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30 years of large river restoration: How long do restored floodplain channels remain suitable for targeted rheophilic fishes in the lower river Rhine?

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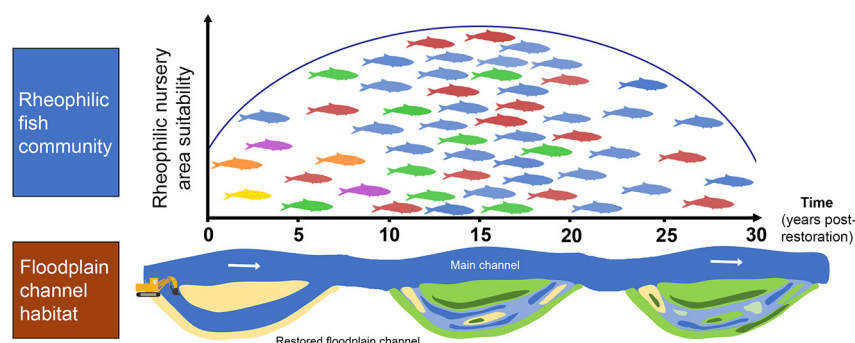
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HIGHLIGHTS

- Long-term evaluation is used for studying ecological efficacy of restoration projects.
- The ecological efficacy of restored floodplain channels changes over time.
- Nursery function for rheophilic fishes was optimal at 13 to 14 years post-restoration.
- Permanent flow was the driving factor in explaining fish community and habitat trends.
- Cyclic rejuvenation maintains optimal fish nursery conditions in restored floodplains.

GRAPHICAL ABSTRACT



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ABSTRACT

The ecological efficacy of river restoration projects may change over time, resulting in the loss of their ecological function for targeted species. The goal of this study was to evaluate the rheophilic nursery function of restored floodplain channels over time, by analysing 30 years of monitoring data from 12 restoration projects in the lower river Rhine. We hypothesised that the nursery function would change over time, caused by the combined effects of decreasing flow conditions and succession processes affecting habitat heterogeneity. We found that nursery area suitability for rheophilic fish was almost 4 times higher in two-sided connected channels than in one-sided connected channels, although the response trends of rheophilic fish were similar for both water body types. These response curves showed clear optima with channel age, for rheophilic fish abundance at 13 to 14 years post-restoration, indicating optimal nursery conditions. On the other hand, rheophilic species richness showed a steadily decreasing trend with channel age, suggesting aging channels became less suitable as nursery areas for most rheophilic fish species. The presence of permanent flow was found to be the main driving factor in explaining both rheophilic fish community trends and habitat succession in individual restored channels. We did not observe an effect of habitat heterogeneity on nursery function for rheophilic fish. To create and maintain optimal nursery conditions in restored floodplain channels of strongly anthropogenically

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Cyclic rejuvenation

influenced rivers such as the river Rhine, we propose a management strategy involving cyclic rejuvenation through human intervention, focusing on restoring permanent flow, with a frequency of on average every 15 years, depending on the rate of aggradation and targeted rheophilic species. We also propose a thorough investigation of the relationship between habitat heterogeneity and nursery success in floodplain channels, as a next step in the identification of suitable nursery areas for rheophilic fishes.

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1. Introduction

There is global concern about the success and effectiveness of stream and river restoration measures, since many projects did not yield the desired ecological recovery (Palmer et al., 2010; Bernhardt and Palmer, 2011; Wohl et al., 2015). Often, the assessment of ecological recovery in restoration projects is based on short-term and local-scale evaluation programmes, resulting in discrepancies between the length of the evaluation studies and the time needed for the restoration measure to reach its ecological potential (Verdonschot et al., 2013; Schmutz et al., 2014; Morandi et al., 2017). Also, restoration effects may vanish over time (Palmer et al., 2014; Kail et al., 2015), causing restored projects to lose their ecological function. The effectiveness of restoration is therefore dependent on both the extent to which the project is self-sustaining and the required maintenance frequency, to ensure continued ecological functioning.

In large lowland rivers strategies for ecological restoration must operate within the constraints of the socio-economic services that these ecosystems support, such as flood protection, navigation, freshwater supply, and agriculture (Buijse et al., 2002). Full restoration to an undisturbed condition is therefore not possible and thus restoration measures are restricted within the boundaries of modified dynamic forces of regulated rivers (Buijse et al., 2005). It is essential to understand whether this type of restoration sufficiently supports natural processes, and what the life span of such interventions is. For instance, in large rivers, hydromorphological processes operate at medium (decades) to long timescales (centuries). Historical interventions, such as normalisation (embankment construction and channelisation) of the river Rhine in the 2nd half of 19th and early 20th centuries, affect channel bed incision and floodplain aggradation up to the present day (Klijn et al., 2019; Havinga, 2020). Similarly, the effects of physical restoration activities, such as reconnecting flow through artificially cut-off side channels, could also have effects over several decades (Schropp, 1995; Simons et al., 2001).

The lower river Rhine is one of the most modified river systems in Europe, with the entire river landscape being modified for the purpose of flood safety, agriculture and navigation (Tornqvist, 1993; Busschers et al., 2005). Much of the modifications of the lower river Rhine have led to floodplain channels being lost or disconnected from the main river (Hudson et al., 2008; Tockner et al., 2009). This has serious negative consequences for ecological processes and river food web functioning (Bayley, 1995; Winemiller, 2004), since floodplain channels function as spawning, nursery and feeding areas for many aquatic and terrestrial organisms (Galat et al., 1998; Ricciardi and Rasmussen, 1999; Ward et al., 2001; Tockner and Stanford, 2002; Tockner et al., 2010b; Pander et al., 2015). Sensitive ecological guilds, such as rheophilic fishes, are particularly affected by the loss and modification of these channels (Kurmayer et al., 1996; Copp, 1997; Aarts et al., 2004; Eick and Thiel, 2013), and their numbers have declined drastically during the last century (Limburg and Waldman, 2009; Araújo et al., 2013; Darwall and Freyhof, 2016; Birnie-Gauvin et al., 2017; Van Puijzenbroek et al., 2019).

In recent decades, the importance of healthy river fish populations has been widely recognised, and restoration of fish nursery habitat has become a priority in riverine nature restoration efforts (Welcomme et al., 2006; Beechie et al., 2010; Hohensinner et al., 2014; Erős et al.,

2019). Since the 1990's, over 30 floodplain channel restoration projects were realised in the Dutch part of the lower river Rhine as part of the European Water Framework Directive and the Dutch 'Room for the River' programme, which simultaneously aimed at flood safety and improved habitat quality (Rijke et al., 2012). This resulted in more natural river-floodplain systems, but not in the expected recovery of rheophilic fish species (Reeze et al., 2017), which may be explained by the sub-optimal functioning of these channels as nursery areas for this specialised ecological guild.

Driving factors of a well-functioning nursery area for rheophilic fish are flow conditions through river-floodplain channel connectivity and sufficient presence, accessibility, and quality of species-specific habitat patches (Ward et al., 1999; Grift et al., 2001; Aarts et al., 2004; Nunn et al., 2007; Górski et al., 2011; Lorenz et al., 2016; Pander et al., 2018). Habitat patches that positively affect rheophilic nursery potential are characterised by the presence of coarse substratum (Keckeis et al., 1997; Jurajda, 1999; Eick and Thiel, 2013), moderately sloping shores (Grift et al., 2003; Pander et al., 2017), and high levels of habitat heterogeneity associated with permanent flow (Schiemer and Spindler, 1989; Grift et al., 2003).

