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ORIGINAL ARTICLE

Lakeshore areas of conservation interest: Characteristics of nursery areas of the threatened lake-dwelling grayling, *Thymallus thymallus*

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Abstract

Research-based knowledge is essential for effective conservation and restoration of threatened aquatic species and habitats. Here, our aim was to gather this knowledge on the lake-dwelling grayling (*Thymallus thymallus*), typically a riverine fish. Such atypical populations are particularly vulnerable to anthropogenic impacts, including fishing pressure, climate change, eutrophication and waterway construction, some of which affect especially the early life stages. However, there is little information available to guide management and conservation of grayling in lakes. Accordingly, we assessed characteristics of the nursery areas in the threatened grayling population of Lake Puruvesi (eastern Finland). In particular, we used beach seines in two consecutive years to sample lakeshore sites (including islands) that were a priori presumed suitable for grayling. We assessed the occurrence of grayling fry (larvae and post-larvae <40 mm in length) regarding depth, year, the site's exposure (fetch), bottom shear stress, substrate coarseness and shoreline's north–south orientation. Overall, we found grayling fry in low numbers at every fourth site, with the sites' exposure and dominant substrate coarseness being most relevant variables. In particular, more exposed sites (i.e. with higher fetch values) and fine-grained substrates dominated by sand or gravel had more grayling fry. Average depth, bottom shear stress or shoreline orientation along the north–south axis did not have a significant effect. Together, the results suggest that the most important nursery areas for lake-dwelling grayling are lakeshore zones that are barren and exposed. Hence, the sites share characteristics with those used for reproduction by the more common riverine grayling. We hope that these findings will facilitate lake-dwelling grayling's management and conservation efforts.

KEYWORDS
biodiversity, environmental ecology, freshwater, habitat choice, lacustrine, population, reproduction, salmonid

1 | INTRODUCTION

Many freshwater habitats around the globe are hotspots for biodiversity, but this biodiversity is also declining particularly fast (Geist, 2011; Wiens, 2015). Global and local threats to freshwater fauna and flora include water pollution, nutrition enrichment, habitat degradation, overexploitation, climate change and species invasions (Dudgeon et al., 2006; Geist, 2011; Heino et al., 2021; Woolway et al., 2020). Conservation of the lacustrine biodiversity under these threats is likely to benefit from research-based knowledge and sufficient public support (Knight et al., 2006). The latter may be advanced, for instance, by increasing public awareness of high profile species (Ebner et al., 2016; Verissimo et al., 2011). Although freshwater fish rarely have such flagship status (Cambray & Bianco, 1998; Ebner et al., 2016), many salmonids (family Salmonidae) make good candidates. These are Holarctic freshwater and anadromous species (Jobling et al., 2010; Klemetsen et al., 2003), many of which are ecologically, commercially and culturally important, especially because of their importance in recreational and commercial fisheries (Klemetsen et al., 2003; Lynch et al., 2016).

One salmonid species that has vulnerable populations requiring attention is the grayling (*Thymallus thymallus*). Compared to other high profile and widely distributed European salmonids, such as the Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and European whitefish (*Coregonus lavaretus*), the ecology, habitat use and migratory behaviours of the grayling are not as extensively studied or well-known. However, there is need for both knowledge and well-thought management and conservation measures, especially given that many grayling populations throughout Europe have been declining for decades (Gum et al., 2009; Ibbotson et al., 2001; Uiblein et al., 2001) due to anthropogenic impact, including overfishing, habitat degradation, discontinued access to breeding grounds, pollution, eutrophication and climate change (Junge et al., 2014; Meldgaard et al., 2003; Northcote, 1995; Uiblein et al., 2001; Wedekind & Küng, 2010). Many of these challenges have contributed to a shortage of breeding and nursery areas.

Interestingly, similarly to a few other salmonid species (Arostegui & Quinn, 2019), certain Fennoscandian grayling populations complete their life cycle in lakes (Amundsen et al., 2010; Northcote, 1995). However, there is very little published information on reproduction and early life stages of these grayling populations. Aside from river populations being more common in most parts of the species' range, another reason for this lack of essential knowledge is the difficulty of obtaining relevant data on the species' habitat use and life cycle in lakes compared to rivers (Lennox et al., 2021). In the lake environment, grayling are likely to be subject to different selection pressures from those experienced in rivers, including different and more diverse competitive interactions (Amundsen et al., 2010; Lennox et al., 2021) and a wider range of potential predators (especially on young fish) (Ibbotson et al., 2001; Lennox et al., 2021). Similarly, grayling eggs may be exposed to different predation regimes, chemical and physical conditions and water level fluctuations in the two habitat types (Bašić et al., 2018; Ibbotson et al., 2001). Finally, grayling's behaviour (Salonen & Peuhkuri, 2007) and even morphological traits (McGuigan et al., 2003; Peres-Neto & Magnan, 2004) may vary with the habitat type, especially due to differences in water movements.

