Assessing Habitat Suitability for Native and Alien Freshwater Mussels in the River Waal (the Netherlands), Using Hydroacoustics and Species Sensitivity Distributions

N. Y. Flores¹ · F. P. L. Collas^{1,2} · K. Mehler³ · M. M. Schoor⁴ · C. K. Feld⁵ · R. S. E. W. Leuven^{1,2}

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Abstract

Longitudinal training dams (LTDs) in the river Waal are novel river training structures that protect the littoral zone from the adverse effects of navigation providing new habitats for riverine macroinvertebrates. In order to inform river management and to better understand their ecological value for native and alien mussel species, it is important to assess the habitat suitability of the protected LTD shore channels. We applied spatial hydroacoustics surveys consisting of side-scan sonar (SSS) and acoustic Doppler current profiler (ADCP) of the substrate type, water depth and flow velocity in three shore channels in combination with species sensitivity distributions (SSDs) to predict habitat suitability for native and alien mussel species. SSDs allowed for the prediction of habitat suitability as a potentially occurring fraction (POF) of a species pool. High substrate type, water depth, and near-bottom flow velocity POFs were found for $\geq 70\%$, 100% , and $4\text{--}51\%$ of the total shore channel area, respectively, suggesting that shore channels provide suitable habitat for both native and alien mussel species. To enhance the shore channels as habitat for native mussel species, we recommend increasing shallow areas dominated by fine (silt/clay) and sand substrate types with low near-bottom flow velocities (near 0 m/s). In contrast, the total area of hard substrate (e.g., boulders) in the shore channels should be reduced as it strongly favored invasive alien mussel species in our study. Future research should include additional abiotic parameters to enhance the habitat suitability predictions and compare the results for different riverine habitats.

Keywords Freshwater mollusks · Habitat mapping · Water depth · Flow velocity · Side-scan sonar · River Rhine

1 Introduction

Globally, riverine ecosystems are continuously threatened by the effects of anthropogenic pressures, such as resource overexploitation, hydromorphological modifications, and the

introduction of alien species [1–7]. Many of the navigable river systems in Europe have been heavily modified in order to accommodate navigation leading to the deterioration of lotic riverine habitats through digging, straightening, and building of hydraulic infrastructure necessary to facilitate inland navigation [8–10]. These structures often consist of training or flow-regulating structures, such as groynes and dams, that serve to sustain water depths that are favorable for navigation [8, 9, 11–13]. In lotic ecosystems, inland navigation has detrimental effects on biodiversity due to an increase in flow velocities, the creation of waves, and high amounts of re-suspended sediments, among other physical effects [10, 13–17]. These effects reduce the quantity and quality of suitable habitat for fish, macroinvertebrate and macrophyte species in riverine ecosystems, and in particular the availability of refuge habitats close to the shoreline [2, 14, 18]. In the future, navigation pressures are expected to increase as inland navigation continues to be preferred over other forms of transportation [14, 19, 20].

✉ N. Y. Flores
n.flores@science.ru.nl

¹ Department of Animal Ecology and Physiology, Institute for Water and Wetland Research, Radboud University, Nijmegen, Gelderland, the Netherlands

² Netherlands Centre of Expertise On Exotic Species (NEC-E), Nijmegen, Gelderland, the Netherlands

³ Great Lakes Center, State University of New York College, Buffalo, NY, USA

⁴ Rijkswaterstaat Oost Nederland, Arnhem, Gelderland, the Netherlands

⁵ Department of Aquatic Ecology, Faculty of Biology, University of Duisburg-Essen, Essen, Germany

In Europe, the implementation of management measures to improve the ecology of heavily modified rivers has become a common goal [21]. In the Netherlands, this resulted in the construction of longitudinal training dams (LTDs) in 2014 with the purpose of increasing the space for the river Waal, an important free-flowing tributary of the river Rhine, while improving navigation, water management, and ecological value [22, 23]. The LTDs were constructed by Rijkswaterstaat (i.e., the Directorate-General for Public Works and Water Management of the Netherlands) as a pilot project to replace groyne fields in an effort to divide the river into two sections, a navigation channel and a shore channel protected from the effects of navigation [22, 24, 25]. The protected shore channels along the LTDs are expected to provide habitats to riverine species and thus could improve the ecology of heavily modified rivers, such as the Rhine and its Dutch branches [22]. There is evidence that some species groups, such as fishes, are already benefiting from the habitats provided by these shore channels [24].

