

Research Article

Individual Growth of European Eel (*Anguilla Anguilla*) Assessed by Mark-Recapture With Passive Integrated Transponders (PIT Tags) in Four Isolated Water Systems in the Netherlands

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Growth rates are generally obtained from back-calculation of increments of otolith readings and based on the assumption that mean annual growth can be scaled directly to the distance between age rings. Although otoliths continue to grow even when somatic growth ceased. To analyse growth rates of yellow eel, a passive integrated transponder (PIT) mark-recapture study was performed in four water bodies (Delfland, Markiezaatsmeer, Süderpolder and Vinkeveense Plassen) in the Netherlands. PIT-tags were used as an alternative method instead of the generally applied back-calculation of annual increments from otolith readings. During 2017–2020, 2209 eels were tagged individually and in the subsequent years, 541 eels were recaptured. The mean annual growth rate decreased with increasing length of eel, with growth rates of 2.2–8.8 cm/year for undifferentiated (sex undetermined) eel between 30 and 50 cm and 1.3 and 5.7 cm/year for female eel between 50 and 80 cm. Differences in growth rate were also observed between the four water bodies, which having consequences to population demographics, such as age at first maturity.

Keywords: *Anguilla*; growth rate; isolated water systems; mark-recapture; PIT tag; yellow eel

1. Introduction

The European eel is a panmictic population, occurring throughout Europe from Norway to northern Africa [1, 2]. After returning from the spawning grounds in the Sargasso Sea, young glass eel migrates into brackish and fresh water, where they feed and grow until they mature into silver eel and migrate back to the spawning ground. Eel has the ability to adapt to all kind of environments [3]. Because eel mature in different water types under different conditions, key demographic parameters such as growth, sex ratio and maturation also differ depending on geographical location,

food conditions, temperature and intra- and interspecific competition [4–7]. Growth is considered a key parameter in population management since it directly affects metamorphosis to silver eel [8, 9] and fecundity [10]. Fast growth shortens the period in which eels are vulnerable to predation to size-selective predators [11, 12] and larger individuals tend to be in a better condition [13] and have a higher reproductive potential [14].

Across geographic areas, variation in eel growth rate can be found over a latitudinal gradient, driven by differences in temperature and food availability. In general, in the northern part of its distribution area, eel grow slower and mature later

than eel in more southern areas [3, 7, 15]. In Norway, where eel grow relatively slowly, age at maturation can regularly be up to 30 years or more [16], whereas in Mediterranean areas, age at maturation is generally under 10 years [7, 17]. Other habitat parameters also affect eel growth. For example, along the Mediterranean, faster growth was observed for eel in coastal brackish sites compared with freshwater sites [8, 18, 19]. This difference in growth rate between estuarine habitats and freshwater habitats was found to be a general pattern [3, 20]. In addition, distance in freshwater to the coast was found to negatively affect the eel growth rate [7, 21].

Within geographic areas, local or regional differences in growth rate can also be considerable [22]. Eutrophic lakes, which are mostly highly productive systems due to a high nutrient content, contain faster growing eels than oligotrophic lakes [23, 24]. Competition due to high eel density has also been suggested influencing the growth rate [25, 26]. As eel show strong dimorphic growth, with females growing faster and much larger than males, observed growth rates of yellow eel can also be a consequence of varying geographic sex ratios [19, 27, 28].

Growth rates of eel are generally obtained by back-calculating annual increments from otolith readings [29, 30]. This back-calculation assumes that the mean annual growth of an individual fish can be scaled directly to the distance between the age rings in the otoliths since a positive correlation between otolith length and fish length has been observed [31, 32]. However, because otoliths continue to grow even when somatic growth ceased, scaling the distance between the rings to the size of the eel does not hold for eel that have reached the stage where somatic growth has stopped [30, 33].

