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Environmental requirements and heterogeneity of rheophilic fish nursery habitats in European lowland rivers: Current insights and future challenges

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Abstract

The large-scale degradation of riparian ecotones and of the connectivity between rivers and their floodplains has resulted in a drastic decline of rheophilic fish populations in European temperate lowland rivers. Recent river restoration projects have had variable success in effectively restoring these fish populations. Knowledge on nursery habitat requirements is considered essential for effective population restoration. However, a detailed understanding of the role of habitat heterogeneity in young-of-the-year (YOY) fish population development is limited. Therefore, we carried out a synthesis of the available knowledge on nursery habitat requirements of rheophilic fish species found in European temperate lowland rivers (<200 m elevation). From a total of 603 papers, 77 studies with primary information were selected, containing 390 associations between habitat features and YOY fish. As expected, most studies focused on static components of physical riparian habitat. Generally, YOY fish require habitats of shallow depth (<0.5 m), with slow-flowing water (<0.2 m/s), gentle bank slope (<20°), variety in substratum types (fine sand to gravel), relatively warm water and high food availability. Surprisingly, no clear ontogenetic habitat shifts between larvae and juveniles were found, which may be explained by the limited spatial–temporal resolution of most studies. Since 2011, studies on habitat heterogeneity have increased, but few have explicitly assessed its role in relation to movement patterns of YOY fish for nursery success. Therefore, we recommend that future research focuses on fish movement patterns between habitat patches in heterogeneous (river-floodplain) environments, to increase the knowledge base for effective recovery of rheophilic fish populations.

KEYWORDS

ecological responses, fish movement, floodplain restoration, ontogenetic habitat shifts, river restoration, riverine fish

1 | INTRODUCTION

Temperate lowland rivers and floodplains are among the most productive and diverse freshwater ecosystems (Junk et al., 1989; Welcomme, 1979) and are home to a wide range of fish species of different functional ecological guilds (Aarts et al., 2004; Noble et al., 2007). The rheophilic fish guild, consisting of riverine fish species that prefer flowing water during certain life stages, make up a significant part of the total biomass and biodiversity of the indigenous fish community in healthy temperate lowland rivers (Aarts et al., 2004; Van Puijenbroek et al., 2019). Rheophilic fish are considered important indicators of the habitat integrity and ecological quality of rivers, because they require a variety of specific habitats throughout their life in a broad spatio-temporal context (Copp, 1989; Schiemer, 2000).

During the course of their life rheophilic fishes require different functional (micro)habitats of suitable environmental conditions for each specific stage (Figure 1). Microhabitat conditions are directly influenced by hydromorphological (presence of structures, substratum type, water flow, depth, bank slope) and biotic variables (food availability, predation; Cowx & Welcomme, 1998). For most fishes, survival is largely determined by rapid growth in their first year, with the bigger, potentially stronger, fish most likely to survive (Mills & Mann, 1985; Nunn et al., 2002). The proper scale, spatial organization (heterogeneity) and interconnectivity of essential microhabitats (for feeding and sheltering) at these early life stages contributes greatly to their survival (Pont & Nicolas, 2001; Schlosser, 1995; Van Looy et al., 2019), as swimming capacity is not fully developed. The spatial scale of daily activity differs among fish species, but generally increases with size (and thus life stage). It varies between tens to hundreds of meters for young-of-the-year (YOY) fish in nursery habitats, to tens or hundreds of kilometres for migratory adults to reach their spawning habitats (Cowx & Welcomme, 1998; Grift et al., 2001; Wolter et al., 2016).

Backwaters and side channels in floodplains fulfil many nursery habitat requirements for rheophilic fish, due to large areas of land-water interaction and (semi-)permanent connectivity with the main channel (Copp & Peňáz, 1988). This results in a dynamic and heterogeneous aquatic environment, in which YOY fish can find many of the essential consecutive microhabitats necessary for their early-life growth and survival, such as shelter and food (Balcombe et al., 2007; Górski et al., 2011; Grift et al., 2001; Junk et al., 1989; Nunn et al., 2007b; Stanford et al., 2005). Such diverse and complex riverscapes are however under severe threat, with as much as 70%–90% of European and North-American floodplains estimated to be ecologically degraded, or even functionally extinct, due to anthropogenic river modifications (Hein et al., 2016; Hohensinner et al., 2004; Tockner & Stanford, 2002; Tockner et al., 2009) The remaining natural rivers in the world are also increasingly affected by extensive modifications, and their floodplains are disappearing at an alarming rate (Belletti et al., 2020; Tockner & Stanford, 2002). Structural degradation of temperate lowland rivers, resulting in fragmentation, disconnected floodplains and degraded riparian ecotones, has led to a drastic decline of rheophilic fish numbers (Birnie-Gauvin et al., 2017; Van Puijenbroek et al., 2019) and has made rheophilic fishes target species for conservation efforts in recent decades (Geist, 2011; Mueller et al., 2018; Schiemer, 2000).

With the aim of conserving and restoring floodplain areas, a variety of lowland river restoration projects was realized (Bernhardt & Palmer, 2011; Buijse et al., 2002). In Europe, at least 1,390 river restoration projects in 31 countries have been carried out since the 1990s (Environment Agency, 2021), boosted by European environmental directives (Water Framework and Habitats Directives) and national programmes (Hering et al., 2010; Szałkiewicz et al., 2017). However, it has proved difficult to evaluate the effectiveness of these projects for the recovery of rheophilic fish populations in European lowland rivers (Van Looy et al., 2019), due to a lack of uniformity in ecological targets (Hein et al., 2016), restoration strategies (Buijse et al., 2002), and ecological evaluation strategies (Erős et al., 2019; Morandi et al., 2017; Schmutz et al., 2014; Verdonschot et al., 2013). Furthermore, the complex and variable nature of aquatic ecosystem functioning is also likely to be responsible for the frequent uncertainty in the evaluation of restoration project effectiveness (Peipoch et al., 2015; Roni et al., 2008).

Effectiveness of restoration projects for fish is often assessed by the use of single biological indicators, whereas a more holistic approach with indicators that simultaneously address fish communities, multiple life stages and habitat characteristics may be more useful (Pander & Geist, 2013). Effective river management and

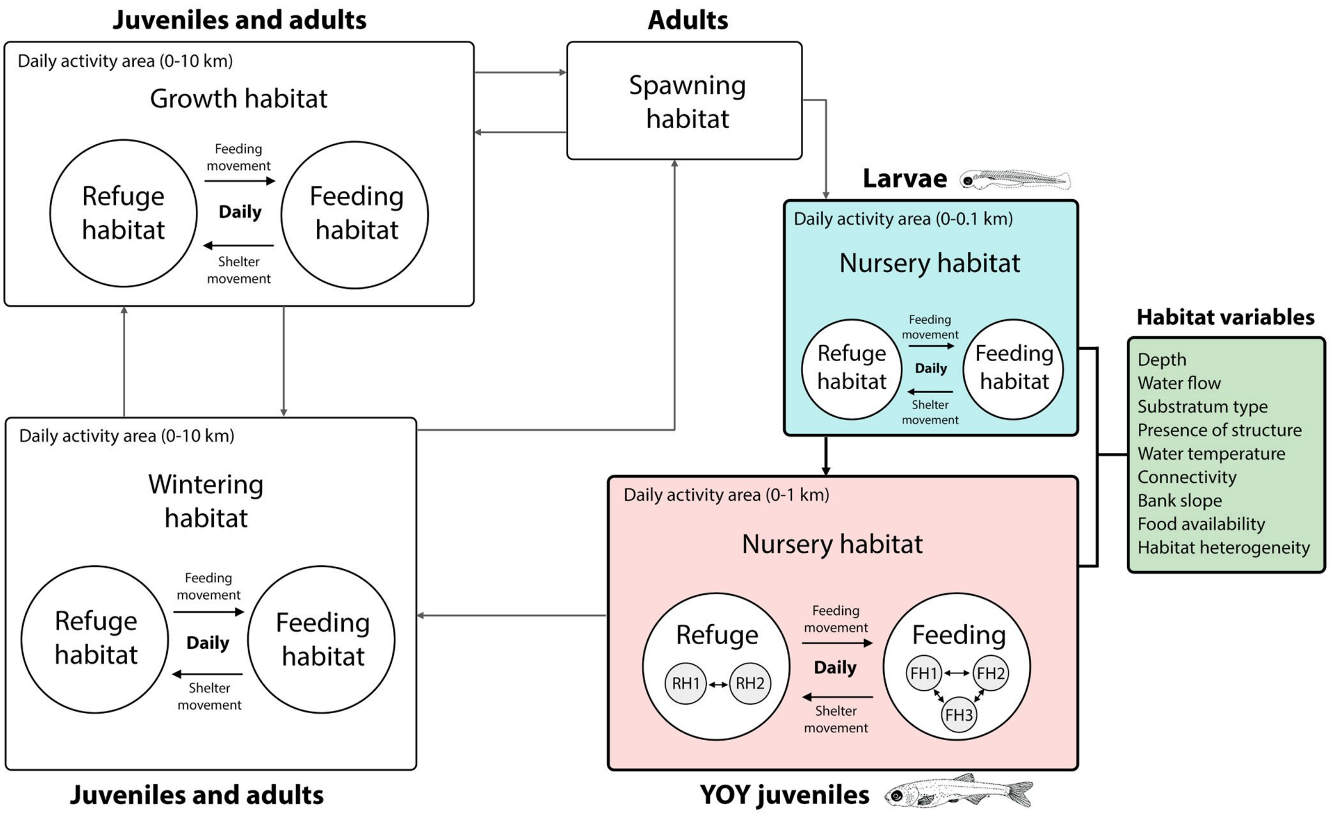

FIGURE 1 Functional units in river fish ecology, with emphasis on nursery habitat characteristics of the larval and YOY juvenile life stages. A dynamic and heterogeneous aquatic environment is important for growth and survival of YOY fish, as they use consecutive microhabitats throughout this early life stage (refuge habitat: RH1, RH2; feeding habitat: FH1, FH2, FH3). Adapted from Cowx and Welcomme (1998) and Schlosser (1991), with daily activity area input from Wolter et al. (2016). Fish drawings were adapted from Pinder (2001)

conservation of rheophilic fish would benefit from such a harmonized and more holistic evaluation of the effectiveness of individual river restoration projects (Van Looy et al., 2019). A synthesis of information on nursery habitat requirements is an essential step in this process. Such a systematic literature synthesis has the potential to strengthen the knowledge base of nursery habitat requirements; reveal possible ontogenetic habitat shifts in YOY fish; identify (shifting) focus and knowledge gaps in current scientific literature; and set future research and management priorities for long-term population recovery (Radinger et al., 2017).