Here, we explore the degree to which the ambient water depth, substrate, and near-bottom flow velocity conditions in the shore channels along the LTDs provide suitable habitats for freshwater mussels. These three abiotic parameters were selected since longitudinal and transversal habitat heterogeneity in riverine ecosystems have been hypothesized to result from varying substrate type distribution, water depth, and flow velocity gradients [26–30]. Many mussel species are threatened or endangered globally, especially native unionids with more than 200 species listed on the International Union for Conservation of Nature (IUCN) Red List [31, 32]. Native mussel species fulfill important functions as ecosystem engineers, such as biofiltration, bioturbation, and shell formation [33–35]. Their decline is partly due to the introduction of invasive alien mussel species by ballast water and hull fouling of ships, many of which are better adapted to the modified abiotic conditions resulting from anthropogenic impacts [4, 36–44]. An approach to predict the potential local mussel species pool is species sensitivity distributions (SSDs) [44, 45, 47, 48]. SSDs are statistical curves that describe the variability in the sensitivities of species to a specific abiotic parameter and are derived by using either laboratory or field data on the mortality and occurrence of species when exposed to stressors [38, 45, 46, 48]. These SSDs enable the prediction of suitable habitats based on measured or modeled abiotic conditions [44, 49, 50]. The potentially occurring fraction (POF) is the fraction of the regional mussel species pool included in the SSD that could be present under an abiotic condition [38].

Since abiotic conditions of riverine ecosystems vary in time and space, it is important to account for spatial variability in abiotic conditions to increase prediction accuracy [27, 51]. Hydroacoustics, such as side-scan sonar (SSS), have been used for riverine habitat substrate mapping, including

mussel beds, whereas acoustic Doppler current profilers (ADCPs) have been used to assess water depth-specific flow velocity in mussel habitats [26, 52–58]. By combining detailed spatial abiotic conditions measurements with available SSDs for native and alien freshwater mussels, a prediction of their POFs may be derived to evaluate the local suitability of habitat in river systems [38, 44, 45, 59]. We hypothesize that shore channels along LTDs provided suitable habitats for native freshwater mussels due to favorable substrate type, water depth, and near-bottom flow velocity conditions. Moreover, these shore channels would also be suitable for invasive alien mussel species, limiting ecological rehabilitation success. The resulting maps are useful for the management of aquatic ecosystems and may guide during the planning phase of river training projects in the future by assessing the ecological value of infrastructure in heavily modified rivers.

2 Materials and Methods

2.1 Study Site

The river Waal is a lowland river and one of the two main branches of the river Rhine in the Netherlands. It has a high inland navigation intensity as it is an important waterway between Germany and the port of Rotterdam. Data collection was performed along three longitudinal training dams (LTDs) in the river Waal constructed with boulders that extended from river 911 to 922 km and divided the river into the main channel and three shore channels (Fig. 1). The LTD shore channels had an average width of 80 m [22, 24]. They had an inflow and an outflow as well as lowered sections that allowed for the exchange of water with the main channel [22, 24, 60]. Two LTDs were situated on the left bank of the river Waal and a third on the right bank (each ~3–3.5 km long). Hydroacoustic data collection techniques, consisting of side-scan sonar (SSS) and acoustic Doppler current profiler (ADCP), were used due to the large area of the study site, high water turbidity, and intensive inland navigation. The abiotic conditions were measured at the microhabitat level, a level seen at a 0.1-m spatial resolution with seasonal variations in substrate type, water depth, and flow velocity, which directly affect the distribution of biota [27, 28, 55, 57, 61, 62].

In order to create maps for the habitat suitability in the LTD shore channels, abiotic conditions field data were collected in April, 2019 at Wamel (N51.880638, E5.471680) Dreumel (N51.848860, E5.431090), and Ophemert (N51.846750, E5.394250). Species sensitivity distributions (SSDs) from the scientific literature [38, 45, Collas, unpublished data] were used to calculate the POFs for the ambient substrate type, water depth, and near-bottom flow velocity

Fig. 1 The three longitudinal training dams in the river Waal with the LTD shore channels enumerated 1 at Wamel, 2 at Dreumel, and 3 at Ophemert. The arrow indicates flow direction. The insert on the bot-

tom-right shows the location of the study site in the Netherlands (red rectangle). Aerial images source: Environmental Systems Research Institute (ESRI) Nederland, beeldmateriaal.nl

(Fig. 2). Then, the data were processed using SonarWiz 7.2 from Chesapeake Technology or Microsoft Excel, converted to POF predictions using R programming, and subsequently mapped using ArcGIS® software from ESRI [52, 53, 59, 63].