An alternative method to analyse individual growth rates is by mark-recapture. Individually marked eels can be recaptured at certain time intervals and the length and weight can be recorded. Although the use of passive integrated transponders (PIT) tags allows for a nondestructive growth rate estimation in which eel can continue their life cycle, this method is hardly been applied [17]. In this study, it is explored whether the use of PIT tags and mark recapture is feasible to determine growth rates of eel in different habitats. The growth rates of eel were estimated in four different water systems in the Netherlands with different nutrient concentrations and salinity by a mark-recapture experiment using PIT tags. The different habitat characteristics between the four water systems may result in growth differences. A better understanding of the growth potential of eel in different water systems can contribute to both conservation and the implementation of management measures.

2. Method

2.1. Study Areas. The mark-recapture study was conducted in four highly regulated water systems in the Netherlands (Figure 1; Supporting Information S1). Delfland, is a typical Dutch polder system in the west of the Netherlands, consisting of relatively deep canals and shallow ditches connected via the Nieuwe Waterweg with the North Sea. The mark recapture study at this location was carried out in four separate subareas within this polder area. In Delfland,

commercial eel fishing ceased in 2016. Markiezaatsmeer is a highly eutrophic artificial lake. The approximately 1200 ha lake, of which 850 ha is shallow water (< 2 m), is located in the southwest of the Netherlands close to the coast and was formed by separating the lake from the Oosterschelde estuary by the building of a dam. The local commercial fisheries also have an annual glass eel stocking program. Süderpolder is another typical polder system in the north of the Netherlands but only consists of (small) shallow ditches and is smaller than Delfland, approximately 63 ha of water surface. Unlike the other study areas, Süderpolder is not managed under the Water Framework Directive and no commercial eel fishing occurred in this water system. Vinkeveense Plassen, an artificial oligotrophic lake system located south of Amsterdam, was created by dredging peat centuries ago. The approximately 1000 ha lake system is connected to the North Sea via the Amsterdam-Rijnkanaal and the Noordzeekanaal, but barriers such as pumping stations and sluices hamper silver eel escapement from the water system. The local eel population is supported by the local commercial fisheries through an annual glass eel stocking program.

The four water systems consist of shallow waters (< 2 m) either completely (Süderpolder), largely (Delfland and Markiezaatsmeer) or partly (Vinkeveense Plassen). The tight coupling of air and water temperatures in Dutch shallow waters (response time < 5 days), irrespective of size, result in highly similar patterns of water temperatures in Dutch water systems [34]. Therefore, water temperatures during the study period were derived from air temperature measurements from meteorological data produced by the Royal Netherlands Meteorological Institute (KNMI) from stations less than 50 km away from the four water systems [35].

2.2. Sampling Program. In total, 2209 yellow eel were used in the study: 1008 eels in Delfland (years 2017 and 2018), 590 eels in Markiezaatsmeer (2019), 168 eels in Süderpolder (2019 and 2020) and 443 eels in Vinkeveense Plassen (2019). All eels were caught with fykes by local fishermen, anesthetized with 2-phenoxyethanol (0.5 mL L^{-1}), measured to the nearest mm below total length and tagged with a 12 mm or 23 mm HDX-PIT tag (Oregon RFID). Except in Delfland, all eels were measured for total weight in gram (Table 1). PIT tags were injected through a hollow needle into the body cavity and no suture were used. These tags transmit a unique code that can be read at a short distance with a handheld PIT tag reader. After normal swimming behaviour reoccurred, the yellow eels were released near the original catch site.

In subsequent years (2017–2023), eels were caught using professional fyke nets in co-operation with local fishermen during the period April–August. Every eel in the catch was checked for PIT tags using a handheld PIT tag reader. This reader can inductively charge a PIT tag and receive the unique code from a PIT tag. Recaptured eels were measured in a V-shaped measuring board. For each water system, recaptured eels were measured by the same operating fishermen and length measurements were done consistently in the same way whether using anaesthesia or not.



FIGURE 1: Map of the study area in the Netherlands and the four water systems (black), from north to south: Süderpolder, Vinkeveense plassen, Delfland and Markiezaatsmeer.

TABLE 1: Overview of the number of (yellow) eels that were marked with a PIT tag, including mean length (L), mean weight (W) and mean condition (K).

