

Article

Hatched Late to Be Fed? Identifying the Origin of Late-Summer Pikeperch Cohorts Using Daily Otolith Increments

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Abstract

Effective fisheries management depends on a clear understanding of the recruitment dynamics of young-of-year (YOY) fish. Analysis of two-decade ichthyological data from Czechia and the Netherlands revealed an unexpectedly small cohort of YOY pikeperch (*Sander lucioperca*) in late summer. The origin of these individuals remained speculative. Building on the long-term patterns documented in these regions, we provide a new empirical contribution by analyzing the daily otolith increments of 29 pikeperch individuals sampled in the Lipno Reservoir (Czechia) in late August 2023. The otolith-based aging revealed that the extremely small pikeperch were not more than 35 days old, indicating they hatched at the turn of July and August. Even with the uncertainty in the exact timing of the first otolith increment formation, this approach disclosed the origin of the extremely small cohort as late-hatched individuals produced by wild late-spawning pikeperch. These extremely small, delayed pikeperch coexist with their normal, earlier-spawned conspecifics, which are often already piscivorous. Although they mostly do not survive the first winter, they still contribute to the recruitment indirectly by serving as prey for conspecifics. Our results highlight the need to revise the current understanding of pikeperch spawning phenology in the temperate zone.

Keywords: demic structure; percid fish; late spawning; hatch date

Key Contribution: We have confirmed the origin of the extremely small pikeperch cohort as offspring of so far unknown late spawners.



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1. Introduction

Pikeperch, *Sander lucioperca* (Linnaeus, 1758), is a key predatory fish species in European coastal, brackish, and freshwater ecosystems that is highly valued by both commercial and recreational fishers [1]. Pikeperch is native to northeastern Europe and western Asia [2]. It is widely used in biomanipulation programs to control zooplanktivorous fish and thus to improve water quality [3]. While it is stocked and reared in aquaculture in northern, eastern, and central Europe [4,5], pikeperch is an invasive and alien species in most parts of western and southern Europe [6–8]. The increasing importance of pikeperch for fisheries and aquaculture led to detailed ichthyological surveys and numerous studies on its population dynamics across the Czech Republic and also in the Netherlands [9–14]. These

studies have been recording an extremely small (ES) or also known as a dwarf intra-annual cohort of pikeperch individuals (Figure 1a). In fact, the ES intra-annual cohort is commonly observed to be the most abundant young-of-year (YOY) pikeperch cohort [9,13]. These ES pikeperch individuals coexist with an intra-annual cohort of normal pelagic and planktivorous fingerlings, sometimes called ordinary fingerlings (Figure 1b) during the late-summer ichthyological surveys [9]. The presence of ES pikeperch has been recorded for the first time in 1978 by Densen 1985 in the Netherlands [15]. Then, at the beginning of the millennium, they were observed in a number of Czech and Dutch reservoirs [9]. Later, these ES individuals became an integral part of the YOY pikeperch community of the Lipno Reservoir in the Czech Republic [11]. Their abundance exhibits high inter-annual variability, ranging from complete absence to numerical dominance [13]. The Lipno Reservoir in Czechia has become a model system with significant research dedicated to exploring fish population dynamics [16].

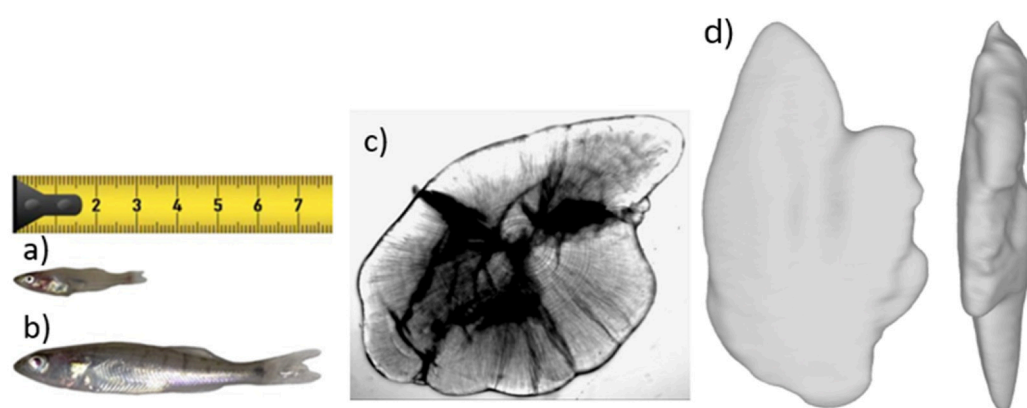


Figure 1. The standard length relationships between the co-existing pikeperch intra-annual cohorts recorded by the night pelagic trawling, and examples of the largest otolith (sagitta) with visible daily rings used in this study. (a) The smallest (extremely small) intra-annual cohort analyzed in this study was identified as the offspring of late-spawner pikeperch. (b) A cohort considered as the normal-sized planktivorous fingerling corresponding to the mostly expected late-August YOY pikeperch individuals. (c) A raw image of an otolith as obtained from the microscope. (d) Morphology of the sagitta medial side (left) and a side view from the dorsal perspective (right) of a 3D reconstruction of dwarf pikeperch obtained from micro-CT scanning of the dwarf pikeperch head (pikeperch individual originated from the 2023 survey).