2.2 Abiotic Conditions

2.2.1 Substrate Type Mapping

On 4–11 April 2019, side-scan sonar (SSS) acoustic backscatter was collected using a Humminbird Helix 10×CHIRP MEGA SI GPS G2N unit and a XM 9 20 MSI T transducer in the LTD shore channels. The transducer was pole-mounted on the starboard side of a vessel at a water depth of 0.2 m. A total of 29 parallel tracklines of SSS acoustic backscatter with a 15-m spacing were collected going upstream and downstream (Online Resource Figs. 1, 2, and 3). The data were collected at a frequency of 455 kHz for the down-facing image and the MEGA (1200 kHz) option for the

side-facing image [64]. Data files (.dat format) consisting of the SSS backscatter were imported into SonarWiz and projected in WGS_1984_UTM zone 31 N. Each data file was automatically bottom tracked [63, 65]. Data were exported as 8-bit backscatter mosaic GeoTIFF tiles with a resolution of 0.1 m per pixel.

A total of 191 ground truthing samples were collected using a Ponar grab sampler, and the locations were recorded using a Garmin eTrex Touch 35 handheld GPS (Online Resource Figs. 4, 5, 6, 7 and Table 1). Photos were taken of each collected grab sample. Grab sample classification was performed based on the Wentworth [66] classification scheme as fine (<0.63 mm), sand (0.63–2.0 mm), gravel (2–256 mm, consisting of granules, pebbles and cobbles), or boulders (> 256 mm) based on visual inspection and any sounds heard during collection [52, 67]. All the construction materials (e.g. boulders, bricks) were classified as boulders. A class for mixed substrates (e.g., two or more substrates and/or woody debris) was included. In ArcMap 10.3.1 (ESRI), the sediments observed in the imported sonar

Fig. 2 Flow chart of the steps to predict the potentially occurring fraction (POF) of native and alien freshwater mussels in LTD shore channels using species sensitivity distributions (SSDs) and hydroacoustic data for substrate type, water depth, and flow velocity

mosaic were correlated with the locations of the grab samples. Polygons representing each substrate type were manually digitized over the mosaics at ~1:375 raster resolution [52, 68] based on the substrate interpretation performed by Richter et al. [58] (Online Resource Fig. 8). Mapping accuracy was assessed by comparing the mapped substrates based on SSS backscatter to the locations of validation grab samples (54% of the total samples) [68, 69].

2.2.2 Water Depth Mapping

Water depth data were collected on 8–10 April 2019 during river surveys in the three LTD shore channels using an

ADCP by Rijkswaterstaat (Online Resource Figs. 9, 10, and 11). ASCII files containing water depth measurements checked and validated by Rijkswaterstaat were imported into ArcMap and interpolated using ordinary kriging [70] fitted to a spherical model [71] with a fixed search radius of 40 m and a 0.1-m pixel cell size. This search radius and pixel size allowed for sufficient coverage and overlap with the substrate classification data. The “extract by mask” tool in ArcMap was used to ensure that the spatially interpolated water depth and the substrate maps had the same extent. The water depth data were exported as 0.1 m per pixel GeoTIFF files.

Fig. 3 Substrate type classification (**a**), spatially interpolated water depth (**d**), and spatially interpolated near-bottom flow velocity (**g**) for the Wamel shore channel in the river Waal. Substrate type (**b**), water depth (**e**), and near-bottom flow velocity (**h**) for the Dreumel shore

channel. Substrate type (**c**), water depth (**f**), and near-bottom flow velocity (**i**) for the Ophemert shore channel. Aerial images source: ESRI Nederland, beeldmateriaal.nl

Fig. 4 Maps of the POFs for native freshwater mussel species for the Wamel shore channel for (a) substrate, (d) water depth, and (g) flow velocity. For the Dreumel shore channel for (b) substrate, (e) water

depth, and (h) flow velocity. For the Ophemert shore channel for (c) substrate, (f) water depth, and (i) flow velocity. Aerial images source: ESRI Nederland, beeldmateriaal.nl

2.2.3 Near-Bottom Flow Velocity Mapping

The measured flow velocity magnitudes contained in the ADCP data files were averaged based on the depth of the measurements. In some parts of the water column, the measured flow velocity had a logarithmic relation to the water depth, which could best be assessed through semi-logarithmic flow velocity profiles. These were created by using the water depth-averaged flow velocity (u) versus the natural logarithm of the vertical distance from the water surface to the measurements (z) as given by each data point measured by the ADCP [72–76]. Although, this logarithmic law relation is thought to only apply to the lowest 20% of the water depth, it has been previously applied throughout the water column in order to estimate flow velocity profiles [72, 73, 77, 78]. The elevation of interest over the riverbed for mussels was chosen to be 0.1 m. This elevation from the bottom is still low enough to the riverbed to impact mussels, yet high enough to avoid the zero flow velocity plane at the riverbed [79]. Since the ADCP measurements were constrained to the top ~6 m of the total water depth, the logarithmic law was applied in order to estimate the near-bottom flow velocity. A linear regression was fitted to the logarithmic region visible in the flow velocity profiles by including at least three successive raw data points nearest to the bottom [74]. Linear regressions were acceptable if $R^2 > 0.9$. Lower R^2 values suggested that the logarithmic region was not represented in the data, or it simply did not exist and was excluded from the data prior to interpolation [74]. The acquired linear regression equations were used to determine the near-bottom flow velocity for every raw data point. The data were then interpolated and exported in the same way as the depth data.