Area	Tagged	L	W	K	Recaptures	Individuals	Proportion of individuals recaptured (%)
Delfland	1008	59			733	376	37.3
Markiezaatsmeer	590	43	157	0.18	98	96	16.3
Süderpolder	168	53	317	0.17	36	30	17.8
Vinkeveense plassen	443	61	446	0.17	41	39	8.8
Total	2209				908	541	24.5

Note: Furthermore, the number of recaptures recorded, the number of individual eels recaptured and proportion of individuals that were recaptured at least once. Bold values are mean values calculated of the total number of eels that were marked (tagged).

Measurement accuracy was checked for each fisherman with eel recaptured within 21 days or less. For Delfland, all recaptured eels were anesthetized (2-phenoxyethanol: 0.5 mL L^{-1}) and measured to the nearest mm below. For the other three locations, recaptured eels were measured without anaesthesia to the nearest cm below.

2.3. Data Analyses. The mean annual growth rate (mm/year) was calculated by dividing the length increment by the number of days between first tagging and recapture, multiplied by 365 (days a year). Growth rates were only determined if the number of days between first tagging and recapture or between two recaptures was more than 60 days.

Sex ratio as function of length for eels collected in Dutch waters from an extensive commercial fisheries sampling program showed fewer than 1% of the eels of 50 cm are male [36]. Therefore, eels having a length greater than 50 cm at the moment of tagging were considered female, while sex was undetermined for eels smaller than 50 cm. Individual growth trajectories were visualised for eels that were recaptured at least three times. To investigate the effect of length on the growth rate of eel, eels were grouped by 100 mm length categories at capture for each water system. Differences in annual growth rate between length categories per water system were assessed by making analysis of variance (ANOVA) and Tukey HSD tests. The same tests were applied to check whether condition of eel (K-factor) differ between the water systems in which weight was measured [37]. To test the relationship between the mean annual growth rate and length of eel, a Pearson correlation coefficient was used. All analyses were done in the software program R Version 4.0.3.

2.4. Ethical Statement. The care and use of experimental animals complied with Dutch animal welfare laws, guidelines and policies as approved by the 'Central Committee Animal experiments' following permit 2016. D-0041.001.

3. Results

Between 2017 and 2023, a total of 908 recaptures were realised, of which 359 were recorded within 60 days following last release. A total of 541 individual eels were recaptured at least once: 376 in Delfland, 96 in Markiezaatsmeer, 30 in Süderpolder and 39 in Vinkeveense plassen (Table 1). Of these recaptured eels, 84 were recaptured more than once and some were recaptured up to 10 times. Deviations under 5 mm occurred in length measurements with individuals recaptured within 21 days, suggesting that measurements were done correctly by each fisherman since some eel could also have grown several millimetres within the 21 days. In Delfland, for each recaptured individual, its location at recapture was noted. With one exception, all were recaptured near the original marking site.

Growth was positively related to the number of days since marked or released (Supporting Information S2). Multiple individuals were recaptured more than twice in Delfland ($n = 21$), and for these individual, growth trajectories were visualised (Figure 2). Although all individuals were tagged as yellow eels, eight recaptured eels had metamorphosed as silver eel (visually identified by the fisherman: silvery colour, larger eyes and larger pectoral fins). Despite their assumed metamorphosis to silver eel, some of these individuals continued to grow substantially and one was even recaptured again in a following year (Supporting Information S3). One individual in Markiezaatsmeer metamorphosed to a silver eel around a length of 50 cm.