The grayling has been declining in recent decades in Finland (Seppovaara, 1982; Koskinen et al., 2002), consistent with a general trend elsewhere in Europe (Gum et al., 2003, 2009; Northcote, 1995). Although this is probably true only for a subset of the Finnish riverine grayling populations, and those in the very north of the country (north of N 65°) are considered to be of low concern (Swatdipong et al., 2010; Urho et al., 2019), populations further south (south of N 65°) are particularly affected by fishing, climate change, eutrophication, waterway construction and trenching, and they are therefore red-listed as vulnerable (Urho et al., 2019). However, these populations are considerably less well studied and understood than those of rivers. The lack of knowledge is unfortunate because information on grayling's habitat preferences, especially during their reproduction and vulnerable early life stages (Miller et al., 1988; Sogard, 1997), is needed to plan their management and protection measures, such as government of lakeshore development plans and areas of more rigorous protection. Accordingly, in the current study, we set out to address some of these knowledge gaps regarding lake-dwelling grayling by assessing the characteristics of their nursery sites (with regard to depth, substrate, orientation, exposure and bottom shear stress). Hence, our goal was to provide information that could potentially be utilised in the lake grayling's management and conservation efforts.

2 | METHODS

In Finland, the most southern grayling populations are those of the Vuoksi watershed, which includes Lake Puruvesi. The lake is oligotrophic (typical Secchi depth: 8 m, colour: 5 Pt mg/L, total phosphorus: 5 μg/L, total nitrogen: 250 μg/L, maximum depth: 61 m, medium depth: 8.8 m and surface area: ~400 km^2; Grönlund et al., 2006; Ollikainen et al., 1993) and located in eastern Finland (~N 61° 80′, E 29° 30′; Figure 1). Our study area included shore sites (see below for sample sizes and other details) in the central parts of the lake (Figure 1), including many island shores within the lake's European Union Natura 2000 area (Evans, 2012). Biodiversity within Natura 2000 areas has been considered particularly important, and the aim is to prevent its significant degradation. However, the primary focus has been on terrestrial biodiversity (with 20% of the European Union's terrestrial area being covered), there are no strict conservation or development guidelines for these areas, and the areas have had limited success in protecting freshwater fish (Gavioli et al., 2023; Hermoso et al., 2015; Trochet & Schmeller, 2013; Tsavdaridou et al., 2019). This seems to be true also for grayling populations in the Vuoksi watershed, including those in Lake Puruvesi, which have been declining during the recent decades (Seppovaara, 1982; Sundell, 2008; Urho et al., 2019). To provide information that could support more efficient management and conservation measures for Lake Puruvesi, its grayling, and other similar lakes and populations, we investigated the characteristics of the sites in which larval and post-larval grayling (less than a month old and below 40 mm, from hereon 'grayling fry'), do and do not occur. We

