture rates and also from marking with alizarin complexone and PIT tags in combination with Sr. If all eels stocked in the Baltic are marked, their contribution to the spawning run can be estimated. Using different combinations of marks in different regions, the relative contribution from separate stocking programmes can be evaluated. To increase the set of suitable marks, barium was tested as an additional tracer.

Key words: Anguilla anguilla; stocking; otolith; marking; strontium; barium

Introduction

The European eel (Anguilla anguilla (L.) is listed as critically endangered (CR) by IUCN (Freyhof & Kottelat 2010). The reason behind this listing is a rapid decline in stock and recruitment all over the distribution area since about 1980 (Dekker 2003). Several hypotheses for this decline have been suggested, including over fishing, pollution, parasitism, obstructed migration, reduced growing areas, turbine mortality and changed oceanic conditions. Probably there is a mix of disturbances and mortalities of this kind and not a single cause for the decline in the eel.

In 2007, the EU issued an eel regulation (EC No 1100/2007) aimed at recovering the European eel population. This regulation demands eel management plans from all member states with significant eel stocks. The main objective is to allow at least 40% of produced spawners (silver eels) from an estimated virgin stock to migrate towards the spawning area in the Sargasso Sea. Besides reduced fishing and hydroelectric power mortalities, restocking with eels taken from areas with a surplus of young recruits (glass eels) is proposed as a possible measure by the eel regulation. Restocking is also eligible for economical support from EU’s Fishing Funds (EFF).

As a consequence of the regulation and the financial support from the EU, the now approved management plans from many European states are more or less based on restocking to improve the production of spawners. This has been discussed and questioned (Westin 2003; EIFAAC/ICES 2011; ICES 2011a), but restocking has de facto become the most significant direct measure to enhance the eel stock. This is especially the case in countries where natural recruits are too few to allow a quick rebuilding of national stocks; Sweden is one of those countries.

When assessing the benefits and costs of restocking, it is of utmost importance to be able to distinguish stocked individuals from eels with a natural
immigration background. It has been difficult to mark or tag yellow eels in general and young eels (as glass eels and elvers) in particular (Nielsen 1988). Recently several methods, such as marking with alizarin, oxytetracycline, elements such as strontium, radiative isotopes, visible implants (VI) and visible implants elastomer (VIE), have been more or less successfully applied to glass eels (Andersson et al. 1991; Thomassen et al. 2000; Skov et al. 2001; Simon & Dörner 2005; Imbert et al. 2007). In slightly larger eels, PIT tags have also been successfully applied (Riley et al. 2011; Hirt-Chabbert & Young 2012).

In this article we describe the preliminary results and experiences from a large-scale marking programme where all stocked eels in Sweden have been marked with SrCl₂ since 2009. This approach has become a de facto requirement from the governmental agency issuing the restocking permits. In Sweden, all eels imported for restocking purposes have to pass through a combined quarantine and eel aquaculture facility where all eels are easily marked. Some experiences and comparisons with alizarin and PIT tags will also be presented. Finally, some recent results from a preliminary test with BaCl₂ are given.

Material and methods

General conditions

Nowadays, there are no wild eel recruits reaching Lake Ymsen situated far up in the river system blocked by numerous hydroelectric power plants. In Lake Mälaren, which faces the Baltic Sea at Stockholm, the relatively few wild recruits are all much older and larger (∼30 cm) than the glass eels and elvers arriving at the Swedish west coast (the Skagerrak–Kattegat). Furthermore, this study mainly aims at estimating the marking success in small eels destined for stocking. In Lake Ymsen, the longevity of Sr marks was checked and corroborated with PIT tag marked and recaptured eels. Thus, for the purpose of this article, the influence of any wild recruits is considered not to be a relevant issue.

The different experiments described below are outlined in Table 1.

Marking with alizarin complexone in Lake Mälaren

In 1997, 5000 pigmented young eels (1.2 g and 95.3 mm, mean weight and length, respectively, originally from the River Severn in SW England) were taken from a quarantine facility and bathed at +16.5 °C for 24 h in an aerated solution of alizarin complexone (50 mg l⁻¹) using water from the nearby Lake Mälaren. The eels were then stocked in the eastern part of this large (1140 km²) mesotrophic lake close to Stockholm (Lat N 59° 20' 00” Lon E 17° 52' 30”) in June 1997 where the water temperature was about +20.5 °C. In this part of Lake Mälaren, the water has a conductivity of about 21 mS m⁻¹ and 20–30 μg l⁻¹ total phosphorous (Lännergren 2010). As part of an existing extensive monitoring programme, all eels were caught using paired fyke nets in the neighbouring area and screened for fluorescence in their otoliths from 1999 onwards. Screening was performed using a compound microscope equipped with an Hg lamp and the appropriate filter packs for excitation and emission. The otoliths were embedded in plastic and ground and polished before the analysis (ICES 2011b).

Marking with SrCl₂ in Lake Ymsen and within the nationwide stocking programme

The first large-scale marking experiment was commenced after some preliminary laboratory experiments which gave positive results. From 1999 to 2002, 17,768 glass eels were bathed for 24 h in water containing 1 g l⁻¹ of SrCl₂ *6H₂O at +20–23 °C before being released in the eutrophic Lake Ymsen (58° 40. N, 13° 58. E, 13 km²). The strontium treatment was carried out at the aquaculture facility responsible for quarantining eels imported into Sweden. From 2009 and onwards, all eels stocked in Sweden were then marked in the same way, a total of about 5.5 million eels. Eels intended for stocking in Finland have been bathed twice to achieve double rings of Sr in their otoliths; these amount to another 5.5 million eels. To facilitate the discrimination of the two rings, the two bathings were made about 52 days apart to allow for sufficient otolith growth at prevailing temperatures. All eels caught and sold from Lake Ymsen since 1999 have been scanned for PIT tags by a local fisherman and subsequently analysed for Sr marks (see below). From the national full-scale marking programme commenced in 2009, we have secured annual samples of eels before they were distributed for restocking to a number of sites. Subsamples were dissected, and their otoliths analysed with

<table>
<thead>
<tr>
<th>Eels analysed for</th>
<th>When</th>
<th>Where</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 ring of raised Sr</td>
<td>Before stocking</td>
<td>Several lakes</td>
</tr>
<tr>
<td>2 rings of raised Sr</td>
<td>Before stocking</td>
<td>Finnish lakes</td>
</tr>
<tr>
<td>1 ring of raised Ba</td>
<td>Before stocking</td>
<td>Lake Mälaren</td>
</tr>
<tr>
<td>1 or 2 rings of raised Sr</td>
<td>In PIT-tagged eels recaptured after 4–12 years</td>
<td>Lake Ymsen</td>
</tr>
<tr>
<td>1 ring of alizarin complexone</td>
<td>In eels recaptured after 3–14 years</td>
<td>Lake Mälaren</td>
</tr>
</tbody>
</table>

Table 1. An outline of the different experiments described in this study.
respect to an induced ring of Sr using an Electron Probe Microanalyzer at the Department of Earth Sciences at the Uppsala University. Imaging was made in BSE mode (i.e. with a back-scattered electron detector) and to verify that the observed rings were indeed induced Sr, the analysis was confirmed using wavelength dispersive X-ray spectroscopy (WDS) line scans for Sr (cf. Barker & Fournelle 1996 and Fig. 2b). This was carried out also when rings were faint or missing.

Tagging with PIT tags in combination with SrCl₂ in Lake Ymsen

PIT tags have been used successfully to mark many different species, including eel (cf. Laffaille et al. 2005). In this study (apart from an analysis of growth not reported here), we used PIT tagging to identify those eels that should have induced Sr rings in their otoliths. In 1999 and 2000, 2627 eels with a mean weight of 17.1 g were both Sr marked and tagged with PIT tags (Table 2). A cursory check during the days after tagging (i.e. before stocking) showed insignificant mortality and tag loss. In 1999, one ring of Sr was induced, and in 2000, two rings were induced, using one or two baths, respectively. On this occasion, the time period between the two baths was 2 weeks. At this time, there was only one eel fisherman in Lake Ymsen, and he screened his catch for PIT-tagged eels; these were sent to our institute, and subsamples were tested for Sr in their otoliths.

Marking with BaCl₂ in Lake Mälaren

To increase the options and possible combinations for marking a large number of young eels destined for restocking, a test with BaCl₂ was conducted in 2011 at the same quarantine facility as above. In this study, the eels were bathed in water containing 0.75 g l⁻¹ of BaCl₂ *2 H₂O for 24 h at the same conditions used for SrCl₂. In August 2011, 1862 individuals (average size 1.9 g and 110.5 mm) from this batch were then stocked at the same site in Lake Mälaren used for the alizarin marked eels in 1997. 30 otoliths from this batch have so far been analysed with respect to a ring of elevated Ba. This was carried out and verified in a similar way as with Sr. Due to practical reasons, these eels were also marked with SrCl₂ as part of the main tagging procedure described above.

Statistics

The marking success data were analysed using least-squared means from generalised linear methods (binomial distribution, i.e. logistic regression). Marking method and year were used as categorical predictors and length and time (days) since last marking as continuous predictors. The analyses were carried out using SAS statistical software (PROC GENMOD).

Results

Generally, the markings remained to a higher extent on larger individuals \( F_{1,165} = 8.16, P = 0.0048 \), and there were differences among the types of marking \( F_{2,265} = 9.14, P < 0.001 \). There was, however, no effect of year of marking \( F_{1,265} = 1.93, P = 0.148 \) and no effect of time between marking and dissection \( F_{1,165} = 0.84, P = 0.361 \). Strontium (one bath) had higher marking success than both strontium (two baths) \( \left( z = 3.68, P > 0.001 \right) \) and barium \( \left( z = 2.59, P = 0.0096 \right) \). Strontium (two baths) did not differ from barium \( \left( z = 0.61, P = 0.542 \right) \). The values for marking success are given below.

Strontium (one bath)

203 eels (including 30 from the Ba experiment and the 45 with PIT tags) were analysed in total, of these all showed the expected first ring with elevated Sr (Table 3). However, in some eels (the smallest at marked), the rings were very faint. If faint, or situated very close to the outer margin of the otolith, the analysis using a line scan with the WDS detector verified a clearly increased level of Sr (cf. Fig. 2b). The marking success based on 158 otoliths (the PIT-tagged ones with one or two Sr rings, respectively

Table 3. Number of eel otoliths analysed regarding marks with elevated strontium and barium, respectively.

