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RESEARCH PAPER

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Reintroduction success of brook lamprey (*Lampetra planeri*) in a lowland stream in the Netherlands

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Abstract – Brook lamprey (*Lampetra planeri*) disappeared in half of its former range in the Netherlands. A reintroduction effort from 2014 to 2018 aimed at re-establishing a population in the Reusel Stream. About 1000 individuals (96% larvae, 4% adults) were translocated yearly from the nearest population. The donor population was not put at risk, and the reintroduced population has successfully established. The new population survives, reproduces, larvae densities increased to >2 individuals per square meter in (sub) optimal habitat, larvae occur in different length classes, and the distribution range expanded to 5 km. In 2024, the population was assessed to be self-sustaining. Due to the impact of droughts and therefore an increased local extinction risk, the best available status estimate of the reintroduced population would be 'Endangered'. The Reusel Stream showed to be highly sensitive to progressive impacts from climate change and intensive land use. Further restoration of the watershed and sustainable land use are crucial for both the ecosystem and agriculture.

Keywords: Lamprey / species recovery / translocation / habitat restoration / climate change

1 Introduction

Lampreys (Petromyzontidae) play an important role in the health of riverine ecosystems, as they link nutrient cycles and serve as ecosystem engineers through bioturbation by their larvae (Wang *et al.*, 2021; Polyakova *et al.*, 2024). The brook lamprey (*Lampetra planeri*) is the most widespread, non-migratory and nonparasitic lamprey species in Europe (Kottelat and Freyhof, 2007). It is considered a paired species with the anadromous river lamprey (*Lampetra fluviatilis*), perhaps even a single species (De Cahsan *et al.*, 2020; Wang *et al.*, 2021). Brook lampreys are rheophilic inhabitants of streams and small rivers. Larvae grow up in the sediment for a period of about 4–9 yr (Hardisty, 1944; Malmqvist, 1978). Larvae ready for metamorphosis go through several stages from June onwards (Bird and Potter, 1979). In September, they show all adult features and become sexually mature over winter. Adults spawn in spring on well-oxygenated gravel beds (Kelly and King, 2001) at close distances to larval habitats, as they display limited migration capacity (Moser *et al.*, 2015). Brook lamprey are semelparous; after spawning in spring, the adults die (Bird and Potter, 1979).

The brook lamprey is listed as being 'Nearly Threatened' by the global IUCN Red List (Ford, 2024). In the Netherlands, the brook lamprey is listed as 'Endangered' due to a 51% decline in distribution (Spikmans and Kranenbarg, 2016). The remaining Dutch populations of brook lamprey are isolated. Their habitats are under continuous pressure from water pollution, canalization, dredging of streambeds and regulating water levels by weirs, mills and sluices (Spikmans and Kranenbarg, 2016; Kranenbarg *et al.*, 2022; Spikmans *et al.*, 2022). Nowadays, climate changes are posing new challenges in the conservation of sustainable brook lamprey populations, with more frequent summer drought events and higher water temperatures on one hand and high precipitation periods leading to flash floods on the other hand (Van Vliet *et al.*, 2013; Bui *et al.*, 2018; Wang *et al.*, 2021; Bartholomeus *et al.*, 2023).

The European Union Habitats Directive (HD), where brook lamprey is listed in annex II (Sands and Galizzi, 2006), resulted in the establishment of Special Areas of Conservation and increased efforts for habitat restoration and improvement of water quality. Also, the Water Framework Directive (WFD) aims at habitat recovery and to facilitate fish migration. Despite conservation and restoration measures, brook lamprey are at present unable to recolonise large parts of their historic range due to remaining barriers, unsuitable river sections and their limited migration capacity.

In the province of North-Brabant only one brook lamprey population persisted, whereas river lamprey became extinct. To ensure long-term conservation and recovery of the regional brook lamprey populations in favor of establishing a meta population in North-Brabant, reintroduction as a conservation

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tool came into view (Spikmans *et al.*, 2013). Reintroduction of a species aims at establishing a new, viable, self-sustaining population within the former range of the species by the introduction of individuals (Seddon, 2010). In this case, translocation of individuals from one or more donor populations was an option. In consideration of potential impact on small populations, the unforeseen risks of mixing the genetics of different populations, and possible disease transmission, the closest suitable brook lamprey population was designated as a donor (Spikmans *et al.*, 2013). This was the population of the Keersop Stream and downstream Dommel River. The plans for reintroduction of brook lamprey in the Reusel Stream, which offered suitable habitat, met the IUCN criteria for reintroduction (IUCN, 1998). In this article, we present the approach and implementation of the reintroduction of brook lamprey in the period of 2014–2018. Because the success of a reintroduction is often declared, but in many cases not well evaluated (Seddon, 1999, 2015), we evaluate the reintroduction success (2018–2024) and impact on the donor population (2014–2024). We also present observations made and discuss future perspectives.

2 Materials and methods

2.1 Reintroduction site description

The Reusel Stream is an upstream reach of the Dommel River basin, which flows into the Meuse River. It is essentially a protected area (Natura, 2000) under the HD. Brook lamprey and river lamprey were observed in the Reusel until the 1960’s (Moller Pillot, 1971; Spikmans *et al.*, 2013), when poor water quality was observed and decline of brook lamprey was already noted (Moller Pillot, 1971). The last documented lamprey observation dates back to 1966 (NDFF, 2024); fish surveys conducted in recent decades have confirmed the local extinction of lampreys. The historical and recent observations are shown in Figure 1. A 4 km long stream section situated in De Utrecht domain was found suitable again in 2012 for all life stages of brook lamprey and therefore, suitable for reintroduction (Fig. 1 and Appendix B) (Spikmans *et al.*, 2013). A complete overview of habitat features of reference streams and reaches within the Reusel is given in Appendix A.

Because of the normalized upper reaches and agricultural land use, the basin is quickly drained after rain, which leads to flash floods and can cause drought (Terink *et al.*, 2023). Stagnation and drying up of the Reusel had never been observed before 2018 in the Utrecht. In 2018, for the first time in recent history, water stopped flowing in the Reusel at De Utrecht domain, and water levels began to drop, leaving behind pools. To mitigate irreversible ecosystem damage from this incident, water from an agricultural groundwater well was pumped into the streambed to keep the reaches in Wellenseind and Utrecht wet and produce some flow between pools (Appendix B). This emergency measure was implemented in many more streams in the Netherlands, including the Keersop. Drought turned into a more structural threat as the summers of 2019, 2020, and 2022 were also among the 10% driest years of the last century (Bartholomeus *et al.*, 2023) and required artificial pumping. In order to remediate the stream and reduce the impact of climate change, many kilometers of Reusel reaches have been restored both upstream and downstream of De Utrecht. Nowadays, the Reusel is also largely connected for fish migration. Since many efforts were completed recently (2022), habitats are still in the process of development.

2.2 Reintroduction

The reintroduction and translocation of brook lamprey from the Keersop and Dommel population was authorized by the Dutch Government (Deetman, 2013) and took place over a five-year period (2014–2018) (Spikmans and Kranenbarg, 2013). Lampreys were sourced yearly from the Keersop and downstream Dommel reaches (Fig. 1). Most larvae were extracted from the Keersop (KD_09). In 2018, the Keersop was not fished because of severe summer drought and potential additional impact on the population. Multi-day fishing events were executed in autumn to minimize impact on spawning and survival (expected favorable water temperature and dissolved oxygen). Manual dip nets (mesh size 3 mm) were used at suitable larva habitats, as this turned out to be more efficient than targeted electrofishing. Small patches of optimal habitat at multiple locations were fished. As larvae densities could reach over 10 individuals per square meter, and operators could search for the best spots; 1000 specimens could sometimes be extracted within a fished area in the order of 100 m^2. All larva stages and adults were kept to provide a demographically diverse population. An exception was first year larvae (<40 mm) (Hardisty, 1961a), which were probably underrepresented due to the used mesh size, alternative habitats of smaller individuals (Malmqvist, 1980; Liedtke *et al.*, 2023), and the fact that they are more easily overlooked. In total 5134 lampreys (204 developing adults and 4903 larvae) were translocated over five years. Yearly numbers and length frequency details are given in Appendix C. Mortality was rarely observed, less than 1‰ of individuals were fatally injured by catching. After capture, lampreys were stored in aerated (100 l/h) 50 liter tanks (maximum density 500 lampreys per tank), for a maximum timespan of 8 h before release. Lampreys were transported ~35 km by road to the reintroduction site on the same day. The vitality of individuals was regularly inspected. No signs of reduced vitality were observed. Release was executed patch-wise in the designated stream section (Fig. 1), over optimal larval habitat, shortly before or during dusk, to minimize potential risks of predation. It was observed that larvae swam away quickly and/or swiftly burrowed into the substrate.

2.3 Data collection

2.3.1 Larvae monitoring

Larvae monitoring took place in both the newly introduced Reusel population and the donor Keersop/Dommel population. Monitoring focused on larva densities and length class distribution, which are indicators for survival of individuals and recent reproduction success.

