1	ragged for fire. Retention rates and effects on growth and condition of tagging - a long-
2	term field study on PIT- and Carlin tagging in European eel
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4	Elin Myrenås ^{1*} <u>https://orcid.org/0000-0003-3894-4501</u> , Joacim Näslund ¹ <u>https://orcid.org/0000-0003-1091-</u>
5	<u>2225</u> , Philip Jacobson ¹ <u>https://orcid.org/0000-0002-3890-4289</u> , Birgitta Jacobson ¹ <u>https://orcid.org/0000-0002-</u>
6	0875-1293, John Persson ¹ https://orcid.org/0009-0002-9780-0559, Håkan Wickström ¹ https://orcid.org/0000-
7	0001-6335-8833, Jennie Strömquist 1 https://orcid.org/0009-0007-9791-101X,
8	Josefin Sundin 1 https://orcid.org/0000-0003-1853-4046
9	
10	¹ Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sci-
11	ences, Stångholmsvägen 2, SE-17893, Drottningholm, Sweden
12	*Corresponding author: Elin Myrenås
13	Swedish University of Agricultural Sciences
14	Department of Aquatic Resources (SLU Aqua), Institute of Freshwater Research
15	Stångholmsvägen 2, 178 93 Drottningholm
16	+46 10-478 42 86, mobil: +46 76-135 01 61
17	elin.myrenas@slu.se
18	
19	Funding information
20	Given the long-time span of the data used in the study, the data have been collected as part of several different
21	monitoring programs, with the most recent being the EU data collection framework in the fisheries and aquacul-
22	ture sector (DCF, Regulation 2017/1004), partially funded by the EU.
23	
24	Abstract
25	Different types of tags and markers are commonly used for various fish monitoring and tracking purposes. Effects
26	of tags and markers on fish and the retention rates can affect the interpretation of mark-recapture data on both the
27	individual (e.g. growth and body condition) and population level (e.g. survival and production estimates), making
28	studies of this issue important. In this study, we investigated the effects of tagging on the European eel (Anguilla
29	anguilla), using two commonly used tag types, Carlin and Passive Integrated Transponder (PIT)-tags. We exam-
30	ined tag retention of Carlin tags and potential effects on growth and body condition of PIT-tags. We used data

from several long-term tagging projects conducted in a natural Swedish lake, combining outlet trap monitoring with catch data from a commercial fisher. The longest of these studies spanned over 27 years, covering the majority of the eel's resident life stage. We found that the retention rate of Carlin tags was 92%, with 64% of the Carlin-tagged silver eels being recaptured. The recapture rate of PIT-tagged eels released as juveniles in the lake was 12%. This recapture rate indicates little or no effect on survival when compared to other studies of both tagged and untagged eels. No major impact of PIT tags on growth and condition in eels was found. We conclude that both Carlin and PIT tags are suitable methods for tagging European eel, each with strengths in its respective area of use.

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Keywords: Anguilla anguilla, long-term monitoring, mark-recapture, Sweden, tag shedding

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Introduction

Various tags and markers for individual identification have been important tools in scientific studies and management of fish for over a century, and the methods are constantly developing (Atkins, 1876; Latour, 2005; Lucas & Barras, 2008). Present-day physical tags and markers make it possible to study behaviour (Lucas & Barras, 2008), migration patterns (e.g. Acou et al., 2005; Piper et al., 2013; Wright et al., 2015), habitat use (e.g. Riley et al., 2011; Herrera et al., 2019), abundance (Cahill et al., 2018), and mortality (Vandergoot & Brenden, 2014) at the individual (identity marking) or group (batch marking) level. Tagging studies can also generate valuable information for stock assessments (Saville & Morrison, 1985; Höhne et al., 2023), and decision-making in fisheries and conservation management (Hays et al., 2019). It is often assumed that neither the tag nor the tagging procedure itself will have an impact on the fish, provided that the fish are not too small in relation to the tags, an assumption that is supported in several empirical studies (e.g. Nyqvist et al., 2023; Závorka et al., 2024). However, this is not always the case. Several studies have shown that tags and markers can cause adverse effects on fish, for example, in altering feeding patterns (Bridger & Booth, 2003), behaviour (Huusko et al., 2016), growth rate, and mortality (Larsen et al., 2013). Fish with conspicuous external tags might also experience higher predation pressure than untagged fish (Kerstetter et al., 2004). The handling and tagging procedure vary among tagging techniques, and some of the more invasive techniques are associated with a risk of inducing inflammation (Semple et al., 2018) and infection (Elliott & Pascho, 2001). In addition to the possible negative impacts of tagging on the studied fish, tag shedding can also affect the result of the study and lead to biased interpretations and inferences, if not accounted for (Cowen & Schwarz, 2005). Currently, there is a smorgasbord of

tagging methods available to enable individual identification of fish, which all come with their own set of pros and cons (Latour, 2005; Thorstad et al., 2013). Some methods suit certain species better than others; therefore, species-specific evaluations are needed to enable informed decisions on what method to use.

Tagging is crucial for European eel (*Anguilla anguilla*) research and management, due to their long life span and long-distance migration undertaken both as larvae/juveniles and adults. The European eel has a complex life cycle that has challenged scientists for centuries (Schmidt, 1912). When the eggs hatch somewhere in the Sargasso Sea, the leptocephalus larvae follow the currents towards the European- and northern parts of the African continents, and on their way, they metamorphose into glass eels (Schmidt, 1912; Miller et al., 2019). When arriving at the coast, they transform into pigmented yellow eels and spend several years in freshwater, estuaries, and/or coastal marine environments (Moriarty and Dekker, 1997; Daverat et al., 2006). Thereafter, they transition into silver eels, begin their maturation process, and embark on one of the longest known spawning migrations for a fish, back towards their spawning grounds in the Sargasso Sea (Schmidt, 1912; Tesch, 1977). It is with the use of various tagging methods that scientists have been able to study the migrating silver eels on their route to the Sargasso Sea (Tesch, 1989; Westerberg et al., 2014; Wright et al., 2022). Even if the spawning of mature silver eels is a thrilling story that is yet to be fully understood, it is important to manage the species throughout all its life stages to support and secure its continued existence, given that the European eel is classified as Critically Endangered (Pike et al., 2020).

