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Mesohabitat Evaluation Reveals Variable Abundances and Habitat Choice in Juvenile Atlantic Salmon Across Diverse Habitats in the Main Stem of a Large Sub-Arctic River

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ABSTRACT

Large main stem rivers typically provide a variety of mesohabitat types, but their abundance, distribution and role in providing habitat for juvenile salmonids have rarely been analysed. The quantity of meso-scale habitats and their juvenile Atlantic salmon abundance was surveyed in the large sub-arctic River Teno in northernmost Fennoscandia. Different habitat types were mapped using the Norwegian Mesohabitat Classification Method (NMCM). Juvenile salmon abundance in different mesohabitats, on various substrates, depths and lateral positions across the channel was estimated by electrofishing boat surveys. Most of the Teno main stem (67%) was dominated by fine substrate and > 50 cm s^{-1} flow velocity. Typical juvenile salmon-rearing habitats, such as rapids, riffles and glides, comprised 32% of the riverbed. Data from NMCM and electrofishing surveys were used in generalised linear models to describe the relationship between habitat variables and juvenile salmon (YOY and parr) abundance. Juvenile abundance varied a lot across and within mesohabitats; in general, abundance was higher in areas with depth ≤ 70 cm than in deeper areas, and in middle sections of the river compared to those near shorelines. Juvenile salmon were documented also in sandy areas, although in low abundances, and in relatively high abundances in areas deeper than typically considered important for juvenile salmon. These areas should be considered in assessing habitat potential for juvenile salmon production. NMCM proved to be a fast, cost-effective method for surveying large areas for habitat assessment.

1 | Introduction

The need for managing fluvial fish populations and restoring their riverine environments has led to increasing efforts to develop methods for quantifying and qualifying riverine habitats for production. Estimating juvenile fish production potential for management purposes by surveying riverine habitats requires upscaling from micro-scale studies (Parasiewicz 2003, 2007), especially in large rivers. Several habitat modelling methods have been developed by creating a link between fish habitat suitability, mostly based on microhabitat studies, and the hydrological features and geomorphology of the drainage area and structural features of the riverbed (Borsányi et al. 2004; Clifford et al. 2006; Parasiewicz 2007; Schwartz and Herricks 2008; Hauer et al. 2009). For evaluating habitats on various scales, especially in large river systems, Rosenfeld (2003) listed three main levels of modelling: distributional or macrohabitat models, which predict the presence or absence of species at larger spatial scales (e.g., catchment); capacity models on the meso-scale; and microhabitat models that predict the habitat associations on a highly local, finer scale. Similarly, Habersack et al. (2014) concluded that micro- and mesoscale models are complementary, especially for large rivers, both relying on dynamic abiotic modelling and biological data. Combining multiple scales may improve the efficiency of habitat models and decrease their uncertainty (Habersack et al. 2014).

Considering different spatial scales within and between catchments, field-based characterisation of habitat requires resources and is often available only for a small portion of the river network, typically focusing on specific stretches or smaller sub-catchments mainly for logistical reasons. Consequently, predicting fish abundances at large spatial scales often requires coarser habitat resolution, for example, by using landscape covariates to model fish-habitat relationships (Malcolm et al. 2019). Recently, Jelovica et al. (2024) applied Machine Learning techniques to model the habitat-abundance relationship for juvenile Atlantic salmon (*Salmo salar*) in the main stem of the large River Teno and two major tributaries in Finland and Norway. However, their habitat data resolution was also on a microhabitat scale, but across a vast river area with a large number of long-term juvenile salmon monitoring sites (Niemelä et al. 2005; Jelovica et al. 2024).

Few studies focus on lowland rivers, in contrast to upland catchments, when relating densities of juvenile salmonid fishes to habitat characteristics. Marsh et al. (2020) listed typical characteristics of lowland rivers where they differ from typical upland river systems as: (i) physically more stable habitats and a smaller and more uniform gradient, (ii) low-energy systems and (iii) a lack of coarse substrate typically important for juvenile salmonids. These characteristics are especially typical in lowland main stems of large river systems, whereas headwaters and tributaries are often characterised by physical and biological conditions of upland rivers (Lotsari et al. 2010; Doretto et al. 2020).

Atlantic salmon is an anadromous species of high economic and conservation value, ranging in river systems on both sides of the North Atlantic Ocean and in the Baltic Sea basin. Juvenile abundance assessment is a typical approach for describing the status of salmonid populations and informing management on needs for action such as fishing regulations, habitat restoration, etc. (Malcolm et al. 2019; Reynolds and Dean 2020). Traditionally, studies on juvenile Atlantic salmon habitat use have focused on micro-scale observations in small streams with depths usually less than 1 m (Heggenes 1990; Gibson 1993; Mäki-Petäys et al. 2004).

Most studies have concluded that the most important microhabitat factors for defining juvenile salmon habitat preferences are depth, flow velocity, substrate size and the amount of shelter (Heggenes 1990; Bardonnet and Bagliniere 2000; Armstrong et al. 2003), and the habitat choice may change as the fish grow (Gibson 1993; Foldvik et al. 2017) or with changing season (Mäki-Petäys et al. 2004; Huusko et al. 2007). However, studies on utilisation of deeper areas of rivers by juvenile salmon are scarce. In the few earlier studies, notable juvenile Atlantic salmon abundances have been documented also in deeper parts of rivers (Bremset and Berg 1997, 1999; Linnansaari et al. 2010), but observations have mostly been restricted to areas close to the shoreline or pools in smaller rivers (but see Linnansaari et al. 2010). In larger rivers (> 50 m bank-full width) most of the channel may be > 1 m deep areas with high velocities, and few studies have attempted classifying habitat and estimating juvenile abundance and distribution in such environments for any salmonid fish species (Murphy et al. 1989; Beechie et al. 2005; Linnansaari et al. 2010).

Fine substrate habitats comprise a large portion of the benthos in large rivers (Doretto et al. 2020), but to our knowledge, studies have not investigated whether and to what degree juvenile salmon use these habitats, even though juvenile salmon exhibit plasticity in habitat use (Gibson 1993; Heggenes et al. 1999; Bardonnet and Bagliniere 2000; Mäki-Petäys et al. 2002; Armstrong et al. 2003). Although the preferred substrate size for juvenile salmon varies typically from coarse gravel to boulders (see references above), even low densities of fish in fine substrate areas could imply significance in overall juvenile salmon production in large lowland rivers running in valleys with post-glacial deposits, since considerable proportions of wetted area in their main stem may consist of reaches with moderate flow velocity and sand-dominated substrate (Lotsari et al. 2010).

A potential study area for investigating the role of a large mainstem for juvenile Atlantic salmon production in a large lowland catchment is the large sub-arctic River Teno in northernmost Finland and Norway (Erkinaro et al. 2019). The long-term monitoring at permanent electrofishing stations in the mainstem of the River Teno covers only the traditionally assumed typical juvenile salmon habitats (shallow, relatively coarse substrate; e.g., Niemelä et al. 1999, 2005). In addition, some information on habitat use of juvenile salmon is available from the Teno mainstem, both in shallow shoreline habitats (Mäki-Petäys et al. 2002) and in deeper areas (Linnansaari et al. 2010), but these studies are restricted to a few sampling sites in the mid-part of the Teno. The aim of this study was to investigate the quantity and spatial distribution of different meso-scale habitat classes, and their utilisation by juvenile Atlantic salmon across the entire main stem of the River Teno. In particular, we investigated juvenile salmon occurrence in typically abundant habitats of a large lowland river characterised by fine substrate (sand, fine gravel), and the possible role of these areas in the conservation and management of Atlantic salmon and their fluvial habitat.