From 2014 until 2018, larvae monitoring was carried out within the reintroduction project by professionals, students and citizen scientists. Nine sites were monitored in the Keersop and Dommel, and six in the Reusel (Fig. 1 and Appendix D).

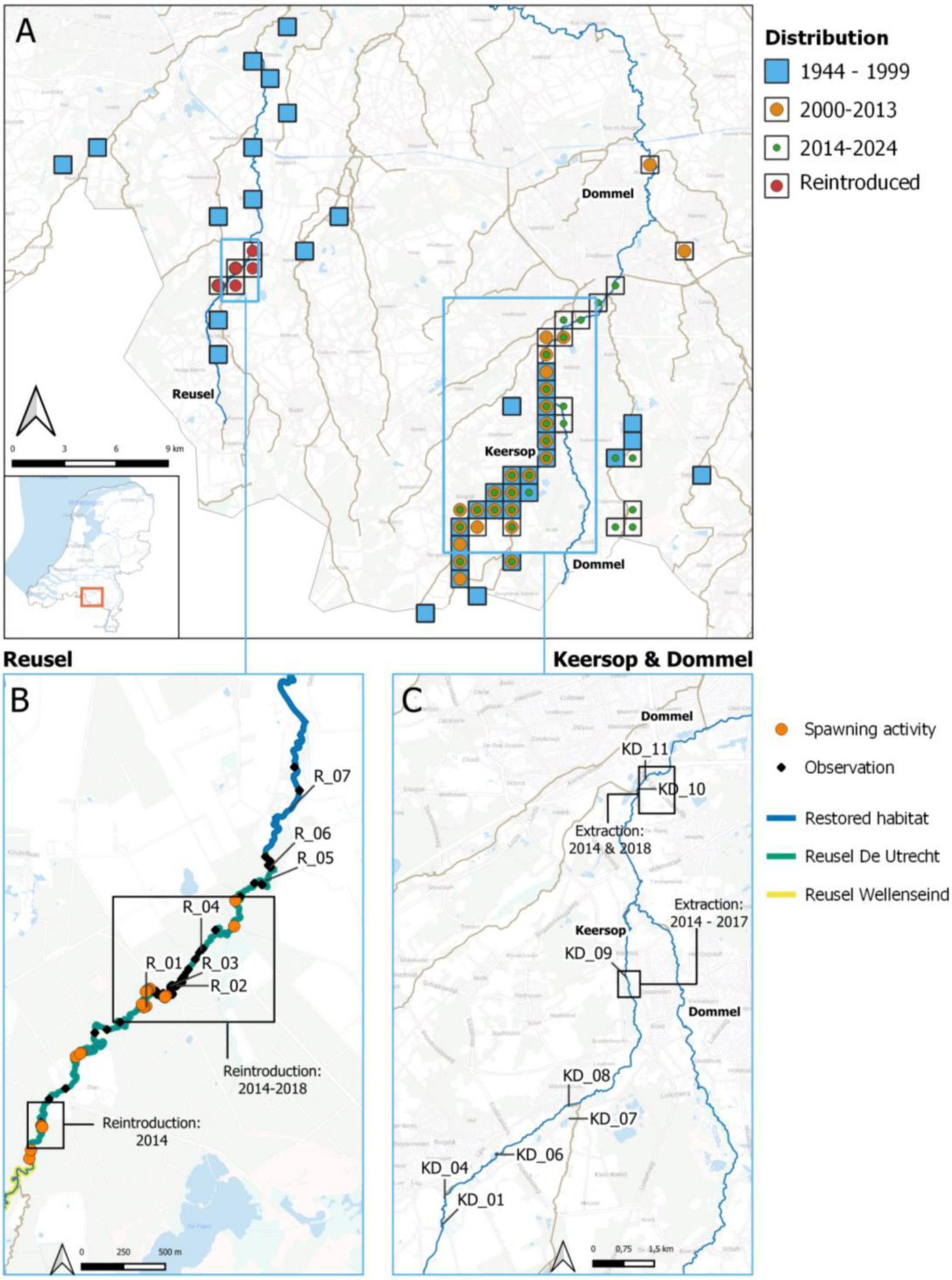

Fig. 1. Map of Reusel and Keersop/Dommel watershed with: a) Distribution of brook lamprey by observations given in occupied kilometer squares in different periods; b) Section of the Reusel stream and locations of reintroduction, larvae monitoring locations and recent (>2014) observations of brook lamprey subdivided into visual observations of spawning and all other observations; c) Sections of the Dommel river and Keersop stream and locations of extraction of larvae and larvae monitoring locations.

Monitoring was executed in autumn, in the years of translocation before extraction and stocking activities. Larvae density samples were obtained by using a cylinder of 46 cm diameter (Appendix B) (Smith *et al.*, 2018). The cylinder was placed on top of the surface and gently pushed down 10 to 20 cm. The soft substrate, in which the larvae are burrowed, within the cylinder was removed using a fine mesh (1 mm) net and collected in a container for further inspection. Suitable sample sites were selected based on the presence of soft substrates preferred by larvae (detritus, silt and fine sand) (Malmqvist, 1980; Polyakova *et al.*, 2024). Twenty samples were taken at each site at the best available larval habitats the operator could find (selective sampling protocol), totalling a bottom surface of 3.32 m^2. Total length (mm) and stage (larva or adult) were noted for each lamprey. Substrate and larvae were gently placed back.

In 2017, monitoring continued under the 'standardized' sampling protocol (Smith *et al.*, 2018). In this protocol habitat selection was standardized, to prevent year to year differences caused by the operators' choices, experience and 'luck'. A fixed stream section of 100 meter, with suitable larval habitat present, was sampled at 5-meter intervals. At these 20 cross sections, the best available larval habitat was sampled by the placement of a cylinder. In the absence of an optimal larva habitat, suboptimal habitat is sampled. Larvae are counted in each sample and assigned to a length class (0-<3 cm, 3-<6 cm, 6-<11 cm, 11-<16 cm or 16-<25 cm).

2.3.2 Observations on distribution range and spawning

Non-standardized visits and surveys of professionals, interns and instructed volunteers result in observations that are registered. In March and April, citizen scientists regularly walked the banks of the stream to search for brook lampreys present at gravel beds and (signs of) spawning activity. In 2024 additional dip net surveys were conducted by interns and professionals. To gain an overview of the observed distribution, all entries in the NDFF were reviewed (NDFF, 2024). Some data entries displayed GPS inaccuracy in the range of <75 m, likely due to the presence of tree cover. Data entries positioned in the forest, were adjusted by coordinates to the nearest position in the stream.

2.4 Data analysis

2.4.1 Larva density and length class distribution

Densities of larvae (individuals per square meter) were calculated for each year and site, based on the average of subsamples. At the catchment scale, averages were calculated based on the densities from different sites to provide a general overview, rather than detailed trends. Brook lamprey larvae densities are considered favorable if they reach over two individuals per square meter (ind/m^2) at a catchment level average for both optimal and sub-optimal habitats (Harvey and Cowx, 2003). In Dutch populations, densities ranging from 0.4–12.7 ind/m^2 have been observed (Spikmans *et al.*, 2013). Comparable densities are also observed in brook lamprey and other lamprey species (Harvey and Cowx, 2003; Mundahl *et al.*, 2006; Harris and Jolley, 2017; Sperone *et al.*, 2019; COSEWIC, 2020; Blanchard *et al.*, 2023), whereas local densities over optimal habitat can sometimes reach over 100 ind/m^2 (COSEWIC, 2020). If recruitment or survival are too low to sustain a population, a decrease in larva densities will be observed, falling below favorable densities.

An assessment of the demographic health of larvae lamprey populations has been proposed by Shephard *et al.* (2019). A population must consist of different length classes with a gradual distribution over recruits, mid-sized classes and larger larvae. In our study, the length class distribution is evaluated based on the occurrence of three length classes. First- and most second-year larvae will remain under a length of 6 cm, indicating that successful spawning occurred recently (Hardisty, 1944, 1961a). The presence of larger larvae between 6 and 11 cm indicates multi-year survival of larvae. The length class over 11 cm are larvae of different year classes which are coming close to transforming into a next generation of adults. The presence of the latter length class is important in securing reproduction in the near future. Adult lengths should not be included in the assessment because of shrinkage of up to 10% (Hardisty, 1961a). Based on references (Spikmans *et al.*, 2013; Shephard *et al.*, 2019), and the observations in the Keersop/Dommel population during translocation, we have set criteria to quickly assess a favorable length class distribution (Appendix G). For a favorable status, these three length classes all occur in a population above a lower range of 5% for < 6 cm; 35% for 6-<11 cm and 5% for >11 cm. When growth or survival is too low to sustain a population, larger length classes will disappear from the population. Impaired recruitment will lead to the ageing of a population, where smaller length classes disappear.