Two types of tags have been widely used in studies of yellow and silver eels: external Carlin tags (e.g., Westin, 1990; Pedersen and Dieperink, 2000; Sjöberg et al., 2009; Westerberg and Sjöberg, 2015), and internal Passive Integrated Transponder tags (PIT-tags) (e.g., Holmgren & Mosegaard, 1996; Laffaille et al., 2005; Riley et al., 2011; Wickström & Sjöberg, 2014). The Carlin tag (sometimes referred to as trailer tag, Eames and Hino, 1983) was developed in the 1950s and consists of a small plastic plate with an ID number and additional text information that is attached to the fish with two steel wires (Carlin, 1955). In eel, it is usually attached straight through the dorsal musculature. In Sweden, data on recaptured Carlin tagged silver eels reported by commercial fishers are used in the stock assessment to assess fishing mortality, "F" (Dekker & Sjöberg, 2013; van Gemert et al., 2024). Since the fishing mortality assessment is dependent on reported recaptures it is influenced by tag shedding, should it occur. The retention rate of Carlin tags has been reported to be relatively low in field studies of some species, for example Atlantic sturgeon (*Acipenser oxyrinchus*) and nurse shark (*Ginglymostoma cirratum*) (28% and 21% respectively) (Carrier, 1985; Kallemeyn, 1989). In other species the retention is high, for example Chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon (*Salmo salar*) (98-99% and 98%

respectively) (Eames and Hino, 1983; Huusko et al., 2016). Given these species-specific differences in retention rates of Carlin tags, assessing retention rates specifically for eels is pivotal for accurate evaluation of recapture data. Currently, such data is largely missing, but tag retention of Carlin tags in eel is considered to be high based on expert opinion (Nielsen, 1988). In addition to the expert opinion, we are aware of only one study, which is a laboratory experiment reporting a Carlin tag retention rate of ca 90% (Vøllestad, 1988).

The other main tag type used in eel, the passive integrated transponder (PIT-tag), was developed in the early 1980s (Prentice and Park, 1984). These tags have an electronic microchip with a unique ID code, enclosed in a glass hull (Prentice et al., 1990). The microchip remains inactive until it comes within range of a PIT-reader/antennae that powers the transponder, and the reader/antennae thereby receives the unique ID code (Prentice et al., 1990). PIT tags have a wide application field, ranging from individual identification of experimental fish (Holmgren & Mosegaard, 1996) and mark-recapture studies (Wickström & Sjöberg, 2014), to active movement biotelemetry in the field using portable PIT antennas (Cucherousset et al., 2005) and passive movement and migration telemetry using larger stationary PIT antennas (Riley et al., 2011). In eel, it is usually inserted in the abdominal cavity or the dorsal musculature (Table 1). Tag retention of PIT-tags in eel is well studied and can be considered relatively high (Table 1), but there are still ambiguities to investigate regarding the effects of PIT-tagging (or implants of micro acoustic tags of comparable size, shape, and construction) on growth and mortality rates in eel. Although such effects have been specifically investigated in laboratories, mesocosms, and field studies, reported results range from no effects to major growth reductions in PIT-tagged eels (Table 1). Given the broad range of previous results, continued testing, for example, under differing environmental conditions, is important and a direct necessity to facilitate reliable meta-analyses on the effects of PIT-tags on European eels.

This study investigated the retention rate of Carlin tags and the potential effects on growth and condition of PIT-tagging in the European eel, using unpublished data from long-term tagging projects (both Carlin and PIT-tagging) in a natural Swedish lake. We predicted high tag retention for Carlin tagged silver eels in the field based on expert opinion and a previous laboratory study (Nielsen, 1988; Vøllestad, 1998). We also predicted no negative effects of PIT-tagging on growth and condition, consistent with most prior research (Table 1).

Table 1 Summary of results from studies on effects of Passive Integrated Transponder (PIT)-tagging on growth and survival, and PIT-tag retention in Anguilla species. Data on eel size at tagging is given as it was presented in the paper (i.e., if it says, "silver eel", then no more specific information on size was provided in the paper). Placement of the tag is noted in the column "Retention" (AC – abdominal cavity; DM – Dorsal musculature (DMD – dorsal fin; DMH – behind the head)). "NR" indicates missing methodological information (Not Reported); "NA" indicates parameters not investigated in the study.

Ref.	Species	Location	Method	Tag	Eel size	Study du-	Growth	Survival	Retention
				length		ration			
Acou et al., 2000	A. anguilla	Mesocosm	NR	NR	Silver eel	30 days	NA	100%	100% (NR)
Morrison & Secor, 2003	A. rostrata	Field	Needle	NR	457 mm (mean)	2 months	NA	NA	89% (AC)
Verdon & Desrochers,	A. rostrata	Field	Needle	14 mm	196-726 mm (mean \pm SD: 472 \pm 79	< 16	NA	NA	98.6% (DMH)
2003					mm)	months			
Verdon et al., 2003	A. rostrata	Field	Needle	12-14	380 mm (mean)	< 3 months	NA	NA	93.9% (DMD)
				mm					
Acou et al., 2005	A. anguilla	Lab	Needle	NR	> 200 mm	1 hour	NA	NA	86% (AC)
Zimmerman & Welsh,	A. rostrata	Lab	Needle	12.5	205-370 mm	9 weeks	NA	NA	100% (AC)
2008*				mm					100% (DMD)
									88% (DMH)
Hirt-Chabbert & Young,	A. australis	Lab	Scalpel	11 mm	$101 \pm 12 \text{ g (mean} \pm \text{SD)}$	108 days	No effect	No ef-	>95% (AC)
2012								fect	