2.3 Biotic Assessment

2.3.1 Potentially Occurring Fractions

The habitat suitability prediction given by the SSDs is the POF, that is the fraction of the regional species pool included in the SSDs that will locally occur at a given substrate type, water depth, or flow velocity (Appendix, Tables 3 and 4; Online Resource Figs. 12, 13 and Tables 2, 3, 4). For instance, a POF of 0.5 for a habitat suggests that 50% of the species can occur in the respective habitat. The highest POF value is 1, suggesting that all of the species can potentially occur, while 0 indicates that none of the species can occur [38]. The substrate SSDs for the river Rhine for 21 native and 5 alien mussels were acquired from F. Collas (unpublished results). These SSDs included the substrate type silt/clay, sand, pebbles, cobbles, boulders, and hard surface. The water depth SSDs of river Rhine for

28 native and 7 alien mussels were obtained from Collas et al. [45]. Only the SSDs for maximum water depth were included, as according to Collas et al. [45], water depth started limiting the occurrence of mussels at depths shallower than 1 m, and the lowest interpolated water depth was 1.07 m. The flow velocity SSDs for the river Rhine for 14 native and 5 alien mussels were acquired from Koopman et al. [38]. Similarly, only the maximum flow velocity SSDs were included, as according to Collas et al. [45], flow velocity started limiting the occurrence of mussels at about 0.05 m/s and lower, and the lowest interpolated near-bottom flow velocity was 0.41 m/s. For each LTD shore channel, the substrate type, water depth, and near-bottom flow velocity maps produced were used with the SSDs in order to calculate the POFs of native and alien freshwater mussels per pixel. SSDs provided predictions of habitat suitability (POFs) for each map pixel based on their unique abiotic parameter values [49, 59]. This was completed by using the “calc” function from the raster package of R statistics to apply the SSDs on the abiotic condition maps based on the mean and standard deviation of the distributions [80]. In order to find the most limiting parameter, the “min” function in R statistics was used on the stacked substrate type, water depth, and near-bottom flow velocity POF maps [81]. This step found the lowest POF value per pixel between the three abiotic parameters by comparing the values of all of the POF maps produced and then calculating which parameter resulted in the lowest POF for each unique pixel and hence was the most limiting. The POFs were separated into the following ranges: 0–0.099, 0.1–0.199, 0.2–0.299, 0.3–0.399, 0.4–0.499, 0.5–0.599, 0.6–0.699, 0.7–0.799, 0.8–0.899, 0.9–1. The POF values were referred to as low (0–0.399; small species pools), medium (0.4–0.699; medium species pools), and high (0.7–1; large species pools). The percentages of the total area of the LTD shore channels covered by each POF range were determined by using the number of pixels for each range calculated from histograms created in ArcMap and the pixel surface area of 0.01 m².

3 Results

3.1 Abiotic Conditions

3.1.1 Substrate Type

Side-scan sonar (SSS) backscatter was used to produce substrate type maps for each of the three longitudinal training dam (LTD) shore channels (Fig. 3a–c). The boulders of the LTDs were visible throughout the mapped area. Areas toward the shore where mixed substrate and boulders were

Fig. 5 Box plots for the POFs ($n_{\text{Wamel}}=20,166,477$, $n_{\text{Dreumel}}=24,222,333$, $n_{\text{Ophemert}}=20,201,274$) of the abiotic parameters including substrate POFs for (a) native and (b) alien freshwater mussel species, water depth POFs for (c) native and (d) alien mussels, near-bottom flow velocity POFs for (e) native and (f) alien mussels and the most limiting POFs for (g) native and (h) alien mussels in all three LTD shore channels. The lines represent the median values, the edges of the boxes the first and third quartiles, the whiskers the 2.5% and 97.5% percentiles, and the points of the minimum and maximum values

mapped coincided with the location of prior groynes. The validation of the substrate classification resulted in an overall accuracy of 67.7% for the Wamel shore channel, 74.2% for the Dreumel shore channel, and 33.3% for the Ophemert shore channel (Online Resource Fig. 14 and Tables 5, 6, and 7). The most accurately classified sediment type was the boulders with an average accuracy of 94.4%, and the least accurate was the gravel substrate type at 0% (Table 1). The SSS backscatter in the Ophemert shore channel showed a high incidence of dunes, usually classified as sand, yet the validation grab samples at these locations were classified as gravel leading to low substrate classification accuracy for the shore channel. Hence, a substrate reclassification was performed for the Ophemert shore channel by using all of the grab samples collected in order to obtain a more accurate substrate map for the POF prediction.