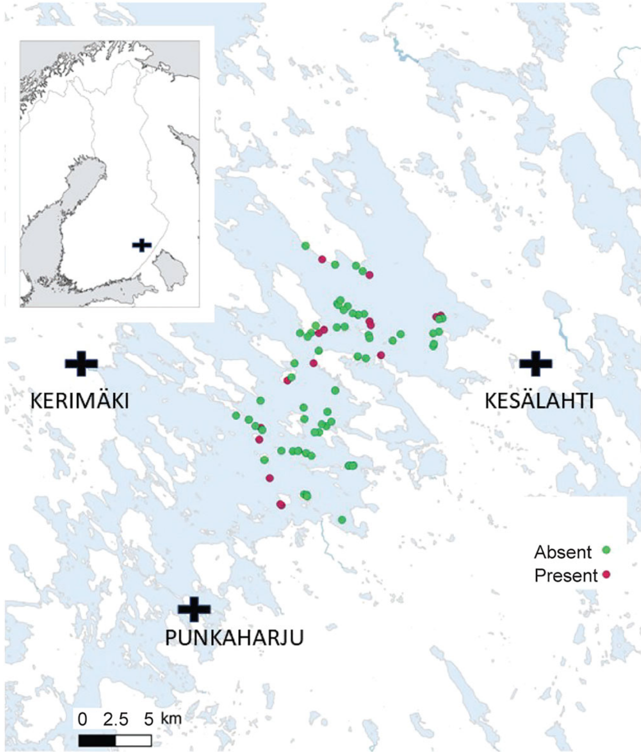

FIGURE 1 The study area. The larger panel shows sites in which we caught grayling fry (present, purple dots) and did not catch any (absent, green dots). The smaller panel shows the location of the lake in northern Europe.

define sites where they occur as nursery areas (see Brown et al., 2023), which are expected to be essential for the life cycle, and hence conservation and persistence, of lake-dwelling populations (Brown et al., 2023; Paufve et al., 2022; Riley et al., 2019). Therefore, knowledge on the sites' characteristics can support efficient management measures.

The behaviour of young grayling in lake environments is poorly known. In riverine environments, they can be first observed in the water column in shallow and slowly flowing river banks at the size of 17–21 mm and they later move towards the river channel and assume a more benthic orientation by the time they have grown to 40 mm (Bardonnet et al., 1991; Nykänen & Huusko, 2003; Scott, 1985; Sempeski & Gaudin, 1995b). We assessed the lake sites in June when the 0+ year class grayling (resulting from eggs laid in May) had presumably started to swim in the water column eating plankton at the time of sampling but had not yet reached 40 mm. Because grayling bury their eggs in nest pits (Nykänen & Huusko, 2002; Sempeski & Gaudin, 1995a) and less than month-old individuals are relatively poor swimmers (Bardonnet et al., 1991; Nykänen & Huusko, 2003; Scott, 1985), we consider it likely that, in the context of a large lake, the nursery sites with such fry tend to be the same as, or at least in close proximity to, where the eggs developed and hatched. In this respect, we are not aware of any directional water currents in the sampled lake areas that would move small fish over significant distances. However, some movement by the fry was possible, especially given that sampling was timed so that the fry was already swimming in the water column.

While we sampled a site, we also measured environmental factors of interest at it (see below for details). To optimise our use of limited resources, we only sampled the following two types of sites. First, we collected local knowledge from fishers and experts on grayling reproductive areas (similarly to Korhonen & Valkonen, 2021), with this knowledge being mostly based on catches of individuals ready to spawn. Second, we included a similar number of additional sites that were comparable to those identified by fishers and hence deemed potentially suitable for grayling reproduction. In particular, using visual land-based assessments and a map, we filled up gaps in the network of sites that were considered to be sufficiently exposed. Hence, we did not include any sheltered bay areas of the lake (Figure 1), in which grayling were considered unlikely to thrive or spawn.

The sampling was conducted in 2017 and 2018, using a type of beach seine that was optimised for catching fish larvae and small juveniles. It was operated by two persons who pulled it from a starting point towards the shore. The seine was 30 m long and 1.4 m tall with a 3 mm mesh on its sides and <1 mm at its rear. Each seine pull started 50 m from the shore and was continued to the shoreline, whereas the width of the sampled section was 20 m. Hence, the area sampled by each pull was ~1000 m^2. The seine was challenging to use amidst dense aquatic vegetation or too many protruding boulders, and we therefore only sampled sites where such obstacles were absent or it was possible to operate around them. The advantages of this sampling method include the general effectiveness in catching a wide range of species and small size classes from a relatively large area. In pilot trials in 2016, we also tested dip nets, a towed round net and bongo nets in front of a boat. Although these pilot methods were effective for catching juveniles of other species, such as the European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), no grayling were caught and hence only the seine was used in the study in 2017 and 2018.

In 2017, we conducted 34 seine pulls during daytime at 22 separate locations between June 27 and 29. In 2018, we did another 52 daytime seine pulls at 19 locations between June 12 and 26. For each pull, we counted the number of <40 mm grayling that we caught. We consider a 'location' to contain all sampling spots (and hence seine pulls) that were situated within so short distance from each other that we could not completely exclude the (in most cases unlikely) possibility that fry could have swum or drifted between them. For example, all seine pulls conducted next to a small island (Figure 1) were considered to have taken place within the same location.