Our current knowledge of ecological patterns and processes in temperate lowland river-floodplain systems is strongly underpinned by subsequent modifications of deep-rooted conceptual models, such as the River Continuum Concept (Vannote et al., 1980), the Serial Discontinuity Concept (Stanford, 1983; Ward & Stanford, 1995), and the Flood Pulse Concept (Junk et al., 1989). These conceptual models focus on river processes on large temporal and spatial scales (>100 km), whereas habitat use and movement of YOY fish generally take place at river reach scale (0–10 km; Thorp et al., 2006; Wolter & Arlinghaus, 2003; Wolter et al., 2016). More appropriate models to help identify nursery habitat requirements of rheophilic fish would be the functional unit concept (Cowx & Welcomme, 1998) and the dynamic landscape model of stream fish (Schlosser, 1991). These conceptual models focus on the whole life cycle of riverine fish and specifically acknowledge the importance of (small-scale) fish movements at early life stages, in relation to the spatial arrangement of aquatic habitats for sheltering and feeding (Figure 1). Therefore, it is important to operationalize both concepts, which is complicated by species-specific differences in habitat use and the interplay between ontogenetic shifts in habitat requirements. Suitable microhabitats vary in availability and quality with fluctuating river discharge during the nursery season in temperate lowland rivers (Cowx & Welcomme, 1998; Fausch et al., 2002; Peipoch et al., 2015).

In the current study, we combine the conceptual models of Cowx and Welcomme (1998) and Schlosser (1991) as a framework for our systematic literature synthesis on nursery habitat requirements of rheophilic fish in temperate lowland rivers. We use European temperate lowland rivers at an elevation of less than 200 m above mean sea level as a case study, because they are among the most heavily used and modified rivers in the world and there are widespread initiatives to restore them (Environment Agency, 2021; Tockner & Stanford, 2002). The conceptual models that we use as framework (Figure 1) address physical habitat requirements of fish, fishes' movements, as well as connectivity between different microhabitats in a heterogeneous environment. Since these models integrate biological and physical processes in river-floodplain systems at relevant scales for local management, they are highly useful for effective conservation and management of lowland rivers (Arlinghaus et al., 2015; Brierley et al., 2012; Meulenbroek et al., 2018). We thus synthesize information from peer-reviewed literature on essential nursery habitat requirements of critical early life stages of representative rheophilic fish species that use (parts) of the selected regions as nursery area. Our aims are: (a) to reveal generalized nursery habitat requirements and identify knowledge gaps; (b) to assess ontogenetic shifts in microhabitat use of early life stages (larvae and YOY juveniles); (c) to identify the shifting focus in scientific literature; and (d) to propose future research efforts to increase the knowledge base for effective recovery of rheophilic fish populations.

2 | METHODS

2.1 | Literature and search terms

To retrieve an overview of scientific literature on rheophilic fish responses in relation to habitat in European temperate lowland rivers, a list of relevant search terms (initial selection criteria) was generated and broken down into six components for the search strategy: (a) life stage, (b) ecological guild, (c) population status, (d) fish response, (e) study system and (f) representative European rheophilic fish species having their main biogeographical distribution in the bream and barbel zones (classified according to Aarts et al. [2004] and Van Treeck et al. [2020]). Search components were combined by using Boolean operators in the search engines of six databases for scientific literature: Aquatic Sciences and Fisheries Abstracts, Scopus, Web of Science, Google Scholar, Zoological Records and the Commonwealth Agricultural Bureaux. Individual search strings for the six aforementioned components are shown in Table 1. All database searches were performed on 12 April 2021.

A total of 603 unique publications met the initial selection criteria in the database search. Publications were screened by the first author in two distinct phases: initial screening of title and abstract and, when necessary, a more detailed full-text screening. Publication inclusion was based on the following predefined selection criteria: (a) the study was conducted in a European temperate lowland river system at an elevation of less than 200 m above mean sea level (see Solheim et al., 2019) and within "ecoregions for rivers and lakes" based on fauna living in European inland waters that cover lowland rivers in Western, Central and Eastern Europe (Schmutz et al., 2007; see Figure 2 for the map); (b) study animals consisted of young-of-the-year (YOY) rheophilic fish that have their main biogeographical distribution in the bream and barbel zones, assessed on either community or individual species level; (c) the study assessed fish responses (recruitment, survival, growth, CPUE, density, abundances) in relation to

TABLE 1 Search string for the execution of the search strategy on 12 April 2021 in all databases

Component	Search string
Life stage	TITLE-ABS-KEY (juvenile* OR young OR "0+" OR larva* OR fry OR fingerling* OR ichthyoplankton OR "early stage*" OR "young of the year" OR "young-of-the-year" OR YOY)
	AND
Ecological guild	TITLE-ABS-KEY ((rheophilic* OR riverine* OR river* OR migratory OR migration OR stream) AND fish*)
	AND
Population status	TITLE-ABS-KEY (presence OR absence OR number* OR existence OR appearance* OR non-appearance* OR distribution OR "spatial distribution" OR "spatial variability" OR "spatial patterns" OR "probability of occurrence")
	AND
Fish response	TITLE-ABS-KEY (CPUE OR densit* OR abundance* OR productivity OR biomass OR growth OR development OR thriving OR maturation OR recruitment OR spawning OR survival)
	AND
Study system	TITLE-ABS-KEY ("floodplain system*" OR "floodplain water*" OR floodplain* OR "flood plain*" OR flood* OR "tidal plain*" OR delta OR "alluvial plain" OR river OR channel OR stream OR brook OR tributary OR riparian OR lowland)
	AND
European rheophilic fish species	TITLE-ABS-KEY ("stream bleak" OR "danube bleak" OR "blue bream" OR "white-eye bream" OR "stone loach" OR barbel OR "mediterranean barbel" OR "crimean barbel" OR nase OR "spined loach" OR gudgeon OR ide OR dace OR "eurasian minnow" OR "white-finned gudgeon" OR "northern whitefin gudgeon" OR "kessler's gudgeon" OR "danubian longbarbel gudgeon" OR "danube whitefin gudgeon" OR "balcan spined loach" OR chub OR vairone OR "vimba bream" OR burbot OR "danube ruffe" OR schraetzer OR "danube streber" OR zingel OR grayling OR bullhead OR "alburnoides bipunctatus" OR "alburnus chalcoides" OR "ballerus ballerus" OR "abramis sapa" OR "abramis ballerus" OR "ballerus sapa" OR "barbatula barbatula" OR "barbus barbus" OR "barbus meridionalis" OR "barbus tauricus" OR "chondrostoma nasus" OR "cobitis taenia" OR "gobio gobio" OR "leuciscus idus" OR "leuciscus leuciscus" OR "leuciscus burdigalensis" OR "phoxinus phoxinus" OR "romanogobio albipinnatus" OR "romanogobio belingi" OR "gobio albipinnatus" OR "romanogobio kessleri" OR "gobio kessleri" OR "romanogobio uranoscopus" OR "romanogobio vladykovi" OR "sabanejewia balcanica" OR "squalius cephalus" OR "leuciscus cephalus" OR "telestes souffia" OR "vimba vimba" OR "lota lota" OR "gymnocephalus baloni" OR "gymnocephalus schraetser" OR "zingel streber" OR "zingel zingel" OR "thymallus thymallus" OR "cottus gobio" OR "cottus perifretum" OR "cottus rhenanus")

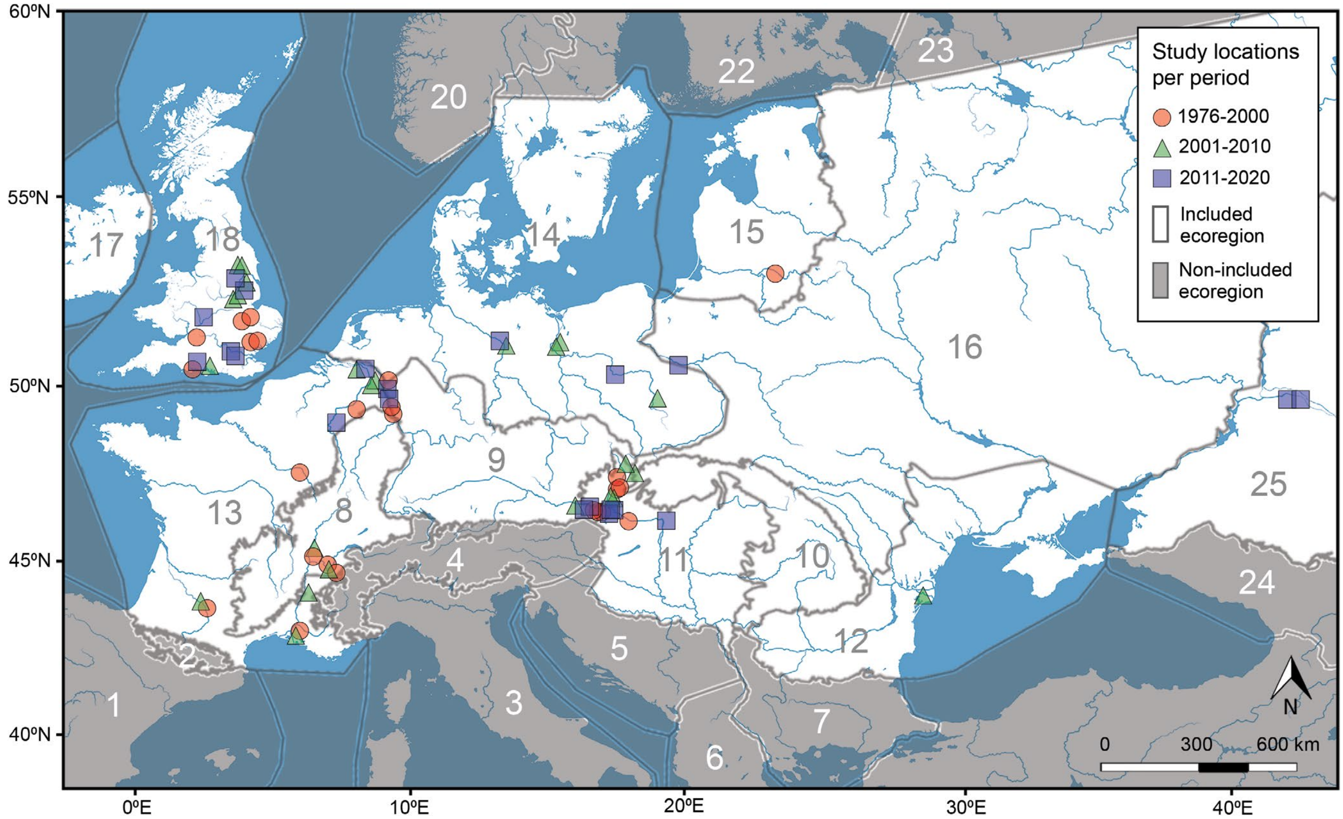

FIGURE 2 Geographical locations of the studies included in the literature synthesis. Selection of studies was limited to temperate European lowland river systems up to an elevation of 200 m above mean sea level within the selected European ecoregions for rivers and lakes (Schmutz et al., 2007). Included ecoregions are shown as transparent areas with grey borders (see Table 4 for ecoregion names). Main rivers are shown with blue lines and filled symbols indicate sampling periods: 1976–2000 (red circles), 2001–2010 (green triangles), 2011–2020 (blue squares)

environmental conditions; (d) the study took place in a river-floodplain system (main channel or stream and/or corresponding floodplain); and (e) the results were based on quantitative research. We focused on obtaining rheophilic nursery habitat requirements from studies in European lowland rivers at an elevation of less than 200 m above mean sea level, because these rivers are among the most heavily used and altered worldwide, resulting in fragmentation and structural degradation of the main channel, disconnected floodplains and degraded riparian ecotones (Birnie-Gauvin et al., 2017; Tockner & Stanford, 2002; Tockner et al., 2009; Van Puijenbroek et al., 2019). Studying these parts of European river systems is essential to set future research and management priorities for long-term rheophilic fish population recovery. We reported on nursery habitat requirements of rheophilic fish species that were found to use (parts) of the selected regions as nursery habitat in the studies. Only peer-reviewed journal articles in the English language were included.