For many restored floodplain channels in the lower river Rhine, connectivity with the main river, and therefore flow conditions, decreases over time (Van Denderen et al., 2019) (Fig. 1). Low or decreasing connectivity levels can be caused by either (poor) restoration project design or by succession processes governed by channel aggradation (Riquier et al., 2015; Van Denderen et al., 2019). Aggradation is a common phenomenon in floodplain channels of lowland rivers (Geerling et al., 2006; Constantine et al., 2010; Dieras et al., 2013; Zinger et al., 2013). Low levels of aggradation can positively affect the rheophilic nursery function of the channel (Stanford et al., 2005; Tockner et al., 2010a). It introduces coarse substratum and creates moderately sloping shores, which increases habitat heterogeneity (Fig. 1). In the long term, the lack of permanently flowing water, due to aggradation at (typically) the upstream connection with the main channel (Van Denderen et al., 2019), causes floodplain channels to gradually evolve into terrestrial environments by the progressively filling with fine-grained materials such as clay and sand (Van der Molen and Buijse, 2005; Citterio and Piégay, 2009; Riquier et al., 2017). Without proper management, this succession eventually causes many restored floodplain channels to lose their function as nursery areas for rheophilic fishes.

No long-term evaluation studies on the functioning of restored channels as nursery areas for fish in lowland rivers have been published; all of the evaluation studies in Western Europe focus on short-term (1–6 years) effects (Simons et al., 2001; Nunn et al., 2007; Schmutz et al., 2014; Daufresne et al., 2015; Pander et al., 2015; Ramler and Keckeis, 2019). As data for a 30-year evaluation study have recently become available in the Netherlands, the goal of this study is to evaluate the development of the nursery function of restored floodplain channels over time, by analysing long-term monitoring data from 12 restoration projects. We hypothesise that the nursery potential of restored channels for rheophilic fish changes over time, with decreasing flow conditions negatively affecting nursery functions with age, while dynamic processes in the channel will increase habitat heterogeneity and the associated nursery function (Cowx and Welcomme, 1998; Grift et al., 2001; Baptist et al., 2004; Van Geest et al., 2005; Geerling et al., 2008). Identification of optimal nursery function of floodplain

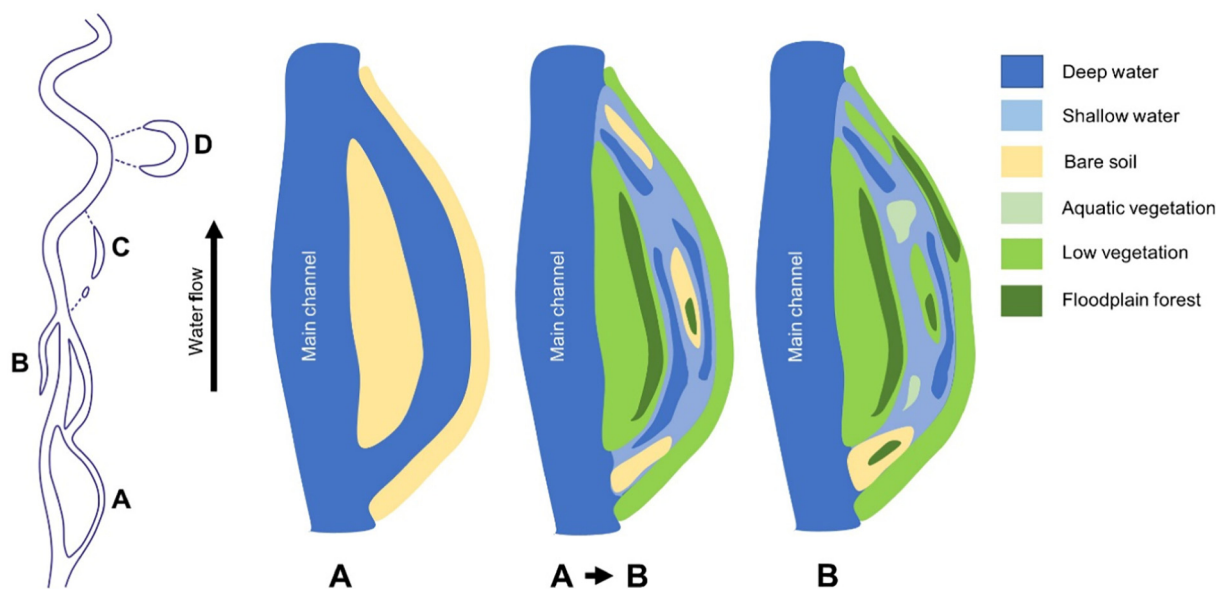


Fig. 1. (Left) schematised natural channel with a gradient of connectivity to the main channel, i.e. a succession series of side-channels: (A) two-sided connected side channel (2SC); (B) over time the upstream connection is blocked by aggradation leaving a one-sided connected channel (1SC); (C) semi-connected side channel whose connections are closed by aggradation enhanced by vegetation succession; (D) isolated oxbow lake only connected at high discharges. (Right) More detailed development of 2SC (A) towards a 1SC. The floodplain channel is aggrading towards a shallower channel with sand banks and pioneer forest development on shoreline and banks. Source: left image adapted from [Petts and Amoros \(1996\)](#).

channels for rheophilic fishes, within the context of anthropogenically modified rivers, will potentially help to guide the effective management of restored floodplain channels.

2. Materials and methods

2.1. Study area and restoration projects

The river Rhine is the second largest river in Central and Western Europe ([Tockner et al., 2009](#)). It originates in the Alps and flows through Switzerland, Austria, France, Germany and the Netherlands, before it flows into the North Sea. The channel of Opijnen (“OP” in [Fig. 2](#)), one of the study locations of this study, was the first major floodplain restoration project in the Netherlands and was constructed in 1994 ([Simons et al., 2001](#)). Since then, 34 water bodies were reconnected with the main river channel through various floodplain restoration programmes. The majority of these restoration projects consists of one-sided and two-sided connected channels, which differ primarily in their flow conditions and habitat characteristics in relation to (semi-)permanent water flow.

Ecological evaluation of these restored channels entailed 50 sampling events spread out over three surveys: (1) a study by [Grift \(2001\)](#) in 1997–1998; (2) a survey by [Dorenbosch et al. \(2011\)](#) in 2009; (3) and an extensive study in 2017–2019 (overview in Supplementary materials A1 and [Stoffers et al., 2020](#)). Sampling strategies for ecological evaluation consisted of monitoring the young-of-the-year (YOY) fish community and characterising habitats. In our evaluation study we included 12 restored channels in the rivers Waal, Nederrijn and IJssel ([Fig. 2](#)), which were all sampled at least twice during the 30-year study period ([Table 1](#)), resulting in the analysis of 27 sampling events. This selection of data enabled for analysis of the impact of succession in individual floodplain channels on their role as nursery habitat for rheophilic fishes.

Study locations consisted of six two-sided connected channels (2SC) and six one-sided connected channels (1SC), the latter connected with the main channel at the downstream end ([Table 1](#)). For the realisation of 7 out of 12 floodplain channels (PA, GW, EP, KL, BK, SW, VR),

floodplains were dredged, whereby side arms were reconnected with the main river channel ([Van den Brink et al., 1992](#); [Grift, 2001](#); [De Leeuw et al., 2005](#); [Schoor et al., 2012](#)). At three other locations (BL, GG, DW) sand extraction pits were connected with the main river through the removal of groynes ([Grift, 2001](#); [De Leeuw et al., 2005](#); [Van Denderen et al., 2019](#)). One channel (BH) was newly created by dyke-relocation ([Schoor et al., 2012](#)), while another (OP) was constructed by opening a 1-km wing dyke at both up- and downstream ends ([Grift, 2001](#)).

All 12 floodplain channels in this study were restored between 1989 and 2002 ([Table 1](#)). Five channels (PA, EP, KL, DW, VR) were subject to a second major modification between 2015 and 2017. Two 1SCs were modified into 2SCs (PA and KL), whereas the inlets and part of the channels of VR (2SC), EP (1SC) and DW (1SC) were extensively modified.