Mazel et al., 2013	A. anguilla	Field	Trocar	12 mm	>200 mm	1-11 years	Reduced	NA	NA (AC)
Mazel et al., 2013	A. anguilla	Corf	Trocar	12 mm	247–732 mm	28 days	NA	NA	100% (NR)
Wright et al., 2015	A. anguilla	Stream	Scalpel	23 mm	$356.0\pm20.1~mm~(mean\pm SD)$	7-14 days	NA	100%	100% (AC)
		enclosure							
Jellyman & Crow, 2016	A. australis	Lab	Needle	15 mm	428–570 mm (mean: 646 mm)	21 days	NA	NA	100% (AC)
Jellyman & Crow, 2016	A. australis	Field	Needle	15 mm	> 400 mm	7 days	NA	NA	99.1% (AC)
Jellyman & Crow, 2016	A. australis	Field	Needle	15 mm	> 400 mm	9 months	NA	NA	95% (AC)
Schmucker et al., 2017	A. rostrata	Lab	Needle	12 mm	Silver eel	5 days	NA	No ap-	100% (DMD)
								parent	
								mortality	
Nzau Matondo & Ovidio,	A. anguilla	Lab	Scalpel	23 mm	215-441 mm	20 days	NA	100%	100% (AC)
2018									
Herrera et al., 2019	A.anguilla	Lab	NR	8-12	$300 \pm 10 \text{ mm (mean} \pm \text{SD)}$	9 months	No effect	99%	100% (NR)
				mm					
Nzau Matondo et al., 2021	A. anguilla	Field	Scalpel	12 mm	2-31.7 g (mean: 8.6 g)	Up to 2	Possibly	NA	NA (AC)
						years	reduced		
							(non-sig-		
							nificant)		
Jepsen et al., 2022	A. anguilla	Ponds	Scalpel	12 mm	16.6-25.1 mm (mean: 21.6 mm)	76 days	No effect	97%; No	99% (AC)
								effect	

^{*} Alternatively, see Zimmerman (2008)

Material and methods

Throughout the material and methods section, we report the author's initials to clarify contributor roles for reproducibility and replicability using the Method Reporting with Initials for Transparency (MeRIT) guidelines (Nakagawa et al., 2023). In this paper, we used previously unpublished data from several projects related to monitoring of European eel in Sweden. This implies that the methods had a monitoring focus, rather than being designed as a specific study. Given the timespan of the data reported here, substantial efforts were made to locate and compile all necessary information and data (performed by JSu, BJ, PJ, EM, HW, JSt, and JP). The general background of the studies, methods, and data hosting has been published in a technical report (Jacobson et al., 2024).

132 Study site

The lake Ymsen (WGS84 dec: 58.666417, 13.965861) is a small and shallow lowland lake (average depth: 2.4 m, max depth: 4m, total surface area: 13 km²) with little vegetation, mainly mud on the bottom, and some rocks and stones in the shore zone. There are no significant tributaries, and the lake drains through one small river, Ölebäcken (WGS84 dec: 58.645019, 13.934244). On the way towards the coast, the water from Ölebäcken flows to the river Tidan and onwards downstream via the much larger lake Vänern and the river Göta älv, where there are several migration barriers for eels (natural as well as human-made). The lake is therefore lacking open, natural fish migration routes, making it a well-controlled natural system suitable for eel monitoring. There are, however, eels in the lake due to translocation of naturally recruiting juvenile eels, caught in an eel trap/collector in the river Göta Älv (located next to an upstream migration barrier at Trollhättan, WGS84 dec: 58.274333, 12.271389), and due to restocking of imported juvenile eels from Europe (from Denmark, England, and France). This translocation and restocking of juvenile eel in Ymsen have been ongoing for at least a century (Nyström and Trybom, 1902; Nordqvist, 1928; van Gemert et al., 2024), with notes on eel presence dating back to at least 1883 (Vallin, 1929).

147 PIT- and Carlin tagging

Between 1998 and 2012, five separate tagging events were conducted in the lake Ymsen, with various sizes of eels and with two kinds of tags.

Small yellow eels were PIT-tagged each fall (September-October), between the years 1998 and 2000, and released in Lake Ymsen (1998: N = 190, mean size = 221 mm; 1999: N = 1527, mean size = 207 mm; 2000: N = 1527

1100, mean size = 231 mm; Table 2). The eels had been purchased from a commercial supplier of imported quarantined glass eels for restocking and aquaculture purposes (Scandinavian Silver Eel AB (SSE), Helsingborg, Sweden; eel origin: Severn, England). Prior to release, the imported eels were held in quarantine at an aquaculture facility from spring to fall each year to ensure they had reached a sufficient size to minimize adverse effects from PIT-tagging (Jepsen et al., 2005). The eels were tagged with PIT-tags (12 mm, 0.1 g, Trovan Ltd, Great Britain) at the SSE facilities (by HW and other staff at the Swedish Board of Fisheries). The PIT-tagging was performed under sedation with 0.12 g L⁻¹ Benzocaine (C₉H₁₁NO₂, Sigma-Aldrich, Inc., St. Louis, Missouri, USA; dissolved in a small amount of 95% ethanol before being mixed in the bath of water). The PIT-tag was inserted using a syringe/needle or by hand into the abdominal cavity after making a small incision at the side of the ventral midline, a few centimetres anterior to the anus, using a scalpel blade. This method was chosen because scalpel incision is easier and safer than using needle injectors to penetrate the skin for tagging of eels due to their soft abdomen and tough skin, which increases the risk of internal organ damage when using needles (Zimmerman & Welsh, 2008; Hirt-Chabbert & Young, 2012). Data on total length (±0.5 mm), total mass (±0.05 g) and PIT tag ID number were recorded for each individual. After tagging, the eels were placed in a recovery tank with aerated water before being moved to a fish holding tank. A few days after the tagging (between 1-6 days), the eels were transported by car to Ymsen (transport time: ca 4h) and released at various sites along the shoreline of the lake. In July 1999, N = 83 yellow eels (mean size: 542 mm, Table 2) caught by a commercial fisher operating in Ymsen, were returned to the lake after PIT-tagging (note that the legal minimum catch-size was not applied since the fishing was performed for monitoring and research purposes). The tagging procedure and data collection were the same as for the tagging in 1998-2000 described above, with the difference that it was performed on-site (performed by HW and other staff at the Swedish Board of Fisheries). After tagging, the eels were kept in a fish corf for approximately two days to recover from the tagging, before being released into the lake. In October 2012, N = 118 silver eels (mean size: 859 mm, Table 2) caught by a commercial fisher operating in Ymsen, were returned to the lake after both Carlin- and PIT-tagging. The tagging procedure and data collection were performed in a similar way as described above for the PIT-tagging of yellow eels in July 1999, with the difference that the eel total weight was measured with ±0.5 g precision, and these eels were tagged with both a Carlin- and a PIT-tag (performed by HW and JSt). The Carlin tag consisted of an 18×4 mm plastic plate (0.12 g, Inplastor AB, Motala, Sweden) with steel wires manually added to the plastic plate [by staff at Swedish University of Agricultural Sciences, Department of Aquatic Resources (SLU Aqua)]. The Carlin-tag was attached