A total of 526 publications were excluded based on being outside the geographical delineation (181), fish species not belonging to the bream or barbel zone and/or to YOY fish (158), no reporting of fish response to environmental variables (79), a different study system than rivers and/or floodplains (68), containing no quantitative research (22), or written in a non-English language (18). The literature selection resulted in 77 peer-reviewed scientific publications for analysis.

2.2 | Coding variables

The full-text of the selected studies was analysed by at least two trained and independent reviewers and relevant information was coded and recorded in a MS-Excel database (available as Supplementary Material). This database was additionally checked by the lead author to ensure consistency in the coding of information. From each study, we collected information on geographical location, period, study system, response unit, life stage and habitat variables (Table 2). We divided the studies into three periods (1976–2000, 2001–2010, 2011–2020), based on status and developments in European river restoration effort and the availability of evaluation studies (Environment Agency, 2021). From 1976 to 2000 only a few European river restoration projects were realized and there were only few project evaluation studies, whereas between 2001 and 2010 numerous river restoration projects were realized throughout Europe, and the effectiveness of some of the older projects was evaluated. In recent years (2011–2020), even more river restoration projects have been implemented on a European-wide scale, with many studies reporting on the effectiveness of both past and recent restoration projects.

We chose to record the effect of nine habitat variables on YOY rheophilic fish responses that were most frequently (minimum

TABLE 2 Coding variables that were extracted from the included studies following full-text screening by the reviewer

Variable	Modality	Information	Type of variable
Location	Coordinates	Latitude and longitude of (the centre of) the study areas in decimal degrees	Numeric
Period	Year	We divided the studies into three periods (1976–2000, 2001–2010, 2011–2020), based on developments in European river restoration efforts	Class
Study system	Main channel	Study area was situated on the shoreline of the main river channel or stream	Class
	Floodplain system	Floodplain system or backwater that was connected with the main channel at least 1 month per year	Class
Response unit	Rheophilic community	Responses were recorded on European YOY rheophilic fish community level	Class
	Individual species	Responses were recorded for individual European rheophilic fish species	Class
Life stage	Larvae	Fish that are in their larval stage of development, according to author(s)	Class
	Juveniles	Juvenile fish that are in their first year of development, according to author(s)	Class
Habitat variables	Water temperature	Water temperature (°C) at study area or difference in water temperature between study area and reference location	Numeric
	Depth	Water depth (m) at sampling site and depth range in study area	Numeric
	Bank slope	The slope/steepness of the bank/shore at the sampling area, measured in degrees and categorized in four classes: (1) flat (<10°), (2) shallow (10°–20°), (3) intermediate (20°–30°), (4) steep (>30°). Also slope of bank range in study area was recorded	Ordinal
	Water flow	Flow rate of water (m/s) at sampling site and water flow range in study area	Numeric
	Substratum	Type/size of the top layer of sediment at sampling site and the range of sediment types present in study area (organic matter, clay, sand, rubble, boulders), in five classes: (1) clay/silt (<0.06mm), (2) fine sand (0.06–0.85mm), (3) coarse sand (0.85–2mm), (4) gravel (2–65mm), (5) cobbles/boulders (>65mm)	Ordinal
	Presence of structure	The presence-absence of morphological complex structures at sampling site, qualified in three classes: (1) (dead) wood, (2) water plants/submerged vegetation, (3) stones/boulders, (4) unidentified	Class
	Habitat heterogeneity	The richness of distinct habitat types in or surrounding the sampling area, in two classes: (1) microhabitat (sample level), (2) river stretch or floodplain level	Class
	Connectivity	Type of connectivity between water bodies in study area in two classes: (1) river–floodplain, (2) river–river/stream	Class
	Food availability	Presence and type of food present at sampling site and study area. Food sources were classified as (1) zooplankton, (2) macro-invertebrates, (3) algae/phytoplankton, (4) unidentified	Class

of 10 times) reported in the selected studies (Table 2) and therefore expected to be most important in structuring nursery habitat. These nine selected variables were: water temperature, depth, bank slope, water flow, substratum type/size, food availability, presence–absence of structures, habitat heterogeneity at sampling site and/or wider area and connectivity with adjacent water bodies. In order to study ontogenetic shifts in responses to habitat variables, we logged responses of both larval and juvenile rheophilic fishes. Limits for species-specific life stages were derived from the selected literature studies (Table 4).

2.3 | Scoring of YOY fish responses

The selected studies reported YOY fish responses in relation to environmental variables (habitat associations) in different ways. Therefore, in the present study, we used the response variables: recruitment, abundance, biomass, growth (rate) and survival as indicators for assessing the effect of habitat variables in nursery habitat.

For each study, the strength and direction of the fish response for five habitat variables was scored on an ordinal scale, as follows. The effect of an increase in temperature, connectivity, presence of structures, food availability and habitat heterogeneity was scored with: ++ (statistically significant positive effect), + (reported positive effect without statistical information), 0 (no effect), − (reported negative effect without statistical information), −− (statistically significant negative effect). Statistically significant effects (++ or −−) were recorded when authors reported p-values < .05, or reported comparable outcomes through a Bayesian data analysis. Positive (+) or negative effects (−) without statistical information were scored when authors, based on their observations and interpretation in their study, indicated that a habitat variable (likely) affected fish responses in a positive or negative way. These effects were generally reported in the discussion section of the publication. No effect (0) was scored when the study reported no fish responses to a particular habitat variable.

For depth, water flow, substratum type and slope of bank, we were able to obtain quantitative data on optimal values or value ranges. This quantitative information was compared to the range of values found in the total study area for each of these habitat variables for an overall perspective. Comparing mean values for these variables between life stages was used to pin-point ontogenetic shifts in habitat requirements.

3 | RESULTS

3.1 | Literature overview

In this literature synthesis on nursery habitat requirements of rheophilic fish in European lowland river-floodplain systems, we analysed 77 peer-reviewed scientific articles in the English language (Table 3). Most of the retrieved studies were performed in the United Kingdom (21 studies), followed by Austria and France (both 11), then Germany (9), the Netherlands (6) and the Czech Republic (6). We analysed three studies from Belgium and Poland, two from Russia and from Hungary, and we retrieved each time one relevant study for Lithuania, Romania and Slovakia (Table 3; Figure 2). The river Danube was the most frequently studied European lowland river, representing 14 studies in four countries, followed by the rivers Ouse (7), Rhine (5) and Rhône (5).

In 49 out of 77 studies, the shoreline of the main channel was studied, and 22 studies focussed on YOY rheophilic fish in floodplain systems (Table 3). Only six studies performed a combined assessment of fishes in both the main channel and corresponding floodplains. Over half of the studies (42) assessed fish responses on a community level, while 35 studies focussed on the habitat associations of one or several rheophilic species separately. The majority of studies (59) focused on the habitat associations of YOY juvenile fish, and only a small part (8) assessed exclusively larval fish responses. Ten studies looked at both larval and juvenile fish responses to changing habitat conditions.

In total, 390 habitat associations (data points) for both rheophilic fish communities and individual species were extracted from 77 studies (Table 4; Figure 3). The most studied individual fish species was chub (*Squalius cephalus*, Cyprinidae; 46 data points), followed by common nase (*Chondrostoma nasus*, Cyprinidae; 41), common dace (*Leuciscus leuciscus*, Cyprinidae; 37) and barbel (*Barbus barbus*, Cyprinidae; 26). A number of species were only studied as part of the YOY rheophilic community, and no habitat associations were reported on the species level. This was true for blue bream (*Ballerus ballerus*, Cyprinidae), white-eye bream (*Ballerus sapa*, Cyprinidae), Danube ruffe (*Gymnocephalus baloni*, Percidae), schraetzer (*Gymnocephalus schraetser*, Percidae), burbot (*Lota lota*, Lotidae), white-finned gudgeon (*Romanogobio albipinnatus*, Cyprinidae), Northern whitefin gudgeon (*Romanogobio belingi*, Cyprinidae), Kessler's gudgeon (*Romanogobio kesslerii*, Cyprinidae), Danube whitefin gudgeon (*Romanogobio vladykovi*, Cyprinidae), vairone (*Telestes souffia*, Cyprinidae), Danube streber (*Zingel streber*, Percidae) and zingel (*Zingel zingel*, Percidae).

Almost half of studies assessed fish responses in relation to depth (40 studies; 75 data points) and water flow (38 studies; 67 data points). Substratum type (30 studies; 59 data points) and the presence of structure (28 studies; 54 data points) were also frequently studied. The effect of temperature (20 studies; 37 data points), connectivity (19 studies; 23 data points), bank slope (17 studies; 40 data points), food availability (15 studies; 21 data points) and habitat heterogeneity (11 studies; 14 data points) on fish responses were studied less. For most habitat variables, at least a quarter of all studies focussed on their effects on larval fish, but for connectivity and habitat heterogeneity 90% of the studies focussed on juvenile fish responses.

3.2 | Literature focus over time

In the 1970s, research started to focus on assessing nursery habitat requirements of rheophilic fish. Since then, continuous research efforts on assessing rheophilic nursery habitat in European temperate lowland rivers have taken place, with the United Kingdom (Ouse, Trent and Lee), Austria (Danube) and France (Rhône and Saône) as study area hotspots (Figure 2). In the 21st century, research additionally focused on temperate lowland rivers in Germany (Rhine, Oder, Elbe) and the Netherlands (Rhine, Meuse).