2.4.2 Population size

Based on the observed area of occupancy, average larval density, and habitat availability, a global estimate of the larvae population could be made for Reusel and Keersop/Dommel. Silt- and detritus-rich substrates, which form an optimal habitat, cover 7% of the area of the Utrecht section (Spikmans *et al.*, 2013). Sandy habitats covered 78% of the total area, and especially the finer fractions serve as suitable habitat (Malmqvist, 1980). We assume that the 10% of the sandy habitats of the Reusel could be considered as (sub)optimal habitats, meaning almost 8% of the area. In total, we consider 15% of the stream to be (sub)optimal habitat, where most larvae live. Some will larvae inhabit coarser (less suitable) substrata (Malmqvist, 1980; Goodwin *et al.*, 2008). We assume that 90% of the larvae population lives in the (sub)optimal habitats and 10% lives in substrata considered to be less suitable. Less suitable substrates cover the remaining 85% of the area in the Reusel. Based on the same assumptions and provided data (Spikmans *et al.*, 2013), the Keersop and Dommel offer, on average, 19% of (sub)optimal substrates for larvae and 81% less suitable substrates.

The yearly production of adults from the larvae population can be estimated using the ratios provided by this study, where in de Dommel/Keersop population during extraction the adult ratio was observed to be 4.0% (one adult to 24 larvae). In the related Northern Brook Lamprey (*Ichthyomyzon fossor*), which has very similar life history traits compared to *L. planeri*, it was calculated one adult corresponds to 16 larvae (Caskenette, 2024); the same order of magnitude as the Keersop/Dommel observation. In brook lamprey populations, most adults will be males, as sex ratios are roughly in the order of two males to one female (Hardisty, 1961a, 1961b).

2.5 Evaluation of reintroduction success

For lampreys (Close *et al.*, 2009), the first signs of success can be described as follows; demonstrating that released individuals survive, breeding by the released generation and their offspring, and persistence of the re-established population (Seddon, 1999). To sustain, populations require sufficient recruitment, favorable growth, and survival rates (Schultz *et al.*, 2017; Caskenette, 2024). For lampreys, it has been emphasized that solid determination of population persistence might take decades (Close *et al.*, 2009). To assess the success of a reintroduced population, IUCN criteria can be applied in a manner to those used for remnant populations (Robert *et al.*, 2015; Shier, 2015). The following criteria are to be elaborated:

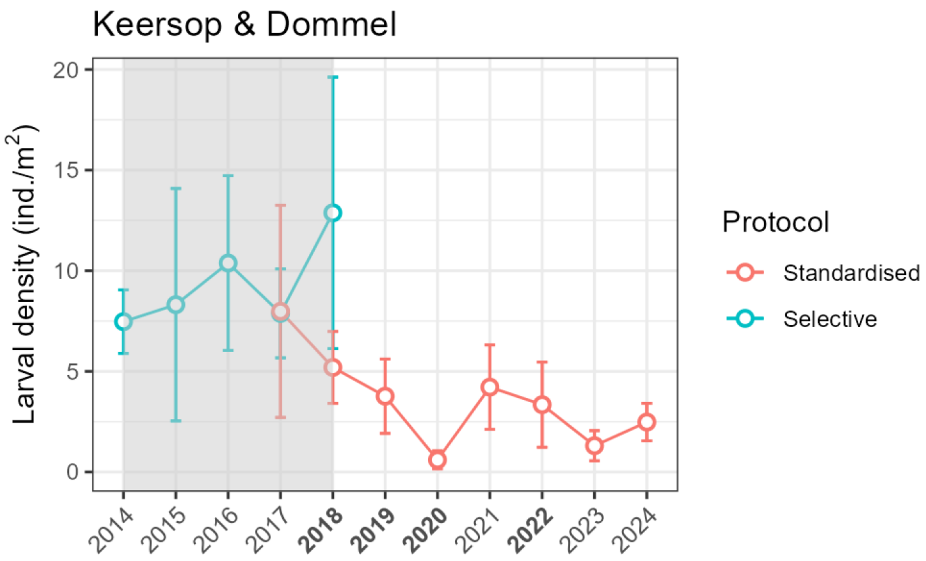

Fig. 2. Observed yearly average densities (and standard deviation) of larvae for Keersop and Dommel monitoring sites in the extraction period (shaded) (2024–2018) and evaluation period (2019–2024) for two protocols. The number and composition of sites deviate between years, see Table A1 for specifications. Years of drought are shown in bold.

Criterion A: a high decline rate in a population; Criterion B: Small range area and decline; Criterion C and D: Population size (and for lampreys we suggest demography); Criterion E: Quantitative analysis of extinction risk. IUCN criteria are not tailored to assess lampreys and the early development stage of this population. We therefore give an interpretation in Appendix F of the directions given (Mace *et al.*, 2008; IUCN, 2012a, 2012b; Shier, 2015; IUCN Standards and Petitions Committee, 2024) for this specific case and evaluate and discuss the results of this reintroduction of brook lamprey accordingly.

3 Results

3.1 Donor population

The larvae population of the Keersop/Dommel in the years of extraction had an observed average density in (sub)optimal habitats of around 8 ind/m^2 (averaging between 5 and 13 ind/m^2) (Fig. 2). The area of occupancy covered approximately 15 ha (25 km at an average stream width of 6 m). A global population estimate, based on 19% of (sub)optimal habitats and 81% of other habitats, yields an average population of around 250,000 larvae (between 157,000 and 408,000) for the years 2014–2018. The site (KD_09) where, until the autumn of 2017, most extractions were made, remained at a moderately high level (5–15 ind/m^2) in monitoring rounds after an extraction (Appendix E). When monitoring continued under the ‘standardized’ protocol from 2018 onward, larvae numbers were observed to decrease at some sites (Fig. 2 and Appendix E). Due to summer drought, die-offs in the larva population were observed. For example, in the Beekloop (Keersop tributary) mass die offs were observed in unshaded pools within 8 h after stream stagnation (Appendix B). The lowest densities were observed in 2020 and 2023, with 2020 being a particularly dry year and 2023 following the summer drought of 2022. The average length-class distributions of the donor population exhibit minor fluctuations over the years and (almost consistently) display a healthy population structure, apart from 2020 (Fig. 4). Since 2014, the Dommel population expanded its distribution range, both a few kilometers upstream of the confluence with the Keersop and downstream into the city of Eindhoven (Fig. 1). Also, the near Tongelreep population (east of Dommel) is expanding in the downstream direction from an upstream Belgian population in the Warmbeek (Fig. 1).

3.2 Introduced population

3.2.1 Stocking period

One year after the first translocation in the Reusel, one 28 mm larva was captured during the larvae monitoring. No larvae released in the prior year were that small, indicating the first sign of reproduction. No other larvae were found in the samples, indicating that densities at this point were still very low. In the spring of 2016, the first visual observations of spawning were made by citizen scientists. From 2016 onward, larvae of larger stages 6–<11 cm and larger than 11 cm occur in the larva monitoring, indicating that larvae survive longer (>1 yr) periods after release and establish a population of mixed demographic composition. In years with stocking, length class distribution showed a high (>40%) abundance of the <60 mm length class. This indicates an effect of successful spawning, as the <60 mm length class was not dominant in stocking. As stocking progressed over the years, numbers of larvae increased in the ‘selective’ monitoring efforts to an average of nearly 2 ind/m^2 over seven sites in 2018 (Fig. 3 and Appendix E). During the 2018 drought, it was observed that larvae left their usual habitat and burrowed in the coarser sand of deeper pools.

3.2.2 After reintroduction

In the years after reintroduction activities, from 2019 onward, numbers fluctuated between sample events (which

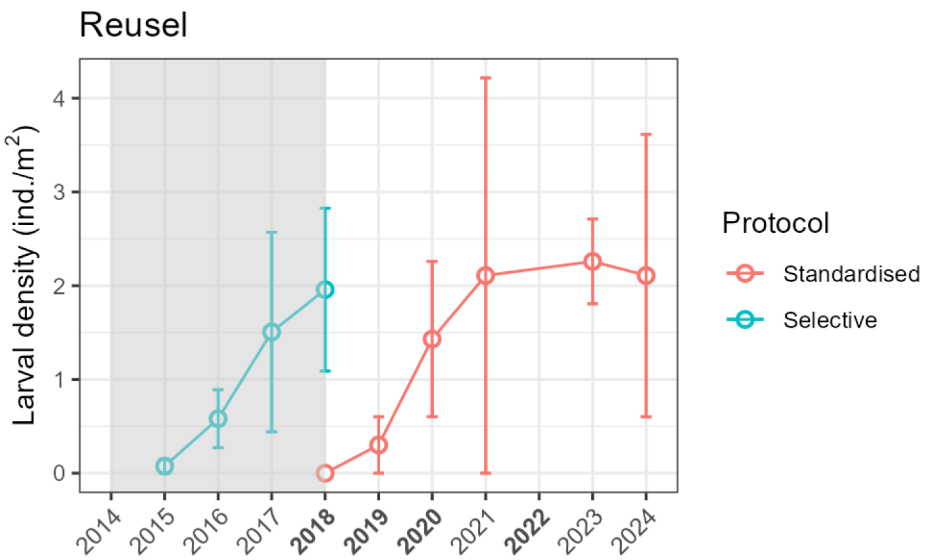

Fig. 3. Observed yearly average densities (and standard deviation) of larvae for Reusel monitoring sites in the introduction period (shaded) (2024–2018) and evaluation period (2019–2024) for two protocols. The number and composition of sites deviates between years, see Table A1 for specifications. Years of drought are shown in bold.