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through the dorsal muscle below the dorsal fin with a double steel wire (while the eel was sedated, as described above for the PIT-tagging). Two injection needles were first disinfected by immersion in 95% ethanol, after which they were pushed through the dorsal muscle approximately one centimetre below and two centimetre in front of the dorsal fin (Fig. 1). One steel wire thread was inserted through each injection needle, the needles were then removed, and the steel wires were wired together to lock the tag in place (Fig. 1). After tagging, the eels were kept in a recovery tank with freshwater until released in Ymsen the same day as they had been tagged.

Table 2 Descriptive statistics of European eel (Anguilla anguilla) tagged with Carlin or Passive Integrated Transponder (PIT) tags and released in Lake Ymsen, Sweden. The table summarizes release date, tagging size (small yellow, large yellow eel, silver eel), total length in range and mean (\pm 1 SD), total mass in range and mean (\pm 1 SD), number of eels tagged with PIT-tags, number of eels tagged with Carlin tags, and origin (caught in Lake Ymsen, or imported from England).

Date re-	Tagging size	Length (mm), range;	Mass (g), range,	N	N Car-	Origin
leased		mean (± 1 SD)	mean (± 1 SD)	PIT	lin	
1998-10-28	Small yellow	171-297; 221 (±23)	8-43; 17 (±6)	190		England
1999-07-29	Large yellow	251-682; 542 (±109)	21-521; 255 (±130)	83		Lake Ymsen
1999-09-15	Small yellow	114-299; 207 (±23)	5-41; 14 (±5)	1512		England
2000-09-14	Small yellow	121-328; 231 (±31)	3-71; 20 (±10)	1087		England
2012-10-11	Silver eel	609-1030; 859 (±68)	452-2120; 1276	118	118	Lake Ymsen
			(±298)			



Fig. 1 Photo of an adult female European eel, Anguilla anguilla, tagged with an external Carlin tag. Photo: Elin Myrenås.

Data collection and dissection, recaptures of Carlin and PIT-tagged eel

Data on recaptures of the PIT-tagged eels have been collected since 1999 (still ongoing in 2025). The only commercial fisher operating in Lake Ymsen continuously scans all captured eels for PIT tags. Eels were caught either in pound nets with 24 mm mesh-size or in an outlet trap with a 20 mm grid located in Ölebäcken (WGS84: 58.644841, 13.93384), which captures individuals migrating out of the lake. All scanned eels with a detected PIT-tag were handled in one of the following ways: a PIT-tagged eel from the 2012 tagging event was checked for the presence of a Carlin tag (since all PIT-tagged eels in 2012 also had a Carlin tag), and the presence or absence of the Carlin tag was noted. For those eels, no additional data was collected. All other PIT-tagged eels (i.e., from any other PIT-tagging event in 1998-2000) were frozen and sent for later dissection to SLU Aqua, except for 21 eels that were measured by the fisher as fresh, and the length and mass data was sent to SLU Aqua. Before dissection, the frozen eels were thawed. Length and mass (scale model: Mettler PC 400; Mettler Instrument AG, Küsnacht) were measured (mass was measured without removing coagulated mucus; Sundin et al. 2025). The abdomen was opened using scissors, from the anal opening to the head. An ocular assessment of the gonads was made for sex determination (Tesch, 1977). All dissection data were stored in a database (Sötebasen), hosted by SLU Aqua, Institute of Freshwater Research. The dissections were performed by JP, JSt, supported by other staff at the Swedish Board of Fisheries/SLU Aqua.

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215 Data collection, untagged fish (control) 216 To compare data from the recaptured tagged fish, we used data from untagged fish as a baseline control, which 217 had been collected for monitoring purposes. Those eels had been sampled from the catch of the commercial 218 fisher operating in Ymsen (using the same pound nets and outlet trap as described above) (2003: n = 85; 2004: n = 85) 219 =30; 2012: n = 11; 2019: n = 123; 2020: n = 129; 2021: n = 130, NA: n = 8). From 2011 onward, all landed eels had 220 a minimum size of 700 mm due to legal minimum catch-size restrictions. The sampled eels were frozen and sent 221 to SLU Aqua for later dissection. The dissections were performed as described above, with the addition that the 222 largest otoliths (sagittae, two per individual) were collected and saved for later age determination in a subset of 223 the eels (according to methods described in ICES, 2009, with otoliths grinded, etched and stained) (untagged 224 eels; aged: n = 440, unaged: n = 76). All dissection data were stored in the database Sötebasen. 225 226 Data analysis 227 All analyses were performed using R, version 4.2.1 (R Core Team 2022) (by EM). Plots were constructed using 228 the R-packages ggplot2 (Wickham et al. 2024) and cowplot (Wilke, 2024). Significance level was set to p =229 0.05. 230 For the Carlin and PIT-tagging studies, data validation had to be performed prior to analysis, since the eels in 231 these studies were released a long time ago, and data collection on recaptures had been performed by several dif-232 ferent staff members over time. Digital data in Excel spreadsheets was validated against original written proto-233 cols. PIT tags that were stored together with samples (otoliths) from recaptured eels were scanned and checked 234 against digital data. When validation and organisation of the data were completed (performed by EM, BJ, JSu, 235 JSt, and PJ), some errors remained, such as certain recaptures missing release data. Data with unresolved errors 236 were excluded from analyses. 237 Data on tagged and untagged (control n = 516) eel from Lake Ymsen were extracted from the database Söte-238 basen on August 20, 2025. Since most of the eels were measured as frozen and thawed, we corrected weight and 239 length using a freeze-shrinking correction factor (Sundin et al. 2025) before further analyses. 240 The recapture rate was calculated as the proportion of individuals recaptured from the total number of re-241 leased individuals per tagging event (Table 2). The mean time between the release event and recapture was cal-242 culated for PIT-tagged eels released as small yellow eels, or larger yellow eels, and for Carlin-tagged eels sepa-243 rately (Table 2). For Carlin tagged individuals, tag retention rate was calculated as the proportion of recaptured 244