<table>
<thead>
<tr>
<th>Type of sample</th>
<th>Sample size</th>
<th>Marking success (estimate ± SE of the mean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marked once with Sr in 2009–2011</td>
<td>158*</td>
<td>0.9939 ± 0.0307</td>
</tr>
<tr>
<td>Marked twice with Sr in 2009–2011</td>
<td>40</td>
<td>0.8006 ± 0.0415</td>
</tr>
<tr>
<td>Marked once with Ba in 2011</td>
<td>30</td>
<td>0.8452 ± 0.0581</td>
</tr>
<tr>
<td>Recaptures (PIT tags) of Sr-marked eels from Lake Ymsen in 2004, 2007 and 2011 (1 and 2 rings, respectively)</td>
<td>45</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

*Including the 1st ring in eels marked twice with Sr.

Table 2. Number of eels marked and tagged with strontium and PIT-tags, respectively in Lake Ymsen.

<table>
<thead>
<tr>
<th>Year</th>
<th>SrCl₂</th>
<th>PIT tags</th>
<th>Number of baths in Sr</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>1987</td>
<td>1527</td>
<td>1</td>
</tr>
<tr>
<td>2000</td>
<td>1500</td>
<td>1100</td>
<td>2</td>
</tr>
<tr>
<td>2001*</td>
<td>200*</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>2002*</td>
<td>12,281*</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Sum</td>
<td>17,768</td>
<td>2627</td>
<td>–</td>
</tr>
</tbody>
</table>

*Not discussed in this article.
were analysed separately and were excluded from this analysis) was 0.99 (C.L. 0.93–1.00).

**Strontium (two baths)**

In the eels marked for stocking in Finland, the second mark was missing in 8 of 40 otoliths, that is, in 20%. The marking success was 0.80 (C.L. 0.72–0.88). Figure 1 shows a double-marked otolith.

**Barium**

Thirty eels were analysed in a similar way for the presence of a ring with increased Ba. Of these, 26 were marked with a more or less clear ring subsequently verified as Ba. The marking success was 0.85 (C.L. 0.73–0.96). There were no differences in success rates between a Ba-treatment and the Sr (two bath) treatment, but in both cases, eels that had been small when marked were more poorly marked than larger individuals \((F = 8.16, \ P = 0.0048\), logistic regression statistics for type 3 analysis). Figure 2a,b shows both the indicative BSE image and the verifying WDS scans for both elements.

**Alizarin complexone**

Unfortunately, no samples were taken or stored from the batch marked in 1997, but it seems all identified eels so far show either very distinct fluorescence or no mark at all. During a number of years, marked eels have dominated the catch in the cove where they were stocked (Fig. 3). So far, a total of 10% of the stocked marked eels have been recaptured. Taken together, these findings indicate a high marking success rate even though we cannot give an absolute figure.

**PIT tags in combination with SrCl₂**

Since 1999, 159 PIT-tagged eels have been recaptured from almost 35,000 scanned eels of commercial size from Lake Ymsen. As 2627 eels were PIT tagged in 1999–2000, this means a recapture rate of 6.1% up to the present. Of these recaptures, 45 eels were analysed for Sr (Table 3). As in all recaptured (PIT tagged) eels, both size at marking and at recapture were known. All were marked accordingly with one or two rings as assumed (Fig. 1). Eels from the 1999 batch dominated in our sample, that is, they had one ring induced. However, the 1999 batch has been exposed to the fishery for one more year than the 2000 batch.

**An applied example**

Since 2010, recruiting young eels have been monitored along the Swedish West Coast using the ‘drop-trap technique’ (Westerberg et al. 1993). At one site in southern Skagerrak in 2011, four of a total of five eels were found to be marked with Sr; these were from stockings in both 2010 and 2011.

**Discussion**

**Technical issues**

When testing different marking methods for small eels destined for restocking on a large scale, we omitted some methods, for example, oxytetracycline (OTC) which is an antibiotic that we did not want to handle or to spread in the environment. Even though visible implants (VI) and visible implants elastomer (VIE) (Imbert et al. 2007) may be possible to use in
small eels, it is not feasible to tag millions of tiny eels in such a way. The same holds for PIT tags (Riley et al. 2011) and coded wire tags (CWT) (Thomassen et al. 2000), added to which, PIT tags are too big for glass eels. Our experience of marking with alizarin complexone is quite good, and the detection is easily achieved with polished otoliths using a normal microscope equipped with a suitable filter pack and a strong illumination. However, handling this chemical compound in large quantities at a commercial eel farm was not considered as an easy or harmless option (Chemical Book 2010). Our choice was to use a bath of SrCl₂, which probably does not differ to an eel from a bath in a NaCl solution or in sea water. Bathing farmed eels in salt water is a common and frequent measure to improve their health and growth (e.g. Mellergaard & Dalsgaard 1987). The test using Ba as an alternative element for marking eel otoliths seems promising, but the method requires some improvements to increase the marking success rate. Larger eels (at marking) were better marked with Ba than smaller eels. This was also the case with the double (two bath) marking with Sr indicating the importance of good growth and high metabolic rates in the individuals to be marked (Yokouchi et al. 2011).

Fig. 2. (a) A BSE image showing two rings with heavier elements in an eel otolith. (b) A WDS line scan verifying both elevated Sr (left peak) and Ba (right peak) concentrations in an eel otolith.
Management issues

There is a demand for an assessment of the current eel stocking programmes, and eels at any stage can quickly be sampled and analysed for an induced ring of Sr in their otoliths. This can be carried out already today from young recruits in open systems or subsequently in silver eels leaving a specific system, as well as in yellow eels. However, as shown by the ‘applied example’ above, in some recaptures from an open coast, the introduced Sr ring seems to coincide with a ‘false’ translucent ‘handling check’ in the otoliths which can easily be misinterpreted as a translucent winter zone when aged (ICES 2011b). This potential bias of one extra year needs to be taken into account if ageing is performed to identify the year or age class.

As most missing marks of Ba and the 2nd Sr mark were related to small individuals with slow growth, both marking procedures, and the time lag between marking and sampling, have to be reevaluated and improved (cf. Yokouchi et al. 2011).

As an extensive stocking programme may influence existing active monitoring series of young recruits, individuals have to be analysed for otolith marks to avoid biases and inference from recaptured stocked eels that might otherwise be counted as wild recruits.

The different marking methods are compared and summarised in Table 4.

Conclusion

There is a need to evaluate the extensive eel stocking programmes being undertaken in many countries. One way to facilitate such an evaluation is to mark all stocked eels. Inducing marks in the otoliths using Sr worked very well for us, and a similar approach using Ba looks promising. However, extensive marking programmes like this require some cross-boundary collaboration and dissemination of information to allow area-specific marking and to avoid mixing eels from different stocking programmes. The Baltic Sea drainage area may be a suitable unit for such a collaborative and co-ordinated marking programme.

The actual conditions in Sweden, with one single importer and a demand for a quarantine period in heated water, probably simplify a marking programme like ours.

Acknowledgements

This work was carried out in close collaboration with Scandinavien Silver Eel AB and Hans Harbyson at the National Electron Microprobe Facility at Uppsala University. Among all colleagues at the Department of Aquatic Resources contributing to this study, Jennie Dahlberg is specially acknowledged and Erik Petersson who helped out with the statistics. This work was financed within a financial agreement between the Swedish University of Agricultural Sciences and the Swedish Agency for Marine and Water Management.

Table 4. A simplified summary of advantages and disadvantages using some otolith marking methods (by bathing) in eels for restocking.

<table>
<thead>
<tr>
<th>Substance</th>
<th>Marking large numbers</th>
<th>Potential risks</th>
<th>Detection/analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alizarin complexone</td>
<td>Fairly easy, but rather expensive bathing</td>
<td>Rather harmful and ‘messy’</td>
<td>Easy and cheap</td>
</tr>
<tr>
<td>SrCl₂</td>
<td>Easy and cheap bathing</td>
<td>Fairly harmless</td>
<td>Laborious and expensive</td>
</tr>
<tr>
<td>BaCl₂</td>
<td>Easy and cheap bathing but needs further improvement</td>
<td>Less harmless than SrCl₂ (Ba is a more poisonous element than Sr)</td>
<td>Laborious and expensive but needs further improvement</td>
</tr>
</tbody>
</table>
References


Traceability of stocked eels
Effects of the swimbladder parasite *Anguillicola crassus* on the migration of European silver eels *Anguilla anguilla* in the Baltic Sea

N. B. Sjöberg*†‡, E. Petersson*§, H. Wickström* and S. Hansson†

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In a mark–recapture study in 2006, migrating European *Anguilla anguilla* silver eels were caught, tagged and released in the Baltic Sea and recaptures in commercial pound nets examined for possible effects on migration of infection with the swimbladder parasite *Anguillicola crassus*. The overall recapture rate was 36%. The prevalence of infection was lowest at the northernmost sampling site. There were no significant differences between infected and uninfected *A. anguilla* in condition indices, body fat content and estimated migration speeds. Parasite infection intensity levels were significantly negatively correlated with times and distances covered between release and recapture, but did not correlate with migration speed. It appears that more heavily infected *A. anguilla* were relatively more vulnerable to recapture in pound nets. It is hypothesized that parasite-induced damage to the swimbladder inhibited vertical migrations and infected *A. anguilla* tended to migrate in shallower coastal waters, relatively close to the shore.

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**Key words:** parasite incidence; parasite infestation; parasite prevalence; swimming speed; tagging experiment; vertical migration.