2 | Materials and Methods

2.1 | Study Area

The sub-arctic River Teno (Tana in Norwegian, Deatnu in Sami; catchment 16,386 km^2) drains the border area between northernmost Norway and Finland (70° N, 28° E; Figure 1). Average discharge of the river is 166 m^3 s^{-1}, with peak levels during spring floods exceeding 3000 m^3 s^{-1}. The 215 km long main stem of the river starts from the confluence of the tributaries River Kárášjohka and River Inarijoki and empties into the Barents Sea at Tanafjorden (Figure 1). The Teno valley is dominated by fine sand sediment of fluvioglacial origin (Mansikkaniemi 1970); thus, the upper and lower reaches of the main stem are characterised by vast sandy areas. The river stretch between the sand-dominated reaches is characterised by rapids and glides with mostly coarser substrate (Niemelä et al. 1999).

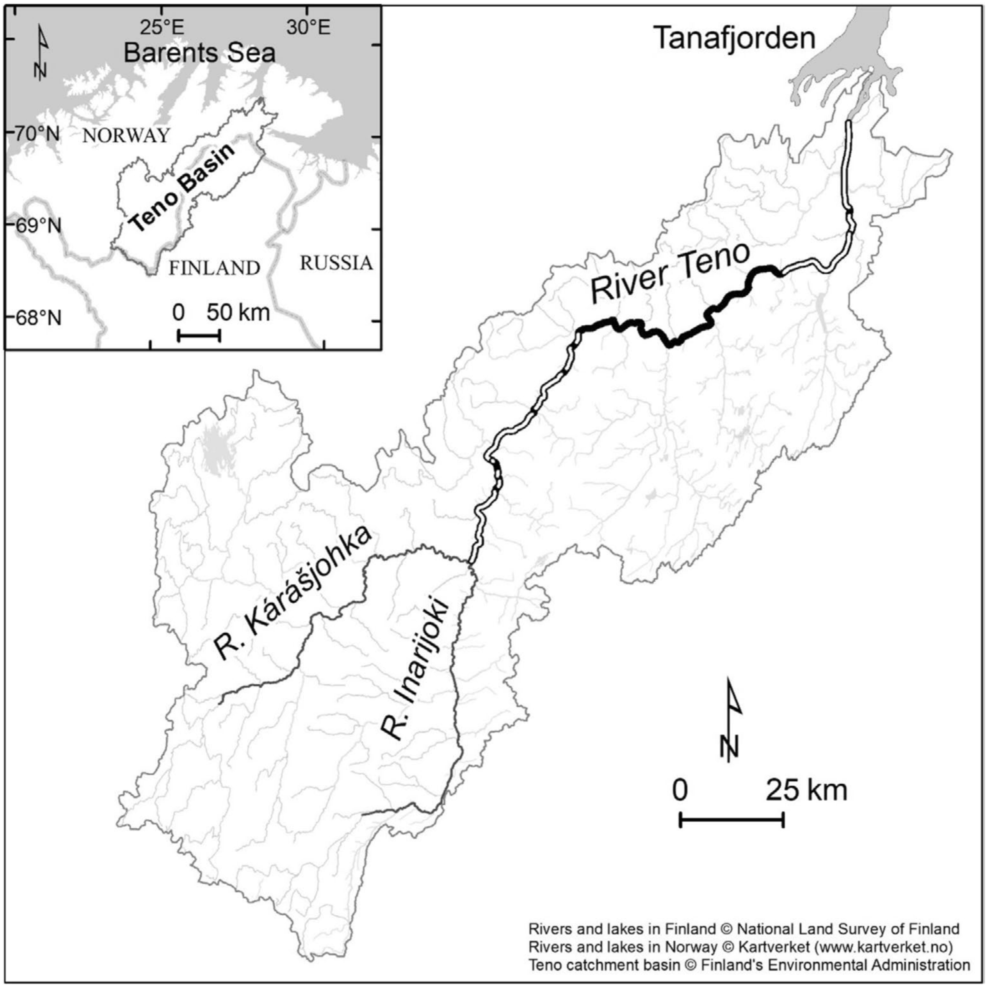

FIGURE 1 | The Teno River catchment. Pooled groups of habitat classes in the Teno main stem are indicated as white (mesohabitat classes S, C, D; sandy or slow-flowing habitats) and black (mesohabitat classes B, G, E; riffle habitats; see Table 1 for class definitions). Map projection: ETRS-TM35FIN.

The Teno River system supports one of the largest Atlantic salmon stocks in the world, with annual river catches varying typically between 40 and 250 t (Erkinaro et al. 2019), although recent estimates of low spawning stock status and pre-fishery abundance have prompted the closure of salmon fisheries in the river and in nearby coastal areas as a precautionary measure (Anon. 2024). There are more than 1200 km of accessible migratory routes for salmon, including the main stem and numerous tributaries (Erkinaro et al. 2019). In addition to multiple tributaries with genetically distinct populations (Vähä et al. 2017), the large main stem of the River Teno is an important spawning and juvenile production area for the genetically distinct main stem salmon population (Niemelä et al. 2005; Vähä et al. 2017), adding to the exceptionally wide diversity in life history strategies of Atlantic salmon in the Teno system (Erkinaro et al. 2019). Juvenile salmon typically spend 3–5 years (range 2–8 years) in this river before migrating to the ocean (Erkinaro et al. 2019). They emerge from spawning redds to the surface of the bottom substrate in early July and are thereafter available for sampling by electrofishing (Niemelä et al. 2001).

The long-term juvenile salmon monitoring program conducted in the Teno River since 1979 does not include sampling sites in the sandy areas since these have not been considered juvenile production areas (Niemelä et al. 1999, 2005). Similarly, deep fluvial habitats of the Teno system are not accounted for in the juvenile monitoring program, also because of methodological constraints (Niemelä et al. 1999, 2000).

2.2 | Habitat Classification

We used the Norwegian Mesohabitat Classification Method (NMCM; Borsányi et al. 2004) to classify the River Teno main stem surface area to different mesohabitat classes for juvenile salmon, either young-of-year (YOY, 0+) or parr (one-year-old and older, > 0+). The habitat variables used in classification included surface flow velocity (< 50 cm s-1 or > 50 cm s-1), water depth (< 70 or > 70 cm), water turbulence (surface broken or not, wave height, etc.) and gradient. These factors combined resulted in 10 different habitat classes (Table 1). In this study, the classification method was complemented by adding an estimation of the substrate composition for each mesohabitat patch. For each mesohabitat patch, we estimated the dominant and subdominant substrate size using a scale consisting of five-grain diameter categories (1 = < 2 cm, 2 = 2–12 cm, 3 = 12–35 cm, 4 = > 35 cm and 5 = bedrock; Forseth and Harby 2014).

