Mesohabitat suitability criteria for the spawning of Twaite shad (*Alosa fallax*, Lacépède 1803)

Critères de pertinence des habitats à méso-échelle pour la fraie de l'alose feinte (*Alosa fallax*, Lacépède 1803)

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RÉSUMÉ

L'alose feinte (*Alosa fallax*, Lacépède 1803) est un poisson anadrome qui dépend des rivières européennes pour sa reproduction. Cependant, ses populations sont en déclin en raison de l'endiguement des rivières et des altérations hydro-morphologiques, qui réduisent et dégradent les frayères adaptées. Cette étude propose les premiers critères de préférences d'habitat (HSC) à l'échelle méso décrits dans la littérature pour la période de reproduction de *A. fallax*. En utilisant l'approche MesoHABSIM (MesoHABitat SImulation Model), nous avons identifié les unités géomorphologiques (GU) et les attributs d'habitat associés préférés pour la reproduction par *A. fallax* dans la rivière Tagliamento (NE Italie). La caractérisation des habitats a été réalisée à l'aide de systèmes aériens sans pilote (UAS), d'un modèle hydrodynamique bidimensionnel (2D), et d'études de terrain menées sur une période de 15 mois. Un modèle de classification par forêt aléatoire (RF), avec une précision élevée (98,8%), a permis d'identifier les principales caractéristiques méso-habitat nécessaires à la reproduction de *A. fallax*. Les critères HSC développés révèlent que *A. fallax* préfère les rifles et les glides pour se reproduire, avec des profondeurs faibles (0,15-0,45 m), des vitesses modérées (0,30-0,75 m/s), et des sédiments de petite taille (0,2-6 cm). Par ailleurs, nous avons utilisé une méthode de surveillance non intrusive avec des caméras infrarouges, qui a permis d'enregistrer avec succès 72 événements de reproduction en surface sur deux nuits. Cette méthode s'est avérée efficace, car il a été possible de définir précisément la localisation, la durée de chaque événement de reproduction et le nombre de poissons impliqués. Les résultats fournissent des informations précieuses pour développer des stratégies de gestion visant à préserver ou restaurer les habitats de reproduction de *A. fallax*.

ABSTRACT

Twaite shad (*Alosa fallax*, Lacépède 1803) is an anadromous fish that relies on European rivers for spawning. However, populations are declining due to river damming and hydro-morphological alterations, which reduce and degrade suitable spawning grounds. This study presents the first meso-scale habitat suitability criteria (HSC) in the literature for the spawning period of *A. fallax*. Using the MesoHABitat SImulation Model (MesoHABSIM) approach, we identified the geomorphic units (GUs) and associated habitat attributes preferred for mating purpose by *A. fallax* in the Tagliamento River (NE Italy). Habitat characterization was conducted using Uncrewed Aerial Systems (UAS), a two-dimensional (2D) hydrodynamic model, and field surveys performed during a monitoring period of 15 months. A classification Random Forest (RF) model, with high accuracy (98.8%) and true skill statistic (97.6%), was employed to identify key meso-habitat features for the reproduction of *A. fallax*. The developed HSC revealed that *A. fallax* prefers glides and riffles to spawn, with shallow depths (0.15-0.45 m), moderate velocities (0.30-0.75 m/s), and small sediment sizes (0.2-6 cm). Additionally, we employed a non-intrusive monitoring method using infrared cameras, which successfully recorded 72 surface mating events over two nights. This method proved effective since it was possible to precisely define the location, the duration of each mating event and the number of fish involved. The findings provide valuable insights for developing management strategies aimed at preserving or restoring *A. fallax* spawning habitats.

KEYWORDS

Anadromous fish, Geomorphic Units, MesoHABSIM, Random Forest, Spawning habitat preference. Poisson anadrome, Unités géomorphologiques, MesoHABSIM, Random Forest, Préférence de l'habitat de frai.

1 INTRODUCTION

Anadromous fish species play a critical role in both riverine and coastal ecosystems, yet they face mounting challenges due to habitat degradation, altered hydrological regimes, and barriers to migration (Almeida et al., 2023). In Italian rivers, these pressures are compounded by a limited understanding of their ecological and reproductive requirements, which hinders the development of effective conservation measures.