Study focus on temperature, depth, water flow and food availability did not change much over time (Figure 4), comprising a steady 45%–55% of the total recorded habitat associations. Literature focus on bank slope, substratum size and the presence of structure however steadily decreased over time, from almost half of the total studied habitat associations in 1976–2000 to <25% in 2011–2020. For connectivity, an increase in scientific interest was found over time, from <3% in 1976–2000 to approximately 15% of the habitat associations focussing on river-floodplain and river-river connectivity in the 21st century. For habitat heterogeneity, interest has increased particularly since 2011 to make up about 20% of the total number of recorded habitat associations.

3.3 | Habitat requirements

For all habitat associations that were analysed on an ordinal scale (149 data points), fish responses to the presence of structure and water temperature dominated the data, scoring 54 and 37 data points respectively (Table 4; Figure 5). Fish responses to connectivity (23), food availability (21) and habitat heterogeneity (14) were less studied. An overall positive fish response for increasing or relatively higher water temperatures (within the floodplain, or the floodplain compared to the river) was found, although two out of 36 associations were negative and eight showed no effect. This effect was similar for larvae and juveniles. The presence of structures (dead wood, water plants and

TABLE 3 Per selected study an overview of the study location, system, response unit, life stage, rheophilic fish species and habitat variables assessed

Paper			Location				System		Response unit				Rheophilic fish species																									Habitat variable								
ID	Author(s)	Year	Country	River basin	Latitude	Longitude	Main channel/stream	Floodplain system	Rheophilic community	Individual species	Larvae	YOY juveniles	*Alburnoides bipunctatus*	*Ballerus ballerus*	*Ballerus sapa*	*Barbatula barbatula*	*Barbus barbus*	*Chondrostoma nasus*	*Cobitis taenia*	*Cottus gobio*	*Gobio gobio*	*Gymnocephalus baloni*	*Gymnocephalus schraetser*	*Leuciscus idus*	*Leuciscus leuciscus*	*Lota lota*	*Phoxinus phoxinus*	*Romanogobio albipinnatus*	*Romanogobio belingi*	*Romanogobio kessleri*	*Romanogobio vladykovi*	*Squalius cephalus*	*Telestes souffia*	*Thymallus thymallus*	*Vimba vimba*	*Zingel streber*	*Zingel zingel*	Depth	Water flow	Substratum	Presence of structure	Water temperature	Connectivity	Bank slope	Food availability	Habitat heterogeneity
1	Stoffers et al.	2021	Netherlands	Rhine	51.89	5.51		•	•			•					•	•	•		•			•	•				•	•		•			•				•	•			•			•
2	Latli et al.	2019	France	Meuse	50.20	4.86	•			•		•																				•													•	•
3	Ramler & Keckeis	2019	Austria	Danube	48.14	16.89	•		•			•	•	•	•		•	•	•	•	•	•	•	•	•	•					•	•			•	•	•	•		•	•		•			•
4	Angelopoulos et al.	2018	United Kingdom	Don	53.40	-1.51	•			•		•				•				•																		•		•						
5	Bašić et al.	2018	United Kingdom	Wylye	51.15	-2.05	•			•		•																						•								•				
6	Collas et al.	2018	Netherlands	Rhine	51.86	5.42		•	•			•					•	•						•	•				•	•		•			•				•						•	
7	Marszał et al.	2018	Poland	Vistula	52.64	19.56	•			•		•	•																									•	•	•	•				•	
8	Meulenbroek et al.	2018	Austria	Danube	48.18	16.48		•	•		•	•	•		•	•	•	•	•	•	•			•	•	•				•	•	•		•	•		•	•	•		•			•		•
9	Roberts & Britton	2018	United Kingdom	Teme	52.30	-2.43	•		•			•					•								•		•					•		•				•	•							
10	Golski et al.	2017	Poland	Warta	52.33	16.91		•	•			•						•			•			•	•	•						•			•							•	•			
11	Lechner et al.	2017	Austria	Danube	48.12	16.83	•			•	•							•																					•							
12	Górski et al.	2016	Russia	Volga	48.47	45.18		•		•	•													•														•				•	•		•	
13	Bolland et al.	2015	United Kingdom	Ouse	54.00	-1.17		•	•			•				•	•			•	•				•		•					•		•									•			
14	Keckeis	2014	Austria	Danube	48.15	16.91	•		•		•				•		•	•			•			•	•			•		•		•			•				•							
15	Lechner et al.	2014	Austria	Danube	48.12	16.83	•			•	•							•																				•	•							•
16	Nunn et al.	2014	United Kingdom	Multiple rivers	53.10	-0.81	•			•		•							•																						•					
17	Weiperth	2014	Hungary	Danube	47.83	18.84	•		•			•	•				•	•			•		•	•	•	•				•	•	•			•	•	•	•	•	•	•					
18	Britton et al.	2013	United Kingdom	Multiple rivers	51.55	-0.90	•			•		•					•																									•				
19	Eick & Thiel	2013	Germany	Elbe	52.93	11.84	•		•			•		•					•		•			•	•	•			•			•							•					•		
20	Lorenz et al.	2013	Germany	Multiple rivers	51.16	6.86	•		•			•				•	•	•		•	•				•		•					•		•				•	•	•						•
21	Scharbert & Borcherding	2013	Germany	Rhine	51.36	6.66		•	•			•					•	•	•					•	•							•											•			
22	Bolland et al.	2012	United Kingdom	Trent	52.98	-1.01		•	•			•				•			•		•				•		•					•											•			
23	Górski et al.	2011	Russia	Volga	48.44	44.97		•	•			•		•					•					•																			•			
24	Copp et al.	2010	Slovakia	Multiple rivers	49.09	17.93	•			•		•	•							•	•				•		•					•			•			•	•		•			•		
25	Janác et al.	2010	Czech Republic	Dyje	48.63	16.93		•	•			•		•				•	•					•	•			•				•			•			•			•		•			
26	Piffady et al.	2010	France	Rhône	45.77	5.22	•		•			•	•				•	•			•				•							•							•			•				
27	Pollux & Korosi	2010	Netherlands	Meuse	51.49	6.17		•		•		•								•												•						•					•			
28	Nunn et al.	2007a	United Kingdom	Ouse/Trent	53.28	-0.78	•			•		•													•							•							•			•				
29	Nunn et al.	2007b	United Kingdom	Trent	52.94	-1.11		•	•			•				•	•			•	•				•							•											•		•	
30	Wolter	2007	Germany	Oder	53.02	14.30	•			•		•												•																		•				
31	Pollux et al.	2006	Netherlands	Meuse	51.41	6.15	•		•			•				•					•																	•	•		•					
32	Sindilariu et al.	2006	Romania	Danube	45.06	29.16	•		•			•						•						•																	•					
33	Copp et al.	2005	United Kingdom	Ouse	51.77	-0.14	•		•			•				•	•			•	•				•							•													•	
34	Davey et al.	2005	United Kingdom	Itchen	51.00	-1.34	•			•		•								•																		•	•	•	•					
35	Hohausova & Jurajda	2005	Czech Republic	Morava	49.64	17.24		•	•			•									•				•							•											•			
36	Mastrorillo & Copp	2005	France	Garonne	43.86	1.24		•	•			•					•				•											•						•					•			
37	Bartl & Keckeis	2004	Austria	Danube	48.20	16.24	•			•	•							•																				•	•	•		•			•	•
38	Copp & Vilizzi	2004	United Kingdom	Ouse	52.32	-0.01	•			•		•				•			•																			•	•	•	•					
39	Grift et al.	2003	Netherlands	Rhine	51.86	5.42		•	•		•	•	•				•	•	•	•	•			•	•							•						•	•		•	•				

(Continues)

TABLE 3 (Continued)