2.2. Data collection

2.2.1. Long-term river trends

To check for trends in long-term discharge and water quality over the sampling period (1990–2018), we retrieved data from the Dutch annual monitoring program of state-managed water bodies (MWTl, <https://waterinfo.rws.nl>). For the water quality trend analysis we used water temperature ($^{\circ}\text{C}$), dissolved oxygen level ($\text{mg}\cdot\text{L}^{-1}$) and phosphate level ($\text{mg}\cdot\text{L}^{-1}$). Data were collected daily at the water surface at the permanent monitoring station at Lobith, where the river Rhine enters the Netherlands from Germany ([Van der Weijden and Roos, 2016](#)). River discharge ($\text{m}^3\cdot\text{s}^{-1}$) data was derived from water level measurements at Lobith.

For the fish community trend analysis, we used MWTl-data on fish abundance and species richness of adult fish in the main channel of the river Rhine. Between 1993 and 2018, 2331 fish samples were collected with a beam trawl from October–April at 113 sampling locations in all three Rhine branches. The beam trawl net used was 3 m wide with a mouth height of 2.9 m, tapering to a width of 0.5 m; the body of the net was 3.6 m long and was constructed (from front to cod end) of 35 mm, 22 mm, and 18 mm stretched mesh ([Van der Sluis et al., 2019](#)). A 10-



Fig. 2. Geographical location of the tributaries of the lower river Rhine delta in the Netherlands. Restored channels are indicated with open circles (two-sided connected channels) and closed triangles (one-sided connected channels). Letter combinations indicate channel name (see Table 1). Width of individual river branches represents relative annual discharge between 1990 and 2011 and arrows indicate flow direction. Source: discharge level overlay adapted from Dörrbecker (2016).

min beam trawl transect in an upstream direction of the main river channel was performed per sampling location, covering a distance of approximately 1000 m. Fish were counted, measured to the nearest cm and identified to species level (Van der Sluis et al., 2019).

Fish species were grouped into ecological guilds based on their flow preference, according to Aarts et al. (2004) and Van Treeck et al. (2020). We distinguished three ecological guilds (ranging from high to low flow preference): rheophilics, eurytopics and limnophilics (overview in

Table 1
General characteristics of the 12 restoration projects selected for this study.

Nr	Code	Location name	Type	River branch	Restoration year	Sampling period		
						1997–1998	2009	2017–2019
1	OP	Opijnen	2SC	Waal	1994	x	x	
2	PA	Passewaaij	1SC ^a	Waal	1996 (2015 ^a)	x	x	x
3	BL	Beneden Leeuwen	2SC	Waal	1997	x	x	x
4	GW	Gameren - West	2SC	Waal	1996	x	x	x
5	GG	Gameren - Groot	2SC	Waal	1999		x	x
6	EP	Ewijkse Plaat	1SC ^c	Waal	1989 (2015 ^c)		x	x
7	KL	Klompewaard	1SC ^a	Waal	2000 (2016 ^a)		x	x
8	BK	Blauwe Kamer	1SC	Nederrijn	1992		x	x
9	BH	Bakenhof	2SC	Nederrijn	2001		x	x
10	DW	Duursche Waarden	1SC ^c	IJssel	1990 (2015 ^c)		x	x
11	SW	Scherenwelle	1SC	IJssel	1989		x	x
12	VR	Vreugderijkerwaard	2SC ^b	IJssel	2002 (2016 ^b)		x	x

^a Restoration project modification: one-sided connected channel (1SC) to two-sided connected channel (2SC).

^b Major modification two-sided connected channel (2SC).

^c Major modification one-sided connected channel (1SC).

Supplementary materials A2). Because we focused on the ecological requirements of fish in this study, no distinction was made between native and alien species. For each ecological guild we calculated fish abundances and species richness per sampling location.

2.2.2. Fish communities in restoration projects

We used YOY fish community data from 227 daytime sampling events in 12 restored channels in July from 1997 to 2019, divided into three survey periods: 1997–1998, 2009, and 2017–2019 (Table 1). To target YOY fish, seine nets were used ranging from 25 to 100 m length, 2.5–4 m depth, and with a maximum stretched mesh size of 14 mm. A minimum of two persons performed the sampling, one guiding the net on the shore and a second person wading or driving a boat through the water. Sample surface per haul was obtained by multiplying transect area length with width and was used for standardising fish abundance and ranged from 700 to 36260 m². For each survey period, we

calculated fish abundance and species richness per ecological guild, per restoration project. Fish abundance was standardised to number of fish per 100 m² per location. For multiple-year surveys (1997–1998 and 2017–2019) we used the geometric mean to assess fish abundance per location per survey. We calculated species richness by using the number of unique fish species per study location over each survey period.

2.2.3. Habitat in restoration projects

An extensive data set was obtained on habitat characteristics for each restoration project per survey period (Table 2). Many of the habitat variables were measured during field sampling, while floodplain channel metrics and data on habitat variability was retrieved from satellite images (<https://www.satellietdataportaal.nl/>) and aerial photographs taken annually (<https://geoservices.rijkswaterstaat.nl/portaal/>). Flow conditions in a particular channel were determined as the proportion

Table 2
General habitat characteristics that were measured per restoration project.

Variable	Description	Type of variable	Levels	Data source
Period	Sampling period	Class	3 classes: (1) 1997–1998, (2) 2009, (3) 2017–2019	Data sets (1997–1998: Grift, 2009: Dorenbosch, 2017–2019: Stoffers)
Location name	Name of channel	Class	12 classes	General information
Delta t (Δt)	Age of channel	Numeric	Range: 1–30 years	General information
River	Branch of the river Rhine	Class	3 classes: (1) Waal, (2) IJssel, (3) Nederrijn	General information
Type	Restoration measure type: one-sided (1SC) and two-sided (2SC) connected channels	Ordinal	2 classes: (1) 1SC, (2) 2SC	General information
Flow conditions	Free-flowing conditions: proportion of months in which the channel is two-sided connected to main river channel in the year prior to sampling (July).	Numeric	Range: 0–1	Monthly river discharge levels (Lobith), calibrated with satellite images**
Mean flow velocity (m·s)	Mean water flow velocity during sampling	Ordinal	3 classes: (0) no flow, (1) 0–0.1 m·s ⁻¹ , (2) 0.1–0.2 m·s ⁻¹ , (3) >0.2 m·s ⁻¹	Field measurements
Depth	Mean depth of channel	Ordinal	3 classes: (1) 0–0.5 m, (2) 0.5–2 m, (3) >2 m	Field measurements
Length (m)	Length of channel	Numeric	Range: 700–3100 m	Measurements from annual photographs
Width (m)	Width of channel	Numeric	Range: 40–150 m	Measurements from annual photographs*
Surface area (m ²)	Surface area of channel	Numeric	Range: 28559–238,007 m ²	Measurements from annual photographs*
Shore length (m)	Shore length of channel	Numeric	Range: 1588–11,471 m	Measurements from annual photographs*
Shoreline vegetation (%)	Percentage of total shore length that is covered with trees and large bushes	Numeric	Range: 0–69	Measurements from annual photographs*
Shoreline index	The amount of shoreline relative to the surface area of the channel. SI = Shore length / Surface area	Numeric	Range: 0.022–0.078 m·m ⁻²	Measurements from annual photographs*
Shore steepness	Mean slope of the bank of channel	Ordinal	2 classes: (1) <15 degrees, (2) >15 degrees	Field measurements
Aquatic vegetation	Overall presence of aquatic vegetation	Ordinal	2 classes: (0) absent, (1) present	Field measurements
Substratum size	Main substratum size/coarseness present at sampling site	Ordinal	3 classes: (1) clay/silt, (2) fine sand, (3) coarse sand	Field measurements
Sand deposition	Overall sedimentation (sand deposition) processes in channel	Ordinal	4 classes: (0) no sedimentation, (1) 0–5 cm·year ⁻¹ , (2) 5–20 cm·year ⁻¹ , (3) >20 cm·year ⁻¹	Field measurements
Silt deposition	Overall siltation (clay/silt deposition) processes in channel	Ordinal	4 classes: (0) no siltation, (1) 0–5 cm·year ⁻¹ , (2) 5–20 cm·year ⁻¹ , (3) >20 cm·year ⁻¹	Field measurements
Habitat heterogeneity	Habitat heterogeneity of channel. Distinction made between uniform and non-uniform habitat.	Ordinal	2 classes: (1) 1–2 habitat types dominant, (2) >2 habitat types dominant	Observations from annual photographs*
Inlet type	Inflow type of channel	Class	4 classes: (0) no inlet, (1) 0–15 m sil, (2) 15–30 m sil, (3) 0–30 m open, (4) >30 m open	Observations from annual satellite images*
Inflow angle	Inflow angle relative to main channel	Class	4 classes: (0) no inlet, (1) 0–25 degrees, (2) 25–45 degrees, (3) 45–65 degrees, (4) 65–90 degrees	Observations from annual satellite images*

*(<https://geoservices.rijkswaterstaat.nl/portaal/>, 2019).