**INTRODUCTION**

Recruitment of the European eel *Anguilla anguilla* (L.) has declined in recent decades, possible causes being unfavourable climatic and oceanographic conditions, fishing mortality, migration obstacles, losses of growth habitats, mortality in hydropower turbines, persistent organic pollutants and diseases (Dekker, 2003). Another factor may be the exotic parasitic nematode *Anguillicola crassus* (Kuwahara et al., 1974) that infects the swimbladder and may affect the spawning migrations of anguillid silver eels. The parasite is native to the Japanese eel *Anguilla japonica* Temminck & Schlegel in East Asia, but was introduced to *A. anguilla* via commercial trade in live *A. japonica* (Neumann, 1985; Peters & Hartmann, 1986; Wielgoss et al., 2008) and since 1980 has become widespread in Europe (Moravec, 1992; Kirk, 2003). Since first found in Sweden in 1987, *A. crassus* has been recorded in a large number

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*Alive Anguillicola crassus inside a swimbladder from a recaptured eel.*
Effects of the swimbladder parasite \textit{Anguillicola crassus} on the migration of European silver eels \textit{Anguilla anguilla} in the Baltic Sea

N. B. Sjöberg*†‡, E. Petersson*§, H. Wickström* and S. Hansson†

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of *A. anguilla* from fresh waters and the Baltic Sea (Höglund & Andersson, 1993; Wickström et al., 1998; Gehlin, 2003). In the most recent sampling in Sweden, the prevalence is between 15 and 94% (H. Wickström, unpubl. data.)

The adult stage of the nematode lives in the fish’s swimbladder, and the eggs produced leave the fish through the host’s gut. The larvae emerge in the water and are ingested by an intermediate host, a crustacean. This or another intermediate host (e.g. a fish) is then eaten by an anguillid eel and the nematode migrates into the swimbladder (De Charleroy et al., 1990). This penetration causes changes in the swimbladder wall that can lead to a thickening of the wall and a bladder size reduction (Haenen et al., 1989; Banning & Haenen, 1990; Beregi et al., 1998). The adult parasite feeds on blood and influences the gas exchange in the swimbladder (Würtz et al., 1996).

It has been shown that both larval and adult stages of the parasite induce stress responses (Sures et al., 2001). The larval stage of the nematode is suspected to have caused mortality in aquacultured American eel *Anguilla rostrata* (Lesueur) (Ooi et al., 1996). Nematode-infected *A. anguilla* may also be more sensitive to other stressors, such as high temperatures or hypoxia, thus resulting in increased mortality (Molnar, 1993). In laboratory studies (Sprengel & Lüchtenberg, 1991), the parasite appears to influence the swimming performance of small *A. anguilla* in the yellow eel stage. The cruising speed of infected anguillid eels in the silver eel stage was reduced in swim-tunnel experiments (Palstra et al., 2007). Vertical diel migration also appears to be an important component of *A. anguilla* and *A. rostrata* silver eel migratory behaviour (Facey & Van Den Avyle, 1987; Tesch, 1989, 1995; Tesch et al., 1991; Westerberg et al., 2007). If parasites cause damage, this may influence the secretion of gas into the swimbladder, thus reducing the fish’s ability to regulate buoyancy and hence affect its vertical migration.

The aims of the present study were to assess whether the swimming and migratory behaviours of *A. anguilla* silver eels attempting to leave the Baltic Sea might be negatively influenced by the parasite’s effect on swimbladder structure and function. This in turn could help indicate whether the ability of infected fish to complete their migration to the Sargasso Sea and to contribute effectively to the spawning stock is compromised. The study comprised part of a major mark–recapture study and involved assessing the prevalence and intensity of parasite infections in recaptured and reference *A. anguilla* silver eels. Correlations between infection intensity and time elapsed, speed of movement and distance covered between release and capture sites (pound nets in coastal waters) were then estimated.

**MATERIAL AND METHODS**

**TAGGING PROCEDURE**

During the autumn of 2006 emigrating *A. anguilla* (*n* = 707) were caught with pound nets (Berntsson, 1971) at four locations along the Swedish Baltic Sea coast (Fig. 1). Total length (*L* _T_) and wet mass (*M*_ _W_) were measured. A digital calliper was used for measuring the eye diameter and the calculated eye index *I* _E_ was then used to determine maturation stage according to Pankhurst (1982). The fish were tagged with a Carlin dangler (a 18 × 4 mm plastic plate with a mass c. 0.12 g (McFarlane et al., 1990)) that was attached in front of the dorsal fin. As the Carlin tags were small, it was assumed that their influence on the large *A. anguilla* used was minimal (Jepsen et al., 2002). Each tag had a unique number and
a text urging the fisherman to freeze the fish and contact the Swedish Board of Fisheries. The tagged fish were released at the site of capture, and recaptured in pound nets along the coasts of the Baltic Sea. The primary objective of this study was to assess the contribution of stocked young A. anguilla to the silver eels leaving the Baltic Sea. The sampling protocol was, therefore, not optimized for studying effects of A. crassus on swimming behaviours.

MEASUREMENTS AFTER RECAPTURE

Because the fish had been frozen, $L_T$ and $M_W$ were corrected for shrinkage (Wickström, 1986). Each swimbladder was searched for adult (from L4-stage) specimens of A. crassus (De Charleroy et al., 1990) and the prevalence (percentage of fish infected in each sample) and intensity (number of parasites per infected fish) were recorded. Standardized muscle samples for fat determination were taken (Svedäng & Wickström, 1997), and the fat content ($F_C$) was measured by the EC-method B (Anon, 1998) and expressed as % fat in fresh muscle on a wet-mass basis. Eye-size measurements were repeated. The condition index ($K$) was calculated according to Fulton (1904) and age readings were carried out by counting the winter zones in the sagittal otoliths (Svedäng et al., 1998). The distance covered between points of release and recapture was measured as the shortest route in open water (and across islands if <2 km in length). The migration speed was derived as the distance covered in km day$^{-1}$.

REFERENCE SAMPLES

To allow for comparisons between recaptured A. anguilla and those caught only once, samples were taken from commercial catches derived at the same sites and by the same

Fig. 1. The four release sites in the Baltic Sea used in the Anguilla anguilla tagging experiment in 2006. Except for Borgholm, these are also the locations where reference samples were collected.
fishermen who supplied fish for the tagging experiment. These reference data are available for two consecutive years (2005 and 2006; Table I) and are used to evaluate possible variation in e.g. K, maturity stage, A. crassus prevalence and intensity between years. Because the references formed a part of the Swedish Board of Fisheries’ extensive sampling programmes according to the Data Collection Regulation (Anon, 2008), not all variables were available (see Table II for details).

Some of the reference A. anguilla from site Hanö (N = 451) and Marsö (N = 265) were collected from the same fisherman but analysed at two laboratories, one of which showed a consistently lower prevalence of A. crassus. This discrepancy was due to the fact that the personnel at the two laboratories were differently skilled in discerning A. crassus in the swimbladder. The worms are not always easy to detect and are sometimes hidden among blood vessels. This error was accounted for as follows: using A. anguilla from a single catch, one laboratory recorded A. crassus in 41.6% (201 out of 483) of the fish, and the other laboratory in 53.5% (107 out of 200). The ratio (53.5:41.6 = 1.3) was used to adjust upwards for the first laboratory and the inverse (0.8) was used to adjusted downwards for the other laboratory. In this way, the total number of A. anguilla was insignificantly changed and hence the G-value (differences in frequencies were analysed with a likelihood ratio \( \chi^2 \) test) and significance value were not exaggerated or diminished.

**DATA ANALYSIS**

Differences between means were analysed using a \( t \)-test (two samples) or with ANOVA (three or more samples). In some analyses, \( L_T \), \( M_W \) and distance covered between release and recapture sites were used as covariates to account for the effect of these variables. In these cases, ANCOVA have been used. For correlations, the effects of \( L_T \) and \( M_W \) were adjusted for, by using residuals from linear regressions. If the data were not normally distributed, normality was achieved using log10 transformation before analyses. Differences in frequencies were analysed (G-value). As mean \( L_T \), infection intensity and prevalence differed between the sites, the correlation between these ‘and other’ variables was estimated by pooled correlations. In order to further analyse the differences between infected and uninfected A. anguilla, a logistic regression was done. For all statistical analyses, SAS statistical software was used (SAS, 2002–2003; www.sas.com).

**RESULTS**

**PARASITE PREVALENCE**

Out of 707 A. anguilla tagged and released, 254 (36%) were reported recaptured. For both infected and uninfected specimens, the overall direction of movement was southward, as expected for A. anguilla silver eels on their way out of the Baltic Sea. They were all caught along the Swedish and Danish shores, but none was recaptured.
in the Kattegat or Skagerrak as there are no fisheries for migratory Baltic *A. anguilla* north of the Öresund.

Of the recaptured fish, 190 were available intact and could be further analysed. Out of these, 58% had *A. crassus* (from L4-stage) in their swimbladders (*N* = 111). The prevalence differed significantly among the release sites (*χ²*, *G* = 24.54, *P* < 0.05) with the lowest values occurring in fish caught at the northernmost location (Väddö; Table II).

The value of *K* and *F*C did not differ between infected and non-infected fish [reference fish *t*-test, *n* = 868, *P* > 0.05 (*K* and *F*C); recaptured fish *t*-test, *n* = 188, *P* > 0.05 (*K* and *F*C)], nor did the migration speed (recaptured fish *t*-test, *n* = 190, *P* > 0.05).

Between marking–release and recapture, the change in *K* of recaptured *A. anguilla* was correlated with distance covered (*n* = 184, *r* = −0.41, *P* < 0.001), the longer they had swum, the higher was the reduction in *K*. An ANCOVA, however, showed that infected and uninfected *A. anguilla* did not differ significantly in this respect (ANCOVA, *n* = 184, *P* > 0.05).

The logistic regression showed that the only variable in this dataset that could be used to separate infected and uninfected *A. anguilla* among the recaptures was covered distance (*χ²*, *P* < 0.05). The other variables included in the analysis (*I*<sub>E</sub>, *L*<sub>T</sub>, *M*<sub>W</sub>, *K*, age, *F*C and number of days) were not significant.

For two out of the release locations, *A. crassus* prevalence was significantly higher among the recaptures (Fig. 2; *χ²*, Marsö *P* < 0.01 and Hanö *P* < 0.001). When comparing prevalence frequencies in recaptured fish with the frequencies in reference fish caught 1 year earlier (2005), only recaptured *A. anguilla* from Hanö had significantly higher prevalence (Fig. 2; *χ²*, *P* < 0.05).