Paper			Location				System		Response unit				Rheophilic fish species																										Habitat variable								
ID	Author(s)	Year	Country	River basin	Latitude	Longitude	Main channel/stream	Floodplain system	Rheophilic community	Individual species	Larvae	YOY juveniles	*Alburnoides bipunctatus*	*Ballerus ballerus*	*Ballerus sapa*	*Barbatula barbatula*	*Barbus barbus*	*Chondrostoma nasus*	*Cobitis taenia*	*Cottus gobio*	*Gobio gobio*	*Gymnocephalus baloni*	*Gymnocephalus schraetser*	*Leuciscus idus*	*Leuciscus leuciscus*	*Lota lota*	*Phoxinus phoxinus*	*Romanogobio albipinnatus*	*Romanogobio belingi*	*Romanogobio kessleri*	*Romanogobio vladykovi*	*Squalius cephalus*	*Telestes souffia*	*Thymallus thymallus*	*Vimba vimba*	*Zingel streber*	*Zingel zingel*	Depth	Water flow	Substratum	Presence of structure	Water temperature	Connectivity	Bank slope	Food availability	Habitat heterogeneity
40	Nunn et al.	2003	United Kingdom	Ouse	54.01	-1.19	•			•		•													•							•							•			•				
41	Penczak et al.	2003	Poland	Warta	51.33	19.91		•		•		•												•	•																		•			
42	Scholten et al.	2003	Germany	Elbe	52.81	12.02	•			•		•												•														•						•		
43	Bischoff & Wolter	2001	Germany	Oder	53.06	14.35	•	•	•			•				•			•		•			•	•	•						•								•	•			•		
44	Cattanéo et al.	2001	France	Rhône	44.61	4.74	•		•			•	•				•	•			•											•	•						•							
45	Grenouillet & Pont	2001	France	Saône	46.11	4.77	•		•			•																				•						•			•				•	
46	Grift et al.	2001	Netherlands	Rhine	51.86	5.42		•	•			•					•	•	•	•	•			•	•							•							•				•			
47	Jurajda et al.	2001	Czech Republic	Morava/Dyje	48.61	16.94	•	•	•			•				•	•	•	•		•	•		•	•	•		•				•							•							
48	Keckeis et al.	2001	Austria	Danube	48.12	16.64	•			•	•							•																								•				
49	Pont & Nicolas	2001	France	Rhône	43.78	4.64		•	•			•					•	•			•											•								•			•			•
50	Berrebi-dit-Thomas et al.	2000	France	Seine	48.55	3.68		•	•			•	•			•	•	•			•				•		•					•						•		•	•		•	•		•
51	Grenouillet & Pont	2000	France	Saône	45.94	4.77	•			•		•																				•						•		•	•					
52	Baras & Nindaba	1999a	Belgium	Ourthe	50.54	5.59	•			•		•					•	•																				•				•			•	
53	Baras & Nindaba	1999b	Belgium	Ourthe	50.55	5.59	•			•	•	•													•							•						•			•	•			•	
54	Copp & Jurajda	1999	Czech Republic	Morava	48.68	16.98	•			•		•													•							•								•						
55	Simonovic et al.	1999	United Kingdom	Lee/Frome	51.77	-0.14	•			•	•	•															•											•	•	•	•	•		•		
56	Stakenas	1999	Lithuania	Neumanas/ Neris	54.99	24.55	•		•			•					•				•				•		•					•													•	
57	Gozlan et al.	1998	France	Garonne	43.71	1.35	•		•			•				•	•				•				•							•						•	•	•	•			•		
58	Copp	1997	United Kingdom	Ouse	52.32	-0.01	•	•		•	•	•									•				•													•		•	•	•		•		
59	Jurajda et al.	1997	Czech Republic	Dyje	48.90	16.63		•	•			•						•						•														•		•				•		
60	Keckeis et al.	1997	Austria	Danube	48.12	16.78	•			•		•						•																				•	•	•	•	•			•	
61	Pilcher & Copp	1997	United Kingdom	Lee/Stort	51.80	0.00	•		•			•									•						•					•						•	•	•	•			•		•
62	Watkins et al.	1997	United Kingdom	Lee	51.77	-0.14	•			•		•					•				•						•					•						•	•	•	•	•		•		
63	Winkler et al.	1997	Austria	Danube	48.13	16.66	•			•	•	•						•																				•	•	•						
64	Bisschof & Scholten	1996	Germany	Sieg	50.79	7.25	•			•	•	•					•																						•			•				
65	Freyhof	1996	Germany	Sieg	50.80	7.16	•			•	•	•					•																					•	•	•					•	
66	Garner	1996	United Kingdom	Ouse	52.36	0.26	•			•	•																					•						•			•					
67	Kurmayer et al.	1996	Austria	Danube	48.11	16.77	•		•			•						•			•				•							•			•			•		•						•
68	Poizat & Pont	1996	France	Rhône	43.76	4.63	•		•			•									•											•						•	•					•		
69	Staas & Neumann	1996	Germany	Rhine	51.57	6.68	•	•	•			•					•	•			•			•	•														•				•	•		
70	Baras et al.	1995	Belgium	Ourthe	50.54	5.58	•		•			•				•	•	•			•				•		•					•						•	•	•	•	•				
71	Jurajda	1995	Czech Republic	Morava	48.69	17.00	•		•			•					•	•			•				•							•						•		•				•		
72	Copp et al.	1994	Hungary/Slovakia	Danube	47.95	17.43	•	•	•			•		•			•	•		•	•	•		•	•			•				•			•				•	•	•			•		
73	Copp	1993	France	Rhône	45.88	5.35	•	•	•			•					•	•				•			•		•					•						•	•	•	•					
74	Copp	1992	United Kingdom	Ouse	45.70	5.55		•		•	•	•						•			•				•							•						•	•	•	•			•		
75	Schiemer & Spindler	1989	Austria	Danube	48.12	16.70	•		•		•	•					•	•			•		•	•	•			•				•			•				•	•			•		•	
76	Scott	1985	United Kingdom	Frome	51.52	-2.49		•		•	•																							•											•	
77	Mann	1976	United Kingdom	Dorset Stour	50.89	-2.21	•			•		•																				•										•				

TABLE 4 General information on the rheophilic fish species that were studied in relation to their habitat preferences in temperate European lowland river systems up to 200 m elevation

General information			Size		Distribution in ecoregions												Number of habitat associations									
Scientific name	Name EN	Reproductive guild	Size Larvae (< ... mm)	Size YOY juveniles (< ... mm)	08. Western Highlands	09. Central Highlands	10. The Carpathiens	11. Hungarian Lowlands	12. Pontic Province	13. Western Plains	14. Central Plains	15. Baltic Province	16. Eastern Plains	17. Ireland and Northern Ireland	18. Great Britain	25. Caspic Depression	Depth	Water flow	Substratum	Presence of structure	Bank slope	Temperature	Connectivity	Food availability	Habitat heterogeneity	Total
Rheophilic community	-	-	-	-	•	•	•	•	•	•	•	•	•	•	•	•	25	28	23	17	15	6	20	6	11	151
Squalius cephalus	Chub	Lithophils	17-21	45-80	•	•	•	•	•	•	•	•	•		•	•	10	6	5	9	4	6	1	4	1	46
Chondrostoma nasus	Common nase	Lithophils	15-20	57-80	•	•	•	•	•	•	•	•	•			•	9	9	7	3	2	5	-	4	2	41
Leuciscus leuciscus	Common dace	Phytolithophils	17-20	60-85	•	•	•	•	•	•	•	•	•	•	•	•	7	5	5	7	5	6	-	2	-	37
Barbus barbus	Barbel	Lithophils	18-22	49-100	•	•	•	•	•	•	•	•	•		•	•	5	6	4	2	2	5	-	2	-	26
Phoxinus phoxinus	Eurasian minnow	Lithophils	18	28-51	•	•	•	•	•	•	•	•	•		•	•	4	4	4	4	4	3	-	-	-	23
Gobio gobio	Gudgeon	Psammophils	13-16	40-58	•	•	•	•	•	•	•	•	•	•	•	•	4	2	4	4	4	3	-	-	-	21
Cottus gobio	Bullhead	Speleophils	9	38-40	•	•	•	•	•	•	•	•	•		•	•	4	2	3	2	1	-	1	-	-	13
Alburnoides bipunctatus	Spirlin	Lithophils	30	45-70	•	•	•	•	•	•	•	•	•			•	2	2	1	2	1	-	-	1	-	9
Leuciscus idus	Ide	Phytolithophils	24-27	101	•	•	•	•	•	•	•	•	•		•	•	2	-	-	-	1	2	1	1	-	7
Cobitis taenia	Spined loach	Phytophils	-	30-60	•	•	•	•	•	•	•	•	•		•	•	1	1	1	2	-	-	-	-	-	5
Vimba vimba	Vimba bream	Lithophils	-	80	•	•	•	•	•	•	•	•	•			•	1	1	1	1	1	-	-	-	-	5
Barbatula barbatula	Stone loach	Psammophils	35	50-61	•	•	•	•	•	•	•	•	•		•	•	1	1	1	1	-	-	-	-	-	4
Thymallus thymallus	Grayling	Lithophils	-	170	•	•	•	•	•	•	•	•	•		•	•	-	-	-	-	-	1	-	1	-	2
															Total		75	67	59	54	40	37	23	21	14	**390**

boulders) resulted in mixed responses between life stages. Generally, larval fish responded positively to complex habitat structures, with a significant positive response for water plants reported twice. For juveniles, on the other hand, over 40% of the recorded responses to physical structures were neutral or even negative. For increased river-floodplain connectivity and, to a lesser extent, increased connectivity between rivers or streams, almost exclusively positive fish responses were found. Increased availability of food items, such as zooplankton, macro-invertebrates and algae/phytoplankton, resulted in a similar positive responses for both larvae and YOY juveniles. Furthermore, 12 out of 14 data points suggested a positive association of both larvae and juveniles with a more heterogeneous habitat, but only one study showed significant results.

Out of the 241 data points for depth, water flow, substratum type and bank slope, 137 enabled quantitative analysis (Figure 6). Fish responses to substratum type (52 data points) were most assessed, followed by water depth (46), water flow (31) and bank slope (8). For all rheophilic species a water depth <0.5 m was optimal and never exceeded 1.0 m (Figure 6a). On average, larvae preferred slightly deeper waters (0.31 m), compared to YOY juveniles (0.26 m). No clear differences between optimal depth ranges were found between species. On a species level, reported optimal water flow levels and ranges were always <0.2 m/s (Figure 6b), with one exception for stone loach (*Barbatula barbatula*, Cyprinidae). Calculated mean values for optimal water flow did not differ much between the larval (0.053 m/s) and juvenile (0.071 m/s) life stage.

For substratum type preference, less uniformity between species responses was observed. Early life stages of chub, common dace, common nase and Eurasian minnow preferred varying substratum sizes ranging from silt to gravel, whereas YOY barbel, bullhead and gudgeon preferred gravel and boulders (Figure 6c). Despite these large ranges in optimal substratum types between species, in general juvenile fish preferred larger-sized substrates (coarse sand and gravel), whereas larvae preferred slightly smaller-sized substrates (fine and coarse sand).

Only seven studies quantitatively assessed fish responses to bank slope, reporting optimal bank slopes to be <20° (Figure 6d). Calculated average optimal bank slopes for larvae and juveniles were respectively 5° and 10°.

4 | DISCUSSION

We combined the conceptual models of Cowx and Welcomme (1998) and Schlosser (1991) as a framework for our systematic literature review on nursery habitat requirements of rheophilic fishes in European temperate lowland rivers (Figure 1). The conceptual model includes the role of small-scale fish movements at different life stages in relation to habitat heterogeneity, as an essential component of a well-functioning nursery area (Schlosser, 1995). Detailed understanding of this dynamic nursery habitat component is however lacking in literature (Erős & Grant, 2015; Van Looy et al., 2019). As expected, most studies focused on single, well-defined physical components of the riparian ecotone, such as temperature, depth, water flow and the presence of structure. Generally, YOY fish require habitats of shallow depth (<0.5 m), with slow-flowing water (<0.2 m/s), gentle bank slope (<20°), variety in substratum types (sand to gravel), higher than average water temperatures and high food availability (Figures 5 and 6). The configuration of the described optimal habitat is strongly associated with the functioning of riparian ecotones, such as refugia and feeding areas (Eick & Thiel, 2013; Grift et al., 2001; Nunn et al., 2012; Pander & Geist, 2018), highlighting the importance of these shoreline habitats for the recovery of rheophilic fish populations (Schiemer et al., 2011). Additionally, since 2011, the number of studies on (micro)habitat heterogeneity has increased (Figure 4), but only one study explicitly assessed the role of habitat heterogeneity in relation to movement patterns of YOY fish for nursery success (the dynamic part of Schlosser's conceptual model). Surprisingly, no clear ontogenetic habitat shifts between larvae and YOY juveniles were found. This indicates that either early life stages of rheophilic fish operate within similar habitat configurations, or that the studies focus on a too large spatial habitat classification, resulting in undetected shifts in microhabitat use between larvae and juveniles.