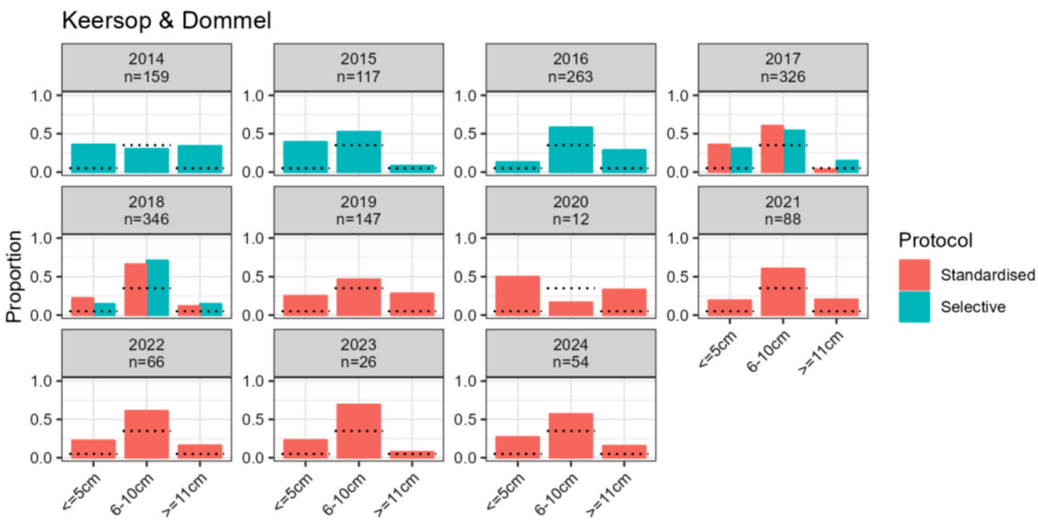

Fig. 4. Length class structure of the Dommel and Keersop larval population by year and protocol, each year shows the total of all sampled larvae (number indicated in graph) for that year over multiple sites. Favorable demographic structure is indicated by a lower range limit (dotted line) of a length class proportion. For a favorable status, all three length classes exceed the lower range limit. Sampled sites are given in Table A1.

might be the result of stochasticity), but on average increased since 2020 (Fig. 3 and Appendix E). In 2019, mid-sized and large larvae were not present in monitoring samples (Fig. 5), although observations of spawning events in 2020 ($n = 3$) and 2021 ($n = 8$) reveal that larger larvae must have been present in 2019. Between 2021 to 2024, average larvae densities levelled off at a point just over 2 larvae per square meter. The increase in larvae numbers observed by the 'standardized' protocol after 2018 could in fact be attributed to the result of successful spawning, as translocation of specimens stopped. This is supported by spawning events observed frequently over the years. A total of 24 spawning events were registered from 2016 to 2022, averaging four individuals per sighting with a maximum of around 20 specimens on March 27th 2022 (NDFF, 2024). All spawning activities were observed between March 22nd and April 12th over the complete length of De Utrecht reach (Fig. 1). A more stable length class distribution at larger numbers of larvae emerges from 2020 onward (Fig. 5). Current larval densities and length class distribution for the Reusel and the Keersop/Dommel, as a reference, show much resemblance.

The brook lamprey in the Reusel remained present in the reintroduced range over the course of 10 yr. Until 2024, some downstream range expansion was observed and observations of larvae were made up to 1.5 km downstream of prior stocking activities. The most downstream observation was made during a targeted survey on October 30th, 2024. Despite efforts further downstream and the presence (of recently restored)

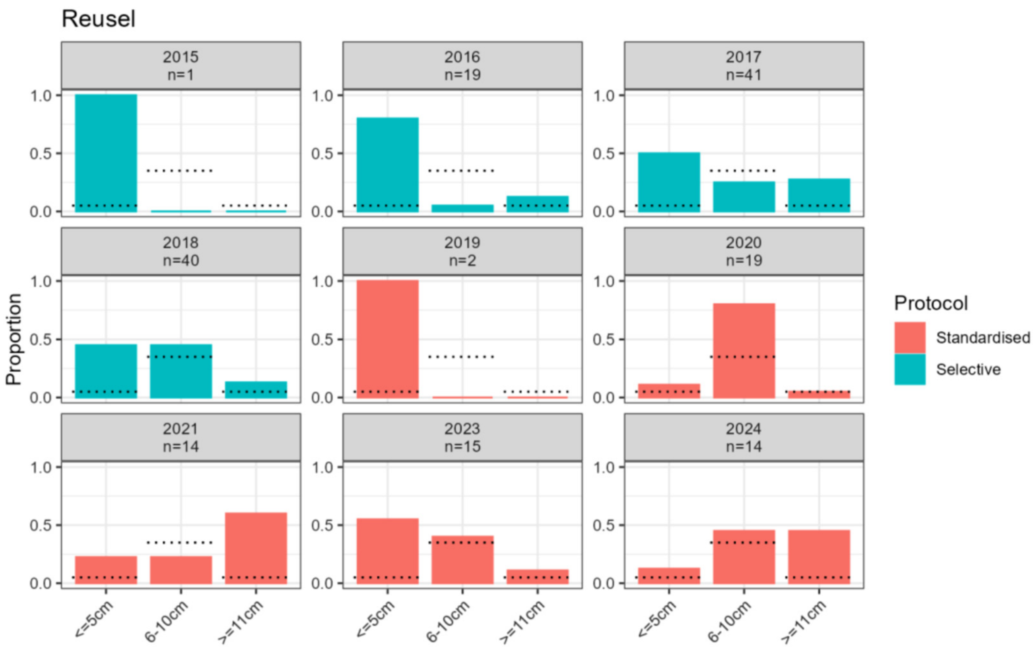

Fig. 5. Length class structure of the Reusel larval population by year and protocol, each year shows the total of all sampled larvae (number indicated in graph) for that year over multiple sites. Favorable demographic structure is indicated by a lower range limit (dotted line) of a length class proportion. For a favorable status, all three length classes exceed the lower range limit. Sampled sites are given in Table A1.

suitable habitat for both larvae and spawning, no individuals were caught. Upstream range expansion has not yet been observed, although a few targeted surveys have also been executed there. At this point approximately 4900 m of stream is occupied with a width of 5 meters, adding up to an area of 2.45 hectares.

Based on the observed average larval density of 2.1 ind/m^2 in autumn of 2024, the given area of occupancy (4.9 km; 2.45 ha) and a (sub) optimal habitat availability of 15% (0.37 ha), the current population of larvae is estimated to be in the range of 8500. At a ratio of 16 to 24 larvae to one adult, a population this size could yearly yield in the order of 354 to 530 spawning adults.

4 Discussion

4.1 Impact on donor population

Monitoring revealed no specific observations of impact on the donor population as a result of extracting over 5000 individuals from the Keersop and Dommel. During the extraction, the estimated population was around 280,000 individuals, which means yearly extractions were in the order of <1%. Local density declines in the donor population were not observed until the first drought of 2018. This phenomenon is also noted in the national monitoring of the complete Dutch distribution range, where, overall, a negative trend is observed (Herder *et al.*, 2024). Interestingly, range expansion was observed for the Dommel, which also corresponds to the positive trend in the national monitoring. Range expansion is attributed to stream restoration (Herder *et al.*, 2024). Our interpretation of these outcomes is that the donor population remains large (in terms of range of occupancy and numbers) and viable, and that the impact of the extraction of individuals should be considered negligible.

4.2 Introduced population development

Initially, the numbers increased during stocking, and the population build-up was evident. In 2018, a trend break in larvae monitoring took place due to further standardization of the monitoring protocol. In 2018 no larvae were captured within the ‘standardized’ monitoring protocol at one site, although sampling was executed at the same site within weeks after the ‘selective’ monitoring, which resulted in a low number of larvae. An explanation is that the operator could not rely on prior knowledge of release sites and previous ‘hotspots’, or could search for the best sampling area. Furthermore, the very dry summer of 2018 might have caused larvae to redistribute and cluster at specific sites (Liedtke *et al.*, 2023), which were not selected under this protocol. After the last stocking event in 2018, very low numbers in the autumn of 2019 of only two small larvae might reflect a population ‘setback’ due to prior drought and/or redistribution of larvae. The population seems to recover, as average larvae densities increase from 2021 and onward and average in 2024 just over 2 ind/m^2 of (sub)optimal habitat, which is at the lower end of a favorable status (Harvey and Cowx, 2003). In autumn 2024, probably no or very few larvae from the stocking remain in the Reusel. If so, they might be young of the year specimens of the 2018 stocking (which were very few) and they should undergo metamorphosis after the average age of 6,5 yr. Therefore, the current population must be composed mainly of first and second-generation lampreys as a result of the natural reproduction of stocked specimens and the reproduction of their offspring. The current numbers in the reintroduced Reusel population are, on average, at the same level as current numbers in the Keersop/Dommel, which declined under pressure of drought. Current habitats in both stream systems are likely not fully occupied, and densities can potentially still increase as they recover from the impact of drought. Future monitoring will reveal if the reintroduced population reaches its regulation phase or carrying capacity (Lorenzen, 2008; Robert *et al.*, 2015). Further range expansion would be possible because habitat availability in the Reusel increased upstream and downstream of the current population due to stream restoration.