TABLE 1 | Mesohabitat classification used in the study (modified from the NMCM classification by Borsányi et al. 2004).

Surface pattern (SP)	Surface gradient (SG)	Surface velocity (SV)	Water depth (WD)	Mesohabitat class	Name	Areal coverage, %
Smooth/rippled (wave height < 5 cm)	Steep (> 4‰)	Fast (> 50 $cm\ s^{-1}$)	Deep (> 70 cm)	**A**	Run	0%
		Fast (> 50 $cm\ s^{-1}$)	Depth not relevant Dominant and sub-dominant substrate size < 2 cm.	**S**	Sandy run	66.6 &
	Moderate (< 4‰)	Fast (> 50 $cm\ s^{-1}$)	Deep (> 70 cm)	**B1**	Deep glide	19.7%
			Shallow (< 70 cm)	**B2**	Shallow glide	6.4%
		Slow (< 50 $cm\ s^{-1}$)	Deep (> 70 cm)	**C**	Pool	0.7%
			Shallow (< 70 cm)	**D**	Walk	0.6%
Broken/riffling (wave height > 5 cm)	Steep (> 4‰)	Fast (> 50 $cm\ s^{-1}$)	Deep (> 70 cm)	**E**	White water	0.5%
			Shallow (< 70 cm)	**F**	Cascade	0%
	Moderate (< 4‰)	Fast (> 50 $cm\ s^{-1}$)	Deep (> 70 cm)	**G1**	Deep rapid	3.3%
			Shallow (< 70 cm)	**G2**	Shallow rapid	2.2%
		Slow (< 50 $cm\ s^{-1}$)	Shallow (< 70 cm)	**H**	Rill	0%

Although the NMCM is designed to be widely applicable for classifying salmon rivers, we constructed an additional habitat class 'S', which included < 2 cm dominant substrate size and water surface velocity higher than 50 $cm\ s^{-1}$. Such areas with fine substrate and relatively fast flow are typical for both the upper and lower sandy areas of the Teno main stem (Niemelä et al. 1999; Figure 1). Unlike the rest of the mesohabitat classes, 'S' had only one depth class. Two depth classes for habitat class 'S' turned out to be too difficult for our surveying method. The depth in sandy areas varied too greatly even in short survey distances, which was likely due to alluvial deposit formation.

The NMCM classification was done by dividing the river channel into mesohabitat polygons based on their habitat characteristics. Based on simple measurements and visual observations, the classification was done by following a simple decision tree (Table 1) in situ. A mesohabitat patch would be divided into sections if the substrate size varied within the patch, but a minimum threshold size for a separate section was set at c. 500 m^2. The level of detail was also considered with other classification criteria, for example if the first 5 m from the shore was shallower than the 70 cm threshold value (defined in NMCM), but the rest of the 150 m wide channel was deeper, the whole channel was assigned to > 70 cm deep mesohabitat class (Table 1). A maximum of three sections, i.e., different mesohabitat classes, were defined for each cross-section of the river.

The c. 200 km stretch of the River Teno main stem, which extends from the confluence of River Inarijoki and River Kárášjohka (N 7703393, E 453189, ETRS-TM35FIN) to the tidal limit, 14 km upstream of the River Teno mouth (N 7810102, E 545292, ETRS-TM35FIN; tidal limit; Figure 1), was surveyed on 26–29 August and 8–12 September 2014. We used an inflatable boat with an outboard motor, aquascope for underwater observations, and a measuring stick for depth measurements. Data were collected by constantly observing changes in substrate, water depth and surface velocity. Defined, distinct habitat patches were sketched to aerial photographs (1:10000 scale; Norwegian National Land Survey, 2008–2012). GPS waypoints were recorded for the whole duration of the survey (Garmin cx60 GPS-device, Garmin International Inc., Olathe, KS, USA). A rough classification of the surface velocity (> 50 $cm\ s^{-1}$ or < 50 $cm\ s^{-1}$) was done with the Garmin cx60 GPS-device by allowing the boat to float freely on the river when a marked change in surface velocity was observed. Because of the large size of the river, it was impossible to measure the velocity in all individual habitat patches of the river. However, most of the River Teno main stem belonged to the > 50 $cm\ s^{-1}$ velocity class. During the survey, the mean discharge was 103 m^3 s,$^{-1}$ which is approximately 15% less than the mean discharge during the same time period between years 1965–2014 (unpublished data: Finnish Environment Center, Onnelansuvanto measuring station).

Field maps were digitised using ArcMap GIS software (version 10.3.1.). A vector file was created for each mesohabitat patch. Due to the large size of the river, only a small proportion of the side channels behind some islets and sand banks of the main stem were classified in situ, but they were classified afterwards based on surrounding, field-surveyed mesohabitats. These areas combined comprised 3.3% of the total classified area.

2.3 | Electrofishing Surveys

The distribution and abundance of juvenile Atlantic salmon and other fish species in different mesohabitats of the study area

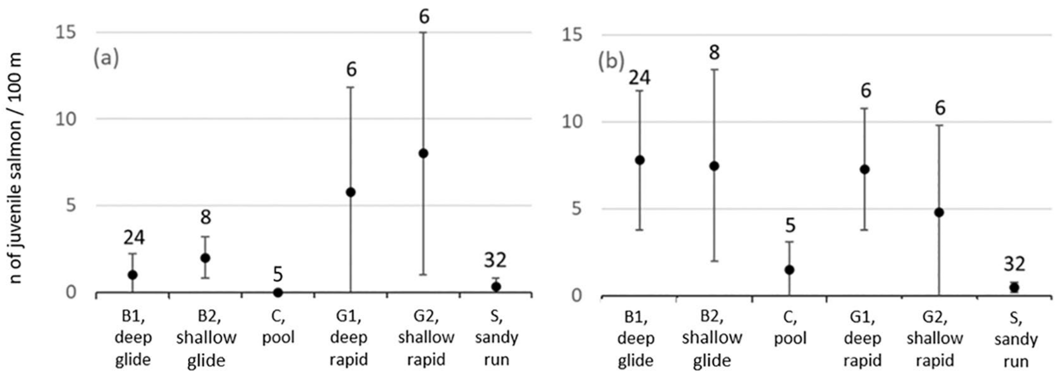

FIGURE 2 | Observed mean abundances (ind./100 m; ±SD) of salmon YOY (a) and parr (b) on different mesohabitats in the River Teno. The number of survey lines electrofished for each habitat class is indicated above the error bars. See Table 1 for the definition of mesohabitat classes.

was studied between 1 and 5 September 2014 using a specifically manufactured, inflatable catamaran boat equipped with a generator-powered electrofisher (https://www.smith-root.com/electrofishers/boats/catarafts). DC power (120 Hz, 1000 V) with current between 2.7 and 5.3 A (mean 3.6 A) was used in the surveys. The surveyed electrofishing lines were selected to cover the various mesohabitat classes in a representative manner and to include areas both near the shoreline and in the middle sections of the river channel. Before conducting the electrofishing surveys, starting points for each survey day were chosen to enable coverage of all mesohabitat classes as the River Teno main stem includes long stretches of sand-dominated areas and, on the other hand, large areas dominated by riffles and glides. The exact selection of lines was done in situ by drifting down the river and searching for stretches of river where the mesohabitat was relatively homogenous and the stretch was long enough to be electrofished. The electrofishing lines were parallel to the shore and were 50–1200 m long. Individual electrofishing lines were conducted to cover one habitat class at a time.