**(<https://www.satellietdataportaal.nl/>, 2019).

of months with free-flowing conditions (two-sided connected) in the 12 months preceding sampling in July. For this we used monthly river discharge levels and channel inlet height. Flow conditions were validated manually by checking river-channels for two-sided connectivity via satellite images. To improve comparability between survey periods, several numerical habitat variables were transformed to class variables (such as mean flow velocity and shore steepness; Table 2). Habitat variables that were measured on the same scale throughout the survey period were analysed as numeric variables.

2.3. Data analysis

2.3.1. Long-term MWTL trends

Long-term data for river discharge, water temperature, phosphate and oxygen levels in the Dutch part of the river Rhine during 1990–2018 were plotted and tested for statistical trends with a linear regression analysis. The temporal developments of mean fish abundances (individuals per 100m²) and species richness per ecological guild were also tested.

2.3.2. Fish and floodplain age

We used age of the restoration project as a proxy for habitat succession processes, hereby assuming a gradual succession over time. Floodplain channel age (Δt) is quantified as the time in years between realisation of a restoration project and the sampling event at that study location. For study locations in the surveys from 1997 to 1998 and 2017–2019, mean year was used to calculate Δt , which was respectively 1997.5 and 2018. Five restoration projects were subject to major

modifications, in which the channel morphology was greatly altered and connectivity with the main channel was restored (Table 1). We considered these modification events to reset the age of the restoration project and therefore fish abundance and species richness were related to the most recent large-scale alteration.

As indices for fish community composition we used species richness, abundance and relative abundance. Based on the best fit, linear or quadratic regressions of log-transformed fish abundances, species richness and relative rheophilic abundances from all 27 sampling events (combining 1SCs and 2SCs) against channel age (Δt) were performed. To check whether observed trends in rheophilic fish abundances were dominated by the most abundant species (ide, *Leuciscus idus* (Linnaeus, 1758)), separate regression analyses were performed for rheophilics with and without ide. Analysis of Variance (ANOVA) on the log-transformed fish abundance data was used to test for fish community composition differences between 1SCs and 2SCs. Mean log abundance and 95% confidence interval per ecological guild were back-transformed to give the geometric mean abundance per 100m². All regressions and ANOVAs were checked for homogeneity of variance assumptions by visually inspecting plots of (standardised) residuals versus fitted values and Q-Q plots.

2.3.3. Fish-habitat relationships

To relate YOY fish community characteristics to multiple habitat variables, multivariate analysis was used. Prior to multivariate analysis, Pearson's product-moment correlations between explanatory habitat variables were checked. In case of variable pairs with correlation levels >0.7, the variable assumed to be most directly related to changes in fish

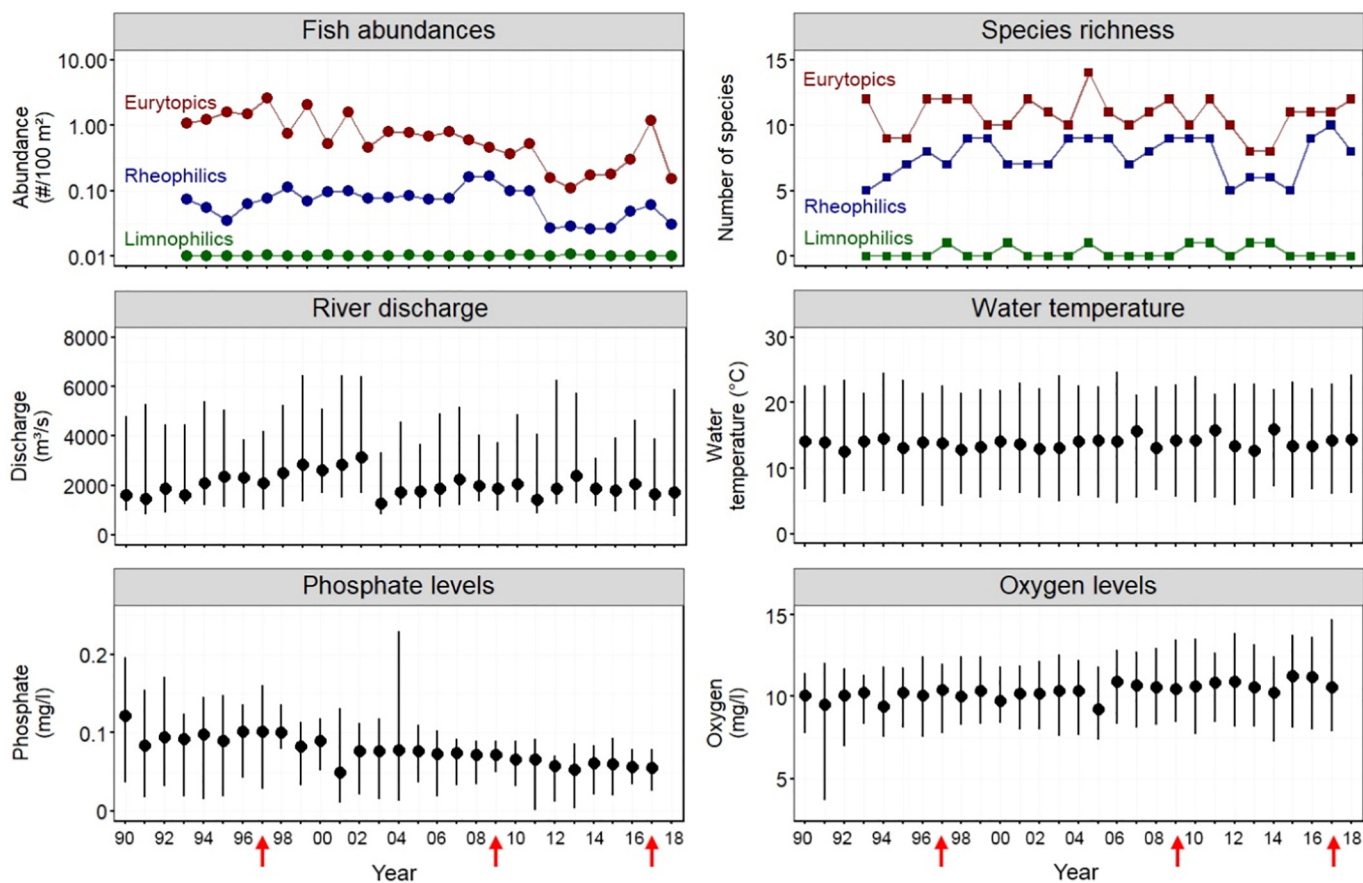


Fig. 3. Long-term river fish community, water quality and discharge trends in the Dutch part of the lower river Rhine between 1990 and 2018. Combined line and dot plots for the mean fish abundance (solid line) and species richness (dotted line) per ecological guild per year are used to show long-term changes in adult river fish community. For river discharge (m³/s), surface water temperature (°C), surface phosphate levels (mg/L) and surface oxygen levels (mg/L) we plotted the median with 95th percentile bars per year. Water quality variables and discharge levels are (in) directly measured at Lobith (NL). Red arrows indicate survey periods in the restored channels of our study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

community composition was retained (Tabachnick and Fidell, 1996). Fish abundance data (response variables) were square-root transformed prior to analysis to decrease the effect of extreme values in the analysis (Ter Braak, 1986).