![Graph](image_url)

**Fig. 2.** Prevalence of *Anguillicola crassus* in the swimbladder of recaptured *Anguilla anguilla* (rec) and reference *A. anguilla* (ref) in 2005 (□) and 2006 (■). Bars denoted with the same lower case letter are not significantly different (*P* > 0.05).
PARASITE INCIDENCE

The number of *A. crassus* in recaptured eels varied considerably (*n* = 0–49). In the analyses below, both infected and uninfected eels were included. For both recaptured and reference *A. anguilla*, neither *F*<sub>C</sub> nor *K* correlated significantly with the number of *A. crassus* (pooled correlation, *n* = 302, *P* > 0.05). Among the recaptures, the infection intensity did not correlate with migration speed (pooled correlation, *n* = 190, *P* > 0.05). Distance covered, however, correlated significantly negatively with the number of *A. crassus* (Fig. 3; pooled correlation, *r* = −0.20, *n* = 190, *P* < 0.05), and the number of days between release and recapture decreased significantly with the number of *A. crassus* in the swimbladder (Fig. 4; pooled correlation, *r* = −0.19, *n* = 190, *P* < 0.05).

DISCUSSION

The principal aim of this study was to assess whether the migration of *A. anguilla* out of the Baltic Sea might be affected by *A. crassus*, leading to possible failure to reach the Sargasso Sea spawning area. Neither the migration speed (this study), nor the short-term swimming activity or capacity (Münderle *et al*., 2004) appears to be influenced by the parasite. These findings contradict the results of Sprengel & Lüchtenberg (1991) and Palstra *et al.* (2007) who found a negative relation between swimming speed and parasite infection. The reasons why these conclusions differ are unclear. Münderle *et al.* (2004) and Sprengel & Lüchtenberg (1991), however, used relatively small *A. anguilla* yellow eels; a comparison with this study’s findings, based on data from emigrating *A. anguilla*, may therefore be inappropriate.
The principal aim of this study was to assess whether the migration of *A. anguilla* is affected by *A. crassus* nor the short-term swimming activity or capacity (Münderle et al. 1991) and Palstra to reach the Sargasso Sea spawning area. Neither the migration speed (this study), &Lüctenberg (1991) and Palstra to be influenced by the parasite. These findings contradict the results of Sprengel correlation, *A. crassus* significantly with the number of recaptures, the infection intensity did not correlate with migration speed (pooled correlation, *A. crassus* negatively with the number of *A. anguilla* recaptured and reference correlation, *A. crassus*.

Palstra et al. (2007), however, used migrating *A. anguilla* silver eels but measured the swimming speed in experimental swim tunnels. The applied mark–recapture approach in this study does not give detailed information about the exact behaviour between release and recapture, and it is certainly more difficult to detect differences in swimming and migration speed at sea. Furthermore, clear comparisons cannot be made with swim-tunnel results because anguillid eels in tunnels cannot rest or make vertical movements and they are not exposed to natural physical factors (e.g., currents and lunar phases) or biological interactions (e.g., predation).

This study is based on data from natural conditions (except that the fish had been caught and tagged) using migratory *A. anguilla* heading towards the Atlantic Ocean. Some of the fish did not fulfil the normal silver criteria suggested by Pankhurst (1982). Besides minor deviations in eye size due to shrinkage during freezing and measurements errors (Acou et al., 2006), migrating *A. anguilla* silver eels from most Swedish localities seem to be in an earlier stage of maturation than those from elsewhere in Europe. One reason may be that *A. anguilla* from remote areas such as Swedish lakes and the Baltic Sea start their spawning migration relatively early, often in August to September, and may be at relatively early stage of maturation. It might be questioned if such fish, with $I_E$ of <6.5, are true silver eels. Such fish had a silvery appearance (e.g., black back, silver–white belly and conspicuous lateral line) and are caught in the same gears, at the same time and at the same fishing sites as more mature *A. anguilla* silver eels. Therefore, it is considered that fish were in the beginning of the spawning migration and could be used for migration studies like this one.

Non-infected *A. anguilla*, or those with low infection intensity, covered longer distances and migrated for longer periods of time before getting caught in the

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**Fig. 3.** Relationship between distance covered between release and recovery sites and log 10 of *Anguillicola crassus* incidence (number per swimbladder). Number of days decreases significantly with number of *A. crassus* (pooled correlation with regard to difference between release sites, $n = 190, P < 0.05$). The curve was fitted by: $y = 27.27 \times 9.90 \log_{10} x$.
fishing gears. It is possible, however, that the effect of the parasite has been underestimated, because some A. crassus-free A. anguilla might have been infected earlier in life and that this still influenced their behaviour. To account for such discrepancies in future studies, more precise measurements of current and historic parasite load should be considered, e.g. classification according to the thickness of the swimbladder wall as a possible proxy for former infestation. Total parasite mass and swimbladder size may also provide more informative and precise data (Palstra et al., 2007).

Westerberg et al. (2007) showed that A. anguilla in the Baltic Sea tended to rest on the seabed during the day and migrated in the night when they also undertook vertical migration. A conceivable explanation for the results reported in this study is that the A. crassus infection has impaired the swimbladder function to such an extent that it affects the fish’s migration behaviour. Infected A. anguilla may avoid deeper waters, where vertical migration can be expected to be more demanding on the swimbladder function. A consequence of this could be that they tend to stay in shallower water closer to the shore and become more exposed to pound nets, thus explaining the faster recapture of heavily infected fish. This theory is also in line with the fact that recaptured A. anguilla had significantly higher A. crassus prevalence than the references when comparing the results from the same year (Fig. 2).

Anguillicola crassus infection does not appear to affect the fat level or condition factor of Baltic Sea A. anguilla, as also shown by Möller et al. (1991) and Moser et al. (2001). Palstra et al. (2007), however, proposed that heavily infected A. anguilla silver eels need at least 20% more energy reserves to manage the spawning migration because of damaged swimbladders. An impaired swimbladder function (e.g. disturbed gas secretion and less flexible wall) can affect the migrating fish in different ways. Inability to inflate the swimbladder may force the fish to swim more intensively to maintain a desired position in the water column or they may sink and be forced to migrate at unfavourable depths. Another alternative effect is that the filling and emptying of the swimbladder will be slower and that the fish in response stay above shallower bottoms where the demand on the swimbladder’s functionality is less. This study’s results support the latter explanation.

An implication of reduced ability for vertical migration, as indicated by this study, is that infected A. anguilla migrating in the Atlantic Ocean may suffer from a decreased ability to obtain a beneficial combination of pressure and temperature that would allow efficient energy utilization by aerobic and anaerobic pathways (Scaion & Sébert, 2008; Scaion et al., 2008). As a consequence, the cost of transport would increase, making the fish less fit for spawning when arriving at the Sargasso Sea. Even if infested A. anguilla reach the spawning grounds in time, they may not be ready to spawn if they have not been normally exposed to high pressures (great depths) because this may be needed to increase the production of hormones associated with the sexual maturation (Dufour & Fontaine, 1985).

Münderle et al. (2004) claim that dysfunctional swimbladders may result in reduced swimming speed. The present study shows that migration speed is unaffected, but the behaviour could result in the fish missing the spawning grounds by getting caught in fisheries along the coastline. If the damaged swimbladder forces the A. anguilla to migrate without undertaking the vertical and deep-water migrations, they may become more exposed to visual predators. Furthermore, irrespective of
whether fish with an impaired swimbladder avoid or sink to deep water, this could lead to navigational problems because vertical migration may be required to derive directional cues, for example, earlier imprinted vertical and horizontal components of magnetic fields (Lohmann et al., 2008).

In Sweden, A. crassus have been frequently found in areas receiving thermal discharge from nuclear power plants (Höglund et al., 1992; Höglund & Andersson, 1993). Larval transmission, parasite establishment and development in A. anguilla is positively affected in these warmer environments (Höglund & Thomas, 1992). This is consistent with the findings presented in this study, i.e. the prevalence was significantly lower among fish from the northern and hence colder location (Väddö). The results thus support the hypothesis that the spread of the parasite is connected with the natural ambient temperature regimes (Knopf et al., 1998).

Stocking is one means of compensating for reductions in natural recruitment, both in Sweden, as in other European countries. The results of this study suggest that stocking should ideally take place in areas where the presence of A. crassus is low and where condition indices are relatively high, so as to maximize chances of A. anguilla being able to reach the Sargasso Sea. Consequently, stocking should preferably be done in the northern Baltic, provided that the fishing pressure they are exposed to when migrating southwards is sufficiently low to allow a high escapement rate.

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Note yellow Carlin tags – used in more recent taggings.
Assessment of the fishing impact on the silver eel stock in the Baltic using survival analysis

Willem Dekker and Niklas B. Sjöberg

Abstract: Restoration of the depleted stock of the European eel (Anguilla anguilla (L.)) requires anthropogenic impacts to be quantified, reduced, and controlled. In this article, we assess the impact of the silver eel fishery on the Baltic Coast in Sweden, applying survival analysis to 60 years of mark–recapture experiments, involving 8000 recaptures out of 18 000 releases. The hazard of being recaptured (overall 46%) varies along the coast and declined substantially over the decades. But, most notably, the hazard for the individual diminishes strongly after the first kilometres en route. This individualized hazard disqualifies the more traditional mark–recapture methodology, which assumes random recaptures. We advocate the general use of survival analysis for conventional mark–recapture data. The result of our analysis indicates that the impact of the fishery just prior the 2009 fishing restrictions was in the order of 10%—in itself well within sustainability limits, though only but one of the factors contributing to the mortality in the Baltic Sea.

Introduction

The population of the European eel (Anguilla anguilla (L.)) is in severe decline. Fishing yield has gradually declined in the past century to below 20% of former levels, and recruitment has rapidly declined to 1–5% over the last three decades (Dekker 2004; ICES 2012). In 2007, the European Union (Anonymous 2007) implemented a regulation establishing measures for the recovery of the stock of European eel (Dekker 2008), obliging EU Member States to develop a national Eel Management Plan, in which the state of the stock and the anthropogenic impacts (fisheries and other mortalities) are assessed. In this article, we assess the impact of the fishery on the silver eel migrating along the Swedish coast of the Baltic Sea, before the fishing restrictions of the Swedish Eel Management Plan (Anonymous 2008) were implemented. This requires the estimation of the (relative) mortality exerted, as well as an estimate of the (absolute) quantity of eel exploited, by this fishery (Dekker 2010).