4.3 Evaluation of reintroduction success

Reintroduction as a measure to restore *L. planeri* populations had not been done before. For other lamprey species, only a few cases of reintroduction are known: *Ichthyomyzon greeleyi* and *Lampetra appendix* (USA) (Spikmans *et al.*, 2013), two cases of *Eudentonmyzon mariea* (Austria), (Spikmans *et al.*, 2013; Ratschan *et al.*, 2021), two cases of *Entosphenus tridentatus* (USA) (Close *et al.*, 2009; Ward *et al.*, 2012) and one case of *Entosphenus minimus* (USA) (Clemens *et al.*, 2021). The long-term successes of these reintroductions remain largely unknown, apart from some early successes in establishment.

The reintroduction of *L. planeri* in the Reusel, based on the presented and potential population developments, reflects to IUCN assessment criterion A (decline rate) and B (range area) positively, but cannot be fully evaluated because at this early stage the population development lacks a reference point. Demographically, the population now displays a balanced distribution among larval length classes and is approaching a point where it is likely to produce over 300 spawning adults annually. Based on population size (IUCN criterion C and D), the current population is still 'vulnerable' (IUCN, 2012b). At this level, the population is sensitive to perturbations and may take more than 10 yr to reach a minimum viable population size (Caskenette, 2024). Although habitat availability has increased, current land use and the progressive impacts of climate change pose a significant risk of summer stagnation and loss of surface water for the Reusel (Terink *et al.*, 2023). These events could have a serious impact on lamprey populations (COSEWIC, 2020), and local mass die-offs have, in fact, been observed in the Keersop watershed within 8 h after stagnation. Brook lamprey in general respond negatively to frequently occurring low flows (Mignien and Stoll, 2023), and (mass) die-offs occur when habitats are dewatered (Liedtke *et al.*, 2023). Stagnation and dewatering of habitat can be survived by (part of) a population, as lampreys also possess traits that make them resilient to some extent. Some larvae (especially larger individuals) emerge when habitats are dewatered and are able to move downslope when habitats dry up (Liedtke *et al.*, 2023). When the stream stagnates and water levels drop, pools remain. Lampreys and other taxa can temporarily seek refuge in these pools (Bogan *et al.*, 2019). Lamprey larvae can survive here on the condition that oxygen and temperature remain outside critical values: water temperatures below 29 °C (*L. planeri*) and oxygen concentration above 0.75 mg/l at 22.5 °C (for the related *Ichthyomyzon hubbsi*) (Potter *et al.*, 1970; Potter and Beamish, 1975). Surprisingly, when surface water completely disappears, some lamprey larvae can still survive in wet substrates (Liedtke *et al.*, 2023). There is one report of a few *Lampetra* sp. larvae which survive without surface water in the Mediterranean climate of California (USA) for at least 22 days in the hyporheic zone (wet parts in the stream bed) (Rodríguez-Lozano *et al.*, 2019). It is doubtful whether *L. planeri* possesses such survival traits and if similar conditions occur in the Netherlands. It is considered very likely that loss of surface water is catastrophic for the brook lamprey population. Although stream restoration efforts have been implemented in the Reusel stream recently, the long-term effects on preserving water are still unknown and might not be sufficient. In light of the progressing climate change, habitat continuity is at risk within the current geographic range. Based on quantitative analyses on northern brook lamprey (*I. fossor*), extinction probability for a population in the order of 100 female adults (comparable to the current Reusel population), which is under a high probability of catastrophic events, is expected to be in the range of 20% over 5 generations (32,5 yr) (Caskenette, 2024). Therefore, the status of 'Endangered' (IUCN Criterion E) would currently be the best estimate for the reintroduced population of *L. planeri* in the Reusel stream.

4.4 Recommendations on future restoration efforts

To further preserve and restore the ecological quality of the Reusel, including the developing brook lamprey population and other rheophilic taxa, future efforts are needed. The hydrological model of the area shows that under the changed climate, these droughts will reoccur when implementation of a set of appropriate measures fails (Terink *et al.*, 2023).These efforts are also necessary to achieve the goals set under the WFD. To restore the water balance on a basin scale, it is necessary to reduce water consumption by crops, irrigation and habitat types (Terink *et al.*, 2023). All impacts can be reduced through a large-scale transformation, including agriculture on higher ground transitioning into natural areas, coniferous forests being converted into less water-demanding habitat types, a ban on irrigation, and adapting agriculture to less water-intensive crops (Terink *et al.*, 2023). The feasibility of this large-scale scenario is, however, regarded as questionable on grounds of societal support (Terink *et al.*, 2023).

Additionally, the resilience of the reintroduced brook lamprey population can be further improved by its continued expansion. Expansion will take place naturally due to dispersion and colonization of suitable habitats. The Reusel reaches have improved accessibility for fish, as almost all weirs have been either removed or mitigated by fish passes in recent years. As adult brook lampreys display limited migration capacity, nearby spawning grounds (gravel) could serve as stepping stones. For example, the Dommel upstream of the Keersop confluence has been colonized in recent years over several kilometers. In the current situation, large stretches of the Reusel do not offer suitable spawning grounds. The Wellenseind stretch upstream of the Utrecht, offers only suitable larva habitat and lacks the presence of gravel for spawning. Placing gravel beds could make this reach suitable for spawning and facilitate colonization (Peeters *et al.*, 2021).

This measure could serve as a stepping stone in expanding the population to the 6 km of upstream restored reaches, where nowadays gravel substrates are naturally exposed. The longevity of placed gravel beds could be an issue (Peeters *et al.*, 2021); however, if colonization progresses to upstream spawning habitats, Wellenseind still offers high-quality larvae habitats. For downstream colonization, a suitable spawning substrate is also a limiting factor. Downstream colonization is also valuable for the survival of the population. Here gravel occurs in the topsoil, but due to weirs and over-dimensioning of the stream bed, suitable gravel beds appear at a very small scale. Further restoration of the stream would benefit lampreys and other rheophilic taxa. It is advised to (locally) narrow the streambed, plant trees in riparian zones, and allow streambed variation and dead wood. Increased variation will increase diversity of habitats, including gravel beds for spawning and deeper zones for summer survival when water levels drop. Trees along the stream fulfil another important role, they provide shading, which is important for temperature regulation in summer. Ideally, further stream restoration and progressive colonization of brook lamprey would lead to a large population occupying over 20 stream kilometers, including tributaries. In the meantime vigilance remains essential; in upcoming dry summers, it might be necessary to repeat emergency pumping of groundwater into the stream.

4.5 Recommendations on future monitoring

To track the development of the brook lamprey population and steer 'post-reintroduction management', monitoring is essential (Close *et al.*, 2009). National NEM monitoring will continue at two sites. For a more detailed insight, it is recommended to periodically conduct targeted surveys for larvae and habitat quality within and outside the current distribution area. When distribution progresses, additional monitoring sites can be designated to get better coverage of the occupied area. As an addition to the current monitoring protocol and ad hoc surveys, it is advised to periodically (*e.g.*, every 5 yr) measure the exact size of a greater number of larvae. This will enable comparison of the demographic features against a reference dataset of length frequency (Shephard *et al.*, 2019). Combined, this knowledge will help safeguard and recover brook lamprey populations, as well as inform future assessments of their status.

5 Conclusion

In conclusion, the translocation of over 5000 brook lamprey from the Keersop and Dommel led to the establishment of a population in the Reusel. The reintroduced population displays the ability to self-sustain by successful reproduction at one generation after restocking, and it shows an increase in larvae numbers and expansion in distribution. Although under new pressure of climate change, the current habitat suitability for brook lamprey of the Reusel at the Utrecht is confirmed. The methods and quantities used for this reintroduction were able to provide a rapid build-up of a new lamprey population. This underlines that the given approach enabled brook lampreys to survive, grow, and recruit in a rate that sustains a population.

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Conflicts of interest

The authors declare no conflicts of interest.

Data availability statement

All datasets produced and/or examined during this study can be obtained from the corresponding author upon reasonable request.