Habitat Suitability Models (HSMs) have emerged as essential tools for evaluating the availability of suitable habitat for freshwater species, aiding in river ecosystem conservation and restoration. Among these, the MesoHABSIM (Meso-HABitat SImulation Model, Parasiewicz, 2007) approach has proven particularly reliable. It is based on a robust hierarchical morphological characterization of river system (Gurnell et al., 2014, Belletti et al., 2017) that assesses available habitat for freshwater species by analyzing physical habitat attributes (such as depth, velocity, and substrate) of geomorphic units (GUs, or mesohabitats). Within the MesoHABSIM approach, machine learning techniques such as Random Forest (RF, Breiman, 2001) are used to develop habitat suitability criteria (HSC; e.g., Vezza et al., 2014). Although HSMs and HSC have been extensively applied to freshwater resident species, their application to anadromous fish remains limited.

This study focuses on the spawning habitat requirements of *Alosa fallax* (Twaite shad), a threatened anadromous fish which relies on European rivers for reproduction. Spawning in spring during nights in both freshwater and tidal waters, *A. fallax* is documented to prefer shallow, fast-flowing areas over different substrate types (Aprahamian et al., 2003). While its general biology is relatively well-documented, significant knowledge gaps remain regarding its spawning habitat requirements, particularly in Italy where this species is classified as vulnerable. To address these gaps, this research aims to develop the first mesohabitat suitability criteria for *A. fallax* during its spawning period. Using high-resolution data from Uncrewed Aerial Systems (UAS), two-dimensional (2D) hydrodynamic simulations, and field surveys conducted in a reach of the Tagliamento River (NE Italy), this study provides a detailed analysis of spawning habitat preferences at the mesohabitat scale. Additionally, innovative use of infrared cameras to capture mating activities offer new insights in understanding the nocturnal spawning behaviour of this species.

2 MATERIALS AND METHODS

2.1 The study site

The study site is located in the lower part of the Tagliamento River (NE Italy), 32 km upstream of the Adriatic estuary (UTM 33N E:343050 m, N: 5075160 m). We surveyed a portion of a hydro-morphologically homogeneous reach (i.e., single-thread channel with alternate bars, Gurnell et al., 2014) that was 1500 m long, with a mean width exceeding 100 m and a mean slope of 0.001. Its substrate consists of small pebbles, gravel, and sand patches. Geomorphic units pattern mainly includes glides and riffles, deep pools (up to 5.5 m) with canopy cover, and occasional backwaters. During low flow periods, discharge remains stable, primarily sustained by groundwater.

2.2 Data collection, analysis and habitat suitability criteria definition

From April 2022 to August 2023, different field campaigns were conducted to investigate the spawning habitat preferences of *A. fallax* within the surveyed reach. Spawning activities were mainly observed in May 2022 and 2023, exclusively in glides and riffles. Uncrewed Aerial Systems (UAS) were deployed to capture high-resolution imagery and generate Digital Elevation Model (DEM) of the study site. Bathymetric surveys, using a combination of an Acoustic Doppler Current Profiler (ADCP) and a flow meter, complemented UAS data, by providing information on submerged riverbed topography. Captured aerial imagery was processed, yielding an RGB orthomosaic (1.6 cm resolution) and a DEM (6 cm resolution). Bathymetric data were employed to correct the DEM for submerged areas by compensating for light refraction effects. A 2D hydrodynamic model was developed and calibrated using the corrected DEM to simulate depth and velocity at discharges of 8.85 and 11.90 m^3/s, representing the 75th and 25th percentiles of flow conditions during the spawning period of *A. fallax*. These simulations, combined with field data on substrate composition and cover distribution, facilitated the delineation and characterization of the GUs mosaic under both flow scenarios according to the MesoHABSIM approach. Water level and temperature data, recorded over 15 months by an onsite sensor, allowed to frame the spawning period for *A. fallax* within the study site. Spawning was assumed to commence when minimum daily water temperatures exceeded 12°C, continuing until the annual temperature peak (i.e., for 3-4 months, Aprahamian et al., 2003). In this way, spawning was defined to take place under relatively stable flow conditions from May to late July in both 2022 and 2023. In May 2023, spawning activity of *A. fallax* was further monitored during nighttime using infrared-equipped trail cameras, which allowed to capture, without intrusion, both the behaviour of individuals involved and the spatial distribution of mating events. Successful spawning events were characterized by sustained circling behaviours lasting between 3 and 11 seconds.