A total of 81 electrofishing lines were sampled with a combined length of 25.9 km. Survey lines close to the shorelines (2–20 m from the shore) included 39 lines and 42 were located in the middle section of the river. Survey lines covered six habitat classes, whereas the two remaining habitat classes identified in the habitat mapping (Table 1) were not sampled because the class E areas were impossible to survey safely with an electrofishing boat, and class D mesohabitat patches suitable for electrofishing were not found at all. Most survey lines belonged to mesohabitat classes S ($n = 32$) and B1 ($n = 24$), while the rest of the mesohabitat classes included 5–8 survey lines each (Figure 2).

In addition to comparing the distribution of juvenile densities across the mesohabitat classes, line-specific habitat characteristics were measured for relating salmon abundance to water depth (nearest 10 cm), surface flow velocity and substrate size (see above for substrate composition estimation) at each survey line. Water depth was measured by using a measuring stick (dipnet) at the start and end of each line, and GPS was used to measure the surface flow velocity.

Electrofishing was done by rowing the boat downstream slightly faster than the current with the electrofisher running, and the stunned fish were collected by three persons using dipnets. The length and position of each survey line were recorded with a GPS device (Garmin Colorado 300, positioning accuracy < 10 m, Garmin 2008). The duration of sampling at each survey line was also recorded. All captured fish were put into a fish tank, their species were identified, and fish were measured to the closest millimetre (fork length for juvenile salmon; total length for other species) and released alive back to the river. Two age groups of juvenile salmon, YOY and parr, were identified based on a set length limit of 55 mm, which was based on earlier data on size-at-age of juvenile salmon in the Teno main stem (Erkinaro and Niemelä 1995; unpublished data; Figure S1). Juvenile salmon abundance index (ind./100 m; one electrofishing pass) was calculated for each electrofishing line.

Catching and handling fish was done in accordance with Finnish legislation concerning animal welfare (see https://www.ruokavirasto.fi/en/animals/animal-welfare/ for more information). Specimens used in this study were sampled during investigations conducted under the permission from the Centre for Economic Development, Transport and the Environment of Lapland (LAPELY 2370/5713–2012) to the Natural Resources Institute Finland (Luke).

2.4 | Modelling the Relationship Between Habitat Variables and Juvenile Salmon Abundance

Generalised linear models (GLM; Tweedie distribution with a log link) were used to describe the relationship between habitat variables and juvenile salmon (YOY and parr) abundance. GLMs are mathematical extensions of linear models suitable for analysing ecological data, which often do not represent classical Gaussian distributions (Guisan et al. 2002). Tweedie distribution is a bimodal distribution that can handle datasets with an excessive number of zeros (over-dispersion, zero-inflated) on which Poisson distribution or negative binomial distributions do not fit. The number of juvenile salmon per 100 m survey line was used as a dependent variable, and the natural logarithm of the electrofishing survey line length was used as an offset variable. All the explaining variables were nominal: mesohabitat class, depth (< 70 cm or > 70 cm), lateral position (near shore or middle, see Section 2.3 Electrofishing surveys), dominant substrate class and sub-dominant substrate class. The mesohabitat class was obtained from the habitat mapping survey (see Section 2.2). The lateral position was first determined in situ and the mean distance of the survey line was later calculated with a GIS analysis. The rest of the variables were measured during the electrofishing surveys.

For both YOY and parr the model was first fitted with main effects of all explaining variables and their two-way interactions (highest level in study setup). The model was simplified in a backward stepwise procedure (stay criteria $p = 0.05$) by first removing the interactions, followed by main effects, to reach the simplest model with best explanatory value (finite sample corrected Akaike Information criteria, AICC; Hurvich and Tsai 1989). The mean estimated values for each parameter were thus produced with their 95% confidence levels. The statistical analyses were conducted using SAS 9.4 statistical software (SAS Institute 2021). Model selection was conducted with SAS PROC GENSELECT and final model fit with SAS PROC GENMOD.

For YOY, survey lines on mesohabitats class C ($n = 5$) were removed from the model as no YOY fish were caught from these lines. The final number of observations used in the model was 76 for YOY and 81 for parr (for distributions and probability plots, see Figures S2 and S3).

2.5 | Habitat Suitability Index

The HSI is a commonly used index of habitat quality and is based on preference curves that present the preference of fish over the range of habitat parameters such as current speed, substrate grain size and depth in a studied river reach (Bovee 1982; Morantz et al. 1987). Hereafter, habitat preference is defined as the habitat that fish use the most, and not as habitat use in relation to habitat availability; see Mäki-Petäys et al. (2004). In this study, HSI for YOY and parr was calculated for each mesohabitat polygon with habitat parameters (see Section 2.2) and a value was calculated for each parameter in the GLM. By dividing the sum of habitat parameter mean estimates by the highest value of the sum of the mean estimates of the GLM, a HSI value between 0 and 1 was obtained for each mesohabitat polygon. The following formula was used to calculate the HSI:

$$HSI = \frac{p_1 + p_2 + \dots p_n}{p_1^{max} + p_2^{max} + \dots p_n^{max}}$$

where p_n is the mean estimated value of habitat parameter, and p_{n}^{max} is the highest mean estimated value of a habitat parameter. Since the dominant and sub-dominant substrate grain size classes could be of same class only on substrates consisting of sand (class 1 substrate), the combination of substrate classes that had the highest combined value was used in the formula.

The mesohabitat classes (Table 1) were divided into four quality categories according to their HSI value. This was considered the maximum realistic number of classes obtainable using the robust methods described earlier.

Due to missing or very low numbers of observations on some habitat parameters, some assumptions had to be made to calculate HSI for all the mapped area. First, in the habitat model for YOY, C and D mesohabitats, which were not included in the GLM (see Section 2.4), it was assumed that they had the same mean estimated value as mesohabitat class S, since both had very low YOY densities. Second, since mesohabitat class S did not have a depth value, mesohabitat class S was assumed to be > 70 cm deep in the models, as juveniles were caught in minimal numbers at all depths on sandy areas in the field surveys. In the parr model, mesohabitat class D was assumed to have the same mean value as class C, since their hydromorphological features were similar, and D was not included in the GLM.