Author contribution statement

M.E.S. and F.S. contributed to the conceptualization of the research and drafting of the manuscript. M.G., M.E.S. and F.S. contributed to the methodology and data-analysis. M.S. provided details on the study area and drafting of the manuscript. M.B. and M.S. contributed to a critical revision of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Appendix A. Habitat reference values for brook lamprey and assessments

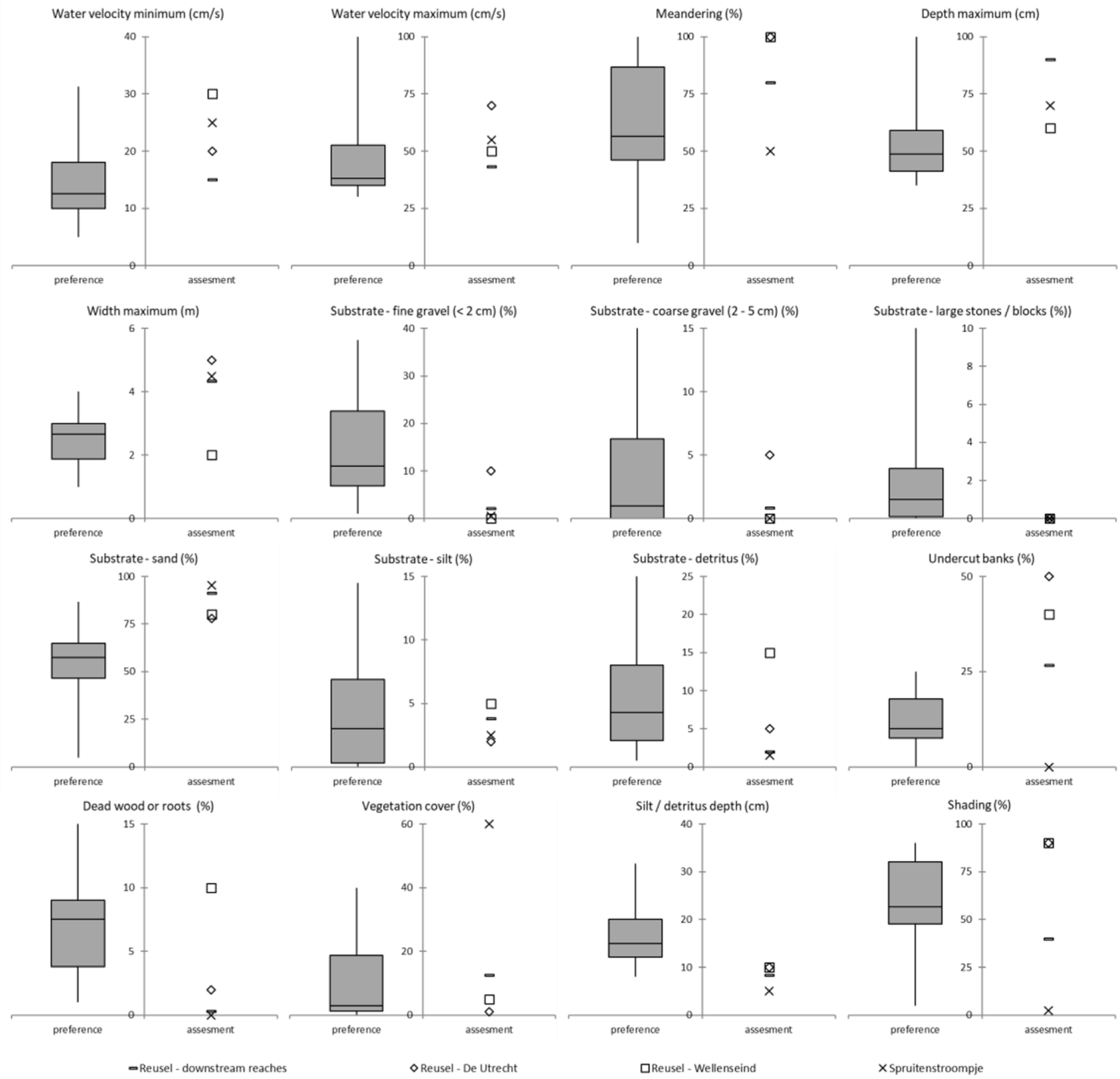

Fig. A1. Brook lamprey habitat ‘preference’ for hydromorphological aspects of reference streams and assessment of potential streams. Preference is based on habitat assessments (field estimates) in current brook lamprey habitats of ten streams (Keersop, Beekloop, Osinkbemerbeek, Willinkbeek, Egelsbeek, Geelmolensche beek, Springendalse beek, Rode beek, Zieversbeek and Kendel) explored by Spikmans *et al.* (2013). Boxplots show the median, 25% lower and 75% upper quartile (gray bars) and the minimum and maximum values (whiskers) observed. Values of the habitat ‘assessment’ (field estimates) by Spikmans *et al.* (2013) are given for the Reusel stretches Utrecht, Wellenseind and the Spruitenstroompje tributary stream. Reusel ‘downstream’ gives an average value which includes three areas; Moleneind, Turkaa and Hilver.

Appendix B. Visual material

Fig. B1. Reusel at 'De Utrecht' during normal late spring conditions (4h of May 2012, picture: M. Schiphouwer).

Fig. B2. Reusel at 'De Utrecht' during summer drought 2018, the stream bed is largely dewatered, some water is flowing from pool to pool as a result of upstream groundwater influx by pumping (23th of July, picture: M. Schiphouwer).

Fig. B3. Groundwater influx to the Reusel by pumping in a ditch upstream of Wellenseind, pumping continued until September (23th of July 2018, picture: M. Schiphouwer).

Fig. B4. Die off of brook lamprey larvae in the Beekloop (tributary to Keersop) (27th of July 2018, picture: M. Scheepens).

Fig. B5. Cylinder sampling for lamprey larvae, bottom right is the 46 cm diameter cylinder placed in the sediment. Citizen scientists remove the soft substrate using an fine mesh net and inspect for larvae (picture: M. Schiphouwer).

Appendix C. Specifications of translocated brook lampreys

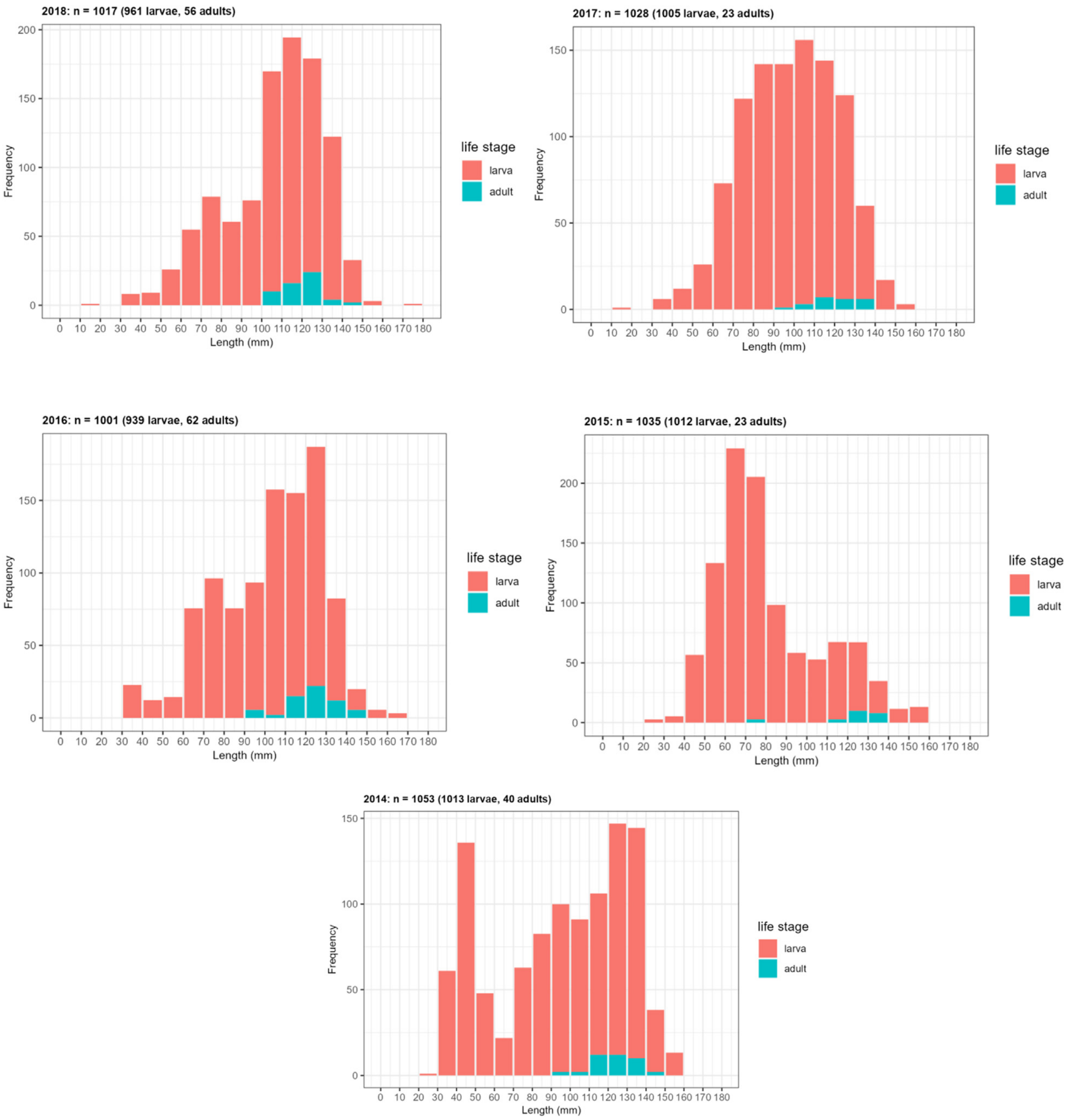

Fig. C1. Specification of yearly extraction of brook lamprey individuals from the Keersop and Dommel in autumn, which were translocated to the Reusel. The frequency of each cm length is given by the number of individuals for adult or larval life stage.