To define the first meso-scale HSC in the literature for the spawning period of *A. fallax*, a probabilistic approach was employed using the Random Forest (RF, Breiman, 2001) classification algorithm. The RF model was developed to distinguish between suitable and unsuitable mesohabitats for spawning, based on local habitat attributes under two considered flow conditions (8.85 and 11.90 m³/s). Specifically, a binary (0/1, unsuitable/suitable) classification model was developed, with a suitability threshold of >50% predicted probability for being a suitable GUs for spawning. For ensuring the highest model reliability a rigorous procedure was implemented which involved (i) balancing the dataset, (ii) identifying the most important predictors (i.e., habitat attributes) for classification results, and (iii) RF hyperparameters tuning. Model performance was assessed using accuracy, sensitivity, specificity, and the True Skill Statistic (TSS). Partial dependence plots (PDPs) were generated to interpret how individual predictors influenced habitat suitability (Figure 1b).

3 RESULTS

Within the study site, 104 GUs were identified, distributed across the two simulated flow conditions (8.85 and 11.90 m³/s). Glides constituted the most frequent GU type (45.2%), followed by pools (21.1%), riffles (20.2%), and backwaters (13.5%). Spawning activity of *A. fallax* was exclusively nocturnal, limited to 8 glides and 4 riffles located upstream of significant slope changes. During daytime, shads retreated to nearby pools, characterized by high water depth (up to 5.5. m), low velocities, fine sediments (sand and silt), and dense canopy cover.

Spawning was considered to take place from May to July in 2022 and from mid-April to July in 2023. Water temperatures during these periods ranged from 12.1°C to 21°C (mean = 17°C), and water levels remained substantially stable (0.77–0.98 m), corresponding to flow rates between 6 and 20 m³/s. Spawning behaviour was recorded during a focused field campaign in May 2023, with 72 mating events and 35 mating attempts observed over two nights. Peak activity occurred between 00:30 and 01:30 (Figure 1a), with individual events lasting 3–11 seconds (mean = 5.5 s). Mating primarily involved single pairs, though up to four fish occasionally participated simultaneously. Pre-mating behaviours, including upstream surface movements and tail splashing, were consistently observed.

The RF model proved highly effective in identifying the key mesohabitat features for *A. fallax* spawning. The final parsimonious model (Figure 1b) achieved very high predictive accuracy (98.8%) and TSS (97.6%), with a sensitivity of 100% and specificity of 97.6%. Twelve mesohabitat attributes were identified as critical predictors. Substrate characteristics emerged as the most important, with microlithal (2-6 cm) positively correlated and psammal (sand) negatively correlated with suitable GUs. Medium water velocities (0.30–0.75 m/s) and shallow depths (0.15–0.45 m) were associated with higher suitability, while low and high values of these attributes reduced the probability for the spawning.

4 DISCUSSIONS AND CONCLUSIONS

This study aimed at investigating the meso-habitat preferences and reproductive behaviours of *A. fallax* in the Tagliamento River, using machine learning models and novel non-intrusive monitoring techniques. The findings revealed that spawning activities were concentrated in glides and riffles characterized by shallow depths, moderate current velocities, and fine-grained substrates. These preferences align with previous studies on other European shads populations, suggesting shared ecological traits (Aprahamian et al., 2003; López et al., 2011).

The application of the RF classification algorithm within the MesoHABSIM framework proved highly effective in identifying habitat requirements, achieving high predictive performance. This highlights the effectiveness of this approach in assessing suitable habitats for anadromous fish species. Furthermore, the study introduced a novel, cost-effective, non-intrusive method using infrared cameras to monitor nocturnal spawning behaviour. The use of infrared cameras represents an unexplored approach in the study of nocturnal surface-spawning fish, offering an unprecedented level of detail in behaviour and spatial distribution monitoring.