For most pulls, we collected the following environmental variables that we considered potentially relevant in the context of breeding and nursery areas of lake-spawning grayling: average depth in proximity of the site, the site's exposure (measured as 'fetch'), bottom shear stress, the site's dominant substrate coarseness class and the compass orientation perpendicular of the shoreline adjacent to the site (see below for why these variables were considered relevant). To collect the data, we conducted side-scan sonar transects in the proximity of the seining sites, using a Lowrance HDS 9 GEN 3 sonar and the ReefMaster software. Side-scan data have previously been used to assess spawning habitats of, for example a lake-spawning salmonid, the lake trout (*Salvelinus namaycush*) (Edsall et al., 1989, 1992). We conducted the transects at a distance of ~25 m from the shore, with the width of each scan being ~25 m at both sides of the centreline of the transect. These data covered a larger area of the site than the seine pull did. This scale was in line with the assumption that physical conditions within a lake vary at the scale of hundreds to thousands of square metres (Riley et al., 2019). We also recoded video footage to support these sonar data. These raw data were later used to assess the following environmental variables.

We obtained the depth at the site (covering a larger area than the seine pull) using our side-scan sonar data and BioBase software. In river environments, grayling often spawn in relatively shallow water (Bardonnet et al., 1991; Darchambeau & Poncin, 1997; Gönczi, 1989; Nykänen & Huusko, 2002; Sempeski & Gaudin, 1995a). We assessed all available data points that were within a 50 m radius from what we had recorded as the 'centre point' of the seine pull. We considered, in separate models, the average depth and the range in depths (the difference between the deepest and shallowest depth reading) at the site. Here, the sample size ($n = 69$) was lower than the number of seine pulls ($n = 86$), because some of the sonar runs were challenged by technical issues, weather conditions or aquatic vegetation.

We analysed the distribution of substrate grain sizes from the side-scan sonar data with the ReefMaster software. Substrate coarseness is presumably important for characterising suitability of a site to at least some lake-spawning salmonids (Riley et al., 2019) as well as river-spawning grayling (Bardonnet et al., 1991; Nykänen & Huusko, 2003). The video footage and written notes were used to support the analysis. This approach allowed us to include a substrate grain size category if covered at least 1% of the area. We initially followed a common Finnish categorisation standard and category names by Blott and Pye (2012): sand (0–2 mm), gravel (2–16 mm), coarse gravel (16–64 mm), small boulders (64–250 mm), medium boulders (250–1000 mm) and large boulders (>1000 mm). The most common (from hereon: dominant) grain size within the seining area was used in the analysis. Because only two of the seine pulls were associated with gravel as the dominant substrate type, we combined this category with sand into a new category 'sand and gravel' (<16 mm). The results (below) would have been qualitatively the same, if we excluded the gravel category due to its insufficient frequency. None of the seine pulls were associated with large boulders as the dominant substrate type.

The orientation of the shoreline at the site was estimated by taking the compass direction perpendicular to the shoreline closest to each site. In particular, we evaluated the shoreline orientation on the north–south axis, because south and north facing sites might differ regarding their temperature profiles and other physiological properties that are relevant for the early life stages (Hudd et al., 2006). Therefore, we transformed the compass direction to a scale between 0 and 180 (at the accuracy of 1), so that shores opening towards the north received the value 0, shores opening towards the east or west received the value 90, and south-facing shore areas had the value 180.

We used the maximum length of the open water section facing each site, fetch, as a measure of the site's exposure. Lake-dwelling grayling have been thought to prefer exposed sites, but published tests of this putative preference have been lacking. Fetch was determined using the Fetch Model tool in ArcGIS 10.3.1 (Environmental Systems Research Institute [ESRI], 2015), with local wind conditions as weights for directions at 10° intervals (method 'SPM', see Rohweder et al., 2012). We obtained wind data (of 2015 and 2016) that covered the area's typical open-water period, from May 1 to October 31, from the nearest weather station (Savonlinna, Finnish Meteorological Institute 2017) and used these to calculate the yearly wind weights with WindRose function in R (Carslaw & Ropkins, 2012). We calculated a mean fetch from these two annual weighted fetches, initially into 5-m resolution-raster data. However, to match the resolutions of our seine data, we extracted the fetch value for each site from a resampled 50-m resolution raster, in which the maximum value was used as the aggregation method (ArcGIS-tool 'Aggregate' with method 'max' was used for the 5-m resolution fetch raster).