Canonical Correspondence Analyses (CCA) were run separately for fish abundances and species richness (Oksanen et al., 2007). If full models (including all selected explanatory habitat variables) showed collinearity (variation inflation factor, VIF > 5), habitat variables were removed, starting with those that showed the highest absolute correlation with another habitat variable. The explanatory significance of final models and individual habitat variables were tested using 999 permutations. All multivariate analyses were performed with the vegan package in R (Oksanen et al., 2007; R Core Team, 2013).

3. Results

3.1. Long-term MWTL trends

From 1993 to 2018, eurytopic fish dominated the Dutch part of the lower river Rhine in abundance and species richness (Fig. 3), with 86.6 ± 7.4 (mean \pm SD) percent of the total catch consisting of eurytopic fish. Rheophilic fish made up $11.4 \pm 6.4\%$ of the total catch, whereas limnophilics were rarely observed ($2.1 \pm 1.7\%$ of total catch) in the main channel of the river Rhine. For eurytopic fish abundances, a long-term declining trend was observed ($F_{1,23} = 19.65$, $p < 0.001$, $R^2 = 0.46$), whereas for rheophilic and limnophilic abundances and species richness, for all ecological guilds no temporal trends were observed. Also, no trends were identified in river discharge and water temperature from 1990 to 2017. For dissolved oxygen levels an increasing trend ($F_{1,26} = 21.04$, $p < 0.001$, $R^2 = 0.45$) was observed over time, whereas for phosphate levels we observed a decreasing trend ($F_{1,26} = 67.05$, $p < 0.001$, $R^2 = 0.72$). Additionally, no clear deviation from the overall long-term development was observed, in either river fish community or water quality variables and discharge levels, within any of the survey periods of this study.

3.2. Fish and floodplain age

The YOY fish community in restored floodplain channels showed a similar composition across ecological guilds, as the fish community in the main channel. Eurytopic fish dominated the floodplain channels, with on average 32.6 ± 3.1 (geometric mean \pm SD) fish per 100m², followed by rheophilics (4.6 ± 6.5 fish per 100m²) and limnophilics (0.1 ± 13.7 fish per 100m²). Species richness per restored channel was highest for eurytopics, with on average 10 ± 3 (mean \pm SD) species observed, followed by rheophilics (4 ± 1 species) and limnophilics (1 ± 1 species).

Although the abundance of rheophilic fish was on average higher in 2SC than in 1SC, this effect was not statistically significant ($t_{23} = 1.55$, $p = 0.13$). Hence we only reported the results of both channel types combined.

Floodplain channel age, Δt , ranged from 1 to 30 years. For abundances, rheophilic fish showed optimum levels at channel age 14 ($F_{2,24} = 16.08$, $p < 0.01$, $R^2 = 0.57$; Fig. 4). We found no significant trends for fish abundance for the other ecological guilds. Rheophilic species richness showed a significant decreasing trend ($F_{1,25} = 11.61$, $p < 0.01$, $R^2 = 0.32$; Fig. 4) with Δt . For eurytopics a similar initial decrease in species richness was observed, followed by an increase, resulting in a polynomial trend with lowest species richness at channel age 13 ($F_{2,24} = 4.61$, $p < 0.05$, $R^2 = 0.28$; Fig. 4). No significant trend was found for species richness of limnophilics.

To explore whether the most abundant rheophilic species (i.e., ide; supplementary materials A2) dominates the observed pattern, we analysed rheophilic fish abundances without ide. For this analysis we also found a significant polynomial trend ($F_{1,25} = 4.95$, $p < 0.05$, $R^2 = 0.29$; Fig. 5), with an optimum at $\Delta t = 13$. For the relative abundance

of rheophilic fish (including ide), indicating preferred environmental conditions compared to other guilds, we observed a polynomial trend ($F_{2,24} = 4.13$, $p < 0.05$, $R^2 = 0.26$; Fig. 6) with an optimum at $\Delta t = 14$.

Despite the fact that rheophilic fish were on average almost four times more abundant (fish per 100m²) in 2SCs (geometric mean: 7.6, 95% CI [6.7, 24.1]) than in 1SCs (geometric mean: 2.0, 95% CI [1.4, 8.4]), no significant difference (ANOVA: $F_{1,25} = 3.5$, $p > 0.05$) was found. Furthermore, we observed no significant differences between 2SCs (4 ± 1 species) and 1SCs (3 ± 1 species) for mean rheophilic species richness (ANOVA: $F_{1,25} = 3.28$, $p > 0.05$).

In contrast to rheophilic fishes, eurytopic species were on average twice as abundant in 1SCs (geometric mean: 50.6, 95% CI [25.9, 154.5]) compared to 2SCs (geometric mean: 25.1, 95% CI [24.9, 26.3]), although no significant difference between channel types was observed (ANOVA: $F_{1,25} = 2.56$, $p > 0.05$). Neither was there a significant difference in eurytopic species richness between 1SCs (11 ± 1 species) and 2SCs (10 ± 1 species) (ANOVA: $F_{1,25} = 0.99$, $p > 0.05$).

3.3. Fish-habitat relationships

For fish abundances in relation to floodplain channel habitat, the final CCA model included mean flow velocity, substratum size, water depth, shoreline vegetation, sand deposition, habitat heterogeneity, shoreline index and aquatic vegetation as explanatory variables (Fig. 7A). This model was significant ($p < 0.05$) and explained 51.2% of the total variance. Rheophilic fishes were mostly associated with increased flow velocity and sand deposition rates, and coarse sand substratum. Eurytopic fish abundances corresponded with high levels of shoreline availability (shoreline index), whereas limnophilic fish were most abundant in habitats with both aquatic and shoreline vegetation present. For species richness in relation to habitat, the final CCA model contained flow conditions, substratum size, water depth, shoreline vegetation, shore steepness, aquatic vegetation, silt deposition, sand deposition and shoreline index as explanatory variables (Fig. 7B). The model was significant ($p < 0.05$) and explained 52% of the total variance. High numbers of rheophilic fish species were associated with the presence of coarse sandy substratum and increased flow conditions in the channel, whereas eurytopics were associated with high levels of silt deposition. Limnophilic species richness was highest in habitats with aquatic vegetation.

High abundances of rheophilic fish were mainly associated with 2SCs (Fig. 7C). Also species richness of this ecological guild was associated with 2SCs, whereas eurytopic and limnophilic species were associated with 1SCs (Fig. 7D). Despite the high levels of variability in the direction and length of the arrows observed for aging 2SCs in both ordinations, most aging 2SCs developed towards decreased flow conditions and sand deposition, increased shore steepness and presence of coarse sand over time (Fig. 7D). Aging 1SCs were subject to less variability in fish community composition and habitat and developed towards increased silt deposition and shore vegetation over time. Despite these differences in habitat succession between 1SCs and 2SCs, both floodplain channel types became less suitable for sustaining high levels of rheophilic fish species with increasing age.