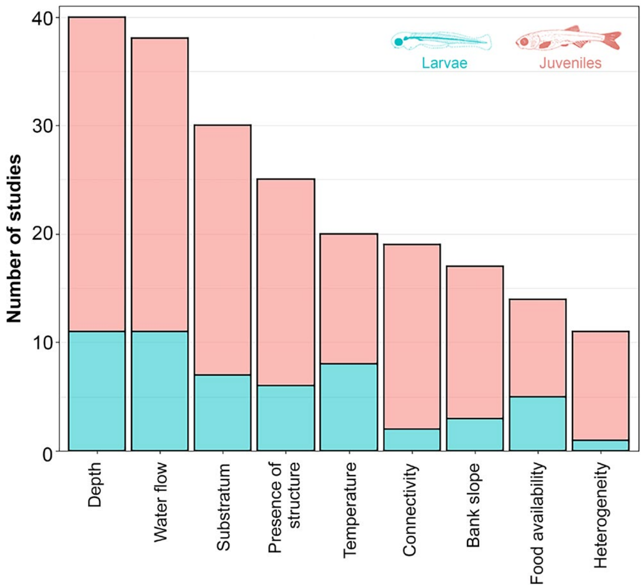

FIGURE 3 Total number of studies that focussed on fish responses per habitat variable. Studies on larval rheophilic fish are shown in turquoise and studies on YOY juveniles are shown in pink. Studies that reported fish responses to more than one environmental variable are counted multiple times. Fish drawings were adapted from Pinder (2001)

4.1 | Literature focus

The physical habitat variables of water flow, depth and temperature, constituted almost 50% of the recorded habitat associations in this synthesis (Figure 4). This is not surprising, given the simple, well-defined and standardized sampling protocols for these variables (e.g. Trudgill et al., 2005). Despite this, research has moved away from studying water temperature in recent years, possibly due to high levels of uniformity in fish responses to shifting temperatures (Górski et al., 2011; Nunn et al., 2003, 2007). Furthermore, the uncontrollable nature of temperature in natural

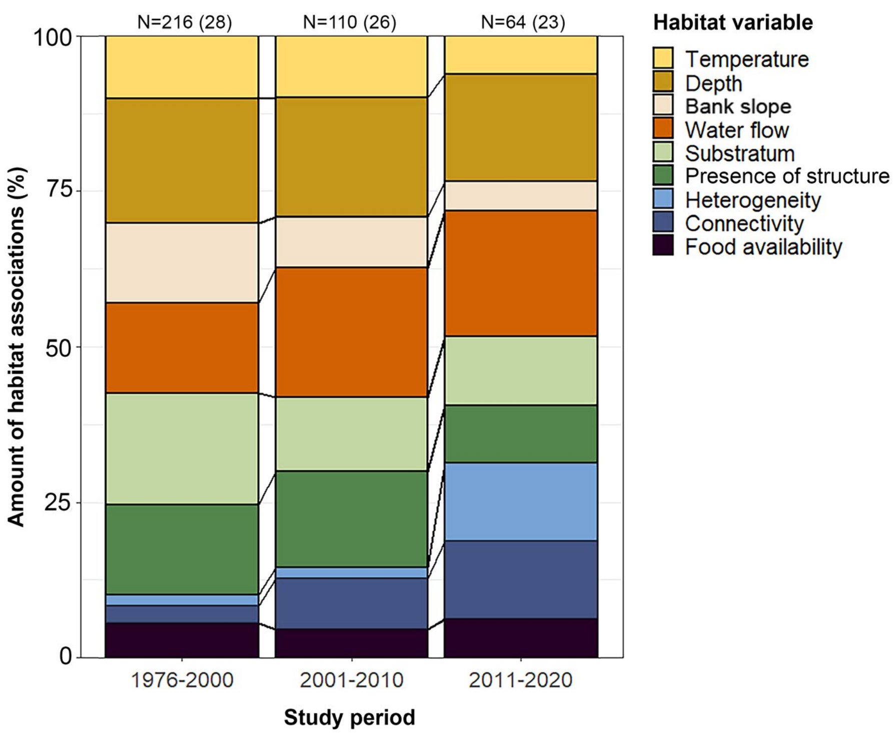

FIGURE 4 Stacked bar plots showing change in study literature focus regarding habitat requirements for YOY rheophilic fish in temperate European lowland rivers (<200 m elevation) over three time periods (1976–2000, 2001–2010, 2011–2020). *N* indicates total number of habitat associations found in literature per time period, and total number of studies are shown between brackets

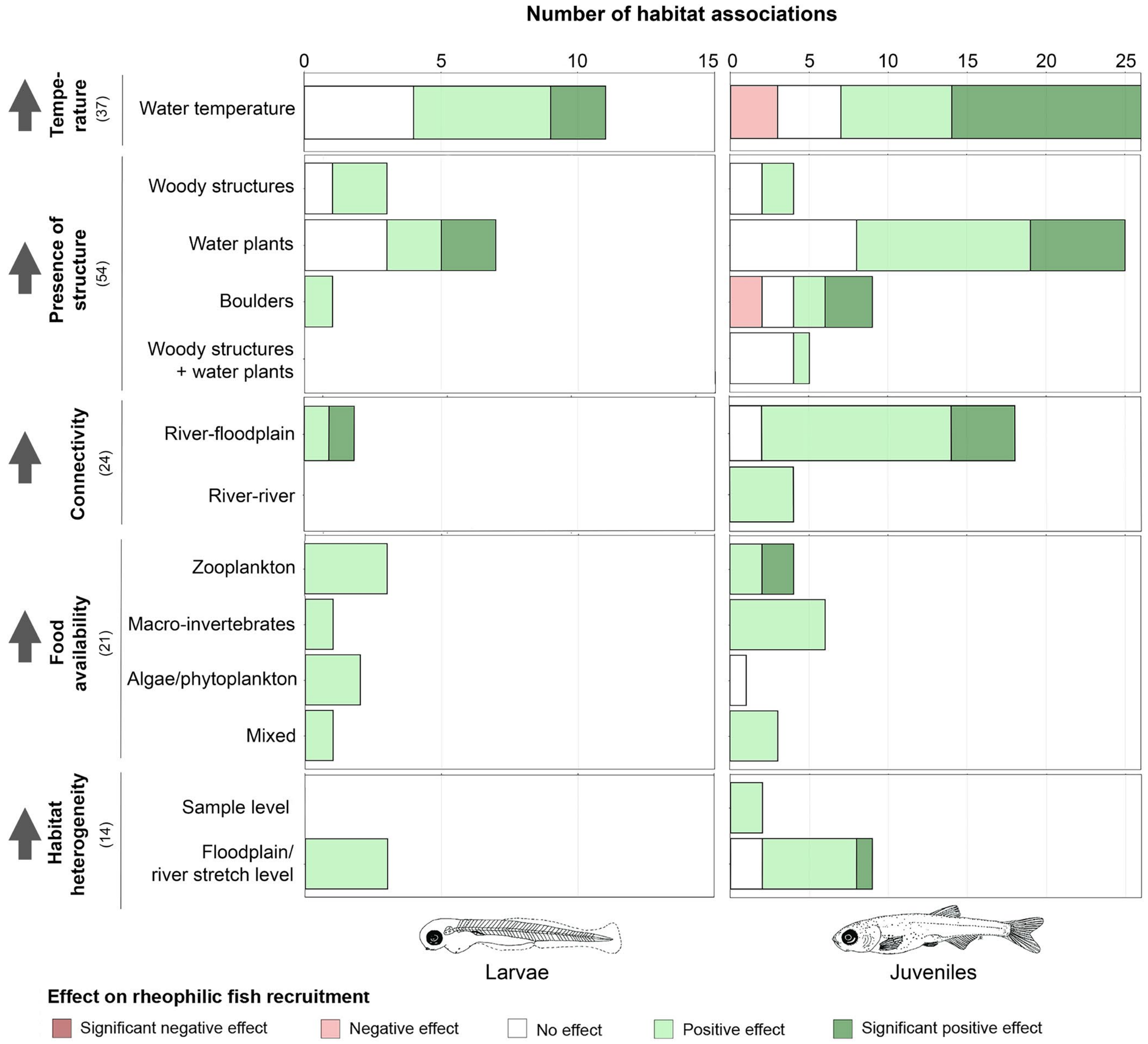

FIGURE 5 Ordinal scoring of larval and YOY juvenile fish responses to an increase in the shown habitat variables per category. Total number of fish-habitat associations per variable are shown between brackets. Bars for both larval and juvenile fish indicate the number of habitat associations per category of each variable. Colours indicate the effect of each category on rheophilic fish recruitment according to literature. Fish drawings were adapted from Pinder (2001)

systems makes it a less effective target in the evaluation of river restoration projects. Additionally, scientific interest in the effect of river-floodplain connectivity on fish responses has increased within the 21st century. This is possibly related to the increased focus on evaluating floodplain restoration projects in recent years (Table 3), and the associated increased perception of the importance of river-floodplain connectivity as an important component of the nursery habitat. Permanent lateral connectivity between the main channel and the floodplain results in floodplain areas with varying flow velocities. This facilitates habitat availability, heterogeneity and YOY fish movement, which is essential for successful recruitment of rheophilic fishes (Nunn, Harvey, Britton, et al., 2007; Pander & Geist, 2018; Schlosser, 1991; Stoffers et al., 2021; Ward et al., 1999; Wolter et al., 2016).