3 | Results

3.1 | Mesohabitat Survey

The main stem of River Teno consisted of 683 mesohabitat polygons with a combined surface area of c. 4600 ha (46 km^2). Most of this area (66.6%; 3050 ha) belonged to the class S mesohabitat in which sand/fine gravel is the dominant substrate, and the water surface velocity exceeds 50 $cm\,s^{-1}$ (Figure 1). Mesohabitats with sand/fine gravel and < 50 $cm\,s^{-1}$ surface velocity (classes C and D combined) covered only c. 1% of the area. These fine substrate habitats were characteristic in the upper and lower reaches of the main stem (Figure 1). Glide-type mesohabitats B1 (19.7%) and B2 (6.4%) covered more than a quarter of the total area. Rapids with moderate (Classes G1: 3.3%; G2: 2.2%) and steep gradient (class E: 0.5%) covered 6% of the surveyed area. Glides and rapids were mostly located in the middle reaches of the main stem where the river is characterised by coarser substrate (Figure 1).

Fine substrates (< 2 cm diameter) were either the dominant or subdominant substrate class for nearly 60% of the river area. Combinations of other substrate sizes in dominant and subdominant classes varied between 0% and 15% (Table 2).

3.2 | Juvenile Salmon Abundance in Mesohabitat Classes

A total of 1830 fish, consisting of 13 fish species, were caught by electrofishing. The most abundant species was Atlantic salmon ($n = 1110$, 60% of all individuals) followed by European minnow (*Phoxinus*; $n = 415$, 23%) (Table 3). The length distribution of juvenile salmon was used to distinguish between YOY and parr, resulting in an estimated 276 YOY and 834 parr captured by electrofishing (Figure S1).

Juvenile salmon abundance was very low in fine-substrate habitats (C, S), whereas the highest abundances were found in rapid areas (G1, G2) (Figure 2). YOY abundances were the highest in shallow rapids (G2: mean 8.2 ind./100 m) and deep rapids (G1: 5.3/100 m). Glides (B1, B2) showed low YOY abundance (1.1 and 1.7/100 m, respectively). YOY abundances in sandy substrates with > 50 $cm\,s^{-1}$ surface velocity (S) were extremely low (0.1/100 m); no YOY were caught at slow-flowing fine-substrate (C) habitats (Figure 2).

Salmon parr were most abundant in deep glides (B1: mean 7.6 ind./100 m), shallow glides (B2: 7.4/100 m) and deep rapids (G1: 7.1/100 m) and slightly less abundant in shallow rapids (G2:

TABLE 2 | Areal coverage (%) of the combinations of dominant and sub-dominant substrate grain size (diameter, cm) classes in Teno River main stem.

		Dominant substrate			
		< 2 cm	2–12 cm	12–35 cm	> 35 cm
Sub-dominant substrate	n/a	59.1%	—	—	—
	< 2 cm	—	1.1%	3.5%	0.1%
	2–12 cm	1.5%	—	14.6%	0.2%
	12–35 cm	6.2%	9.3%	—	2.4%
	> 35 cm	0.4%	0.01%	1.6%	—
		67.2%	10.3%	19.7%	2.8%

TABLE 3 | Abundance indices of different fish species caught by boat electrofishing (ind./ 100 m transect) in two main mesohabitat types: Rocky riffle areas in habitat classes B1, B2, G1, G2 and sandy or slow-flow areas in classes S, C, D; see text for habitat classification.

		Mesohabitat type	
Common name	Scientific name	Riffle	Sandy or slow flow
Atlantic salmon	*Salmo salar*	8.45	0.47
Brown trout	*Salmo trutta*	0.05	0.02
European grayling	*Thymallus thymallus*	0.31	0.12
Whitefish	*Coregonus lavaretus*	0.02	0.02
Perch	*Perca fluviatilis*	0.02	0.02
Pike	*Esox lucius*	0.01	0.07
Burbot	*Lota lota*	0.07	0.04
European minnow	*Phoxinus phoxinus*	1.78	1.45
Three-spine stickleback	*Gasterosteus aculeatus*	0.31	0.30
Nine-spine stickleback	*Pungitius pungitius*	0.02	0.07
Bullhead	*Cottus gobio*	0.02	0.01
Flounder	*Platichthys flesus*	0.14	0.68

4.6/100 m). Similar to YOY, a low abundance of parr was also observed in fine-substrate habitats (C: 0.8/100 m; S: 0.3/100 m; Figure 2).

By multiplying juvenile salmon density by each mesohabitat class areal coverage (see previous chapter) and then dividing by the sum, rough estimates of proportions of juvenile salmon using each habitat class were calculated. For YOY, these proportions were: B1 = 29%; B2 = 15%; G1 = 23%; G2 = 24%; S = 9% and C = 0%. For parr, proportions were more concentrated on glide mesohabitats: B1 = 60%; B2 = 19%; G1 = 9%; G2 = 4%; S = 8% and C = 0%. Mesohabitat class D was not sampled by electrofishing.

Juvenile salmon abundances obtained by electrofishing varied greatly between different survey lines with different substrate sizes; areas with coarser substrate as dominant or sub-dominant substrate showed the highest mean abundances, whereas the survey lines with fine substrate showed very low abundance of juvenile salmon (Table 4).

3.3 | Habitat Models

The selected GLMs used for calculating HSI values for juvenile salmon (YOY and parr) were

$$\text{YOY abundance} = M + \mathrm{D} + \mathrm{S}^{\mathrm{S}}$$

$$\text{Parr abundance} = M + P + \mathrm{S}^{\mathrm{D}} + \mathrm{D} + \mathrm{S}^{\mathrm{S}} + \mathrm{D} \times \mathrm{S}^{\mathrm{S}}$$

where *M* is mesohabitat class, D is depth class (< 70 cm = shallow, > 70 cm = deep), P is lateral position (shore < 14 m from shoreline), S^D is dominant substrate class and S^s is sub-dominant substrate class. For YOY salmon *M*, *D* and S^s parameters were fitted for the model (Wald $\chi^2 = 31.80$; df = 4; $p < 0.001$, Wald $\chi^2 = 12.80$; df = 1, $p < 0.001$ and Wald $\chi^2 = 8.26$; df = 3; $p = 0.02$, respectively)[1]. Rapid type mesohabitats (G1 and G2) had by a large margin the highest YOY densities, while sandy mesohabitats showed very low densities of salmon overall. Shallow water habitats (mean depth < 70 cm) showed considerably higher estimated YOY densities than deeper habitats (Figure 3).

Estimated parr abundance was linked with the mesohabitat class (Wald $\chi^2 = 16.64$; df = 5; $p < 0.001$), lateral position in the river channel (Wald $\chi^2 = 23.10$; df = 1; $p < 0.001$), dominant substrate class (Wald $\chi^2 = 11.12$; df = 3; $p = 0.01$) and the two-way interaction of water depth and sub-dominant substrate class (Wald $\chi^2 = 19.99$; df = 3; $p = 0.02$). Salmon parr abundance estimates were the highest on deep glide (B1) and rapid (G1) mesohabitats. Parr were notably more abundant on survey lines near the shoreline, and the model estimated the highest densities on substrates with 12–35 cm grain size. Lowest parr densities were estimated on substrates with < 2 cm grain size, but the model indicated moderate densities on substrates with mixed < 2 cm

TABLE 4 | Juvenile Atlantic salmon abundance (ind./100 m, age groups combined) in electrofishing surveys, divided by different substrate categories estimated at the survey lines located either near shorelines or in the middle section of the river.