4. Discussion

In this long-term study, we evaluated the nursery potential of 12 restored channels for rheophilic fishes in the Dutch part of the lower river Rhine, over a 30-year period. We hypothesised that channel nursery function would be influenced during aging through channel aggradation and other succession processes. Dynamic processes directed by the main river would create a mosaic of habitats, which are favourable for the nursery of rheophilic fishes (Ward et al., 1999; Grift et al., 2001; Aarts et al., 2004; Wolter et al., 2016; Pander et al., 2018). However, aggradation would also lead to decreasing connectivity with the main river channel, thereby negatively affecting flow conditions in the

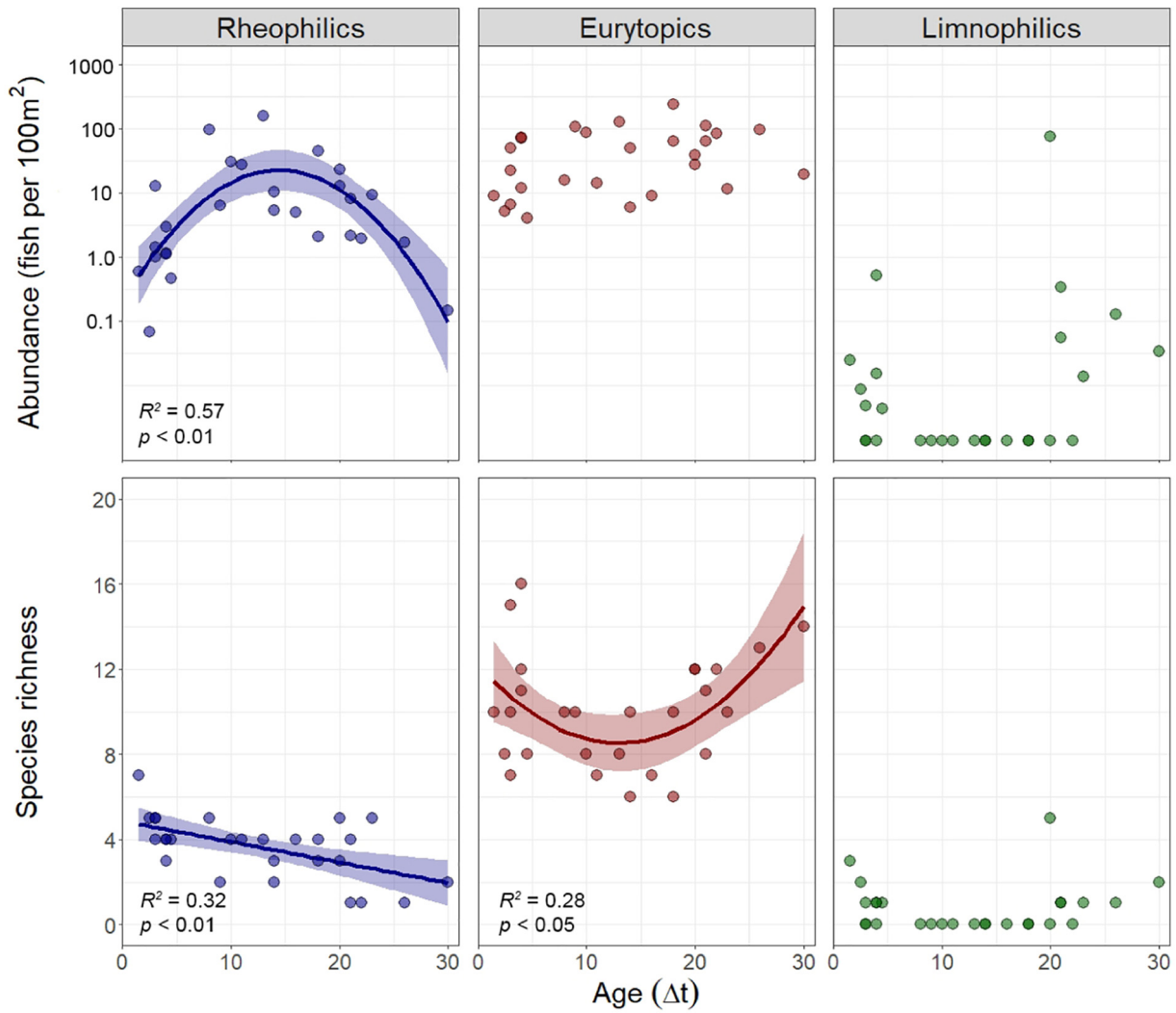


Fig. 4. Fish community response trends in terms of abundances (top figures) and species richness (bottom figures) per ecological guild are plotted against restored channel age (Δt) for all channels combined. Fitted regression lines with 95% confidence intervals are used to indicate significant trends ($p < 0.05$).

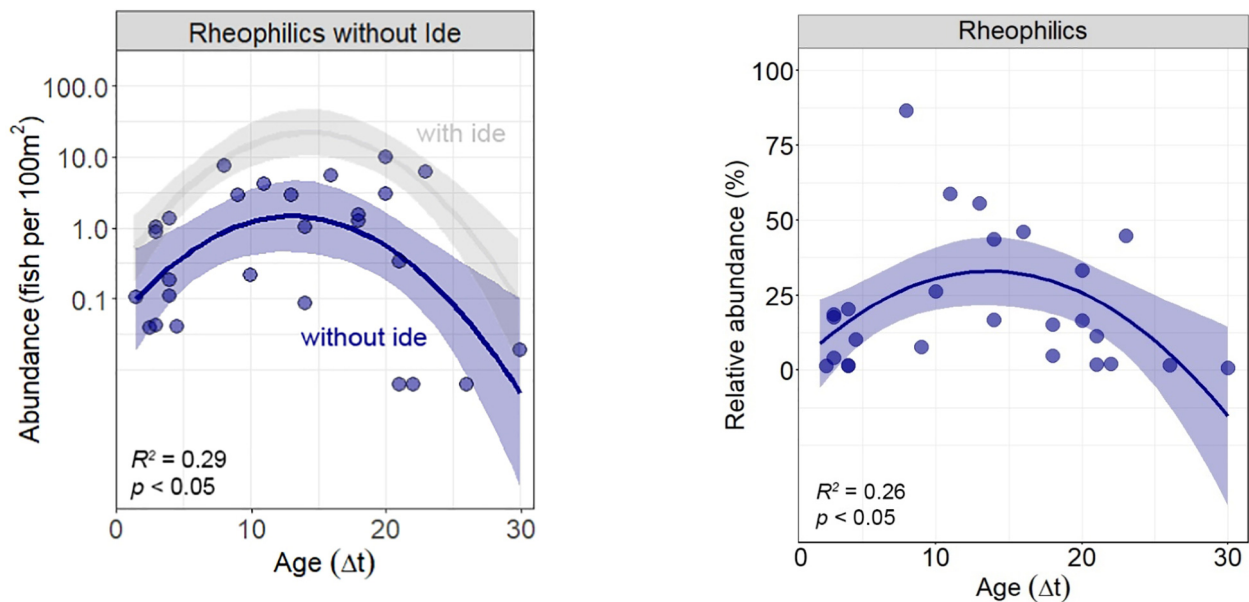


Fig. 5. Regression analysis for rheophilic fish abundance responses to channel age (Δt) for rheophilics without the most dominant species. In grey the original analysis including all rheophilic species is plotted for comparison. A fitted regression line with 95% confidence interval is used to indicate the significant trend ($p < 0.05$).

Fig. 6. Relative abundance (%) of rheophilic fish in restored floodplain channels plotted against channel age (Δt). A fitted regression line with 95% confidence interval is used to indicate a significant trend ($p < 0.05$).