With our literature search, we aimed to retrieve literature from temperate European lowland rivers below 200 m elevation. We only selected English-language peer-reviewed studies that focused on habitat associations of YOY rheophilic fish species. The resulting literature selection was dominated by western European studies and only a few studies were from the Carpathians, Pontic Province and Eastern plains (Figure 2). We do not expect this geographical bias to have affected the overall outcomes of this study, since we have included studies from 29 different rivers in 14 countries (Table 3) and in these under-represented geographical areas no other common

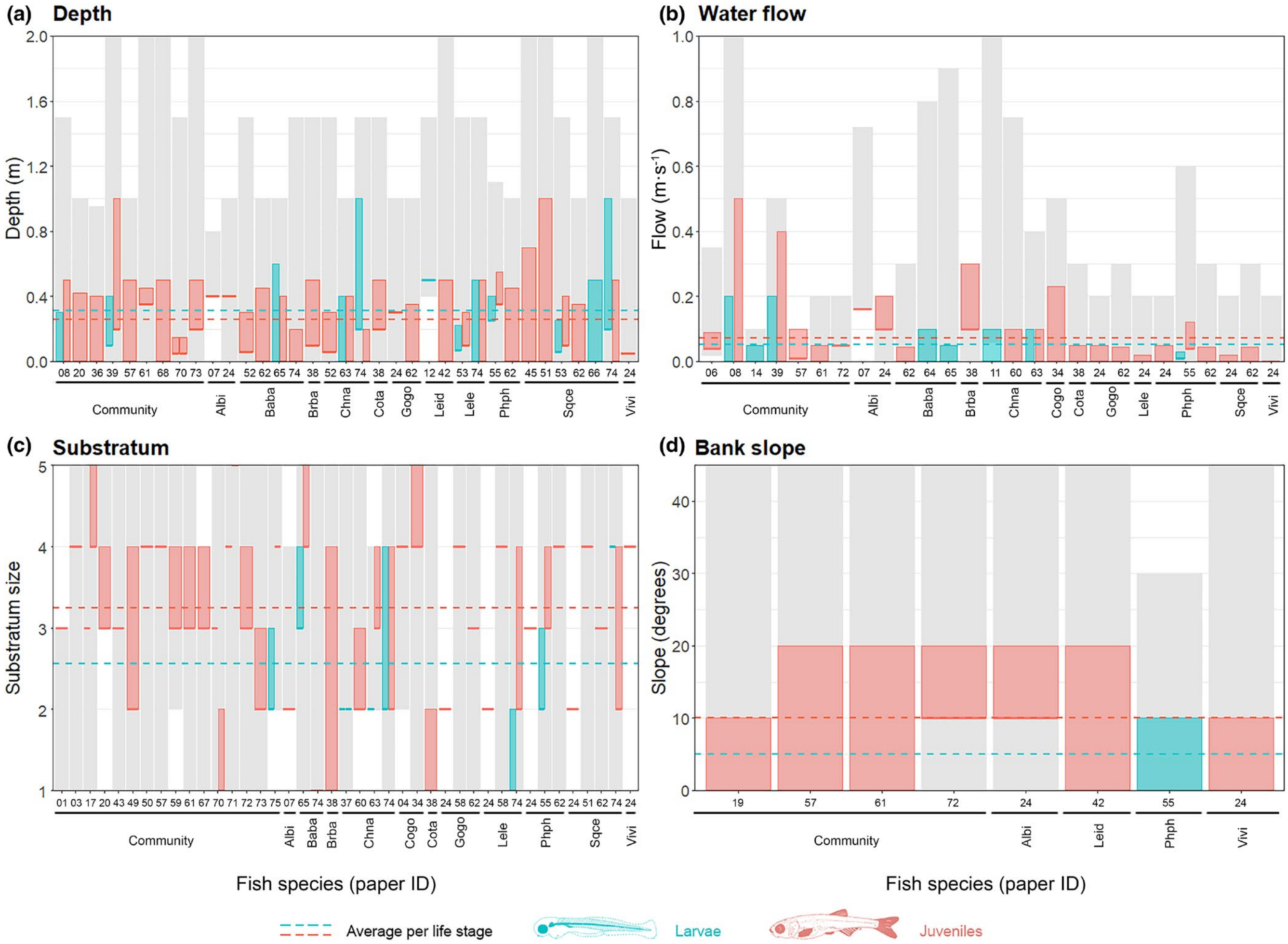

FIGURE 6 Range plots representing optimal ranges for the habitat variables from which their effect on YOY fish recruitment was quantitatively assessed: (a) depth ranging from 0.0 to 2.0 m; (b) water flow ranging from 0.0 to 1.0 m/s; (c) substratum type in five classes: (1) clay/silt (<0.06 mm), (2) fine sand (0.06–0.85 mm), (3) coarse sand (0.85–2 mm), (4) gravel (2–65 mm), (5) cobbles/boulders (>65 mm); and (d) bank slope ranging from 0° to 45°. Turquoise plots represent optimal ranges/values for larval fish and pink plots YOY juvenile fish. Grey areas indicate the range an individual habitat variable was assessed in each study. Average per life stage per habitat variable is indicated with a dashed line (turquoise: larvae; pink: juveniles). Optimal ranges were plotted per rheophilic fish species and show corresponding studies (paper ID corresponds with study information in Table 3). Species abbreviations are comprised of the first two letters of genus and species names, except for Brba: Barbatula barbatula. Fish drawings were adapted from Pinder (2001)

rheophilic species occur. Surprisingly, for a large number of rheophilic species having their main biogeographical distribution in the bream and barbel zones of temperate European lowland rivers, we could not find information on their nursery habitat preferences. Although we included 25 different rheophilic species in our study (Table 3), the analysis of habitat associations for individual species was greatly dominated by the cyprinid species chub, common nase, common dace and barbel (>60% of all obtained habitat associations). For other common rheophilic species in our study area we obtained only few (e.g. spirlin, ide, vimba bream, grayling) or even no habitat associations (e.g. blue bream, Danube ruffe, schraetzer, burbot, vairone) at the species level (Table 4). This could be the result of the framing of our study area, since some of the under-represented species prefer nursery areas in the grayling zone (grayling, Eurasian minnow), or even in the trout zone (bullhead, stone loach; Aarts & Nienhuis, 2003), and their YOY individuals are therefore less commonly observed in our study area (below 200 m elevation). Furthermore, the speleophilic spawning habit of bullhead may have resulted in the general lack of information on nursery habitat requirements for this species, as this habitat is more difficult to sample compared to that of other rheophilics in this study (Balon, 1975). The general lack of habitat associations of Ponto-Caspian gobies in our synthesis is probably the result of the limited number of studies we retrieved from lowland rivers in eastern Europe, where these species are common.

4.2 | Habitat heterogeneity and fish movement

Spatial habitat heterogeneity, temporal habitat variability and the limited mobility of YOY fish are key aspects influencing growth and survival of early life stages of rheophilic fish (Angeler & Allen, 2016;

Pont & Nicolas, 2001; Schlosser, 1991; Van Looy et al., 2019; Ward et al., 1999; Winemiller et al., 2010) and are increasingly recognized as part of a well-functioning nursery area (Meulenbroek, Drexler, et al., 2018; Stoffers et al., 2021; Figure 4). When both local fish biodiversity and habitat heterogeneity are high, and habitat patches are inter-connected, river fish populations may exhibit high levels of resilience against flood pulses, global warming and other environmental changes (Elmqvist et al., 2003; Meulenbroek, Drexler, et al., 2018; Van Looy et al., 2019).

Unfortunately, habitat heterogeneity in dynamic river systems is difficult to define (Li & Reynolds, 1995; Palmer et al., 2010), just as its role in small-scale fish movement (active dispersal) or drift (passive or active dispersal) between habitat patches. This has led to diverse approaches to study its effect on local fish population development. Most studies describe (micro)habitat heterogeneity as a spatial combination of shoreline habitat patches (1–100 m^2) on a river reach scale (100–1,000 m), which is assumed to be the average scale over which individual YOY fish move (Wolter et al., 2016). The size of a nursery area plays an important role in the distribution and spatial connectivity of habitat patches and therefore in the overall functioning as nursery area. Generally, the quality of (restored) rheophilic nursery areas on a river reach scale increases with size (Schmutz et al., 2014). On a smaller scale however, the quality of individual patches is expected to be more important than the size of an individual habitat patch (Pander et al., 2017). Both Pander and Geist (2018) and Ramler and Keckeis (2019) described the importance of transition zones and spatial connectivity between different habitat patches (within 500-m distance) for recruitment and resilience of the rheophilic fish population. Other studies assessed the quality of restoration projects for rheophilic fishes by characterizing habitat patches of good quality (higher juvenile abundance, richness and diversity of target species indicating better quality) and their interconnectivity (Lorenz et al., 2013; Mueller et al., 2014; Pander et al., 2017; Schmutz et al., 2014).

Surprisingly, most of these studies only performed a correlative analysis of habitat heterogeneity on fish responses and movement patterns, which makes it difficult to separate its effect from other confounding habitat variables. Lorenz et al. (2013) performed the only study within our synthesis that quantified (micro)habitat diversity and tested its effect on fish recruitment for a restricted number of environmental variables (water flow and depth). Per river reach they calculated coefficients of variation for flow velocity and depth (higher values indicating higher diversity levels) and summarized total coverage of every microhabitat. Subsequently, they calculated the Shannon–Wiener index of habitat heterogeneity (Pielou, 1975) using the mean relative proportion of habitat coverage (see also Lorenz et al., 2016). Although both depth and flow velocity are key aspects of nursery areas for rheophilic fishes, the quantification and testing of the effect of habitat heterogeneity on nursery habitat success should ideally also include other habitat variables important in early life stages such as substratum type, bank slope and the presence of structure.

Furthermore, only two studies in our synthesis explicitly assessed fish movement between spatially separated habitat patches despite this being an essential aspect of the life cycle of rheophilic fishes (Figure 1). Movement patterns of rheophilic fishes in bays and between backwater and river habitats (50-m distance) were mainly driven by changes in water temperature (Baras & Nindaba, 1999a, 1999b) and oxygen levels (Bischoff & Scholten, 1996), caused by differences in water flow, depth and bank slope between these habitats.

In marine ecosystems, the effect of nursery habitat heterogeneity on YOY fish movement has been studied more extensively than in river ecosystems (Beck et al., 2001; Sheaves et al., 2015). Generally, most marine fish species prefer nursery areas with high levels of habitat heterogeneity (Perry et al., 2018; van Lier et al., 2018), although some species avoid heterogeneous habitats due to predation risk at the edge boundaries (Staveley et al., 2017). In Western Australia, van Lier et al. (2018) observed that nursery success was dependent on both the habitat quality of nursery areas and the presence and complexity of habitat patches in the surrounding area (within 500 m), highlighting the importance of fishes' movement between habitats. For many YOY reef fishes, daily movement is limited to small distances (<300 m), and most daytime movements to adjacent habitat patches take place within a 50-m range of their nursery area (Appeldoorn et al., 2009; Verweij & Nagelkerken, 2007). These ranges correspond with the average scale over which individual YOY rheophilic fish move (Wolter et al., 2016). Fish movement in relation to habitat heterogeneity is more difficult to study in the turbid waters of most of the European temperate lowland rivers and floodplains. Although some studies have used otolith marking and release and recapture techniques to study (passive) dispersal patterns of larval fish (Lechner et al., 2014, 2018), especially YOY juvenile fish movement patterns in relation to habitat heterogeneity remains an important missing link in our understanding of rheophilic nursery areas.

4.3 | Consistency in nursery habitat requirements

The high level of consistency in overall fish responses to most physical habitat variables implies that no large differences between larvae and YOY juveniles of rheophilic fish species exist (Figures 5 and 6). Habitats with varying flow velocities are important for the productivity and biodiversity of rheophilic fishes in nursery areas (Poff & Zimmerman, 2010), with low-flow areas being particularly favoured (Grift et al., 2001; Nunn et al., 2007c; Ward et al., 1999). Low-flow, as a habitat characteristic, is often confounded with other physical habitat characteristics, and within low-flow areas rheophilic fish prefer shallow habitats with a gentle bank slope (Eick & Thiel, 2013; Scholten, 2013).