individuals retaining their tag from the total number of recaptured individuals.

Growth was evaluated by examining the relationship between length of the PIT-tagged eels and time (in years) elapsed since stocking ("years since release") by fitting a LOESS (locally estimated scatterplot smoothing) curve for each size group at tagging separately (small or larger yellow eel) (Table 2). This non-parametric method fits multiple local regressions across the data range to produce a smooth trend without assuming a specific functional form. Each eel contributed with only two observations—length at release and length at recapture—and no repeated-measures data from the same individuals were available.

Specific growth rates (SGR) (Crane et al., 2020), expressed as annual change in percentage growth rate was calculated for the eels released as small yellow eels. The instantaneous growth rate constant (g) was first calculated from changes in weight (W) or length (L) between release date (t_1) and recapture date (t_2), for each eel, as:

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$$g = (\ln(W_2) - \ln(W_1))/(t_2 - t_1)$$

where W_1 and W_2 are the weights at release and recapture, respectively, and $(t_2 - t_1)$ is the time interval in months. An equivalent formula was used for length, replacing W with L. Then SGR was calculated by converting g from log scale to annual percentage change:

260 SGR (% per year) =
$$(e^{(g \cdot 12)} - 1) \cdot 100$$

We compared several candidate Pütter-von Bertalanffy growth models (von Bertalanffy, 1938) to determine the model that best described growth differences between control and PIT-tagged small yellow eel. For this, only untagged aged eels and eels tagged as small eels (since they have a known age) were used. Candidate models differed in which parameters (asymptotic length $L\infty$, growth rate K, and theoretical age at length zero t_0) were allowed to vary between groups, and model selection was based on Akaike's Information Criterion (AIC). We also used the same method to compare Pütter-von Bertalanffy growth curves between eels tagged with PIT-tags, as small and as large yellow eels.

To evaluate differences in body condition between tagged and untagged eels, we used linear models including treatment (fixed factor, two levels: PIT-tagged and untagged). Mass and length variables were log₁₀-transformed to linearise the allometric length-mass relationship before model fitting.

274 Results

Recaptured Carlin tagged silver eels

Out of the 118 individual silver eels that were tagged with both Carlin and PIT-tags and released in Ymsen in 2012, 76 (64%) have been recaptured (monitored until 2025). Data on catch year were only available for 64 recaptures, but these were all recaptured within four years after being released [mean time until recaptured = 1 year (± 0.76)]. For the 76 recaptured eels, tag retention was 92% (restrictive number) or 97%, with data interpretation being the reason for the two numbers (due to issues regarding data quality on four recaptured individuals, with one source indicating that the tag was retained, while another source indicated that the tag was lost). The calculations of tag retention rates disregard the unlikely possibility that both the Carlin and PIT tags would have been lost, in which case the eel would be registered as untagged in the data.

Recaptured PIT-tagged yellow eels

Out of the 2872 PIT-tagged eels released in Ymsen in 1998-2000 (Table 2 and 3), 344 (12%) have been recaptured (until 2025), with recapture rates varying among the different release batches (0 - 15%; Table 3). The eels released as small yellow eels were recaptured after 4-22 years (Fig. 2A) [n = 337, mean time between release and recapture = 12 years (\pm 4), with the longest possible duration being 27 years; 1998-2025]. The eels released as larger yellow eels (in summer, 1999) were recaptured after 3-15 years (Fig. 2B) [n = 7, mean time = 9 years (\pm 4)]. All recaptured PIT-tagged eels were females.

Table 3 Recaptures of Passive Integrated Transponder (PIT) -tagged European eels (Anguilla anguilla) released in Lake

Ymsen in Sweden: release date of respective PIT-tagging event, year 1998-2000, tagging size of released eel (small yellow or large yellow eel), number of PIT-tagged eels released, number of PIT-tagged eels recaptured, and recapture percentage.

Date released	Tagging size	N PIT-tag released	N recaptured	% recaptured
1998-10-28	Small yellow	190	0	0
1999-07-29	Large yellow	83	7	8
1999-09-15	Small yellow	1512	172	11
2000-09-14	Small yellow	1087	165	15

The relationship between mass or length and years spent in the lake after being released show large individual variation both for eels released as small yellow eels (Fig. 2A, Table 4) and as larger yellow eels (Fig. 2B).

Table 4 Mean (\pm 1SD) percentage increase in specific growth rates (SGR) for each year since release (Δ Time= recapture – release date), calculated based on mass (g/year) and length (mm/year), along with the number of individuals (n) in each group. Only eels PIT-tagged as small yellow eels were included.