	Substrate	Mean ind./100 m	Std. deviation	Survey lines *n*	Total survey line length, km
All survey lines	Coarse	9.3	±8.2	47	13.0
	Mixed	0.9	±0.8	10	5.8
	Fine	0.2	±0.3	22	6.7
Lines near shores	Coarse	11.1	±9.1	32	7.0
	Mixed	1.7	±1.0	3	1.1
	Fine	0.6	±0.4	6	2.1
Lines at middle sections	Coarse	5.5	±3.6	15	6.0
	Mixed	0.5	±0.5	7	4.7
	Fine	0.01	±0.03	16	4.6

Note: Substrate class coarse: Dominant and sub-dominant grain sizes > 2 cm; Fine: Substrate size < 2 cm; Mixed: Either dominant or sub-dominant grain size < 2 cm.

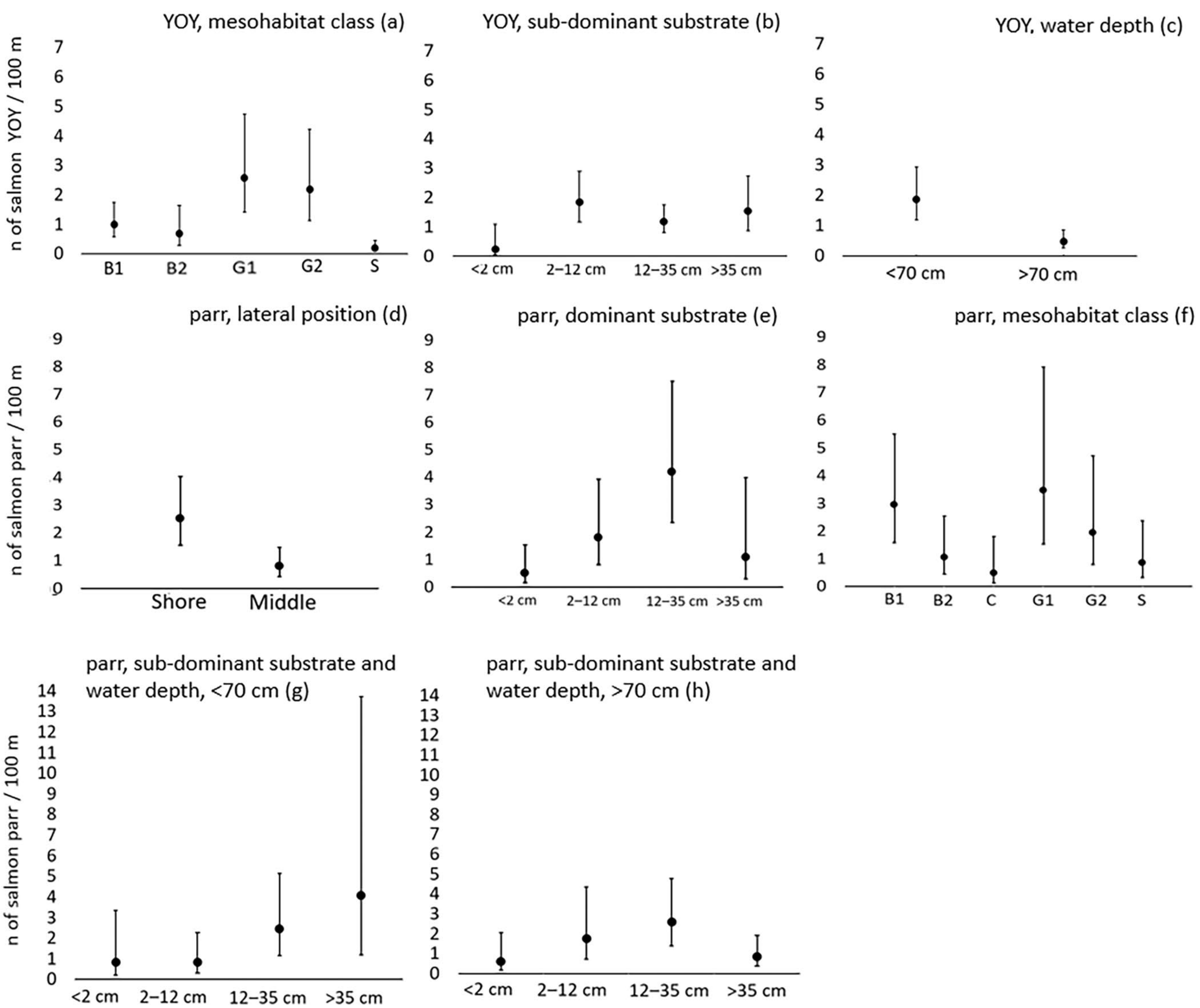

FIGURE 3 | Mean estimated abundance of salmon per 100 m predicted by the habitat parameters fitted for the GLM model for salmon YOY (a, b and c) and parr (d, e, f, g and h). The error bars show 95% confidence intervals for the mean.

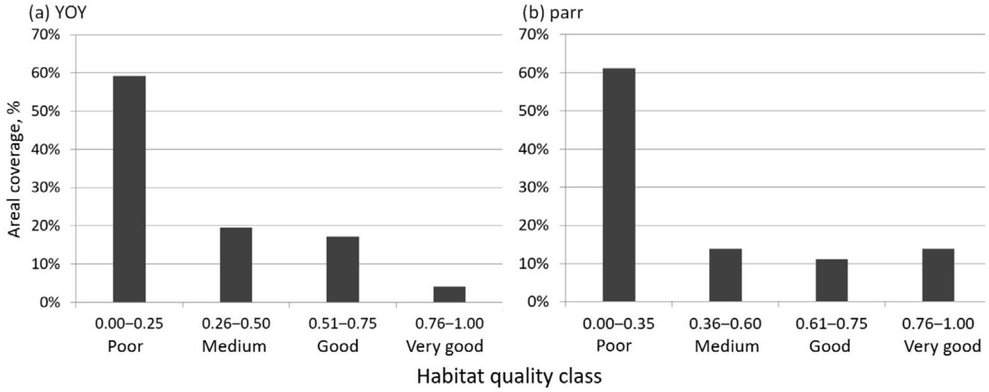

FIGURE 4 | Relative areal coverage of four habitat quality classes (HSI) in the River Teno mainstem for juvenile Atlantic salmon: (a) YOY and (b) parr.

and > 2 cm grain size classes (Figure 3, panels e, g and h). (See Tables S1 and S2 for GLM model parameter estimates and goodness of fit).

3.4 | Habitat Suitability Index

According to the calculated HSI values, most of the wetted area of the River Teno mainstem is of poor habitat quality for juvenile Atlantic salmon, both for YOY and parr 59% and 61% of the mapped area, respectively; (Figure 4). Poor habitats consisted mainly of sand-dominated mesohabitat class S. For salmon parr, sandy mesohabitats with coarse sub-dominant substrate near the shorelines were classified as medium-quality mesohabitat. Overall, 20% of the surveyed area was medium-quality habitat for YOY and 14% for parr. A total of 21% was classified as good or very good habitat for YOY and 25% for parr. Habitat quality class thresholds were higher for salmon parr due to higher average HSI value, which was caused by the higher number of habitat parameters included in the GLM model (Table 5; Figure 4).