Appendix D. Specifications of larval monitoring sites

Table D1. Monitoring sites for larva monitoring in Keersop/Dommel and Reusel reaches, Site codes are used in other maps and graphs. Coordinates are given in Dutch Grid (RD) X and Y and refer to the center of the site. The number of cylinder subsamples (46 cm) is given for each year and include the protocol used: **Selective** or *Standardized*. High subsample numbers (>25) indicate two sampling rounds.

Stream	Site	X	Y	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Keersop_Dommel	KD_01	152755	368117			**20**	**20**–*20*	**20**–40	*40*	*20*	*20*	*20*	*20*	*35*
Keersop_Dommel	KD_04	152823	368896		**20**	**20**	**20**	**20**	*40*	*20*	*20*	*20*	*20*	*26*
Keersop_Dommel	KD_06	154078	369967	**25**	**20**	**20**	**20**							
Keersop_Dommel	KD_07	155888	370851		**25**	**40**	**20**							
Keersop_Dommel	KD_08	155872	371169	**25**		**60**	**40**–*20*	**20**–*20*	*40*	*20*	*20*	*20*	*20*	*20*
Keersop_Dommel	KD_09	157292	374323	**25**	**25**	**20**	**40**	**20**–*20*	*40*	*20*	*40*	*40*	*20*	*20*
Keersop_Dommel	KD_10	157567	370851						*10*	*20*	*20*		*20*	
Keersop_Dommel	KD_11	157751	379202					*20*	*40*	*20*	*20*	*20*	*20*	*40*
Reusel	R_01	139586	383104		**20**	**20**	**20**	**20**						
Reusel	R_02	139708	383310			**20**	**20**	**20**	*20*	*40*	*20*		*20*	*20*
Reusel	R_03	139622	383392		**20**	**20**	**20**	**20**						
Reusel	R_04	139820	383534		**20**	**20**	**20**	**20**						
Reusel	R_05	140268	384022			**20**	**40**	**20**–*20*	*20*	*40*	*20*		*20*	*20*
Reusel	R_06	140437	384352		**20**	**40**	**40**							

Appendix E. Observed larvae densities each monitoring site

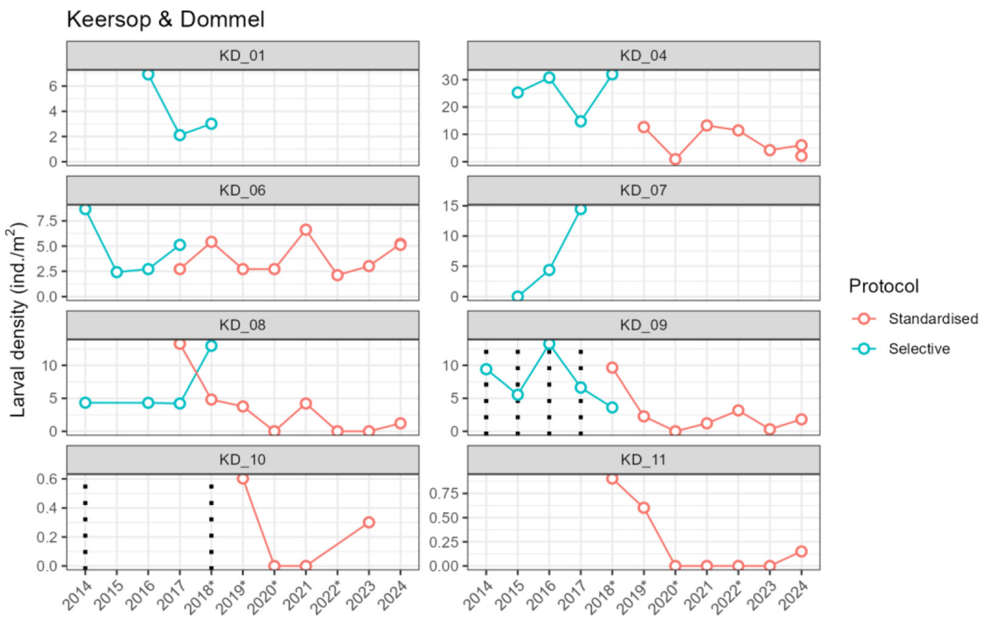

Fig. E1. Observed average densities of larvae for Dommel and Keersop monitoring sites by year and protocol. Each observation is the average of subsamples, normally based upon 3.32 m^2 of sediment surveyed for larvae. Details concerning sites and number of subsamples are given in Appendix D. Years with extreme drought are indicated by *. Extraction sites and years are indicated with a dotted line. Note: *y*-axis is scaled upon maximum observed density for each site to provide maximum detail on fluctuations.

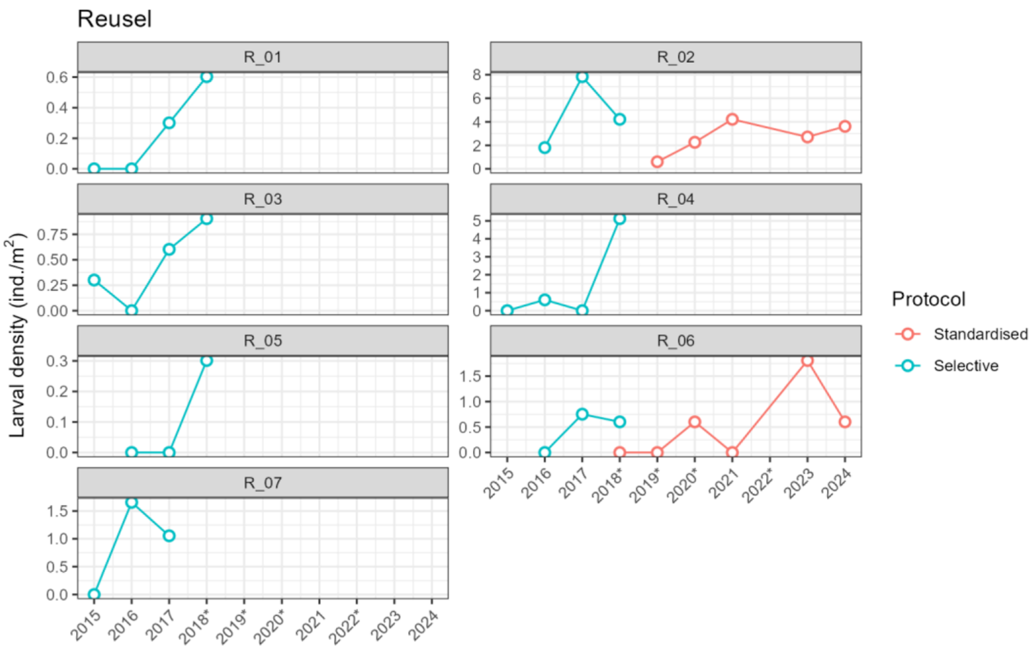

Fig. E2. Observed average densities of larvae for Reusel monitoring sites by year and protocol. Each observation is the average of subsamples, normally based upon 3.32 m^2 of sediment surveyed for larvae. Details on site and number of subsamples are given in Appendix D. Years with extreme drought are indicated by *. Note: *y*-axis is scaled upon maximum observed density for each site to provide maximum detail on fluctuations.

Appendix F. Criteria for evaluation of lamprey reintroduction

In this appendix an elaboration is given on IUCN Criteria and interpretation for evaluation of introduction success in early development of a lamprey population.

Criterion A: a high decline rate in a population

Decline rates in mature individuals are projected over generation lengths and assessed over a period of at least 10 yr or preferably three generations (Mace *et al.*, 2008; IUCN Standards and Petitions Committee, 2024). Brook lamprey has an average generation time of about 6,5 yr, a preferred assessment period would be 20 yr and needs a relevant reference point. Being a semelparous species with a very short and difficult to observe adult life stage, it is most practical to measure decline of brook lamprey by larvae numbers. An observed decline in larvae numbers over these first generations would mean that survival of larvae and/or reproduction success of the adult life stage is too low to sustain the population. To our opinion, at this point in time a successful population should be in a growth phase in numbers and in distribution, moving toward a regulation phase in the future as described by Robert *et al.* (2015). When the regulation phase has been reached after a number of generation times, this could serve as a reference point to measure increase or decline in the future. A regulation point could be defined when larvae reach favorable densities (>2 ind./m^2)(Harvey and Cowx, 2003) over (sub)optimal habitats and the potential distribution range matches the observed one.