3.1.2 Water Depth

In general, water depth maps revealed deeper areas to be located close to the center of the shore channels and the LTDs. In contrast, shallower areas were located toward the shoreline (Fig. 3d–f). Mean spatially interpolated water depths were 4.19 m (range 2.14–6.89 m), 3.95 m (range 2.46–5.57 m), and 4.69 m (range 1.07–6.80 m) in the Wamel, Dreumel, and Ophemert shore channel, respectively (Online Resource Table 8).

3.1.3 Near-Bottom Flow Velocity

The logarithmic region of the flow velocity profiles was found at water depths ranging from 1.28 to 4.78 m and included at least 3 and up to 9 raw data points (Online Resource Figs. 15, 16, 17). One flow velocity data file was excluded from the water depth and flow velocity analyses due to a low R^2 value of 0.0229. The spatially interpolated near-bottom flow velocities were generally higher toward the center of the LTD shore channels (Fig. 3g–i). Mean spatially interpolated near-bottom flow velocities were 0.65 m/s (range 0.41–0.79 m/s), 0.73 m/s (range 0.44–0.86 m/s), and 0.85 m/s (range 0.51–1.10 m/s) in the Wamel, Dreumel, and Ophemert shore channels, respectively.

3.2 Biotic Assessment

3.2.1 Potentially Occurring Fractions

In general, POF median values were higher for alien species than for native species among the three abiotic parameters (Figs. 4a–c and 5a, b; Appendix, Fig. 7a–c; Online Resource Table 9). The only exception was the substrate POF median values in the Ophemert shore channel due to a large percent of gravel and mixed substrate types (POF native = 0.91 and POF alien = 0.80). In the two other sites, the substrate POF median values for the native and alien species were 1, which means that the substrate type is suitable for both native and alien mussel species. In the LTD shore channels, the substrate POF minimum values were 0 for native species and 0.60 for alien species while the maximum values were 1 for both. For native mussel species, substrate POF values were equal to 0 (red areas of maps) where boulders were present and as high as 1 (green areas of maps) in areas with fine and sand substrate types.

Water depth POF median values were equal for the Wamel and Dreumel shore channels due to suitable water depth ranges for both native and alien mussel species (POF native = 0.82 and POF alien = 0.92; Figs. 4d–f and 5c, d; Appendix, Fig. 7d–f). The lowest median values were found in the Ophemert shore channel where the highest spatially interpolated mean water depth was observed (POF native = 0.78 and POF alien = 0.90). Generally, water depth POF values were high (0.7–1) throughout the LTD shore channels meaning that the water depth ranges were suitable for most of the mussel species.

Near-bottom flow velocity POF median values were lower compared to substrate and water depth for both native and alien mussel species due to flow velocities that were relatively high for the tolerances of the mussel species assessed (Figs. 4g–i and 5e, f; Appendix, Fig. 7g–i). The highest median values were seen in the Wamel shore channel due to the lowest mean near-bottom flow velocity compared to the other channels (POF native = 0.69 and POF alien = 0.71). In contrast, the lowest median values were seen in the Ophemert shore channel which had the highest mean near-bottom flow velocity (POF native = 0.48 and POF alien = 0.51). Generally, the near-bottom flow velocity POF values decreased toward the center of the LTD shore channels due to an increase of the near-bottom flow velocities from the shore to the center.

The lowest most limiting POF (Figs. 5g, h and 6) median values for native and alien mussel species were found in the Ophemert shore channel due to the high near-bottom flow velocities (POF native = 0.46 and POF alien = 0.51). The highest most limiting POF median values for native and alien mussel species were found in the Wamel shore channel. This was due to a combination of all three abiotic parameters

Fig. 6 Maps of the most limiting abiotic parameter POFs for (a) native and (b) alien freshwater mussel species for the Wamel shore channel, (c) native and (d) alien mussels for the Dreumel shore channel and (e) native and (f) alien mussels for the Ophemert shore channel. Aerial images source: ESRI Nederland, beeldmateriaal.nl

Table 1 Shore channel overall accuracy, sediment classification accuracy, and percent area of each substrate type mapped using SSS backscatter

Shore channel	Gravel percent area (%)	Boulders percent area (%)	Mixed percent area (%)	Sand Area percent area (%)	Fine percent area (%)	Other percent area (%)	Trees percent area (%)
Wamel	1.1	29.7	8.4	59.6	1.2	0	0
Dreumel	0.5	23.9	3.6	71.5	0.6	0	0
Ophemert	34.2	18.0	26.1	16.9	4.7	0	0.1
Sediment classification accuracy (%)	0	94.4	13.9	85.8	33.4		

that were within the tolerances of the mussel species (POF native = 0.61 and POF alien = 0.63).