	Mean %	Mean %	
$\Delta Time$	mass in-	length in-	n
	crease	crease	
4	56(8)	16(1)	3
5	52(13)	15(3)	8
6	62(14)	16(3)	6
7	55(4)	15(1)	8
8	58(6)	15(1)	18
9	57(7)	15(2)	35
10	49(6)	13(1)	26
11	48(4)	13(1)	30
12	47(4)	13(1)	30
13	41(5)	11(1)	46
14	38(4)	11(1)	40
15	36(3)	10(1)	23
16	33(4)	9(1)	18
17	31(3)	9(1)	11
18	30(3)	9(1)	11
19	29(2)	8(1)	14

	Mean %	Mean %	
ΔTime	mass in-	length in-	n
	crease	crease	
20	28(7)	8(2)	3
21	26(2)	7(1)	4
22	28(-)	8(-)	2

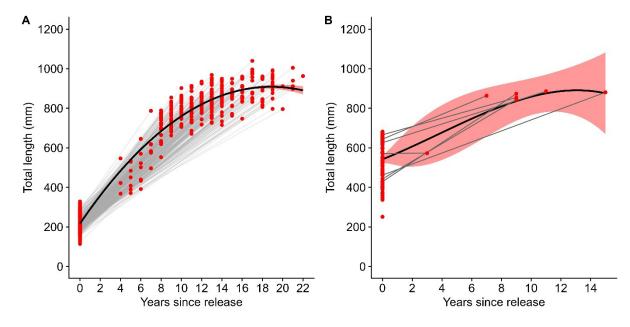


Fig. 2 Length differences between release and catch for PIT-tagged European eels (Anguilla anguilla) released in Lake Ymsen, Sweden, for A) released as small yellow eels (year 1998, 1999 and 2000), and B) released as larger yellow eels (year 1999). Total length for all eels when released is shown at year 0 (i.e., irrespective of actual release year) and recaptured as the number of years since release. For each individual that has been recaptured (small yellow N = 335, larger yellow eels N = 7), a line (grey) between length (mm) at release and recapture are shown. The solid black line represents a locally estimated scatterplot smoothing (LOESS) curve, which models the relationship between years since release and total length (mm), with the red shaded region representing the 95% confidence interval for the estimated curve.

The growth of eels was analyzed using Pütter-von Bertalanffy growth models, with parameters estimated separately for different tagging groups (Table 5).

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The growth of eels tagged with PIT-tags as small yellow eels and untagged control eels was modelled with separate asymptotic lengths $(L\infty)$ and theoretical ages at zero length (t_0) for the two groups. The growth rate parameter (K) was shared across groups. The estimated asymptotic length $(L\infty)$ was slightly higher for the untagged control group compared to the tagged group (Table 5). The theoretical age at zero length (t_0) also differed between the two groups; the tagged eels had a lower estimated t_0 (Table 5). These results suggest that both groups grew at the same rate but differed in their initial size and asymptotic length (Fig. 3A).

The growth of eels tagged at different sizes (small, yellow or large, yellow eels) was modelled with separate theoretical ages at zero length (t_0) for each group. The growth rate parameter (K) and the estimated asymptotic length ($L\infty$) was shared across groups (Table 5). The theoretical age at zero length (t_0) differed between the two groups; the larger yellow eels had a lower estimated t_0 (Table 5). The negative t_0 value indicate that the model extrapolates to zero length before age zero, a common outcome when early life stages are not represented in the data and t_0 is not fixed (Pardo et al. 2013). These results indicate that both groups are expected to reach the same asymptotic length at a similar growth rate, but they differ in their effective starting point of growth (Fig. 3B).

Table 5. Summary table for the Pütter- von Bertalanffy growth model for PIT-tagged European eels and untagged control eels in Lake Ymsen. The table shows the model fit relative standard error (RSE), parameter estimates with their standard errors (SE), and the results of t-tests (t(df), p-value) assessing parameter significance. "Group comparison" indicates the experimental groups, i.e., tagged as small (SY) vs. large yellow (LY) eels or tagged as small yellow vs. control (C) eels. Notes include details on parameter constraints or fitting remarks.

Group com-	Model fit	Parameter	Estimate ± SE	t(df)	p-value	Notes
parison	(RSE)					
SY vs. C	63.66	K	0.23 ± 0.01	19.93 (770)	< 0.001	Shared across
						groups
		$L\infty$ (C)	$956.79 \pm 7.44 \ mm$	128.62	< 0.001	_
				(770)		
		$L\infty$ (SY)	$924.68 \pm 8.53 \text{ mm}$	108.34	< 0.001	_
				(770)		
		$t_{\circ}\left(\mathrm{C}\right)$	$3.91\pm0.20\;yr$	19.62 (770)	< 0.001	_
		$t_{o}\left(\mathrm{SY}\right)$	$1.85 \pm 0.22 \text{ yr}$	8.45 (770)	< 0.001	_

SY vs. LY 58.27 K 0.23
$$\pm$$
 0.02 14.11 (338) $<$ 0.001 Shared across groups L ∞ 924.61 \pm 10.55 mm 87.68 (338) $<$ 0.001 Shared across groups t_{\circ} (SY) 1.87 \pm 0.27 yr 6.86 (338) $<$ 0.001 $-$ (338)

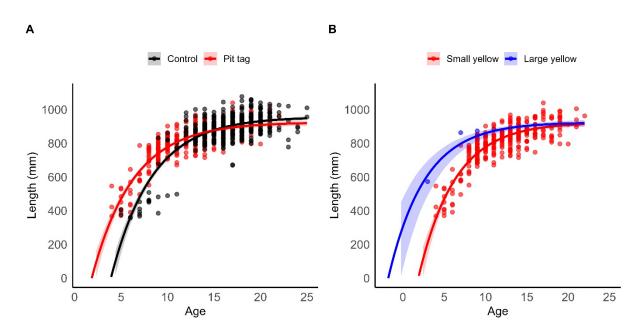


Fig. 3 Length at age data with Pütter-von Bertalanffy curves and 95% confidence intervals in shaded colours, for A) untagged control eels (black) and Pit-tagged eels released as small yellow eels (red), and for B) Pit-tagged eels released as small yellow eels (red) and as large yellow eels (blue).