The mean annual growth rate of eel decreased as length increased (Supporting Information S4). No differences in condition (K-factor) were revealed between eels from the areas Markiezaatsmeer, Süderpolder and Vinkeveense Plassen (Table 1). For all areas, the highest mean growth

rates were observed for the smallest length classes (undifferentiated) and differences in mean annual growth rate between the areas was observed (Figure 3; Supporting Information S4). The mean annual growth rate for the undifferentiated length classes varied between 2.2 cm/year in Markiezaatsmeer and 8.8 cm/year in Vinkeveense Plassen, with maximum observed mean annual growth rates above 10 cm/year. For the length classes above 50 cm, the mean growth rate ranged from 1.3 to 5.7 cm/year in Vinkeveen. The observed growth rate for the overlapping length classes (40–50 cm and 50–60 cm) was lower in Markiezaatsmeer than that in the other three areas. Large individuals (> 80 cm) in both Delfland and Vinkeveen were observed to have a mean growth rate between 2 and 3 cm/year.

4. Discussion

In this study, the mean annual growth rates of eel (1.2–8.8 cm/year), as obtained with a mark-recapture method using PIT tags, are in line with previously estimated growth rates at similar latitudes based on the most commonly used method of back-calculation via otolith readings [6, 20, 31, 36, 38]. In Markiezaatsmeer, Süderpolder and Vinkeveense plassen annual mean growth rates might be slightly underestimated since length at recaptures were measured without anaesthesia. Anaesthesia results in the relaxation of the muscles and the length of eel while measuring tends to be slightly longer. However, the results indicate a large variability in individual mean annual growth rates (0.1–14.6 cm/year) in a small geographic area and show the plasticity of the eel. Eel is known to show high variation in annual growth rates over its distribution area in Europe as a whole [3, 12]. Although water temperatures hardly differed between the study areas, other environmental conditions may explain part of the growth difference within this study between areas (Supporting Information S1).

Except for the smallest size class, the mean annual growth rates in Delfland were found to be rather constant across the length classes. The constant mean annual growth in this water system was also found by individual growth trajectories. In both Markiezaatsmeer and Vinkeveense plassen mean annual growth rate seems to decrease with increasing length, whereby mean growth in Markiezaatsmeer is generally lower compared to the other water systems. Hardly any individuals were recaptured multiple times in these two water systems to confirm decreasing annual growth rates with increasing length by individual growth trajectories. Mean annual growth rates were indicated to be variable across length classes due to the limited number of recaptures. In Süderpolder, too few individuals were recaptured to indicate consistency in mean annual growth rates across length classes.

The low growth observed in Markiezaatsmeer, while this water system is recognised as a eutrophic lake, is remarkable and might be due to a larger proportion of the eel population being male. Male eels have been shown by several studies to have lower annual growth rates than females [19, 27, 36]. Studying the sex ratio of the eel population in Markiezaatsmeer, i.e., the length frequency of escaping silver eels