We also observed that almost all reported associations of larval and juvenile fish with food availability were positive. This highlights the underlying importance of food availability for the well-functioning of nursery habitat for rheophilic fish. With relatively low water temperatures in European temperate lowland rivers, shallow habitats with a gentle bank slope warm up relatively fast in spring and summer. They often contain broad temperature gradients, which is beneficial for zooplankton production (Dzialowski et al., 2013; Górski et al., 2016) and for the metabolic processes in small fishes (Schiemer et al., 2002). The way in which both YOY fish and their prey respond to the interplay of river discharge, flow patterns and temperature, plays a major role in the population success of river fish (Humphries et al., 2013). In the floodplains of the Volga river, for example, Górski et al. (2016) observed that YOY fish were more abundant at the shoreline of permanent waterbodies, compared to the adjacent flooded terrestrial habitats, where food production was orders of magnitude higher. The authors hypothesized that these shallow flooded terrestrial habitats function as nursery areas for zooplankton, rather than for fish, and that food items will become available for YOY fish with the retreating water. These fish thus avoid the risk of getting stranded on the flooded habitats when the water quickly retreats (Wilzbach et al., 2002). In the Danube river, Pander et al. (2017) observed that early life stages of rheophilic fish also preferred shoreline habitats with a gentle bank slope (<10°) over habitats with steeper bank slopes, even though the latter had increased shelter opportunities due to the presence of boulders and dead wood.

The presence of physical structures also plays an important role in the nursery area of many rheophilic fish species (Górski et al., 2011; Grift et al., 2003; Smokorowski & Pratt, 2007), as structurally complex habitats give shelter against stressful environmental conditions, such as strong currents (Copp, 1992; Schiemer & Spindler, 1989), waves from shipping activity (Collas et al., 2018) and predation (Grenouillet et al., 2002; Schneider & Winemiller, 2008). Although responses to the presence of water plants and woody structures varied, probably due to species-specific differences in habitat use (Copp, 1992; Copp et al., 2010), larval fish tend to respond more positively to the presence of structure than juveniles (Figure 5). Increased vulnerability to predatory fish may explain the preference of larval fish for the presence of structure in their nursery habitat (Baras et al., 1995; Copp, 1992); although the presence of piscivorous invertebrates inside these structures may also explain the reported larval avoidance of such habitats by Pander et al. (2017).

Substratum type was the only habitat variable for which we observed clearly contrasting fish responses. This is probably due to differences in substratum preferences between roughly two groups of rheophilic fishes (Copp et al., 2010). Early life stages of many rheophilic fish species (i.e. chub, common dace, common nase, Eurasian minnow) appear to be less specific in their substratum use and can cope with highly varying substratum sizes ranging from silt to gravel (Copp, 1992; Copp et al., 2010; Keckeis et al., 1997; Kurmayer et al., 1996; Simonovic et al., 1999; Watkins et al., 1997), whereas YOY barbel, bullhead and gudgeon generally prefer larger-sized substratum types, such as gravel and boulders (Britton & Pegg, 2011; Copp et al., 2010; Davey et al., 2005; Freyhof, 1996; Figure 6c). Contrasting fish responses to substratum in the first group can also be explained by varying ranges of available substratum between studies, or the lack of a standardized classification system to describe substratum type (Blott & Pye, 2012), making it difficult to compare fish responses. Furthermore, river beds often consist of a combination of differently sized substrates, and especially in larval lithophilic fish there is evidence that this combination of substratum types is important in larval emergence and early-stage survival (Bašić et al., 2018; Nagel et al., 2019, 2020).

4.4 | Ontogenetic habitat shifts

The vicinity of a local spawning habitat and subsequent drift processes determine the presence of larval rheophilic fish in nursery areas (Oesmann, 2003; Reichard et al., 2004) and connectivity between these functional habitats is an essential component for successful recruitment of rheophilic fish (Figure 1). Recent studies show that drifting fish larvae can perform rheoreaction, in which they actively move in the current of the main channel to increase their chances of reaching a suitable nursery area (Glas et al., 2020; Lechner et al., 2016, 2018; Pavlov, 1994; Zens et al., 2017). Upon arrival or after hatching, larvae are generally bound to small-scale nursery habitat conditions (0–100 m) due to their limited swimming performance. Since swimming performance increases with fish size and depending on physical factors within the microhabitat (temperature, oxygen levels, viscosity effects) and changes in species-specific biological factors (body shape, muscle function, fin form, swimming mode; Kolok, 1999; Wolter & Arlinghaus, 2003), a wider range of microhabitats (0–1 km) in the same nursery area becomes available for juveniles (Wolter et al., 2016). This may explain why we found that habitat heterogeneity and connectivity of microhabitats becomes more important with increasing size (Figure 5). For juveniles, connectivity between habitats in the main channel and adjacent backwaters becomes more important, as many rheophilic species start to show daily migrations between these habitats to find food (Baras & Nindaba, 1999b), avoid predation (Baras & Nindaba, 1999a; Copp & Jurajda, 1993) and choose optimal temperatures (Bischoff & Scholten, 1996).

Temporal changes in the quality, availability and accessibility of important physical nursery habitat (e.g. for shelter and feeding), combined with considerable changes in habitat requirements and behaviour, may lead to ontogenetic shifts in habitat use by rheophilic fishes (Copp, 1997; Eick & Thiel, 2013; Gaudin, 2001; Schiemer & Spindler, 1989). For most physical habitat variables assessed in this study, we were unable to find clear differences in fish responses between larval and juvenile life stages. This may imply that differences in tolerance between the larval and juvenile life stages of rheophilic fish might not be as large as generally believed. Also the lack of detail in the studies on microhabitat preferences may explain why we did not find an ontogenetic shift. The mentioned studies may have focused on a (too) large spatial scale of habitat classification to enable identification of especially larval microhabitat preferences. However, for water flow and depth we do not expect this to be the case, since both variables were assessed in great detail by many of the studies, resulting in a detailed overview of optimal depth and water flow ranges (Figure 6a,b).

Although we did not observe clear ontogenetic nursery habitat shifts, species-specific ontogenetic diet shifts can cause YOY fish to use different physical habitats at different life stages (King, 2005; Werner & Hall, 1988). For example, ontogenetic shifts in flow preference for common nase and barbel have been explained by shifts in feeding behaviour and increased swimming capabilities (Bischoff & Freyhof, 1999; Reckendorfer et al., 2001). Similar ontogenetic shifts in flow preference caused by food availability were reported for YOY grayling (Gaudin, 2001), with larvae inhabiting stagnant shallow areas with fine substratum, and YOY juveniles increasingly using shallow gravel banks in lotic habitats. Gaudin (2001) hypothesized that these shifts may be due to high energy demands in these early life stages, as single microhabitats cannot regularly provide sufficient food.

4.5 | Recommendations for future research

We observed a geographical bias in the literature towards western European countries (Figure 2), which resulted in a knowledge gap on rheophilic nursery requirements in lowland rivers in eastern Europe. It is not easy to judge whether these under-represented areas are genuinely lacking research, or whether these studies simply have not reached English-language scientific literature. We did find some peer-reviewed literature written in the local language for this geographical region, but did not include it in our synthesis for consistency. Either way, future studies on under-represented temperate lowland rivers in eastern Europe will increase our understanding of nursery habitat requirements, for a wider range of rheophilic fish species, and help guide river conservation efforts (Erős et al., 2019).

Additionally, ecological research in European rivers and river conservation would also benefit from a more streamlined methodology to obtained YOY fish samples and habitat conditions. No formal meta-analysis (truly quantitative analysis) of the data was possible due to large differences between studies in sampling techniques and strategies, reporting of fish responses and quantifying habitat variables. We noticed major differences in fish (and habitat) sampling techniques used between countries, geographical areas, and even in similar habitats. This resulted in the general lack of clear means and standard deviations to determine effect sizes per study, necessary to perform a meta-analysis.

Literature bias towards the evaluation of fish responses for single physical habitat variables may be caused by the complex nature of these ecological patterns and processes and the associated complex evaluation strategies (Peipoch et al., 2015). It could also be that these complex ecological patterns and processes, across spatial scales, do not fit well within the more classical guidelines and criteria for assessing the ecological status of restoration projects within the Water Framework Directive. Therefore, classical biotic-index-based evaluations are preferred (Angermeier & Karr, 1994; Moss, 2008).

With the large number of studies on classical biotic indices, and the unified fish responses found regarding these physical habitat variables, we were able to outline the contours of the microhabitats necessary for rheophilic nursery areas. We found that refugia and/or feeding areas generally consist of (a combination of) habitats with shallow depth (<0.5 m), slow-flowing water (<0.2 m/s), gentle bank slope (<20°), variety in substratum types (fine sand to gravel), relatively warm water and high food availability. However, the effect of habitat heterogeneity on habitat use and movement patterns of YOY fish remains a caveat in research on rheophilic fish nursery areas. Since YOY fish movement and habitat use generally take place at relevant scales for local management (0–1 km; Thorp et al., 2006; Wolter et al., 2016), it is essential to understand what drives these processes for the effective management of restoration projects (Brierley et al., 2012).

We are aware that in order to do this, extensive field surveys and modelling effort is required on different spatial and temporal scales (see also Erős et al., 2012). We propose five key steps that need to be taken to enhance our understanding of the effect of habitat heterogeneity on habitat use and movement patterns of YOY rheophilic fish in European temperate lowland rivers: (1) the collection of a detailed data set on physical habitat preferences (preferably day and night) for both larval and juvenile rheophilic fish in river habitats (riparian ecotones of the main channel and adjacent backwaters/floodplains) on relevant spatial and temporal scales (see also Wolter et al., 2016); (2) the modelling of the general effect of habitat variables on fish population responses (biodiversity and total abundances) and selection of the habitat variables that best explain the variation in fish population responses; (3) the development of a standardized methodology for the quantification of important habitat patches, based on the selected habitat variables (10–100 m); (4) the characterization of habitat patches, and assessing size and quality, over the relevant spatial scales; (5) the modelling of the effect of patch size, quality and connectivity on fish population responses and testing of the hypothesis that an increase in habitat heterogeneity positively affects nursery success.

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CONFLICT OF INTEREST

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

AUTHORS' CONTRIBUTIONS

Twan Stoffers: Conceptualisation, Methodology, Software, Validation, Formal analysis, Investigation, Writing—original draft, Visualization, Data curation. *Antonie D. Buijse*: Conceptualisation, Writing—review and editing, Supervision. *Johan A.J. Verreth*: Conceptualisation, Writing—review and editing. *Leopold A.J. Nagelkerke*: Conceptualisation, Writing—review and editing, Visualization, Supervision, Funding acquisition.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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