There were no significant differences between PIT-tagged eels and untagged controls in mass corrected for length, i.e. relative body condition ($F_{3,854} = 1.52 \cdot 10^4$, p < 0.001) (Fig. 4, Table 6).

Table 6 Summary table for the linear model of log-transformed mass (M) as dependent on log-transformed length (TL) (i.e., relative body condition) for Passive Integrated Transponder (PIT)-tagged European eels (Anguilla anguilla) (n=344) released and recaptured in Lake Ymsen. The reference group (intercept) was the untagged eels, the control group (from Lake Ymsen) (n=516).

Response	Coefficient	Estimate (β)	SE	T	p
variable					
log ₁₀ (M)	intercept	-6.49	0.05	-130.73	< 0.001
	$\log_{10}(TL)$	3.27	0.02	191.41	< 0.001
	treatment [PIT]	0.04	0.11	0.39	0.70
	$log_{10}(TL) \times treatment [PIT]$	-0.01	0.04	-0.37	0.71

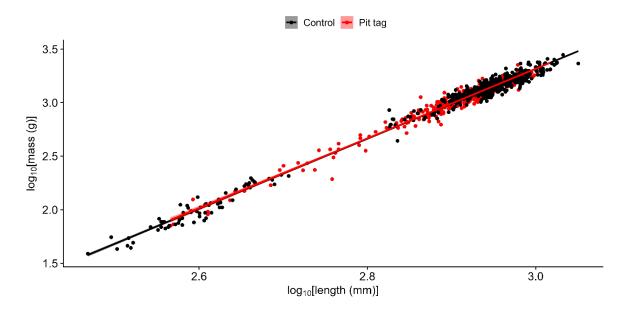


Fig. 4 Linear regressions of log-transformed mass (g) as dependent on log-transformed length (mm) (representing relative body condition) for Passive Integrated Transponder (PIT)-tagged European eels (Anguilla anguilla) released as small yellow eels and later recaptured in Lake Ymsen (red data points and line), n = 344, and untagged, control eels captured in Lake Ymsen (black data points and line), n = 516. The shaded regions in grey and red represent the 95% confidence intervals for the regression lines (note that the 95% CI are very close to the regression line and therefore difficult to see in the figure).

Discussion

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In this study, we investigated tag retention of Carlin tags in silver eels, and any potential effects on growth and condition of PIT-tagged yellow eels by utilising data from several long-term field studies conducted in a natural lake in Sweden. We found that the tag retention rate of the recaptured Carlin tagged eels was 92%, with six out of the 76 recaptured eels having lost their Carlin tag. The retention rate could be as high as 97%, given uncertainties between different data sources regarding four recaptured individuals. Our results are in line with a laboratory study performed by Vøllestad (1988), where he could see a retention rate of Carlin tags at 90%. In general, certain behaviours of fish, such as passing through crevices and burrowing, can lead to loss of external tags (Jepsen et al., 2015). Since the eel is a bottom-dwelling fish that inhabits hollows and burrows, sometimes several eels together, and can spend a long time within the sediment during winter dormancy (Nyman, 1972; Tesch, 1977; Westerberg & Sjöberg, 2015), this could be considered as one potential factor underlying the 8% Carlintag loss. The study by Vøllestad (1988) only monitored tagged eels during seven months in a laboratory environment, hence possibly not covering tag losses due to such types of behaviour. With a possible recapture period of more than twenty years in our study, any seasonal variation in tag loss should be sufficiently covered. The comparable retention rates between the studies suggest that burrowing is not the primary cause of tag loss. Also, if the eel would get entangled and lose the tag in the fishing gear, there would likely be a wound noted during the dissection. But there are other specific behaviours of the eel, like the ability to tie their body into a knot, rolling around, or reaching and biting at the tag, that could mean that the eel might not be an ideal species for external tags (Økland et al., 2013; Jepsen et al., 2015). The retention rate has been found to be as low as 0-9% of larger external telemetry tags on eels (Cottril et al., 2006; Økland et al., 2013), and these types of behaviour might be the reason for tag loss of Carlin tags as well. Considering the very low retention rate of larger tags, the tag retention of Carlin tags at 92%, as found in this study, could be considered high. In precaution, when accounting for retention rate in statistical models and analyses using recaptures of Carlin tagged eel, the use of the lower retention rate found in this study (92%) is recommended, but more research is needed to confirm these results. All recaptured Carlin tagged eels with known recapture date were recaptured within four years after being released, despite continued monitoring for 27 years (continuing in 2025). A possible explanation could be that some of the remaining tagged individuals died. Vøllestad (1988) found a mortality rate of 13% in the laboratory study monitoring Carlin-tagged eel, which would correspond to 15 individuals in our study, much lower than the

43 individuals that were not recaptured (corresponding to a mortality rate of 36%). There are several reasons

why tagging might lead to mortality: direct (e.g. infections) or indirect effects (e.g. increased predation due to a

visible external tag) of the Carlin tag, and these might be higher in a natural environment than in a laboratory. Tag-related mortality was, however, not possible to evaluate in this study, and similarly, natural mortality of untagged eels cannot be evaluated here. Tags should ideally not influence the survival, growth or behaviour of the tagged individuals and should last as long as possible to fulfil their purpose. Future work should investigate the mortality rate caused by Carlin tagging, specifically to separate different possible adverse effects, like infections and increased predation pressure, from natural mortality.