The total area of our study sites within the Wamel, Dreumel, and Ophemert shore channels were 0.20, 0.24, and 0.20 km², respectively. The Ophemert shore channel had the highest percentages of the total area with high substrate POF values (0.7–1) for native (82%) and alien (82%) mussel species. This was due to a combination of fine, sand, mixed, and gravel substrate types, the last two substrate types being less abundant in the Wamel and Dreumel shore channels (Table 2).

Water depths correlated well with the tolerances of large mussel species pools (70–100% of the species assessed) in larger areas (100% of the total area for all three LTD shore channels) than the substrate type (70–82%) and near-bottom flow velocity (4–31%) results. The Wamel shore channel had the highest percentages of the total area with high near-bottom flow velocity POF values for native (47%) and alien

(51%) mussel species since the near-bottom flow velocity values were more suitable than in the other LTD shore channels.

The Wamel shore channel had the largest percentages of the total area with most limiting POF in the high range for native (28%) and alien (31%) mussel species meaning that larger areas of habitat are suitable for a large species pool compared to the two other LTD shore channels. For native mussel species, the percentages of the total area with most limiting POF in the medium range were 42%, 71%, and 68% for Wamel, Dreumel, and Ophemert, respectively. For alien species, the percentages of the total area with most limiting POF in the medium range were 69%, 92%, and 92%, for Wamel, Dreumel, and Ophemert, respectively. This suggests the LTD shore channels offer both native and alien mussel species suitable habitats in most of their total areas ($\geq 70\%$) for medium to large species pools based on the three abiotic parameters assessed, albeit alien species have larger

Table 2 POF percentages of the total area per shore channel for native and alien mussel species

Shore channel	Mussels species group	POF range	Substrate POF percentage of the total area (%)	Water depth POF percentage of the total area (%)	Near-bottom flow velocity POF percentage of the total area (%)	Most limiting POF percentage of the total area (%)
Wamel	Native	0–0.399	30	0	0	30
		0.4–0.699	0	0	53	42
		0.7–1	70	100	47	28
	Alien	0–0.399	0	0	0	0
		0.4–0.699	30	0	49	69
		0.7–1	70	100	51	31
Dreumel	Native	0–0.399	24	0	0	24
		0.4–0.699	0	0	94	71
		0.7–1	76	100	6	5
	Alien	0–0.399	0	0	0	0
		0.4–0.699	24	0	90	92
		0.7–1	76	100	10	8
Ophemert	Native	0–0.399	18	0	11	28
		0.4–0.699	0	0	85	68
		0.7–1	82	100	4	4
	Alien	0–0.399	0	0	3	3
		0.4–0.699	18	0	92	92
		0.7–1	82	100	5	5

suitable habitats due to the boulder areas (Online Resource Figs. 18, 19, 20 and Tables 10, 11, 12).

4 Discussion

4.1 Abiotic Conditions

The substrate map for the Ophemert shore channel was reclassified due to the possible presence of gravel dunes, which were not present in the other two LTD shore channels. Gravel dunes are likely to occur in the river Waal since it has a sand and gravel riverbed with up to 60% gravel, which could be mobilized as dunes during high discharges [82]. This is in line with findings by Van Weerdenburg [83] suggesting 66% gravel composition for the riverbed in the upstream section of the Ophemert shore channel. This channel also had the highest flow velocities, which were high enough to move gravel of up to about 10 mm in diameter [84]. The formation of underwater gravel dunes has been documented in the field for grain sizes of up to 60 mm [85]. In the future, a better image resolution (<0.1 m per pixel) may help to visually differentiate between dunes composed of sand and those composed of gravel [86].

4.2 Biotic Assessment

Habitat suitability studies for mussels in the past have focused on experimental approaches and predictive modeling of species abundance or richness. These studies took hydraulic parameters into account and focused on a single species or a few species at most. Detailed studies on spatial substrate distributions within mussel habitats are scarce [26, 55, 57, 61, 87]. Habitat suitability studies have found that substrate is a good indicator for mussel habitat, and thus, it is important to include detailed measurements of this parameter in suitability predictions [61, 88].