Comprehensive monitoring and multi-scale conservation strategies are urgently needed for anadromous populations of *A. fallax*. Key priorities include safeguarding spawning habitats, ensuring basin-wide connectivity, and maintaining adequate flow regimes and sediment supply. This study's innovative habitat evaluation methodology and monitoring tools align with these objectives as recommended also by the recently approved European Nature Restoration Law, offering practical solutions to restore river ecosystems, enhance connectivity, and protect *A. fallax* and similar species.

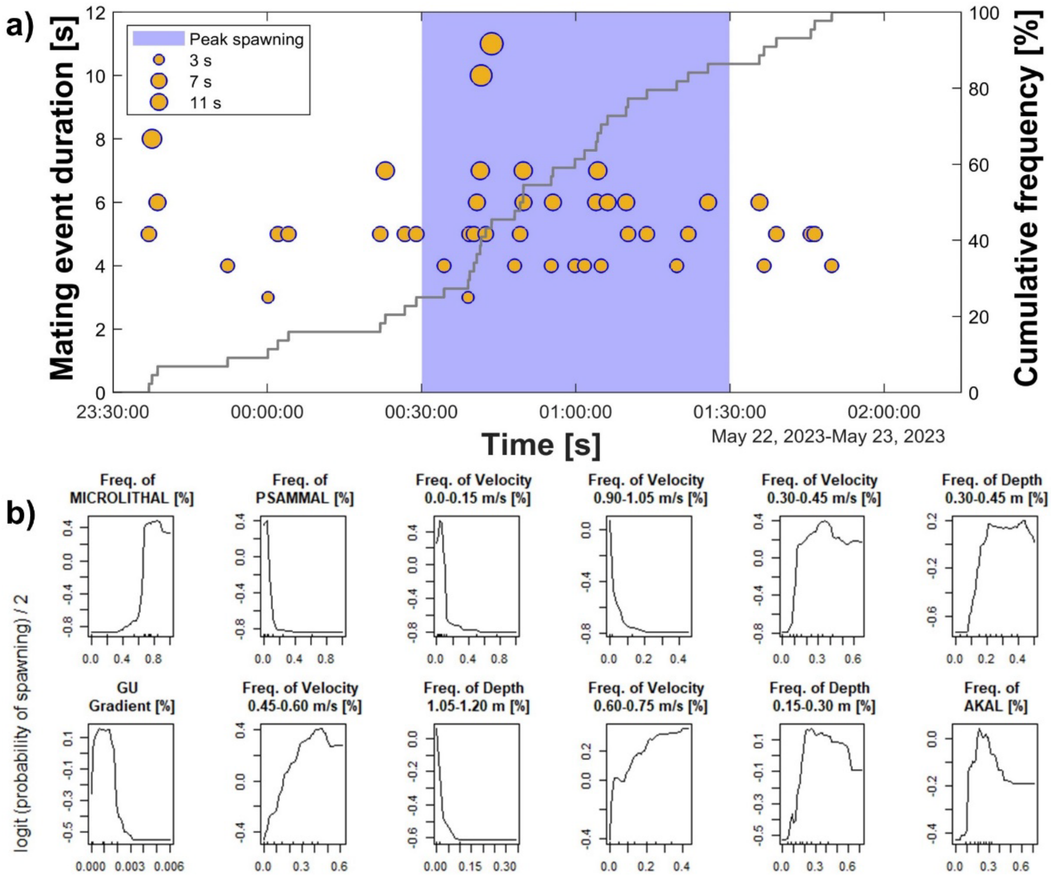

Figure 1. a) Occurrence (orange dot) and duration (dot size) of mating events recorded by the infrared camera during the first night of observation of the field campaign of May 2023. b) The Random Forest parsimonious model for the spawning period of *A. fallax*. Habitat attributes are presented in decreasing order of importance through partial dependence plots.

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