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Our results add to the collection of studies that do not find any major impacts of PIT tags on growth or condition in eels. No major effect related to the size at which the eels were tagged was found, even though few eels were recaptured that were tagged as large yellow eels. In general, the PIT-tagged eels were found to have a similar growth rate as untagged eels. The conclusion that PIT tags do not have any clear effects on eels was further strengthened since there was no significant difference in relative condition (length-mass relationship) between tagged and untagged eels in our study. There were, however, no recaptures from the first stocking year of PITtagged eels in Ymsen in 1998, and the reason for that is unknown. The number of released PIT-tagged eels that year was rather low, n = 190, in particular compared to the other two years when eels were PIT-tagged and restocked (n = 1512 and 1087, respectively, in 1999 and 2000). However, there were 7 recaptured eels from the even smaller summer batch of larger tagged yellow eels in 1999, n = 83. These tagged yellow eels were large enough to get caught in the fishing gears relatively soon after being released, while the tagged small yellow eels from the batch in 1998 had to grow for a longer period before being large enough to possibly be caught in the gears. Importantly, if any of those eels were male, they would have migrated from the lake at a size too small to be caught in the fishing gear, since males are much smaller than females (Vøllestad & Jonsson, 1986). An important aspect to consider in tagging studies that rely on recapture reports by fishers is the uncertainty associated with the fishers' recognising the tag and/or the willingness to report having captured a tagged fish (Pollock et al., 2001). There is no reason to believe that the cooperation with the fisher in Lake Ymsen is anything but good, since the communication over the years has worked well and since small-scale fisheries in general may feel a higher responsibility for their work and resource than large-scale fisheries (Berkes et al., 2001). The reason for no recaptures from the stocking in 1998 more likely lies in some of those eels being male and hence not being recaptured, and/or there could have been a methodological problem during tagging or health issues in the supplied eel, even though no such reason is known.

An important and unusual aspect of this study is that the fisher has reported catches from both fishing gear and the outlet trap for more than 27 years (still ongoing in 2025). Only a few recaptures of PIT-tagged eels have

been made in recent years, the most recent in 2022. Most of the tagged eels are expected to have matured into silver eels during this period and should have a natural urge to leave the system (hence being caught in the outlet trap), although eels in the northern hemisphere can reach a considerable age (30 years or more, Durif et al., 2020). Consequently, this long-term field study likely covers the majority of the yellow eel growth phase of the released PIT-tagged eels (from restocked small yellow eel to mature silver eel), under the rare conditions of a well-controlled natural lake system. The recapture rate of PIT-tagged eels (on average 12% for eels released as small yellow eels) was lower than for Carlin-tagged eels (64% recapture rate). This is, however, not surprising since the eels tagged with Carlin tags were large and most likely old eels. Compared to young individuals, older fish can have a substantially lower natural mortality (Bevacqua et al., 2011) and a higher natural urge to leave the system, leading them to the outlet trap (i.e. being recaptured). From 2011 onward, catches from the commercial fisheries had a size limit of 700 mm, which could have biased recapture rates. However, given the long study period, allowing eels to grow and age, increasing the possibility of being caught in the outlet trap, this effect is likely minimal. Compared to other long-term field studies with PIT-tagged young eels, the recapture rate (12%) lies at the same level as for both tagged and untagged eels. One example is a study performed in France where they found a 15% recapture rate of PIT-tagged eels after 11 years in a natural system (Mazel et al., 2012). Another example is a study of untagged restocked eels in a Swedish lake (the lake had no eels prior to the restocking event), where 11% had been recaptured in the outlet trap after 14 years (Wickström et al., 1996). Overall, our results suggest no clear negative effect of PIT-tagging on the survival of yellow eel in natural lake systems, despite survival not being directly assessed in this study.

Conclusion

Based on the relatively high retention rate of Carlin tags, high recapture rates of both Carlin and PIT tags, and the lack of negative effects on condition or growth rates of PIT tags, we conclude that these are suitable methods for tagging European eel. For the Carlin tags, the results only regard silver eels, and these kinds of tags might not be as suitable for yellow eels which have less thick skin. In addition, there are other aspects of Carlin tagging that are not covered in this study that also need to be considered in tagging studies, such as tagging mortality. While the results from this study regarding Carlin tags can significantly contribute to improving stock assessments and mortality estimates based on mark-recapture studies using Carlin tags, the results regarding PIT tags can further improve meta-analyses and welfare legislation. This, in turn, may facilitate the implementation of appropriate management strategies and conservation endeavours for the critically endangered European eel.

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447	Statements and Declarations
448	
449	The authors declare no competing interests. The authors have no relevant financial or non-financial interests to
450	disclose.
451	
452	CRediT author contributions
453	Author contribution roles are listed here according to the Contributor Role Taxonomy (CRediT) guidelines
454	(<u>https://credit.niso.org</u>): Conceptualization: JSu, HW, JN, EM; Investigation: EM, JN, JP, HW, JSt, JSu; Data
455	curation: JSt, EM, JN, BJ, JP, PJ; Formal analysis: EM, JN; Funding acquisition HW, JSu; Project administra-
456	tion: JSu, HW; Validation: EM, BJ, JN; Visualization: JN, EM; Writing - original draft: EM, JSu; Writing - re-
457	view & editing: all authors.
458	
459	Data availability statement
460	The data and script for this study are archived in the figshare repository: (preliminary links for review purposes:
461	https://figshare.com/s/d3b3e3eefa67de34f33f and https://figshare.com/s/80af7c2266cce86dd6bc), following best
462	practices (Roche et al., 2015) and were available to editors and reviewers upon initial submission.
463	
464	Ethical statement
465	The PIT- and Carlin tagging performed in 1998-2000 and 2012 were performed in accordance with the animal
466	ethical legislation valid at that time.
467	
468	Acknowledgements
469	We thank the local fishers, the family Grönlind, who helped with the field PIT- and Carlin tagging studies con-
470	ducted in Lake Ymsen, by monitoring all eels caught in Lake Ymsen for the presence of PIT- and/or Carlin tags
471	since 1999. Thanks to staff at the former Swedish Board of Fisheries, and at the present Swedish University of
472	Agricultural Sciences, Department of Aquatic Recourses (SLU Aqua), Institute of Freshwater Research, for as-
473	sistance with tagging, animal care, data handling, and dissections, and that have conducted data collection over
474	the years, leading to the important and substantial database "Sötebasen". Thanks to Scandinavian Silver Eel
475	(SSE) for assistance with obtaining the juvenile eels and providing work premises during the tagging procedure.

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