4 | Discussion

The NMCM habitat classification method (Borsányi et al. 2004) proved to be a fast, cost-effective way to quantify meso-scale habitats of the large River Teno. In 9 days of field work, a survey of the surface area and spatial distribution of different mesohabitats with their dominant and sub-dominant substrate grain size classes was completed in the c. 200 km long main stem of the river.

Typically for a large lowland river (Lotsari et al. 2010), most of the riverbed (67%) had totally or predominantly sandy substrate and only a third of the river consisted of riffle or glide type habitats with coarser substrate. By electrofishing extensive reaches across different habitat types, marked variation was observed in juvenile salmon densities and occurrence among different mesohabitats and substrate and depth classes, as well as across lateral positions in the river.

As expected, juvenile salmon were largely absent in the vast sandy areas which covered roughly 67% of the surveyed area of the Teno main stem. While juvenile salmon have been observed to exhibit great plasticity in habitat utilisation by migrating from classical fluvial rearing habitats to for example estuaries, lakes and small tributary streams (Cunjak et al. 1989; Erkinaro et al. 1998, 1997, 2017), the sandy areas of the wide River Teno mainstem do not seem to offer suitable conditions for juvenile salmon. Habitats with fine substrate provide very little shelter from current or predators, and their production of macroinvertebrates is also very low compared to coarser habitats (Armitage et al. 1995; Foldvik et al. 2017). These factors combined may result in an unfavourable combination of high metabolic costs and poor energy intake for juvenile fish (Waters 1995; Suttle et al. 2004; Finstad et al. 2007). Although juvenile salmon clearly preferred habitat with coarser substrate, there was a large variation in juvenile densities within all compared habitat classes. This indicates that the suitability of a habitat is typically dependent on multiple habitat features, including micro-scale habitat variability and macro-scale assemblage and juxtaposition of habitats (Kocik and Ferreri 1998; Bouchard and Boisclair 2008). Although mesohabitat classes are characterised by similar gradient, channel structure and shape, they also typically comprise various microhabitat types with varying suitability for the juvenile salmon (Bovee et al. 1998).

Despite the less profitable characteristics of the fine substrate habitats, some juvenile salmon were observed in these areas as well. This may be explained either by transient fish occupying these areas temporarily, or by density-dependent mechanisms where locally increasing population density of fish (Rodríguez 1995) may force part of the fish population from their preferred habitat. The ideal free distribution theory (Fretwell and Lucas 1970) predicts that habitat selection equalises the mean profitability among habitats, resulting in equal realised fitness for all individuals. While the very low densities of salmon parr in the sandy areas could be a result of poor habitat quality and the consequent large size of individual territories (see Grant et al. 1998), the earlier information on juvenile densities elsewhere in the system does not indicate obvious density-dependent effects (see Niemelä et al. 1999, 2001, 2005). In some earlier studies conducted elsewhere, large parr have been observed to emigrate downstream, especially in the autumn, possibly exiting their nursery habitats for more suitable areas for their increasing size or moving downstream towards the estuarine areas in

TABLE 5 | GLM model-based mesohabitat quality classes in the Teno River, their habitat suitability indices (HSI values), descriptions and examples of mesohabitats in them. Class descriptions are modified from the habitat quality classes defined by Falkegård et al. (2014) for the River Teno and its tributaries.

Mesohabitat quality class	Poor	Medium	Good	Very good
HSI value for YOY	0.00–0.25	0.26–0.50	0.51–0.75	0.76–1.00
HSI value for parr	0.00–0.35	0.36–0.60	0.61–0.75	0.76–1.00
Description	Mostly unproductive, zero to very low catch of juvenile salmon	Habitat quality and catch of juvenile salmon varies, mainly low	Mostly productive, high-juvenile salmon catch	High-quality habitats, very high juvenile salmon catch
Examples of YOY habitat	Sandy, slow flowing (class S)	Deep glide habitats (B1). Slow-flow (class C, D) with coarse substrate	Deep rapids, shallow glides (G1, B2)	Shallow rapids (G2)
Examples of parr habitat	Sandy (class S) slow-flowing habitats (C, D) and sandy habitats (S) with some coarse substrate in mid-channel	Slow flow (class C, D) with coarse substrate. Sandy habitats are located near shore with some coarse substrate. Shallow glides and rapids (B2, G2) in mid-channel, coarse substrate mixed with sand.	Deep rapids and glides (G1, B1), coarse substrate located in the mid-sections of the river channel	Rapids (G1), glides (B1) and cascades are located near the river shore with coarse substrate

preparation for smolt migration in the following spring (Riddell and Leggett 1981; Cunjak et al. 1989; Youngson et al. 1994). It may therefore be possible that some of the juvenile salmon caught in the fine substrate areas of the Teno main stem might be transient, gradually moving downstream from their original nursery habitats. While middle sections of the sandy parts of the Teno showed very low abundance of juvenile salmon, moderate amounts of juveniles were caught near the shore in these areas, usually when the shoreline was stippled with coarser substrate and some vegetation. These strips of better habitats may be important oases for salmon on their way downstream through the sandy areas of the Teno.

It should be noted that the highest abundances of both pike (*Esox lucius*) and flounder (*Platichthys flesus*) were observed in the sandy or slow-flowing areas (Table 3). Flounders ascend the river from the Barents Sea (Hemmer-Hansen et al. 2007) but are not able to pass the strong rapid section c. 60 km from the river mouth (the point where the sandy area (white) changes to the riffle area (black) in the lower part of the river; Figure 1). Pike is a major predator of juvenile salmon (Falkegård et al. 2023) and their presence in slow-flowing habitats may further decrease the suitability of these areas for juvenile salmon production.

Armstrong et al. (1997) suggested that typically only a small portion of the juvenile salmon population exhibits high mobility and actively explores alternative habitats from their nursery areas. However, relatively large-scale habitat shifts from the Teno main stem and its large tributaries to small tributaries and lacustrine habitats have been documented (Erkinaro and Niemelä 1995; Erkinaro et al. 1998, 2017), which indicates active, far-reaching explorative behaviour in search of favourable habitats, at least in a certain proportion of the population (Erkinaro et al. 1997). Moreover, the patchy sand-dominated habitats occupied by some juvenile salmon documented in this study are often located several kilometres from the nearest apparent spawning habitats (see Louhi et al. 2008 for general spawning area criteria), which further indicates active search for new habitats.

While the riverine habitat of salmon is widely studied, studies investigating lateral variation in juvenile salmon abundance in large rivers are largely lacking. There was a clear lateral pattern in habitat utilisation by juvenile salmon: nearshore areas showed higher abundance of juvenile salmon than those in mid-channel. In some areas, both lines close to shoreline and in the middle section were sampled in the same cross-section of the river and were longitudinally overlapping (altogether nine lines; Table S3). In these situations, the difference in salmon abundance between the shoreline and mid-river was following the general pattern: abundances on survey lines close to riverbanks were higher than on middle sections (Table S3). Habitats close to shore typically show higher habitat heterogeneity, in for example flow velocity, substrate size and the amount of vegetation (Armstrong et al. 2003) and in general, fluvial habitat heterogeneity increases the abundance of macroinvertebrates and juvenile salmonids (Negishi and Richardson 2003; Dolinsek et al. 2007). It should be noted, however, that our observations have been made at the mesohabitat scale, but the effects of habitat heterogeneity are likely functional at the microhabitat scale (Armstrong et al. 2003; Mäki-Petäys et al. 2002, 2004).