Direct estimates of the population of silver eel escaping from a river have been made using traps spanning the river mouth (e.g., Wolf traps; Vallestad and Jonsson 1988; Poole et al. 1990; Poole 1994; Wickström et al. 1996; Feunteun et al. 2000; Acou et al. 2008) or fish counters (Biolletta et al. 2011). These techniques are by their very nature restricted to smaller rivers and thus excluding all stocks in major river systems and coastal waters (Dekker 2003). In recent years, an increasing number of studies have used mark–recapture experiments to quantify the size of the silver eel run and the impact of the fishery. The silver eel population, however, does not constitute a standing stock in the classical sense of mark–recapture analysis, but a run of individuals migrating through a study area during a prolonged season. This introduces inherent spatial and temporal heterogeneity in capture probabilities, which causes a simple mark–recapture analysis (e.g., a pooled Petersen index) to severely underestimate the population number. A time-stratified variant of the Petersen model allows for varying recapture probabilities (Darroch 1961; Plante et al. 1998). However, most mark–recapture studies on silver eel use an unstratified estimator (Feunteun et al. 2000; Pedersen and Dieperink 2000; Rosell et al. 2005; Klein Breteler et al. 2007; Winter et al. 2007; McCarthy et al. 2008; ICES 2011; Charrier et al. 2012). We could find only two studies applying the procedure of Darroch–Plante (Caron et al. 2003; Amilhat et al. 2008).

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1Different life stages of the eel have specific names: the transparent youngsters coming from the Atlantic Ocean towards the European coasts are called glass eels; in the growing phase, they are known as yellow eels; when finally starting maturation and returning towards the ocean, they are called silver eels.

2All eels in Europe and northern Africa are considered to belong to a single panmictic stock, forming one “biological population”. In mark–recapture techniques and in statistical analyses, the animals at large from which a sample is taken are conventionally indicated as the “statistical population” being sampled—in our case, the run of silver eels towards the ocean during a specific season in a restricted area (but not the yellow eels that belong to the same local stock). In this article, we use “silver eel population” to avoid potential confusion.
Resident yellow eels occur from the river headwaters out to the coastal areas and silver eels may recruit to the run at any place or time within this range, i.e., both the mark-and-release and the recapture-sampling of silver eel necessarily take place within productive habitats. Mortality estimates from mark–recapture studies relate to the site and time of marking, disregarding the eels recruiting downstream and thus biasing the assessment (Winter et al. 2007). Consequently, the size of the most downstream stratum is critical. Making this stratum as small as possible reduces the bias mentioned by Winter et al. (2007)—but that will also reduce the number of recaptures in the last stratum and hence increase statistical uncertainty in the estimates. Rather than choosing between this devil and the deep blue sea, we opt for the use of survival analysis—the continuous and more versatile generalization of discretely stratified mark–recapture models (Pollock et al. 1995; Yip et al. 2005). Survival analysis and mark–recapture analysis have been compared by Viallefont et al. (1999) using a data set concerning 995 women with metastatic breast cancer, concluding that capture–recapture models should obviously not be used when the dates of death are available, as is the case in almost all fish tagging experiments. We know of no previous study applying survival analysis to classical fish tagging data.

Survival analysis has been applied to study American eel by Castro-Santos and Haro (2003), analysing the delay in migration that eels incur when approaching a hydroelectric facility. Their study being focused on individual time delays, it has no relevance to the present analysis. Survival analysis is frequently applied in telemetry studies (Pollock et al. 1995), but results are rarely, if ever, used for estimating population characteristics.

We apply survival analysis to more than half a century of mark–recapture data from the Baltic coast in Sweden and derive an estimate of the total silver eel run, using historical landings records. Though using survival analysis for the analysis of conventional fish mark–recapture data constitutes a methodological step forward, our main focus is on the Baltic silver eel population. Having said that, adapting to the complexities of the eel case and testing the basic assumptions of mark–recapture studies is probably the best means of demonstrating the value of survival analysis for analysing conventional fish tagging data.

Materials and methods

Study area and fisheries

The Baltic Sea is a 377 000 km² brackish sea in northern Europe, which is almost completely enclosed by land (Fig. 1). In the southwest, it drains through narrow and shallow connections via the Kattegat and Skagerrak into the North Sea and on into the Atlantic Ocean. On the Swedish coast, the Kullaberg hill (56.30°N, 12.45°E) marks the outlet. The average depth of the Baltic is 62 m, with a maximum of 459 m. Our analysis is focused on the Swedish coastal areas, which are dominated by rocky shores and an extensive archipelago in the north. Towards the south, there is a more open, sandy shore. The salinity of surface waters varies from 5‰ in the north to 10‰–15‰ in the southern parts.

The Swedish territory is divided into counties, referred to by their official code (and name) as indicated in Fig. 1. Eel occurs in many different coastal and inland habitats all over the Baltic area. Stock densities vary, naturally as well as by restocking of young eel. North of county AB (Stockholm, 60°N), stock densities rapidly decline, though eels have been found all over the area. Upon silverying in summer (north) and fall (south), eels leave their habitats in rivers and along the coast, and migrate toward the Baltic Sea outlet. All along the Baltic coast, but especially in the vicinity of the outlet, an extensive coastal fishery for silver eel occurs, using very large fykenet-type nets, called pound nets or bottengarn (Berntsson 1971). Beyond Kullaberg, there is no directed fishery for silver eel; the silver eel that pass by do not come close enough to the shore to be fished (Lundberg 1881). It is generally believed that the pound net fishery targets silver eel derived from all over the Baltic area. In addition, there is a smaller fykenet fishery, primarily targeting resident yellow eel. Both fisheries are operated by small-scale, rural companies.

For the purpose of this study, we identify a position along the coast by its distance from Gävle (shortest route in kilometres (km) along a convex hull around the Swedish coastline, ignoring potential short-cuts in-between the islands); Gävle is the town just north of the northernmost release site. The outlet of the Baltic at Kullaberg is almost exactly 1000 km from Gävle. In addition to this, we use the relative distance travelled by an individual, as the distance from its release to its actual position. To avoid confusion, we use the terms “position” for the distance from Gävle and “kilometrage” for the distance from the individual’s point of release.

The simplification from a two-dimensional spatial position to a one-dimensional distance along the coast generates some distortion, notably for 49 recaptures at far westerly positions (Great and Little Belt, Denmark, up to 1100 km from Gävle. In total, 1130 recaptures were reported from Danish waters). These westerly positions are coded as being beyond the outlet at Kullaberg, while strictly speaking they were still inside the Baltic. Given the low numbers involved, this was not corrected for. Our results show only a very minor mortality beyond Kullaberg.
Data

Tagging experiments

Tagging experiments have been executed throughout the 20th century. In 1903, the first experiment was performed 150 km north of Stockholm (Trybom 1905) to identify the migration routes of the silver eel. Later on, experiments were held to investigate what impact various anthropogenic activities (paper mills, bridges, electric supply cables, etc.) had on fish and fisheries. More recently, Westin (1998) investigated whether silver eel of re-stocked and of natural origin showed the same migration behaviour.

Two types of tags have been used (Fig. 2). Until the late 1960s, tags made of silver plate were applied (Trybom 1905); later on, Carlin tags were preferred (Carlin 1955). Why this change was made is not recorded, but presumably, the price of silver became an obstacle for larger tagging experiments. There are only two years (1967 and 1968) in which both tag types have been used in parallel (four experiments), but unfortunately, tag types were not recorded for the individual recaptures. To our knowledge, differential tagging mortality and catchability for these two tag types have never been analysed. Therefore, we can but tentatively assume that differences are negligible.

In all tagging experiments, eels were collected from pound nets along the coast, visually classified as silver stage, tagged, and released. Biological measurements (length, weight, etc.) were probably taken during all decades, but except for the most recent years, these records appear to have been lost.

Throughout the 20th century, ongoing experiments were advertised in newspapers and fishery officials were kept informed. Fishers were rewarded for their recaptures, often via local fishery officers.

Data collection

Records from historical and more recent tagging experiments were extracted from archives and combined into a single database (Table 1). Data were thoroughly checked and groomed where necessary. If only the month was given, the 15th day was assigned to the record. Similarly, where only the county but not the exact location was given, a tentative position in the middle of the county was assigned.

In several experiments (1959, 1974, and intermittently since 1982), eels have been experimentally manipulated (e.g., blocking of nostrils, deliberate translocation between capture and release site, etc.). These data have been excluded from the current analyses.

Before 1980, the number tagged (3095) was much lower than in later experiments (17 960). We, therefore, excluded all experiments undertaken prior to 1950 from our analyses.

In parallel to the experiments in coastal areas, eels have also been tagged and released in inland lakes and rivers, and some of these have been recaptured in the coastal fishery. These recaptures from inland releases were not included in the current analyses.

Landings data

Statistics of catch and landings have been kept since 1914, but the time series are far from complete, and the reporting system has changed several times. Before 1978, data were broken down by county (lin); after 1998, individual landings locations were reported (which we grouped by county); for the years in-between (1978–1998), only a rough breakdown into three areas (east/south/west) has been used. For these in-between years, the more detailed breakdown by county is reconstructed on the assumption that the relative contribution of each county has remained stable between 1970 and 2010. A few remaining location problems (e.g., confusion caused by traders living exactly on the border between counties) have been resolved on an ad hoc basis. Figure 3 shows the (reconstructed) time series by year. In most recent years, the detailed data and the official statistics show an increasing discrepancy. The calculation of fishing impact uses the landing per county averaged by decades, prioritizing data sources giving the most detailed information.

There is little historical information on the composition of the landings by life stage. Fishermen report that the fraction of yellow eel on the east coast has declined, but the decline in the absolute quantity might have confused these observations. Certainly, in recent years yellow eel constitutes less than 10% of the total in the east and south (in contrast to 90% on the west coast, beyond Kullaberg). In the absence of pertinent information, all landings on the east and south coast were supposed to consist of silver eel only (i.e., a bias of some 10% is accepted). The west coast is not considered in the current analysis, because of the absence of silver eel in this fishery.