The bottom shear stress (unit: Pascal) can be used to estimate the effect of water flow on resuspension at the lake floor (Evans, 1994). The friction between the lakebed (hereon: bottom) and moving water generates a force directed along the bottom, with any loose material on the bottom being more likely to move with a higher force when shear stress is higher. In the current study, the bottom shear stress was obtained from a 3-D flow model prepared for Lake Puruvesi with a horizontal resolution of 50 m and 16 variable thickness layers (as per Heino et al., 2022). The effect of waves was not included in the flow model and the value for bottom shear stress was determined by the modelled advection only. The effect of waves was estimated by fetch (see above) instead.

We measured the total length of a subset ($n = 62$) of the grayling we caught. We also collected records of the by-catch, which is all other species besides grayling, in 2017.

2.1 | Statistical analyses

Statistical analyses were performed using the R software version 4.2.2 (https://www.r-project.org/). To assess factors that influence the number of grayling fry we caught, we used glmmTMB package (and function) to fit a GLMM (generalized linear mixed model) with a negative binomial distribution and the log link function, as appropriate for such overdispersed count data (Zuur et al., 2013). The response variable was the number of fry and the initial explanatory variables were the depth, dominant substrate grain coarseness class, fetch (exposure), bottom shear stress value, north–south orientation of the site (on scale 0–180) and year (2017 or 2018). To address non-independence of the sites/seine pulls that were located close to each other (as defined above), we also added location ID as a random effect. Due to logistic challenges, we did not have all environmental data for some of the seine pulls. In particular, of the total of 86 seine pulls, depth data were only available for 69 pulls and the dominant grain size for 85 pulls. Because the analysis only considers the replicates for which all explanatory factors are available, we first fitted the above model separately with the depth (which had clearly fewer observations than other variables), after which we fitted another model without the depth to consider the rest of our explanatory variables. It is important to note that our results

TABLE 1 Results of a negative binomial GLMM assessing the effects of environmental variables on the occurrence of grayling fry.

Effect	Estimate	SD	*z*	*p*
Bottom shear stress	3.605	3.209	−1.124	0.26
Fetch (exposure)	0.00081	0.00037	2.158	**0.031**
Coarse gravel	−1.334	0.819	−1.628	0.10
Small boulders	−0.3565	0.5010	−0.712	0.48
Medium boulders	−1.811	0.822	−2.204	**0.028**
Shore orientation	−0.0015	0.0043	−0.357	0.72
Year	−0.2708	0.4724	−0.573	0.57

Note: The three substrate coarseness categories (coarse gravel, small boulders and medium boulders) are compared to the finest substrate category, sand + gravel.

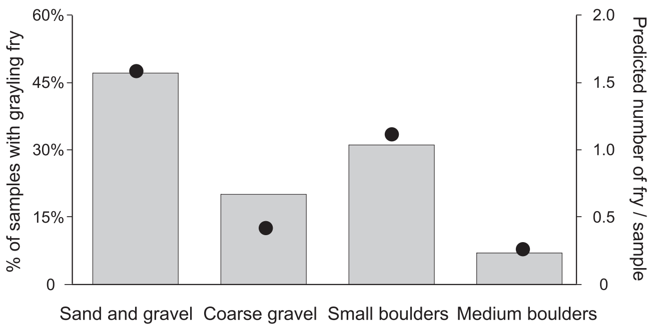

FIGURE 2 The relationship between the dominant substrate grain coarseness and the occurrence of grayling larvae. The bars show the proportion of seine pulls with at least one grayling (left axis), and black dots show the model-predicted number of grayling fry per seine pull (right axis).

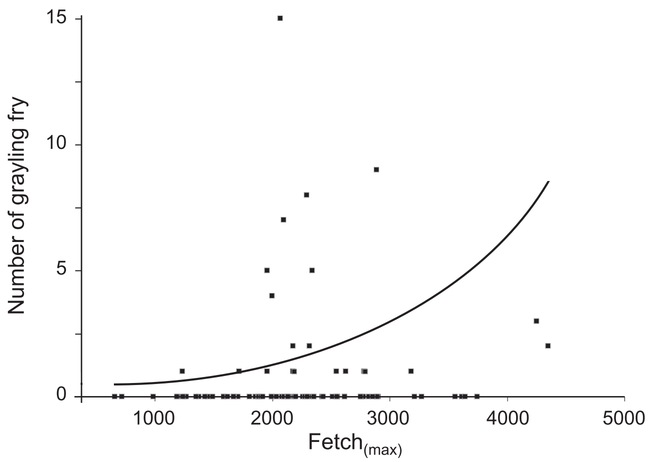

FIGURE 3 The actual (dots) and model-predicted (black curve) numbers of grayling fry per seine pull as a function of $fetch_{max}$ (our proxy of site exposure).