Moderate abundances of salmon parr and YOY were caught at depths of 1–2.5 m, which is in line with the findings of the few earlier studies on juvenile salmon in deep habitats (Bremset and Berg 1997, 1999; Linnansaari et al. 2010). In our study, salmon parr occupied deeper habitats than YOY, and the overall abundances were clearly higher closer to the shoreline than further out in mid-channel of the river. These general preferences are comparable to those discovered elsewhere: In the large River Tornionjoki in the Baltic Sea area, Linnansaari et al. (2010) also found that salmon parr preferred deeper habitats compared to YOY. In markedly smaller rivers than the Teno, Bremset and Berg (1999) found that salmon YOY (0+) preferred nearshore habitats while older parr preferred the middle sections of pool habitats. In their study the depth increased rapidly towards the middle part of the pools, and the mean depths occupied by salmon were somewhat deeper than in our study, between 0.3–1.7 and 0.8–2.4 m for YOY and older parr, respectively. Sufficient water depth itself has been suggested to provide cover for young salmon (Gibson and Erkinaro 2009), and in the absence of severe predation threat or competition, which is often the case in northern rivers with depauperate fauna, juvenile salmon are more inclined to use slow-flowing deep habitats, even lakes (Gibson 1993; Erkinaro et al. 1998). However, our results suggest that juvenile salmon in the wide main stem of the Teno preferred habitats near the river banks even if depth, substrate and flow velocity were somewhat similar in the mid-channel. However, this topic requires more rigorous studies before strong conclusions can be made. Such patterns should be taken into account when assessing and modelling potential salmonid fish habitats in large rivers.

Despite some differences found, comparable abundances of YOY and parr were observed across all habitat types with no major differences in preferences between age groups. Salmon YOY generally prefer shallower depths than older parr (Bardonnet and Bagliniere 2000; Armstrong et al. 2003; Mäki-Petäys et al. 2004; Jelovica et al. 2024), and most studies have been conducted in shallower habitats than most of the electrofishing areas covered by our study, including those carried out in the River Teno system (Mäki-Petäys et al. 2002, 2004; Jelovica et al. 2024). However, even the sampling lines in the shallowest areas were typically dominated by parr. This might be partly because of methodological difficulties and partly due to the semi-random selection of survey lines. Fishing from an electrofishing boat might involve some bias in the capture probability of different-sized fish (see Bremset et al. 2012), but it is difficult to disentangle the effects of the electrofishing method and the natural habitat preferences of juvenile salmon of different sizes. Furthermore, greater water depths may cause technical difficulties in fishing the deeper areas, especially considering the capture efficiency of small salmon YOY which might be less visible for the netting crew than larger fish. Roy et al. (2012) showed that juvenile Atlantic salmon occupying pools with low velocity exhibited higher mobility than their counterparts in more shallow areas with higher flow velocity. The deep sandy areas in this study might have contributed to a higher probability of fleeing compared to shallow areas with higher flow velocity and coarse substratum. Finally, supporting information on the possible effect of fleeing behaviour has been provided by Bremset et al. (2021) who documented clearly higher electrofishing boat catches of juvenile salmon in sandy, lower parts of a Norwegian river fished at night when compared with daytime catches. It is possible that declining visibility and difficulty in operating the hand nets, together with increasing mobility of fish may have negatively affected the capture probability in deeper areas and especially in smaller fish. In summary, the methods used in this study could have moderately underestimated the use of deep and sandy habitats of both YOY and parr, and the catch efficiency for YOY was weaker in all habitats.

The absolute and relative amounts of different fluvial habitat types vary temporally with varying discharge (Borsányi et al. 2004; Hauer et al. 2009). In the River Teno, where seasonal variation in discharge is particularly large, tens of square kilometres more wetted area can be found during high flows compared to periods with low discharge. This is especially characteristic in the vast, relatively shallow fine substrate areas, where sand banks form dry islands during low discharge, but are submerged during high discharge. As the depth increases with discharge, large portions of shallow rapids (G2) may also turn into glide-type mesohabitats (B1 or B2; see also Harby et al. 2005). Changes in flow create and eliminate different habitats, causing temporal variation in mesohabitat availability for fish.

The criticism raised against correlative habitat models such as PHABSIM (Railsback 2016) includes their inability to consider spatio-temporal changes, use of inappropriate spatial scales and production of output that lacks clear ecological meaning. The habitat suitability modelling used in this study could have benefited from the application of individual-based models (IBM) which have been found to better incorporate ecological effects on habitat use, like temporal patterns, competition, predation and bioenergetics, with the advantage of linking physical stream habitat with realistic measures of fishes' ecophysiology and ecology (Hajiesmaeili et al. 2023). IBMs enable assessment of river habitat quality and their production potential (Railsback 2016) and are able to capture dynamic habitat responses to variable environmental factors such as changes in the flow regime (Hajiesmaeili et al. 2023). Although the present study was not able to consider the various ecological and ecophysiological effects, future research would benefit from exploiting the avenues provided by IBMs with ecologically meaningful assessments of habitat qualities for juvenile salmon in a dynamic spatio-temporal context.

In conclusion, deep glide and riffle habitats (classes B1 and G1) comprised more than one-fifth of the overall wetted area of the Teno, and their juvenile salmon densities were mostly comparable with those representing the typically assumed shallow, primary fluvial habitats. Moreover, although the sandy habitats showed very low abundances of salmon in general, narrow habitat strips close to shorelines with coarser substrate within the otherwise sandy areas revealed at least moderate juvenile salmon abundances. Given the large absolute area of both deep glides and sandy areas in the Teno main stem, such areas should not be neglected when assessing the importance of different habitats for juvenile salmon production. Considering meso-scale evaluation together with finer spatial scales in habitat mapping often produces a more precise understanding of the availability of fluvial fish habitat (Habersack et al. 2014). Accounting for a wider spatial scale can also help understand fish distribution and production potential for informing riverine habitat management in large heterogeneous rivers. Moreover, the increase of less productive sandy areas in rivers through bank erosion and riverbed siltation caused by human activities like road construction should be avoided by firm environmental governance.

Author Contributions

Tuomas Metsäniemi: conceptualisation, methodology, fieldwork, formal analysis, writing – original draft and writing – review and editing. **Panu Orell:** conceptualisation, methodology, writing – original draft and writing – review and editing, supervision and funding acquisition. **Anders Foldvik:** methodology and writing – review and editing. Jorma Kuusela: methodology, fieldwork, writing – review and editing. **Mika Kurkilahti:** methodology, formal analysis, writing – review and editing. **Jaakko Erkinaro:** conceptualisation, methodology, writing – original draft and writing – review and editing, supervision and funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Shared data is not available. Data generated or analysed during this study are available from the corresponding author upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.