We presented an approach for assessing suitability in a novel habitat for large mussel species pools based on the spatial distribution of three ambient abiotic parameters, including detailed substrate type distribution maps. Our results showed that the three protected longitudinal training dam (LTD) shore channels provide suitable habitats for native and alien mussel species offering spatial heterogeneity based on substrate type, water depth, and near-bottom flow velocity gradients. Thus, these habitats were suitable for different mussel species pools throughout the study site, including native species such as *Anodonta cygnea*, *Sphaerium rivicola*, and the regionally extinct *Unio crassus*, but also invasive alien species such as *Corbicula fluminea*, *C. fluminalis*, and *Dreissena polymorpha*.

The predictions suggest that water depth was the most suitable of the three abiotic parameters for both native and

alien mussel species, followed by substrate type and near-bottom flow velocity. However, alien mussel species had larger species pools due to suitable habitat covering larger areas than native species, which could limit the success of ecological rehabilitation of native mussels. Additionally, the suitable areas for both native and alien mussel species overlap, while 18–30% of the habitat mapped in the LTD shore channels was not suitable for native mussels due to the presence of boulders. Newton et al. [54] found that stable substrate was a requirement for the establishment of healthy mussel assemblages, and the LTD shore channels could offer more stable substrate compared to the main channel due to a reduction of inland navigation effects [24]. Areas with suitable habitat for large native mussel species pools were larger in the Wamel shore channel due to lower near-bottom flow velocities, followed by Dreumel and then Ophemert shore channels. The same results were found for alien mussel species. However, a disadvantage of the Wamel shore channel is the large percentage of the total area covered by boulders compared to the other two LTD shore channels.

4.3 Implications for Management

Based on our findings, a management option to provide more suitable habitat for the largest native mussel species pools would be the creation of more areas with fine and sand substrate types and low near-bottom flow velocities close to or at 0 m/s. Although, this will still benefit alien species such as *Corbicula fluminea* and *C. fluminalis* which do well in fine and sand substrate types. Therefore, controlling alien species is imperative for the ecological success of these novel habitats as alien species are able to affect the biochemistry, hydrology, and biological linkages within an ecosystem [42, 43]. When adapting the LTD shore channels to create more suitable habitat for freshwater mussel species, it should be noted that most species have minimum flow velocity requirements of 0 m/s and occur most often at a water depth of about 1 m [45]. These conditions are consistent with those provided by natural large rivers where lotic, semi-lotic, and lentic flow conditions may occur, and seasonal changes in the abiotic conditions allow for the continuous development of important microhabitats [27, 89]. Depending on the management needs and target species, other minimum abiotic condition thresholds may be required. For example, Collas et al. [45] found minimum flow velocity requirements as high as 0.05 m/s (*Unio crassus*) and water depth requirements as high as 2 m (*Pisidium pulchellum*) for specific mussel species. For some native species, such as unionids which have complex life cycles involving host fishes during the glochidia life stage, the habitat suitability of host fish populations should also be assessed and managed within the habitats [28, 57, 87]. In order to reduce and control alien species,

including *Corbicula fluminalis* and *Dreissena polymorpha*, which also benefited from the ambient abiotic conditions within these novel aquatic habitats, reducing the total area of boulders present may be beneficial [4, 38, 41–43, 45]. This may be done in areas where the substrate type no longer serves a purpose, such as the previous groyne fields where debris were mapped. *Dreissena polymorpha* and *D. bugensis* are well known for attaching themselves on native unionids in areas with high dreissenids densities competing for hard substrate ultimately leading to high unionid mortality rates [6, 90]. However, anthropogenic modifications in the form of groynes, sluices, and bridge pillars likely provide enough hard substrate for dreissenid mussels even if boulders in the LTDs were removed.

4.4 Limitations of the Assessment

The substrate POF was based on the presence or absence of a species in a given substrate type, without taking into account the preferences of each unique species. This could have led to an overestimation in the substrate POF results for native and alien species. The near-bottom flow velocity regression analysis likely resulted in an overestimation of the near-bottom flow velocities and hence lower POF values, since velocities near the riverbed are influenced by drag from the bottom features causing them to deviate from the logarithmic law [76, 91]. Hence, the logarithmic law provided results that adhered to an ideal flow velocity profile [76].

4.5 Future Research

The integration of substrate mapping into ecological assessments is crucial for a reliable representation of the habitat and could serve as the basis from which more parameters are added for a more comprehensive prediction. In the future, adding more abiotic parameters, such as water temperature, pollutants, and dissolved oxygen would lead to a more complete assessment of habitat suitability for freshwater mussel species [45, 50, 57, 92, 93]. This should result in more accurate habitat suitability predictions which would make validation possible by using monitoring data as done by Kefford et al. [94], Smetanová et al. [93] and Collas et al. [44]. Currently, validation is limited by the lack of monitoring data on the occurrence of mussels within the LTD shore channels.