Survival analysis

Survival analysis studies the time until an event occurs for the individual, rather than the number of events observed in a particular time interval. In our case, the recapture and reporting of a tagged eel is the event and the interval between release and recapture is the quantity analyzed. In the following, we consider the choice of the primary axis (time or distance); the influence of tag-loss, natural mortality, and under reporting; and the level of detail in the analysis that the historical data can support.

Temporal or spatial axis

Survival analysis has been applied in sociology, engineering, economics, medical research, epidemiology, and many other disciplines (Allison 2010). In actuarial science, limits on product warranties can be related to either the time since the product was acquired or to the usage of the product (e.g., mileage for a car, number of copies for a photocopier, etc), or even to both (Wu 2012). For our silver eel, the hazard of capture might be related to the time between release and recapture or to the kilometrage the individual has made since release. The choice of time or kilometrage affects our ability to adequately analyze the non-recaptured individuals. For a space-structured analysis, the observation ends when either the eel has been recaptured (event) or the eel passes Kullaberg—and thus escapes from further observation (censoring). Any eel that has not been recaptured and has not crossed Kullaberg is still at large somewhere between the release site and Kullaberg; thus, this eel is still at risk of being recaptured. Kullaberg is the natural censoring location for any eel that has not been recaptured.

For a time-structured analysis, the censoring is less evident. Any individual eel that has not been recaptured might or might not be at large, depending on whether that individual has or has not left the Baltic on the date considered. After it has left, time continues; however, being outside the area, the eel is no longer at risk. This
individual should have been censored on the date it left, but that
date remains unknown for the individual.
For the silver eel population as a whole, the earliest recaptures
close to the outlet occurred in mid-August (disregarding 6% of the
recaptures that had stayed over the winter) and latest releases
occurred in November (crossing Kullaberg in November or later).
Eels might have passed Kullaberg on any date in-between August
and November, or even later. Whatever generic censoring date
between August and November is chosen, some individuals had
already left before, while others had not been released yet. An
earlier generic censoring date would result in a higher number of
individuals released afterwards, while a later date increases the
number of individuals that actually left before. Hence, there is no
acceptable generic censoring date.
Because of the inability to specify a censoring date for a time-
structured model, we select the spatial structure. This choice pro-
hibits all time-related covariates from the analysis (including the
time passed since the release), since it is unknown at what date an
individual has crossed any specific point in space. However, the
date of the release itself is fixed for each individual, and it could be
included as a covariate. This date expresses the effect of early or
late tagging and release—not of early or late migration or fishing.
The most recent tagging was done in 2008, releasing 221 eels;
the data set was updated in spring 2011, more than two years later.

Table 1. Data sources on silver eel tagging experiments and numbers of individuals involved. Publications in which the eels were experimentally manipulated have been excluded.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Releases</th>
<th>Recaptures</th>
<th>Years</th>
<th>Counties*</th>
<th>Tag type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trybom 1908</td>
<td>250</td>
<td>53</td>
<td>1905</td>
<td>H, M</td>
<td>Silver</td>
</tr>
<tr>
<td>Trybom and Schneider 1908</td>
<td>300</td>
<td>63</td>
<td>1906</td>
<td>E, H, M</td>
<td>Silver</td>
</tr>
<tr>
<td>Hessle 1929</td>
<td>600</td>
<td>41</td>
<td>1927–1928</td>
<td>I, H</td>
<td>Silver</td>
</tr>
<tr>
<td>Hessle 1931</td>
<td>200</td>
<td>12</td>
<td>1930</td>
<td>H</td>
<td>Silver</td>
</tr>
<tr>
<td>Ask and Erichsen 1976</td>
<td>10 749</td>
<td>5306</td>
<td>1941–1968</td>
<td>C, AB, H, K, M</td>
<td>Mix†</td>
</tr>
<tr>
<td>Neuman and Thoresson 1979</td>
<td>800</td>
<td>341</td>
<td>1975–1977</td>
<td>H</td>
<td>Carlin</td>
</tr>
<tr>
<td>Unpublished data (authors’ archives)</td>
<td>409</td>
<td>95</td>
<td>1984–1994</td>
<td>AB, H, I, K</td>
<td>Carlin</td>
</tr>
<tr>
<td>Westin 1998</td>
<td>219</td>
<td>77</td>
<td>1991</td>
<td>D</td>
<td>Carlin</td>
</tr>
<tr>
<td>Sjöberg and Wickström 2008</td>
<td>600</td>
<td>217</td>
<td>2006</td>
<td>AB, H, K</td>
<td>Carlin</td>
</tr>
<tr>
<td>Sjöberg et al. 2008</td>
<td>200</td>
<td>33</td>
<td>2008</td>
<td>AB</td>
<td>Carlin</td>
</tr>
<tr>
<td>Total before 1950</td>
<td>3095</td>
<td>849</td>
<td>1903–1949</td>
<td>AB, E, H, I, K, M</td>
<td></td>
</tr>
<tr>
<td>Total after 1950 (inclusive)</td>
<td>17 960</td>
<td>8224</td>
<td>1950–2009</td>
<td>C, AB, D, H, I, K, M</td>
<td></td>
</tr>
<tr>
<td>Grand total</td>
<td>21 055</td>
<td>9073</td>
<td>1903–2009</td>
<td>C, AB, D, E, H, I, K, M</td>
<td></td>
</tr>
</tbody>
</table>

* C, Uppsala; D, Södermanland; E, Östergotland; H, Kalmar; I, Gotland; K, Blekinge; M, Skåne; AB, Stockholm (see Fig. 1).
† 10 359 silver tags and 390 Carlin tags released; tag type of 5306 recaptures unknown.

Fig. 3. Trend in landings from the coastal fisheries, by county (colours) and area (black lines). In the years 1978–1998 (faded), due to a lack of
detailed records, it has been assumed that the percent-wise contribution of each county had remained constant. Note that the total landings
on the Baltic coast come predominantly from six counties (AB, E, H, K, M, O) and that the contribution from other areas is barely visible in
this graph.
Earlier experiments indicate that after two years less than 0.2% of the releases are recaptured—less than 1 eel from the 221 released in 2008 would be expected to be reported after 2011. The finite observation period thus leads to an insignificant loss of information.

**Model specification**

An introduction to survival analysis can be found in Allison (2010); our terminology and notation follows his. In particular, we use the word hazard, where in population assessment one would use the word mortality.

Standard applications of survival analysis most often concern the time until an event occurs, denoted by \( t \), while \( T \) is the moment the event actually occurred. Our analysis relates to positions along the coast rather than time, but in keeping with the literature (e.g., Duchesne and Lawless 2000), we keep the time-related notation and wording, using \( t \) and \( T \) also for the positions reached. The kilometrage of an individual thus belongs to the time-dependent variables.

We developed a series of four models of increasing complexity. The more complex models make less stringent assumptions, but they place higher demands on the statistical “design” of the experiments. For our historical data, the design is far from being optimal, so a best balance between assumptions and statistical power has to be found.

We define the survival function \( S \) as the probability to survive up to \( t \), that is the probability that the event (recapture) happens at some \( T \) beyond \( t \), i.e.,

\[
S(t) = \Pr(T > t)
\]

The hazard function \( h(t) \) is defined as the probability that an event actually happens at \( t \)

\[
h(t) = \frac{\text{number of events at } t}{\text{number at risk at } t} = \frac{dS(t)}{S(t)} = -\frac{d \log S(t)}{dt}
\]

In the first step of our analysis, the survival and hazard functions were estimated directly from the data by the Kaplan–Meier method (Kaplan and Meier 1958). The Kaplan–Meier estimate of the survival function \( S(t) \) is the ratio of the number of individuals alive (released, but not recaptured before \( t \)) to the total number of individuals (released before \( t \)). We present the total hazard from any position \( t \) towards the outlet at Kullaberg, numerically summing the Kaplan–Meier estimate from \( t \) to Kullaberg.

Kaplan–Meier estimates reflect the sample rather than the population sampled. The representativeness of the historical data for the population of silver eel is questionable, because of the very unequal spatial distribution of releases between decades (Fig. 4).

For the second step, the most commonly used model is the proportional hazards model (Cox 1972), which assumes that hazard rates \( h(t) \) can be expressed as a baseline hazard function \( h_0(t) \) multiplied by an effect of known covariates \( Z \) (with estimated parameters \( \beta \)), so that for the \( i \)th individual the hazard is

\[
h_i(t) = h_0(t) \times \exp^{\beta Z_i}
\]

which separates the time-dependent effect \( h_0(t) \) shared by all individuals from the covariate-dependent effects \( \exp^{\beta Z} \) which differ between individuals. The baseline hazard \( h_0(t) \) is estimated, as well as the parameters \( \beta \) that scale the individual’s hazard proportionally to the baseline. We present the hazard from any point \( t \) to Kullaberg,

\[
\int_{t}^{\text{Kullaberg}} h_0(u)\,du = \exp^{\beta Z_i} \times \int_{t}^{\text{Kullaberg}} h_0(u)\,du
\]

which does not depend on the point of release \( t \). We present this hazard from \( t \) to Kullaberg for standardized individuals (modal week of release, for each decade separately, for all observed positions), approximating the integral by numerically summing the predicted hazard over all intervals (\( N = 2738 \), mean interval = 0.4 km) in-between \( t \) and Kullaberg.

In the third step, the Cox proportional hazards model is generalized to include time-dependent covariates

\[
h_i(t) = h_0(t) \times \exp^{\beta Z(t)}
\]

in which the hazard develops differently over time, depending on the time-dependent covariates of the individual. The kilometrage \( t - t_i \) is the only time-dependent variable, since no other information for the eel en route is known. There might be different processes leading to a kilometrage-dependent hazard, including initial tagging-related mortality, natural mortality while en route, tag loss, and under-reporting. Tagging-related mortality is expected to level off soon after release, while the other processes would continue until the end (recapture or censoring, whichever comes first). Fitting both kilometrage and kilometrage-squared, the model can accommodate for both.