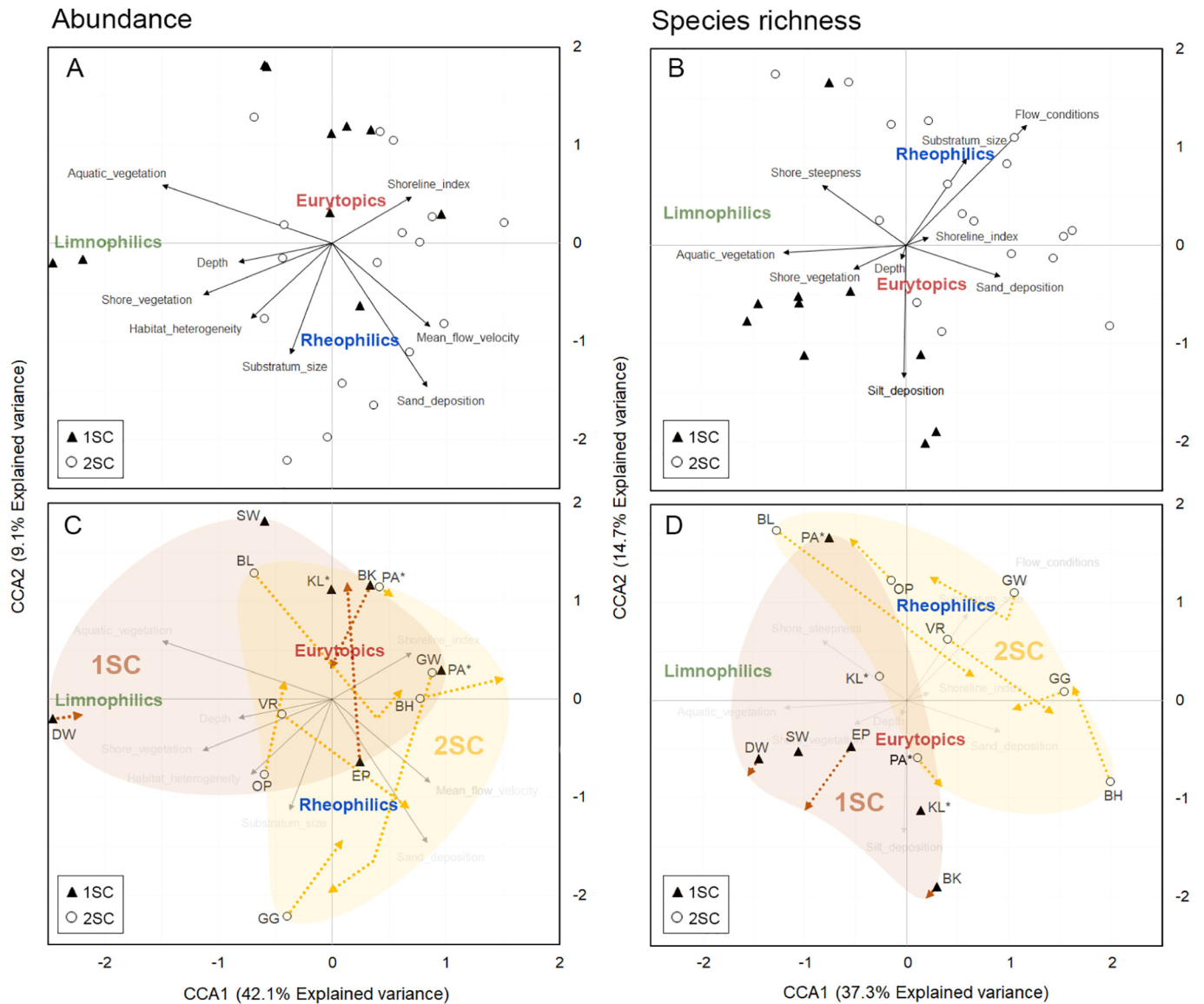


Fig. 7. Canonical Correspondence Analysis (CCA) for YOY fish community responses in relation to habitat variables in restored floodplain channels of the river Rhine. The final CCA model after variable selection is presented for fish abundance (A) and species richness (B) data. Aging individual restored channels are indicated with dotted arrow lines and are plotted on top of the original ordination for fish abundance (C) and species richness (D) analysis. Closed triangles with brown dotted arrow lines indicate aging 1SCs while open circles with yellow dotted arrow indicate aging 2SCs. Yellow (2SC) and brown (1SC) ellipses indicate the field in the ordination in which individual study locations are found. Channels marked with an asterisk (*) have undergone major reconstruction during the survey period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

side channel. Both permanent water flow (Ward et al., 1999; Grift et al., 2001; Nunn et al., 2007; Lorenz et al., 2016) and high levels of habitat heterogeneity (Aarts et al., 2004; Wolter et al., 2016; Pander et al., 2018) are proven to be important for a successful nursery habitat in floodplain channels. Therefore, it seems likely that there is an optimum state of channel succession for rheophilic YOY fish, in which permanently flowing water through river-floodplain channel connectivity is still present, with well-developed habitat heterogeneity.

In this study we evaluated the nursery potential of 1SCs and 2SCs, which primarily differ in flow conditions and therefore in the presence of habitats with permanent water flow. We performed a combined analysis, since similar trends in rheophilic fish responses were observed for the two channel types (Supplementary materials B1, B2). As the presence of permanent water flow is one of the driving factors in determining rheophilic nursery potential (Ward et al., 1999; Grift et al., 2001; Bolland et al., 2012; Lorenz et al., 2016; Pander et al., 2018), we expected

1SCs to have an overall limited nursery function for this ecological guild. Although only marginally significant, our results provide support for this hypothesis, since we observed almost 4 times more rheophilic fish in 2SCs compared to 1SCs. Additionally, more rheophilic species were observed in 2SCs than in 1SCs. These results showed that, although fish response trends for different channel types were similar over time, nursery potential for rheophilic fish was higher for 2SCs than for 1SCs.

We observed a steep increase in rheophilic fish abundances within the first 5 years after (re)construction of restored channels (Fig. 4). Highest abundances were found in channels between the age of 10 and 20 years, indicating the presence of optimal nursery conditions for rheophilic fish at these ages. Starting from 20 years post-restoration, a steep decrease in the numbers of rheophilic fish was observed. This trend was observed for the whole of the rheophilic guild, not only for the most dominant species (ide) (Fig. 5). A similar increase in rheophilic abundances in the first years post-restoration was reported in

floodplain channels in the river Trent (Nunn et al., 2007) and the Danube river (Pander et al., 2015), although the subsequent levelling off and decrease in fish numbers that we observed was not previously assessed.

For relative abundances of rheophilic fish we also observed an optimal trend (Fig. 6), indicating that, in the first years post-restoration, rheophilics generally benefit more from floodplain channel restoration than eurytopic fish species, which dominated the rest of the catches. This initial increase in relative rheophilic abundances post-restoration was also observed in floodplain channels in the river Rhône (Daufresne et al., 2015) and Danube river (Ramler and Keckeis, 2019).

For rheophilic species richness, our findings were less in line with other studies. We observed a steadily decreasing trend in rheophilic species richness with channel age (Fig. 4), whereas the few studies that report on temporal changes after major disturbance events found at least partial support for an initial increasing trend (Meffe and Minckley, 1987; Pander et al., 2015). Since rheophilic species richness was positively associated with channels with free-flowing conditions and the presence of coarse substratum (Fig. 7B), we expect that this decreasing trend was caused by a combination of (1) channel aggradation, reducing permanent flow levels (Van Denderen et al., 2019), and (2) differences in individual species sensitivity for (the lack of) habitats with permanent water flow (Aarts et al., 2004). We observed that, with increasing age, all restored channels became generally less associated with the rheophilic fish community, permanent flow and coarse substratum (Fig. 7D) and thus that most channels became less suitable as nursery areas. This was also apparent from the more sensitive rheophilic species that were frequently observed in the first years post-restoration, but almost disappeared at later stages, such as the European barbel (*Barbus barbus* (Linnaeus, 1758)), dace (*Leuciscus leuciscus* (Linnaeus, 1758)), and chub (*Squalius cephalus* (Linnaeus, 1758)). These species are specifically known for their preference for habitats with permanently flowing water (Copp et al., 1994; Aarts et al., 2004; Britton and Pegg, 2011), and are therefore expected to be less frequently observed in channels with non-permanent or no flow. Rheophilic species that were less dependent on permanent flow, such as ide, whitefin gudgeon (*Romanogobio belingi* (Slastenenko, 1934)) and nase (*Chondrostoma nasus* (Linnaeus, 1758)), were observed in a large range of channel ages (Supplementary materials B3). Furthermore, in floodplain channels of the Danube river, where permanent flow did not decrease over time, no decline in rheophilic species richness was observed (Pander et al., 2015). This implies that, due to the initial design and current management strategy of Dutch restored floodplain channels, they are only temporarily suited (up to 5 years) as nursery area for the more sensitive rheophilic fish species.