were very similar and our conclusions were qualitatively the same if we fitted the model without the random effect (i.e. as a GLM, generalized linear model). Similarly, a binomial analysis using the absence versus presence data, without the random effect, provides the same conclusions (whereas a binomial model with location as a random effect cannot be fitted due to complete separation). Finally, we ran a similar model for the by-catch, except that year was not included, because by-catch data were only available for 2017. In particular, we ran a GLMM with a negative binomial distribution, with the number of by-catch per seine pull as the response variable, dominant substrate grain coarseness, fetch, bottom shear stress and north–south orientation and the response variables and location ID as a random effect.

3 | RESULTS

We caught grayling fry with 29% (10/34) of the seine pulls in 2017 and with 21% (11/52) in 2018. The numbers of individuals were low (total of 27 in 2017 and 46 in 2018). Their mean total length was 28.5 mm (SD = 4.5, *n* = 27 and range: 17–37 mm) in 2017 and 21.9 mm (SD = 8.3, *n* = 35 and range: 13–39 mm) in 2018.

When investigating the factors that influence the occurrence of grayling fry at a site, our first model indicated that the average depth (GLMM: estimate (β) ± standard deviation (SD) = 0.0474 ± 0.3409; $z = 0.139$, $p = 0.89$) or depth range ($\beta \pm$ SD = −0.0403 ± 0.1151, $z = -0.350$ and $p = 0.73$) did not have a significant effect. The average depth at these 69 sites (i.e. within 50 m of the coordinates of the seine pull) varied between 0.62 and 4.12 m and the range of depths per site between 0.58 and 13.53 m. Because of the large number of missing values in the depth data, we then refitted the model without depth. This final model with 85 seine pulls indicated that bottom shear stress, north–south orientation of the shoreline and year did not significantly affect the grayling's occurrence (Table 1). In contrast, the dominant substrate grain size had an effect, with the highest grayling occurrence at sites dominated by sand (and gravel) and the lowest at sites dominated by boulders (Figure 2; Table 1). Fetch (exposure) also had a significant effect (Table 1): more exposed sites (i.e. with higher fetch values) had more grayling fry (Figure 3). This effect may have been driven by grayling fry being rare at sites with fetch values below 1900 (present at 2/25 sites = 8%; Figure 3) and more common when fetch exceeded 1900 (present at 19/61 sites = 31%; Figure 3). Similarly, by considering (arbitrary) fetch categories of 500, we find that the occurrence of grayling was 0% (0/2) for fetch values ≤1000 , 8% (1/12) for fetch values 1000–1500, 22% (4/18) for 1501–2000, 33% (8/24) for 2001–2500, 24% (5/21) for 2501–3000 and 33% (3/9) for >3000 (Figure 3).

In the by-catch (in 2017), the European perch was by far the most common and numerous species: We caught ~4000 small (larvae and small juveniles) European perch, with the species being present in 94% (32/34) of the seine pulls. Both pulls without perch provided grayling fry, which is notable because the total number of pulls with grayling was only 10 (out of the 34) that year. The next most common by-catch species were the smelt (*Osmerus eperlanus*) and unspecified cyprinids. Low numbers of seine pulls also contained young ruffe (*Gymnocephalus cernua*), Eurasian minnow (*Phoxinus phoxinus*) and burbot (*Lota lota*). The overall number of by-catch significantly decreased with increasing bot-

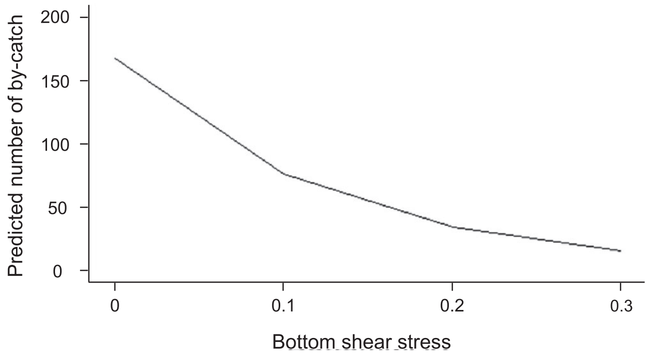

FIGURE 4 Model-predicted numbers of by-catch in relation to bottom shear stress (by advection only).

tom shear stress (GLMM: $\beta \pm SD = -7.860 \pm 2.997$, $z = -2.623$ and $p = 0.0087$) (Figure 4), whereas none of the other variables had a significant effect (comparisons between dominant substrate grain size types: $p \geq 0.13$, the rest of the effects: $p \geq 0.17$).