For this model, the hazard from any point \( t \) to Kullaberg is

\[
\int_{t}^{\text{Kullaberg}} h_0(u)\,du = \int_{t}^{\text{Kullaberg}} h_0(u)\times \exp^{\beta Z(u) + t_i u}du
\]

which now does depend on the point of release \( t_i \). Though this hazard can be calculated for any position \( t \) for all release points \( t_i \), we present results only for \( t = t_0 \). This expresses the hazard from any release point to Kullaberg. We present this hazard to Kullaberg for standardized individuals (modal week of release, for each decade separately, for all observed positions), approximating the integral by numerically summing the predicted hazard over all intervals in-between \( t_0 \) and Kullaberg, as before.

In the fourth step, the assumption that the spatial pattern in hazard is indeed proportional between the decades is tested by including the interaction term \( t \times \text{decade} \) in the analysis. Beyond this, more complex models than the proportional hazards model make assumptions on the functional form of the (baseline) survival function. For our silver eel, the (baseline) survival function might vary irregularly in time and space, because of seasonality and topographic features. We, therefore, did not pursue these parametric models any further.

For all models, a conventional presentation of hazard functions would show the cumulative hazard and survival from the origin (Gävle) to the point of observation \( t \). For our silver eel, however, there is no common origin: “late entry” is the rule and individuals may originate from all over the coast. Expressing hazard and survival from our artificially chosen origin at Gävle in the north would present a hazard and survival that no individual actually experiences. The survival and hazard functions are, therefore, presented as the accumulated survival and hazard from any point \( t \) to the common endpoint, the outlet of the Baltic at Kullaberg—as specified above.

**Implementation**

SAS/STAT software Version 9.3 of the SAS System for Windows (SAS 2010), proc PHReg was used to derive Kaplan–Meier estimates and to apply the Cox proportional hazards model, testing the significance of covariates and estimating the baseline survival and hazard functions, in so-called counting-style mode.
Every data record indicates where and when a tagged eel has been released (late entry into the risk set), where and when it has been recaptured (response), and what covariate values apply for that eel. For those tags that have never been recaptured, it is assumed that the eel has escaped from the Baltic (right censoring at the outlet, Kullaberg). The assumption of no tag loss and no non-fishing mortality, however, is tested as discussed above (step three).

Covariates include the year of tagging (grouped into decades), the distance from the release site (time-dependent variable: kilometrage) and its square, and the date the release was made (week number, absolute in the season). Unfortunately, biological characteristics of the individual eels (e.g., length) have been recorded in less than 5% of the cases; therefore, these were not included in the analysis.

Silver eel population

Survival analysis estimates the hazard per individual, but does not estimate the abundance and spatial distribution of the silver eel population at risk. We calculate the silver eel population biomass as the historical landings mass divided by the fishing mortality, for each decade and county. This represents the average biomass over the interval to which the mortality estimate applies.

The hazard estimate of survival analysis quantifies the risk of being captured. Though usually focused on time-continuous estimates, this is fundamentally identical to the concept of fishing mortality in fish stock assessment, where the focus is more on time-interval averaged estimates (often by year). For our model without time-dependent covariates, the difference in cumulative hazard between the northern and southern border of a county provides an estimate of the fishing mortality in that area.

For models with time-dependent covariates, the hazard varies from individual to individual and no reconstruction of the silver eel population can be derived. Though mortality can be estimated for individuals from different origins, it is not known which part of the catch corresponds. The time-dependent models indicate that mortality (hazard) is highest for eels from nearby areas, and most of the catch will probably be derived from that part of the stock. Only a small part of the catch stems from more distant origins and these eels experience only a low mortality. Our attempts (not shown) to disentangle the nearby and distant parts of

Fig. 4. Spatial distribution of the releases and recaptures, by decade and month of release. The size of the larger symbols is proportional to the number of eels released (the legend symbols are 100 eels each). The small dots represent recaptures of single eels. Seventeen recaptures that were released in June 1960 and 44 in July 1973 have not been plotted.
the stock (deconvolution) failed, because of the numerical instability of the ratio of low catches to low mortalities.

Finally, the total mortality (hazard) for the average eel in the population is estimated as the population-weighted sum of the hazard by county.

Results

Since 1950, a total number of 17,960 tags have been released, and 8,224 recaptures (46%) have been reported (Fig. 4). Only 204 recaptures (2%) were reported to have migrated in an unexpected direction, towards the north or away from the outlet; these were omitted from further analysis. The recapture rate per experiment varied between 1% and 75%, with an average of approximately 40%. Sjöberg and Petersson (2005) provide a detailed description of the individual experiments.

Kaplan–Meier curves

The most northern releases were made close to Östhammar (150 km from Gävle) in most decades but near Karlskrona (at 600 km) in the 1950s (Fig. 5). Survival to the outlet at Kullaberg (1000 km) varied from 25% in the 1960 to 65% in the 2000s.

In the 1950s, releases were made only at 650 km from Gävle and further south. Survival over the remaining stretch to Kullaberg was extremely low. This cannot easily be compared to other decades, because of the limited spatial coverage.

The survival curve for the 1990s starts near Stockholm (300 km), rises above all other curves north of Västervik (600 km), but levels off to an average survival beyond Karlskrona (700 km). This suggests that survival in the 1990s was below that of the other decades north of Västervik, but above the other decades further south.

Model fit

The Cox proportional hazards model was fitted using the covariates decade, date of release, and kilometrage (linear and squared) between release and (potential) recapture in all possible combinations and interactions. Figure 6 summarises the goodness of fit in a Venn diagram of the deviance explained. All terms are significant at the 5% level, except the date of release. Kilometrage is the dominating factor, showing a maximal effect (a minimal hazard) at 715 km from the release. In interaction with decade, the kilometrage having the extreme effect varies from −14 to 1815 km, with the mode near 700 km. Plotting the residuals of the model decade + release date (but not kilometrage) versus kilometrage, indicates that the hazard declines rapidly after release, stabilizing at a low level at greater distance (around 700 km) from the point of release (Fig. 7). Nevertheless, the deviance explained by kilometrage is dominated by the linear term, not the quadratic.

In addition to these proportional hazards models, a non-proportional hazards model was fitted, including decade × t, where t is the distance from Gävle. This reduced the unexplained deviance by another 30 units, which is significant at the 5% level too.

Hazard and survival functions

The survival functions estimated by the different model variants differ considerably.

For the basic model of proportional hazards without time-dependent covariates (Fig. 8a), survival increased gradually over the decades, from 10% for the most northern eel in the 1950s up to 60% in the 2000s. The highest hazard (steepest decline in survival) is found in county H (Kalmar) and the first half of county M (Skåne). In line with the assumption of no time-dependence, the cumulative hazard increases (survival decreases) the further north an eel originates.

Including the time-dependent covariate kilometrage (Fig. 8b), the estimated total hazard until Kullaberg for releases in the northern counties (X, Gävleborg and C, Uppsala) is lower than that for releases mid-way (in the south-east: E, Östergötland and H, Kalmar). The local hazard in the northern counties is lower than in the southern, and the kilometrage-effect makes these northern eels less vulnerable to the southern hazard. Assigning recaptures at unknown positions in M (Skåne) to a central position

Fig. 5. Hazard and survival by decade, estimated by the Kaplan–Meier method. The horizontal axis gives the distance from Gävle, just north of the northernmost release. Major cities (names) and counties (bars and character codes) are indicated along the bottom. The left vertical axis expresses the net survival observed in the recapture data; the right vertical axis expresses the same in terms of the accumulated hazard over the remaining interval.

Fig. 6. Venn diagram of the deviance explained for the main effects, the co-linearity between main effects, and the interaction decade × kilometrage. All effects, except the release date, are significant at 5% level.
Fig. 7. Hazard residuals as a function of the kilometrage (the distance between the point of release and the recapture position) for each recaptured eel. The residuals were estimated from a Cox model of decade and date of release, not containing the kilometrage. High residuals indicate an increased hazard.

Fig. 8. Hazard and survival estimated by three different analysis models. The left vertical axis expresses the net survival from the release position $t_0$ to the outlet of the Baltic at Kullaberg; the right vertical axis expresses the same in terms of accumulated hazard over that interval. (a) Estimated by Cox proportional hazards model, by decade, without time-dependent covariates. (b) As plot (a), adding an effect of individual kilometrage (time-dependent covariate). (c) As plot (b), additionally allowing the baseline hazard to increase or decrease linearly from Gävle, relative to the baseline hazard in decade 2000 (non-proportional hazards).
Recapture frequencies were achieved. Direct comparison across coast, varying in numbers, location, and timing; highly variable have been conducted on the silver eel along the Swedish Baltic.

**Discussion**

Over the past century, numerous mark–recapture experiments have been conducted on the silver eel along the Swedish Baltic coast, varying in numbers, location, and timing; highly variable recapture frequencies were achieved. Direct comparison across the decades fails, because of the extremely unbalanced historical design; however, our application of survival analysis adequately addresses this unbalance. Results show that the hazard of being caught in the fishery has gradually declined, and that the highest hazards occur for silver eel in the middle region (Västervik to beyond Karlskrona, 400–700 km from Gävle)—not in the furthest north.

We introduced survival analysis, an unusual technique for conventional mark–recapture experiments, for the following three reasons: (i) to accommodate for late entry of marked individuals all along a 1000 km long coast, even close to the outlet; (ii) to avoid the arbitrary choice on the size of the "last bin", the final stratum in a stratified mark–recapture analysis; and (iii) to allow for variation in recapture probability between individuals.

For the individual recapture probability, results indicate a large variation related to the kilometrage of the individual (and a negligible variation to the date of release), contradicting the central assumption of mark–recapture studies of equal catchability for all individuals. Applying survival analysis, even the effect of individual characteristics (e.g., body length) could have been included in the regression, but unfortunately, our historical database does not contain such information.