The abundances of YOY rheophilic fishes were similarly affected by the presence of permanent flow, coarse substratum and sand deposition (Fig. 7A), which are particularly associated with early-stage habitats in Dutch 2SCs (Simons et al., 2001; Geerling et al., 2008; Van Denderen et al., 2019) (Fig. 7C). We could not find support for our hypothesis that rheophilic nursery habitat was positively affected by high levels of habitat heterogeneity, as this variable did not have a significant influence in the CCA ordination (Supplementary materials A3). This may be due to the predominance of flowing water in explaining rheophilic nursery potential, and high variability in the directions in which the habitat of individual 2SCs developed (Fig. 7C/7D). Another reason for observing a limited effect of habitat heterogeneity could be that we measured this variable through aerial photographs, which is a crude measure for estimation of floodplain channel habitat. Habitat heterogeneity acts on both macro- and microhabitat level for YOY fish (Kurmayer et al., 1996; Wolter et al., 2016) and especially the latter cannot be addressed through the visual inspection of aerial photographs. Furthermore, it is questionable whether Dutch restored channels will ever reach their full potential regarding habitat heterogeneity. Dutch national floodplain management related to water safety results in the constant removal of woody vegetation, dead wood, and other habitat-

enriching structures from the channel and its surrounding habitat (Harezlak et al., 2020), thereby limiting the channels' capacity of reaching optimal habitat heterogeneity levels. The combined effects of additional floodplain management, and other pressures in the landscape matrix in which the floodplain channels are embedded, are an important knowledge gap.

In our study we obtained two or three snapshots of fish communities and habitat characteristics per restored location over a 30-year period. Although a declining trend was observed in eurytopic fish abundances in the main channel of the lower river Rhine from 1992 to 2018, we found no indication that long-term trends could have affected the observed developments in rheophilic fish community composition (Fig. 3). Rheophilic fish abundances and species richness remained constant over time and no aberrations from the general pattern were observed in our survey periods 1997–1998, 2009 and 2017–2019. Over the whole period, phosphate levels significantly decreased and oxygen levels significantly increased, which may indicate that water quality conditions have improved slightly during the study period. However, these trends were minimal and unlikely to have affected the outcomes of our study. No trends in water temperature was observed during the study period, which was in line with other studies over similar time ranges in the river Rhine (Van Slobbe et al., 2016; Zobrist et al., 2018) and the river Rhône (Daufresne et al., 2015). Also, similar median discharge levels and variability within and between sampling years were observed, despite yearly variability. Therefore we conclude that the observed trends in the fish community reflect actual changes in the suitability of the studied side channels as nursery habitats for rheophilic fish species.

The results of our analysis are robust and are not significantly different when other choices in data selection are made. In this study we chose to include the 12 restoration projects that were sampled at least twice in the period 1992–2018, since we wanted to focus on the effects of habitat succession processes within individual channels. Similar trends in rheophilic fish community responses were however also observed when we analysed the complete data set (a total of 47 surveys in 1997–2019). When we performed a 'snapshot' analysis of all 34 restored channels only using recent data (2017–2019), similar patterns were observed, although only marginally significant (Supplementary materials B4/B5). This may be caused by an underrepresentation in recent data of channels with an age between 10 and 20 years. Furthermore, with the use of age as proxy for habitat succession, our study assumes a static rate of succession. It is possible that aggradation of floodplain channels is not homogeneous over time, but our habitat data did not allow us to study this in more detail. However, we are confident that our approach will not have produced artificial trends, rather that the trends would have been even clearer had we been able to model habitat succession in a more precise way.

Fish community responses were mostly reported to vary both within restored channels (Pander et al., 2015; Pander et al., 2018), and between floodplain channel habitats (Nunn et al., 2007; Ramler and Keckeis, 2019). All of these studies based their conclusions on relatively short evaluation periods (1–6 years) in a small number of restored channels (1–6 channels). Many studies report that channel restoration initially improves rheophilic fish abundance and biodiversity (Grift et al., 2001; Schmutz et al., 2014; Daufresne et al., 2015; Pander et al., 2015; Collas et al., 2018; Ramler and Keckeis, 2019), but the long-term suitability of these restored channels for the rheophilic fish community is poorly understood. This emphasises the need for the long-term evaluation of multiple projects, such as our study, to provide guidance for adaptive management of restored floodplain channels (Morandi et al., 2014; Schmutz et al., 2014).

Restored floodplain channels should develop and retain suitable environmental conditions to remain effective for specific restoration aims, such as the occurrence of target species and habitats (Palmer et al., 2005). Such restoration aims can either be to initiate a trajectory of ecological succession or to remain within a desired stability range. In our

case the aim of the channel restoration projects was to remain suitable for rheophilic species for several decades. In order to achieve this, we propose a management strategy involving cyclic rejuvenation through human intervention, in which interventions need to be repeated on average every 15 years, depending on the rate of aggradation (Baptist et al., 2004; Breedveld et al., 2006; Vreugdenhil et al., 2008). More frequent interventions are proposed when channel restoration is targeting sensitive rheophilic species, which are most frequently present in the first years post-restoration. A less invasive alternative to these interventions to prevent or slow down channel aggradation is the construction of so-called sediment traps upstream of the channel, such as wooden structures (Piton and Recking, 2016; Wohl et al., 2019) or the development of river bank vegetation (Zen et al., 2017). Even a combination of consecutive floodplain channels may be useful to help limiting aggradation of the more lateral or downstream channels (Van Denderen et al., 2019).

Maintaining optimal nursery conditions is restricted within the boundaries of the current river management regime and context of the river Rhine, in which very limited river dynamic processes, such as spontaneous flooding events or evolution of new side channels, is allowed. On the other hand, existing side channels become disconnected and may eventually disappear through aggradation, causing nursery areas for rheophilic fishes to gradually disappear. Therefore, cyclic rejuvenation interventions should primarily focus on restoring permanent water flow in 2SCs, since the rheophilic fish community positively benefits from the presence of permanently flowing water, coarse sediment and sand deposition. The restoration of permanent water flow can also be achieved by transforming existing 1SCs into 2SCs. Furthermore, the role of habitat heterogeneity in nursery areas is considered potentially important (Ward et al., 1999; Grift et al., 2001; Aarts et al., 2004; Wolter et al., 2016; Pander et al., 2018), but remains poorly understood. As our study was not able to adequately address this potentially important driving factor we propose a thorough investigation of the relationship between habitat heterogeneity and nursery potential as a next step in the identification of suitable nursery areas for rheophilic fishes.

CRediT authorship contribution statement

T. Stoffers: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization, Data curation. **F.P.L. Collas:** Conceptualization, Methodology, Software, Formal analysis, Writing - review & editing, Data curation. **A.D. Buijse:** Conceptualization, Methodology, Writing - review & editing, Supervision. **G.W. Geerling:** Writing - review & editing, Visualization. **L.H. Jans:** Methodology, Writing - review & editing, Project administration. **N. van Kessel:** Writing - review & editing. **J.A.J. Verreth:** Writing - review & editing. **L.A.J. Nagelkerke:** Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - review & editing, Visualization, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Research data

Research data to this article is available upon request at: <https://doi.org/10.4121/12999575> (Stoffers et al., 2020).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.142931>.

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