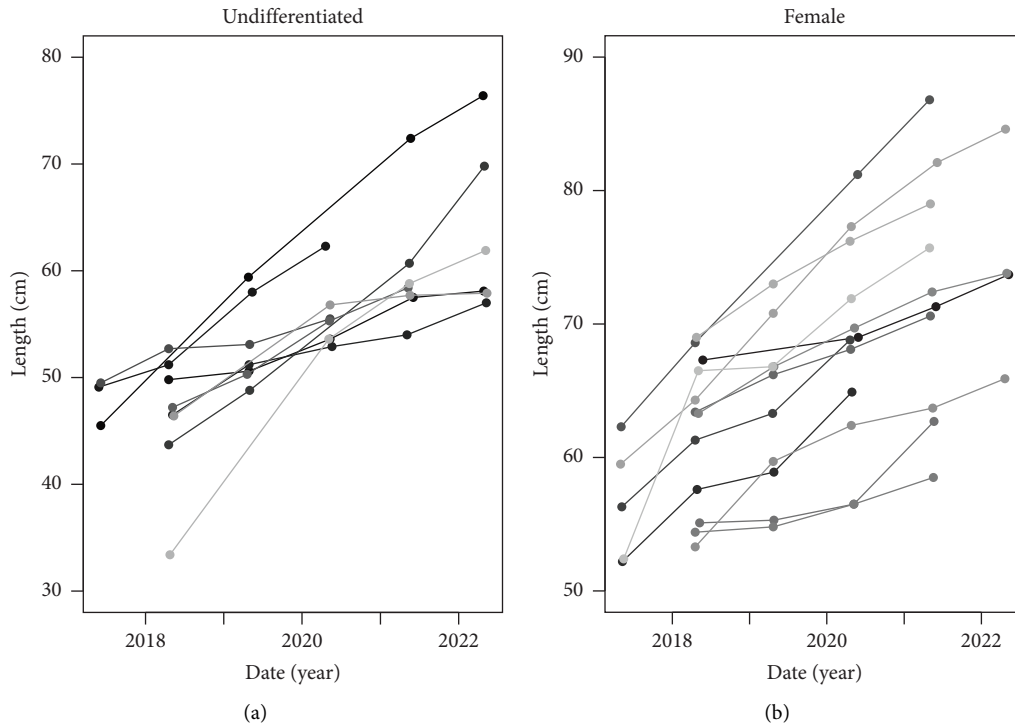


FIGURE 2: Individual growth trajectories of sex undetermined yellow eels (a) and female yellow eels (b) in Delfland, only individuals that were recaptured for more than two times were selected. Recaptures are indicated with a dot.

gives an impression of the ratio of males in a water system [19, 38, 39] indicated that the proportion of males in the population could be substantial [40], while in most Dutch waters, the eel population is assumed to be female dominated [36]. It has been observed in other areas that a high density of eel in a water system results in the development of proportionately more males [12, 41]. This density dependent sex ratio might be the case in Markiezaatsmeer since restocking of glass eels is extensively done. However, eel density and population estimates of Markiezaatsmeer are not yet available.

Multiple studies have found no significant effects of surgically implanted electronic tags on the growth of eel [42, 43]. Although the effects of surgically implanted electronic tags on the growth of anguillids are divergent according to Mazel et al. [44], the growth rates of PIT tagged eels in this study, and in the study of Panfili et al. [17], were in line with previously reported growth rates indicating that the growth performance of eel was not negatively impacted by the implantation of a PIT tags using a hollow needle.

A methodical limitation of the mark-recapture method is that less than 50 cm long, the gender cannot be defined. Thus, for these length classes mean annual growth rates could not be grouped by sex. Eels larger than 50 cm were considered to be female in this study [36] and this assumption is in line with studies addressing the maximum length of male eels [3, 28, 38, 39]. However, within this study, marked eels showed metamorphosis to silver eel. One individual was recaptured again as silver eel in a following year and still grew substantially. Previous research shows that although visual features of silver eels occur, some eel

postpone seaward escapement [45]. Only one individual metamorphosed, at about a length of 50 cm. Ideally, a large amount of small sized eels (< 40 cm) should be marked with a PIT tag to potentially sample a sufficient number of males.

The relative high percentage of recaptures within this study is probably the result of the studied water systems being isolated, e.g., buffered lake and polder. In a more open water system like rivers, the proportion of recaptures is likely to be lower and makes this mark-recapture method using PIT tags less applicable. By selecting isolated water systems, this study was able to focus on an accurate growth estimation of eel by making use of a mark-recapture method using PIT tags. Mark-recapture with PIT tags can also be combined with otolith readings and back-calculated growth to compare (for the same individuals) the observed growth over a given number of years. Furthermore, depending on the research question and research setup, multidisciplinary research can be conducted by making use of PIT tags. PIT tags can also be used for population estimates via mark-recapture [46] and migration and dispersion of individuals can be tracked with PIT tags if eels are recaptured or when detection stations are installed.

In conclusion, this study demonstrates that a mark-recapture method using PIT tags is suitable to accurately obtain mean annual growth rates of eel in isolated water systems. Observed mean annual growth rates of eel revealed large variability between individuals and between different areas on a small geographic scale and mean annual growth rates decrease with increasing length. Accurate growth estimates can contribute to improve population models of eel in managing the eel stock.