However, the abundance of juvenile unionids is higher in the LTD shore channels than in the groyne fields [95]. Hence, a future approach could be to compare the POFs for the ambient abiotic conditions of the LTD shore channels to the conditions in the groyne fields and main channel of the river Waal in order to assess any spatial differences in the current ecological value. Additionally, the temporal variability of water depth, substrate type, and near-bottom flow velocity in the LTD shore channels could be assessed, as mussel distributions have been found to be affected by different river discharges [28]. Future research linking POFs and ecological status or potential of water bodies, as required by the European Water Framework Directive 2000/60/EC [21], would be beneficial for water managers and ecologists as Europe progresses toward more natural conditions for riverine ecosystems.

5 Conclusion

Our results showed that the shore channels along the longitudinal training dams (LTDs) in the river Waal provide suitable habitat for both native and alien freshwater mussel species. The LTD shore channels may be enhanced as habitats for native mussels by increasing shallow areas with fine (silt/clay) or sand substrate types and low flow velocities. Another important management option that would benefit native mussels would be the removal of artificial hard substrates, such as boulders and groyne construction materials, which often provide habitat for alien mussel species. We also recommend that LTDs not be constructed using boulders, but instead using materials that provide less surface area or have antifouling properties. In the future, more abiotic parameters should be included to enhance the habitat suitability predictions and to better spatially characterize the habitat. It would be beneficial for further understanding of the ecological value of the LTD shore channels to assess the habitat suitability in the main channel and groyne fields for comparison. Validation may also enhance the predictive power by using monitoring data in order to link the predicted habitat to the actual species occurrence. Habitat suitability predictions have the potential to bridge the gap between scientists and water managers by making the results of fundamental scientific research more accessible.

Appendix

Fig. 7 Maps of the POFs for alien freshwater mussel species for the Wamel shore channel for **(a)** substrate, **(d)** water depth, and **(g)** flow velocity. For the Dreumel shore channel for **(b)** substrate, **(e)** water

depth, and **(h)** flow velocity. For the Ophemert shore channel for **(c)** substrate, **(f)** water depth, and **(i)** flow velocity. Aerial images source: ESRI Nederland, beeldmateriaal.nl

Table 3 Summary of native species included in the SSDs

Species	Substrate type	Water depth	Flow velocity
<i>Anodonta anatina</i>	x	x	x
<i>Anodonta cygnea</i>	x	x	x
<i>Cerastoderma glaucum</i>	x	0	0
<i>Margaritifera auricularia</i>	x	0	0
<i>Margaritifera margaritifera</i>	0	x	0
<i>Musculium lacustre</i>	x	x	x
<i>Pisidium amnicum</i>	x	x	x
<i>Pisidium casertanum</i>	x	x	x
<i>Pisidium conventus</i>	x	x	0
<i>Pisidium henslowanum</i>	x	x	0
<i>Pisidium hibernicum</i>	0	x	x
<i>Pisidium lilljeborgii</i>	x	x	0
<i>Pisidium milium</i>	x	x	0
<i>Pisidium moitessierianum</i>	x	x	0
<i>Pisidium nitidum</i>	x	x	x
<i>Pisidium obtusale</i>	x	x	0
<i>Pisidium personatum</i>	x	x	x
<i>Pisidium pseudosphaerium</i>	0	x	0
<i>Pisidium pulchellum</i>	0	x	0
<i>Pisidium subtruncatum</i>	x	x	0
<i>Pisidium supinum</i>	x	x	x
<i>Pisidium tenuilineatum</i>	0	x	0
<i>Pseudanodonta complanata</i>	0	x	0
<i>Sphaerium corneum</i>	x	x	x
<i>Sphaerium nitidum</i>	0	x	0
<i>Sphaerium nucleus</i>	0	x	0
<i>Sphaerium rivicola</i>	x	x	x
<i>Sphaerium solidum</i>	x	x	0
<i>Unio crassus</i>	x	x	x
<i>Unio pictorum</i>	x	x	x
<i>Unio tumidus</i>	x	x	x

x was assigned if the species was included and 0 if it was not

Table 4 Summary of alien species included the SSDs

Species	Substrate type	Water depth	Flow velocity
<i>Corbicula fluminalis</i>	x	x	0
<i>Corbicula fluminea</i>	x	x	x
<i>Dreissena bugensis</i>	0	x	x
<i>Dreissena polymorpha</i>	x	x	x
<i>Musculium transversum</i>	x	x	x
<i>Mytilopsis leucophaeata</i>	x	x	0
<i>Sinanodonta woodiana</i>	0	x	x

x was assigned if the species was included and 0 if it was not

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Availability of data and material Once the manuscript is accepted the data will be archived in the repository of the Radboud University and a link will be made available.

Declarations

Competing interests The authors declare no competing interests.

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