For the last bin size, Caron et al. (2003) indicate that strata had to be regrouped to avoid low recapture numbers, and Amihat et al. (2008) report zero recaptures in the last stratum, while all non-stratified studies (Feunteun et al. 2000; Pedersen and Dieperink 2000; Rosell et al. 2005; Klein Breteler et al. 2007; Winter et al. 2007; McCarthy et al. 2008; ICES 2011; Charrier et al. 2012) effectively ignored the problem, leaving it unclear what part of the silver eel population the estimates refer to. In survival analysis, the a priori chosen stratification is avoided and replaced by a stratified mark–recapture analysis; and Amilhat et al. (2008) report zero recaptures in the last stratum, while all non-stratified studies (Feunteun et al. 2000; Pedersen and Dieperink 2000; Rosell et al. 2005; Klein Breteler et al. 2007; Winter et al. 2007; McCarthy et al. 2008; ICES 2011; Charrier et al. 2012) effectively ignored the problem, leaving it unclear what part of the silver eel population the estimates refer to. In survival analysis, the a priori chosen stratification is avoided and replaced by a continuous survival function. The estimated confidence interval for our survival functions (mean 5%, max 12%) allows discriminating between survival curves per decade as far out as Copenhagen (915 km from Gävle)—no releases and only 12% of recaptures were made beyond that point. An a priori determined stratification might have used a last bin starting at the southern tip of Sweden (Trelleborg, 864 km from Gävle) or taken the whole

<p>| Table 2. Estimated silver eel population biomass, by decade and county, in metric tons. |</p>
<table>
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<td>5555</td>
<td>42801</td>
<td>55754</td>
<td>49351</td>
<td>27209</td>
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<td>2470</td>
<td>2772</td>
<td>2306</td>
<td>632</td>
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<td>612</td>
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<td>1086</td>
<td>975</td>
<td>718</td>
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<td>196</td>
<td>404</td>
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<td>616</td>
<td>625</td>
</tr>
<tr>
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<td>1088</td>
<td>445</td>
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<tr>
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<td>802</td>
<td>914</td>
<td>618</td>
<td>716</td>
<td>514</td>
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<tr>
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<td>1668</td>
<td>1413</td>
<td>933</td>
<td>1071</td>
<td>670</td>
</tr>
<tr>
<td>M Skåne</td>
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<td>1376</td>
<td>814</td>
<td>682</td>
<td>693</td>
<td>638</td>
</tr>
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<td>14739</td>
<td>11075</td>
<td>50679</td>
<td>63679</td>
<td>56816</td>
<td>31501</td>
</tr>
<tr>
<td>Sum Landings &gt;10 t</td>
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<td>5041</td>
<td>5003</td>
<td>4577</td>
<td>4543</td>
<td>2985</td>
</tr>
<tr>
<td>Sum Landings &gt;100 t</td>
<td>3912</td>
<td>3846</td>
<td>3141</td>
<td>1301</td>
<td>1409</td>
<td>1152</td>
</tr>
</tbody>
</table>

**Note:** Individual silver eels might cross several counties before being caught or escaping, contributing to the population biomass in each of these counties. The sum over the counties might double-count individual eels. Counties with reported landings of <10 t per year are in italics.

<p>| Table 3. Average hazard (instantaneous fishing mortality) between the place of origin and the outlet of the Baltic, weighted by the estimated population biomass per county, by decade. |</p>
<table>
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</tr>
</thead>
<tbody>
<tr>
<td>All counties</td>
<td>0.16</td>
<td>0.17</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Landings &gt;10 t</td>
<td>0.50</td>
<td>0.37</td>
<td>0.17</td>
<td>0.15</td>
<td>0.13</td>
<td>0.09</td>
</tr>
<tr>
<td>Landings &gt;100 t</td>
<td>0.56</td>
<td>0.45</td>
<td>0.24</td>
<td>0.25</td>
<td>0.19</td>
<td>0.13</td>
</tr>
</tbody>
</table>
last county (Skåne, starting at 716 km from Gävle), which would have put the major part of the catch (and silver eel population?) into the last bin.

We analysed a series of four models (Kaplan–Meier, proportional hazards, time-dependent proportional hazards, non-proportional hazards) of increasing complexity, decreasingly stringent assumptions, but increasing demands on the statistical design of the historical experiments. The survival curves for these models (Figs. 5, 8a, 8b, 8c) differ considerably. Though each step up in complexity improves the model fit, the final model (non-proportional hazards) is obviously a step too far: the confidence intervals on the survival (20%–60%) are much wider than the effects being analysed. Close inspection of the data shows that the number of marking events is the limiting factor. The analyses assumed that all individual variations are known and, of course, absolutely true. Batches of silver eels (mid-spread: N = 50–200) share time and place and the tagging experience, while their individual recapture events are independent. In the 1990s, for instance, only three batches were released, on two sites (Fig. 4). For whatever reason, the northern release showed a much lower survival than the two southern ones, which is extrapolated by the non-proportional hazards model to a decline in survival of 60% along the estimated 1682 km from Gävle to Kullaberg—with a disappointingly wide confidence interval. We did not pursue a much more complex analysis of variance components (e.g., Petersen et al. 1996), which would have disentangled the experiment-specific from the individual variation.

All in all, the greater flexibility of survival analysis allowed us to show significant deviation from the basic assumption of the more conventional (stratified) mark–recapture analyses, supporting the recommendation by Viallefond et al. (1999) to prefer survival analysis over capture–recapture models when the dates of death are available—as in most conventional mark–recapture experiments. We even advocate the general use of survival analysis for conventional mark–recapture data.

According to Westerberg et al. (2007), migrating silver eels follow the Baltic coastline, but at some distance offshore: their map indicates a depth of 10 to over 20 m. Pound nets, in contrast, are set at depths up to 6 m (Henck 1965, cited in Tesch 2003) or anchored at depths up to 12 m (Bobzin 1965, cited in Tesch 2003). Consequently, migrating eels will be out of reach for the fishing industry the most of the time. Releases have (nearly) always been made in shallow water, often on the coast, and emigrating eels will initially avoid shallow waters when leaving. This agrees with our current finding that hazard starts high and declines to only 10% of its initial value as the eel moves the first kilometres away from its release position. Because of tag loss and natural mortality, the hazard further declines slowly up to 700 km kilometrage, but that is a minor effect in comparison to the steep decline in hazard over the first 100 km (Fig. 7).

The time-dependent proportional hazards model (Fig. 8b) fits the historical data substantially better (Fig. 6) than the plain proportional hazards model (Fig. 8a). Especially in the northern counties, we find a considerable difference in hazards estimated by these two models. The reconstruction of the silver eel population size for these counties, however, fails for both hazard models. Noting the low abundance and catches in these areas, the historical mark–release experiments have been over-representing the northern counties considerably. Though this enables the estimation of the time-dependent component in the hazard (Fig. 8b), the northern counties and the reduced hazard at very high kilometrage are probably less relevant for the assessment of the silver eel population as a whole (and for the historical research objectives on migration routes as well).

In the 1950s, the landings in the Swedish silver eel fisheries fluctuated around 2300 metric tons per annum, declining to less than 300 metric tons in the 2000s (before fishing restrictions applied). Our estimate for the fishing impact (Table 3) starts at −40% (instantaneous fishing mortality $F = 0.5$) and declines to −10% ($F = 0.1$), while the estimated silver eel population biomass (Table 2) declines to about half of its initial value. Over the same period, Andersson et al. (2012) present fishing effort data on the local pound net fishery near Oskarshamn (525 km from Gävle), indicating that local fishing effort declined from 5000 net-nights per annum to 1000 net-nights, agreeing well with our trend in estimated hazard (Table 3). A five-fold decline in fishing impact on a stock that was reduced to about half its origin size over the economic pressures of a declining stock. The catch per unit of effort CPUE reported by Andersson et al. (2012), however, has remained remarkably stable—following an initial decline in the 1960s, CPUE remained at ~5 eels (nearly 5 kg) per net day. This appears to contradict the trend in landings and the trend in our hazard estimates. However, we question the relevance of the CPUE trend, since commercial CPUEs have a lower bound at minimum economic profitability and today’s analyses positively select for fishers who survived the economic pressures of a declining stock.

We assumed (implicitly) that all tagged eels start their migration somewhere along the Swedish coast and that the fishing impact can be deduced from the Swedish landings and tagging data. The estimated silver eel population size ranges from 5000 to 30000 metric tons. This is far more than the estimated production and escapement from Swedish waters. ~500 metric tons (Dekker 2012). Adding the escapement from Denmark, Germany, and Poland (ICES 2012; no estimate available for Estonia, Latvia, Lithuania), the estimated total for the Baltic comes to 2959 metric tons—reasonably in agreement with the current estimates. ICES (2010) presented data on silver eel tagging in all Baltic countries. Of 29241 individuals released in eastern Baltic countries, 10346 were recaptured in the country of origin, 1601 in Denmark, and 113 in Sweden. Obviously, the Swedish fishery exploits a mix of “home-grown” and “foreign” silver eel. Quantitative analysis of cross-Baltic effects will require a much more complex statistical analysis and a larger data set than currently available.

Finally, the impact of the recent silver eel fishery is estimated at $F = 0.1$; this is within the pre-ery morality limits for the currently depleted stock (ICES 2012), though other impacts (hydropower generation related mortality on silver eel and impacts on other life stages, most often in other countries) have not yet been taken in consideration, because they have not been quantified yet. The impact of the Swedish silver eel fishery is at the lower end of the range of reported mortality rates (ICES 2012); however, for capture frequency data in Sweden (2011), the probability of release is taken in the middle. Obviously, the methodology for assessment of silver eel fisheries needs careful reconsideration, in Sweden and elsewhere.

Acknowledgements

This work was funded by the Swedish Agency for Marine and Water Management, as part of the assessment of the Swedish eel stock. We are thankful to Johan Wagström for locating recapture data from county Skåne; to our colleagues Håkan Wickström, Johan Andersson, Joep de Leeuw, Johan Östergren, and the anonymous reviewers for their comments on (earlier) drafts.

References


Dekker and Sjöberg 1683


Eels (*Anguilla* spp) are in decline worldwide and the signs of a reduced recruitment have been observed in continental Europe ever since the early 1970s. In order to protect and recover the European eel, EU (the European Union) decided in 2007 to establish a recovery plan, aiming at protection and restoration.

The unifying link in this thesis is that the selected papers describe subjects and results that could be used in our Swedish eel stock management. The main question is to investigate whether stocked eels manage to migrate towards the spawning area in the same way as naturally recruited fish do. But I will also briefly address the question of cues, circumstances or characteristics that make them migrate in a certain direction. The tool is silver eel tagging experiments, both historical (started in 1903) and recently conducted, made by myself and colleagues.