Criterion B: Small range area and decline

The area of occupancy quantifies where the species is found during its life cycle (Mace *et al.*, 2008). In this criterion the continuous habitat suitability needs to be included. As brook lamprey live in linear habitat, a single perturbation event (like drought or pollution) could affect an entire population. To this respect the reintroduced population can only be successful if the current suitable habitat remains large and stable enough to sustain lampreys. Preferably a larger range of suitable habitats become gradually occupied and the population expands to adjacent stream reaches and tributaries. Expansion to other tributaries and forming a meta population structure, would reduce extinction risk compared to a 'linear' population.

Criterion C and D: Population size (and for lampreys we suggest demography)

IUCN considers population size being mature individuals taking part in reproduction. For brook lamprey the most stable and measurable population indicator is the number of larvae (Harvey and Cowx, 2003) and their demography (Shephard *et al.*, 2019). From the larvae population, the yearly yield of mature adults could be derived (Caskenette, 2024). For these criteria, we suggest to focus on the larval population of a favorable size and displaying healthy demographic composition (Shephard *et al.*, 2019; Caskenette, 2024). An exact number for a favorable population size is difficult to obtain. Spikmans *et al.* (2013) calculated a population size up to 25.000 larvae would be self-sustaining. Caskenette (2024) modelled a minimum viable population (MVP) for Northern Brook Lamprey (*Ichthyomyzon fossor*) a lamprey species with strong similarity in life history and ecology to *Lampetra planeri*. This MVP included resistance to severe perturbation events. For a 1% probability of extinction over 60 yr an MVP was calculated to be in the order of 2,569 adult females, the equivalent of over 150,000 larvae. Lower numbers increase the probability of extinction, for a population in the order of 300 adult females, approximately a 10% probability is given (Caskenette, 2024).

Criterion E: Quantitative analysis of extinction risk

An analysis to estimate the extinction probability of species based on ecology, life history, habitat requirements, threats and any specified management options. The best example of a quantitative analysis for extinction risk of a lamprey species is the study of Caskenette (2024). We will discuss our results and future perspectives in relation to this model, in absence of a quantitative analysis for this specific species and case.

Appendix G. Quick assessment of larval demography

Based on reference datasets and directions (Shephard *et al.*, 2019), assessment criteria on the occurrence of different length groups within the larval demography were made for Dutch populations (see figures and tables below). For a favorable status of the demography all length groups should be present, a lower range for the favorable status of each fraction is discussed here. We conclude that for a favorable status three length classes occur in a population above a lower range of 5% for < 6 cm; 35% for 6-<11 cm and 5% for >11 cm. For a favorable status, criteria on all three length classes should be met. A rationale per length class and supporting material is found below.

Length class <60 mm

Shephard *et al.* (2019) consider an optimum of 35% on the fraction of <60 mm larvae. Although they consider populations without this fraction and with sufficient variation in longer larvae already favorable, we consider that larvae smaller than 60 mm should be present in a population. Presence of this length group represents recent (last or second to last spawning season) successful reproduction. In most Dutch populations the fraction of <60 mm larvae observed is around 12% (Data Spikmans *et al.* (2013)), in the translocation efforts a minimum fraction of 4% was found, where smallest larvae were probably underrepresented. In a healthy population where spawning recently occurred, this length class must be present. We therefore consider a 5% lower range for a favorable status of the <60 mm fraction of a larva population.

Length class 60-<110 mm

The population should include larvae in the middle length range of 60-<110 mm, this range includes probably most year classes and therefore should account for a relative large fraction. Shephard *et al.* (2019) consider the fraction to be favorable between 50% and 90% of a population and a 55% optimum. As observation in Dutch populations tend to be less dominated by this class (Spikmans *et al.*, 2013), we consider a 35% lower range for a favorable status of the 60-<110 mm fraction of a larva population.

Length class 110 mm and larger

Shephard *et al.* (2019) consider an optimum of 10% on the fraction of 110 mm larvae and larger. They consider populations without 110 mm larvae and larger and with sufficient variation in shorter larvae favorable, contrastingly we consider that the largest fraction of larvae should be present in a population. Presence of this length group will ensure a population to yield adults and reproduce in the nearby future. In Dutch populations this largest length class tends to take up a larger share (Spikmans *et al.*, 2013), mostly over 10%. We therefore consider a 5% lower range for a favorable status of the 110 mm and up fraction of a larva population.

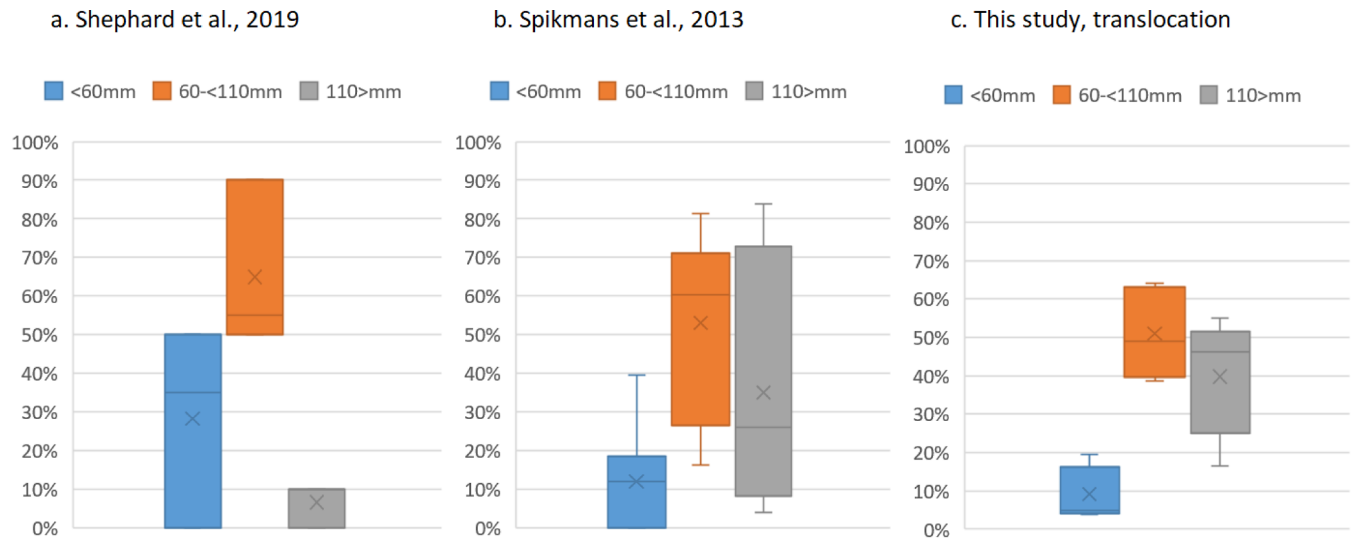

Fig. G1. a) Upper range, lower range, optimal fraction, and average fraction (x) for a favorable status of three length classes in a larva population derived from Shephard *et al.* (2019)/Table A2 b) Boxplot on observed occurrence and an average (x) of three length classes in 9 larva populations based on a dataset by Spikmans *et al.* (2013)/Table A3. c) Boxplot on observed occurrence and an average (x) of three length classes in 5 translocated larva batches (Table A4 / data Appendix C).

Table G1. Fractions for a favorable status derived from Shephard *et al.* (2019) for three larva length ranges.

Shephard *et al.*, 2019	<60 mm	60-<110 mm	110>mm
Threshold to less favorable (lower range)	0%	50%	0%
Favorable (optimal)	35%	55%	10%
Threshold to less favorable (upper range)	50%	90%	10%

Table G2. Fractions for three larva length ranges observed in Dutch populations calculated on a dataset provided by Spikmans *et al.* (2013), only populations where >20 individuals where measured are included.

Spikmans *et al.*, 2013	<60 mm	60-<110 mm	110>00	n
Egelbeek	40%	51%	9%	52
Keersop	0%	29%	71%	35
Kendel	12%	68%	20%	82
Osink Bemersbeek	18%	70%	13%	40
Rode beek	22%	74%	4%	74
Springendalse beek	14%	81%	5%	43
Warmbeek	0%	68%	32%	65
Willinkbeek	3%	20%	77%	35
Zieversbeek	0%	16%	84%	37
Total	12%	53%	35%	464

Table G3. Fractions for three larva length ranges observed in fishing efforts for translocation based on this study (Data Appendix C).

Translocation	<60 mm	60- <110mm	110>nm
2014	13%	39%	48%
2015	19%	64%	16%
2016	5%	49%	46%
2017	4%	62%	34%
2018	4%	41%	55%
Average	9%	51%	40%