4 | DISCUSSION

Shore exposure and substrate grain size (coarseness) contributed to the suitability of a site as lake-dwelling grayling's nursery area. In particular, more exposed sites (with higher fetch values) and those with less coarse substrate (dominated by sand or gravel) were more likely to have grayling fry (<40 mm) present. Hence, among shore sites that had a priori appeared potentially suitable for grayling, especially these types of sites seem to be particularly good for successful reproduction.

The finding that exposed shore areas are suitable for lake-spawning grayling is in accordance with previous anecdotal evidence (Korhonen & Valkonen, 2021; Seppovaara, 1982; Sundell, 2008). In this respect, our study provided more detailed information than merely mapping specific regions of the lake that are suitable for grayling. Even among shore areas that were considered potentially suitable for grayling (and therefore chosen for the current study), the more exposed ones tended to be better nursery areas. Potential reasons for this include lower sedimentation rates and higher water oxygen content (see Ventling-Schwank & Livingstone, 1994). Moreover, grayling eggs, larvae and juveniles at less exposed areas may be subject to higher densities of potential predators and competitors, such as cyprinids and the European perch. However, it is relevant to note that while we did find grayling fry at some of the sites with the very highest fetch values, fetch values slightly below 2000 seemed to be sufficient for grayling numbers/occurrence to improve (see the raw data points of Figure 3). Hence, when attempting to predict likely locations of nursery areas of lake-dwelling grayling, in terms of exposure, the focus should probably be on sites with fetch values close to 2000 or over.

The dominant grain size of the substrate was also important: grayling fry were more likely to be present above finely grained substrates with sand and/or gravel (<16 mm, in most cases ≤2mm), especially when compared to substrates dominated by boulders (250–1000 mm). This finding lines up with previous results from river environments, where grayling have been found to prefer spawning sites that are dominated by sand and gravel (Darchambeau & Poncin, 1997; Gönczi, 1989; Nykänen & Huusko, 2002), and smallest size classes have been found to seek river banks with fine substrate and low velocity (Ibbotson et al., 2001; Nykänen & Huusko, 2003; Sempeski & Gaudin, 1995b). Hence, the results imply that sites that are favourable to lake-spawning grayling are similar to those of the more common river breeders, despite the differences in the populations' life histories and environmental conditions in their habitats.

Although bottom shear stress estimates the potential for on-the-substrate water movements, which can be beneficial for the developing eggs, this hydrodynamic measure did not significantly affect numbers (or presence) of young grayling. Therefore, bottom shear stress, due to advection only (as here), does not seem to directly measure the conditions that make good lake-dwelling grayling's nursery areas. In other words, the results do not advocate the use of this measure for locating grayling breeding and nursery areas. Although the importance of exposure (fetch) suggests that wave action is probably beneficial, at sites of high bottom shear stress (by advection), the eggs could be displaced and then move to potentially unsuitable locations (Ventling-Schwank & Livingstone, 1994). Therefore, suitable bottom shear stress could represent a balance between costs and benefits of high mechanical energy (Riley et al., 2019). Interestingly, the non-significant bottom shear stress result in the case of grayling contrasted with that for by-catch (mostly consisting of European perch): Higher bottom shear stress values were associated with lower numbers of by-catch.

The average water depth of the area (or the range of depths) did not have a significant effect on the occurrence of grayling fry. Although the available sample size for the depth analysis was smaller than that of the other variables, we assume that the lower sample size did not drive this result, because we did not detect any trend towards an association. The lack of a depth effect can be seen to contrast with previous findings from river environments, which showed that shallow areas were both favoured by reproducing adults (Bardonnet et al., 1991; Darchambeau & Poncin, 1997; Gönczi, 1989; Nykänen & Huusko, 2002; Sempeski & Gaudin, 1995a) and occupied by larvae and small juveniles (Nykänen & Huusko, 2003; Sampeski & Gaudin, 1995b). It, therefore, seems that the depth is less important in the lake environment than in rivers. In river habitats, grayling fry are assumed to be associated with shallow habitats because these areas are often also those with the lowest water velocity, making them more suitable for weak swimmers (Bardonnet et al., 1991; Scott, 1985). The lake environment, in contrast, does not have as clear association between the depth and water movement. Moreover, even in river environments, deeper sections might be used by grayling for spawning, but it is generally more challenging to verify reproduction that takes place in deeper areas (Nykänen & Huusko, 2002). It also remains possible that grayling only need a small area of their preferred depth, which could then be surrounded by sections of other depths (and therefore not necessarily detected by our depth measures). Finally, we also tested the hypothesis that north versus south facing shores may differ in their suitability as grayling nursery areas, for example due to different temperature profiles (Hudd et al., 2006). However, we did not find any support for this hypothesis.