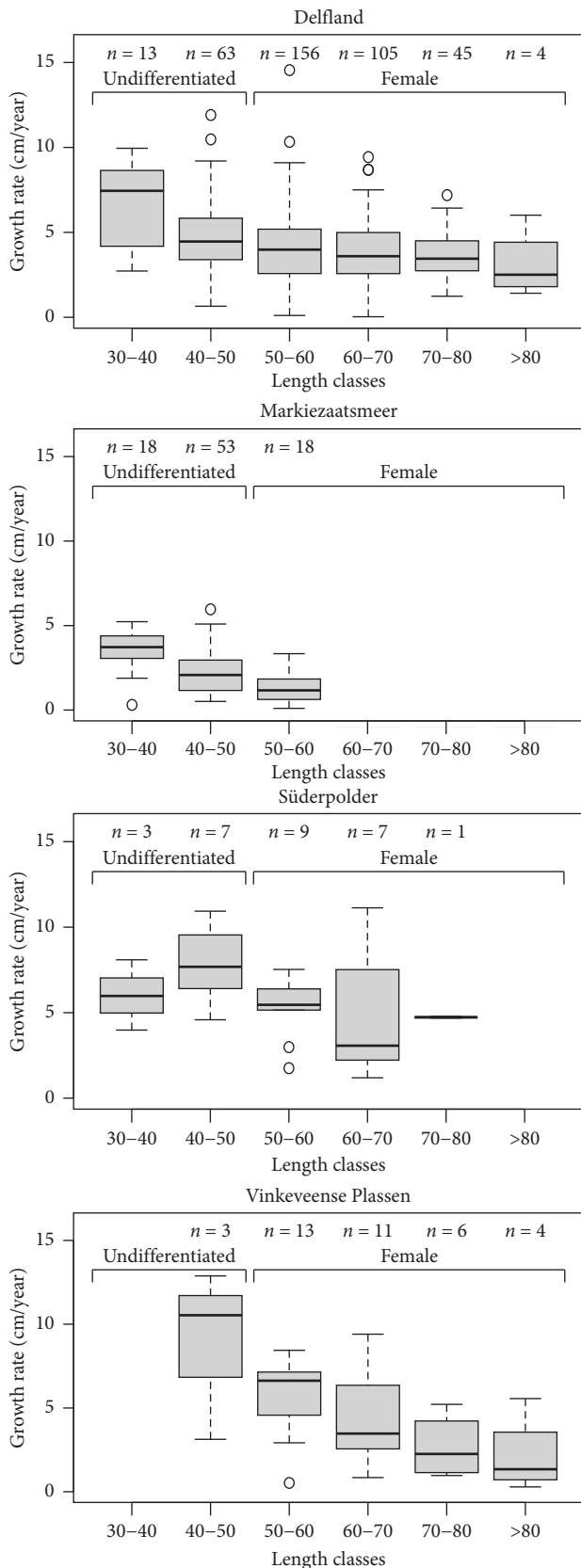


FIGURE 3: Annual growth rate of undifferentiated and female eels for the four different water systems per length class. Length classes are grouped based on the length at release after marking or recapture.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*)

S1: Overview of environmental parameters of the different study areas. The values are average values for the months April–September in the period 2019–2021 (summer mean values). Chlorophyll, nitrogen, phosphate, Secchi depth, Chlorine and pH values were obtained from the corresponding waterboards as part of the Water Framework Directive (WFD). Water temperatures were derived from air temperature measurements by the Royal Netherlands Meteorological Institute (KNMI) from stations Hoek van Holland (Delfland), Tholen (Markiezaatsmeer), Leeuwarden (Süderpolder) and Schiphol (Vinkeveense plassen). S2: Length increment of eel for the four different water systems. Length increment is the difference between the length at recapture and the length at release. S3: Individual growth trajectories of eels that metamorphosed into silver eels during the study period. The recaptures that an individuals was recaptured as silver eel are indicated with a black dot, other recaptures are indicated with a grey dot and growth trajectories of silver eels are shown as black line. S4: Results of ANOVA and Tukey HSD between each length class per area and the Pearson's correlation coefficients between mean annual growth rate and length of eel per area.

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