Given the commonness of between-year variation in the weather conditions and lake water levels, the timing and even locations of lake-dwelling grayling's spawning may also vary. To account for this variation, we collected the data over two consecutive years. Although it would be preferable to conduct even more extensive sampling within and between years, this was not logistically feasible in the current study. We also cannot completely rule out the possibility that the type of the substrate at the sites we sampled might have affected the efficiency of our sampling seine. Such an effect could, for instance, have decreased the probability of catching fish on coarse-grained substrates. However, we argue that this does not explain our substrate-related results for the following three reasons. First, we did not include sites where seining would have been too compromised. Note, however, that this also means that our sampling may not include the full range of substrates that could be suitable as nursery areas. Second, we expected the young grayling not to take a benthic orientation before the size of approximately 35–40 mm (Sempeski & Gaudin, 1995b). Therefore, we assumed that we had a high chance of catching them if they were present where we sampled. Third, the by-catch, assessed using the same samples, did not follow the same pattern as grayling did: The effect of the dominant grain size (or fetch) was not significant for the by-catch. Moreover, bottom shear stress had a significant effect on the occurrence of the by-catch but not grayling: the higher the stress the lower the number of by-catch individuals. Hence, the patterns of the by-catch and that of the grayling appeared to be partly inversed.

The inverse patterns between grayling and by-catch may have resulted, for example from species-specific habitat requirements, competitive interactions or higher predation rates on grayling eggs and fry at sites preferred by the European perch (see Amundsen et al., 2010). Regarding habitat requirements of the early life stages, eggs and larvae of the perch and most other by-catch species may be less sensitive to sedimentation than those of the grayling (Chapman et al., 2014; Kemp et al., 2011), which could allow the former to use more sheltered areas. Here, it is relevant to note that we were not able to sample the sites of particularly dense vegetation. However, we assume that such sites do not provide good habitat for young grayling because they are usually too sheltered (as suggested by the current results) and, indeed, more suitable for their competitors and would-be predators, such as cyprinids, European perch and northern pike (*Esox lucius*).

To conclude, we suggest that with sufficient research and media attention, the lake-dwelling grayling has the potential to gain a local flagship species status, which could advance its conservation; there is already pre-existing general public fascination towards this peculiar-looking salmonid that is relatively unusual in the lake environment. We trust that our study promotes such awareness by providing knowledge on lake-dwelling grayling's nursery areas, in particular by showing that grayling fry can be found at sites that have the combination of high exposure and relatively fine-grained substrate but not particularly high bottom shear stress. These sites are also different from those with high numbers of more common lake species, which are associated with low bottom shear stress but not with exposure or particular substrate coarseness. Such information can prove to be useful when planning measures to manage and protect lake-dwelling grayling populations and habitats. As management measures, we propose preservation of good quality nursery areas (identified here), for instance, by regulating development projects and by limiting nutrient loads to these areas, as well as to the lake overall, in order to minimise the effects of sedimentation and eutrophication on the lakebed types that the grayling use for reproduction.

AUTHOR CONTRIBUTIONS

Topi K. Lehtonen: Formal analysis; project administration; writing—original draft; writing—review and editing; visualization. **Esa Hirvonen**: Conceptualization; investigation; methodology. **Irma Kolari**: Investigation; methodology; project administration. **Janne Ropponen**: Formal analysis; writing—review and editing. **Kristiina Nyholm**: Formal analysis; writing—review and editing. **Tapio Keskinen**: Investigation; visualization. **Teppo Vehanen**: Conceptualization; methodology; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data are available from the corresponding author upon a reasonable request.

ETHICS STATEMENT

The study followed all relevant institutional and national guidelines for handling animals.

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