The body size of ES pikeperch recorded in Lipno at the end of August (Figure 1a; 20–30 mm of standard length, SL, i.e., without tail) roughly corresponds to the planktivorous pelagic stage obtained during ichthyoplankton trawling in June of recent years [17,18]. The pikeperch fry community regularly recorded during the June trawling is supposed to originate from the main April-to-May pikeperch spawning season, as generally known [19] and as recorded specifically for Lipno [11,18]. The stage of June pikeperch pelagic planktivores turns into benthivores and finally into demersal piscivores during the first year of life [14]. Having undergone this sequence of stages as soon as possible is crucial for YOY pikeperch to survive the first winter [20]. Recent results revealed that the abundance of the ES pikeperch cohort positively correlated with the summer copepod density and with the increased densities of large cladocerans in July [13]. At the same time, the higher abundance of ES pikeperch individuals in late summer positively impacted the abundance of its conspecific intra-annual cohort at the piscivorous stage [20]. The extremely small pikeperch individuals are thus considered to serve as feed for more advanced YOY conspecifics and to contribute to their earlier switch to piscivory, thus increasing their chances to survive the

first winter [14]. To the best of our knowledge, the origin of these extremely small pikeperch individuals, both in the Lipno Reservoir and elsewhere, has not yet been explored.

Available literature on pikeperch reproduction biology considers this species a total (i.e., determinate) spawner with synchronized egg development and therefore also synchronized hatching [2,19,21]. The recognized spawning period in the central European region falls into the range from April to May [2,19]. Since this generally accepted knowledge contradicts any existence of a potential second spawning batch in pikeperch, the specific origin of extremely small individuals remained obscured and merely speculative and was ascribed to environmental factors [14]. However, the role of environmental factors is highly relevant regarding the ongoing climate change, including extreme and unpredictable climate events [13]. Therefore, any estimate of pikeperch responsiveness to changing environment and to anthropogenic impact, or both, is crucial for fishery management, potential conservation measures, as well as for the highly desired wild pikeperch populations.

On the other hand, the literature on the North American congener of the Eurasian pikeperch, the walleye (*Sander vitreus* (Mitchill, 1818)), revealed its response to climate change and unpredictable environmental variability [22–25] that might potentially result in the situation observed in pikeperch. Although not specifically mentioning the existence of extremely small walleye individuals, indications of prolonged and/or shifted spawning in response to the changing environmental factors have been recorded [22–25]. Numerous detailed studies on walleye show some ecological similarities with pikeperch. However, biological and geographic differences between the two species must be taken into account, as they may limit the applicability and transferability of this knowledge to the context of European aquatic ecosystems [26,27].

The discovery of daily otolith increments by Pannella (1971) [28] revolutionized early life-history research and provided a powerful tool to investigate the dynamics of juvenile fish cohorts. The largest otolith, the sagitta, is the most informative one and undergoes distinct morphological changes during the early fish ontogeny [29,30]. The sagitta is initially globular and forms a simple spherical core lacking any pronounced features. Later, it becomes complex, increasingly elongated, and develops species-specific traits [31,32]. Otoliths show unparalleled time-keeping properties initiated during the embryonic stages and continuing to grow gradually through daily deposits of calcium carbonate aragonitic crystals onto a fibroprotein organic matrix [33]. Reading these microstructural chronologies present on the sagitta enables estimating daily growth, mortality, and the precise timing of spawning and hatching events when these events have been experimentally validated [34]. The ecological utility of these metrics largely depends on rigorous validation to confirm both the daily periodicity of increment deposition and the exact timing of the first daily increment formation [35]. As in other teleosts, within the family Percidae, where pikeperch belongs, early life transitions leave diagnostic marks on the otolith structure; e.g., in European perch (*Perca fluviatilis* (L., 1758)), a distinct check marks the day of hatching, and a subsequent check typically corresponds to final yolk-sac absorption and the onset of complete exogenous feeding [36]. Sagittae generally exhibit a reliable relationship between increment counts and age in days post-hatching, which validates their use for back-calculating growth rates [35]. However, differences can arise between wild individuals and those reared under stable laboratory conditions that are still crucial to validate the daily increments [37]. These interpretive complexities are pronounced within the genus *Sander*, where replicate validation studies on walleye have reported the onset of the first daily ring spanning from 7 days before hatch to 7 days after hatch, as summarized by [35]. A single study on early juvenile pikeperch otoliths originating from another water reservoir in Czechia (Římov) is not specifically focused on daily increments themselves [38]. The study reports marking pikeperch of exactly known hatch dates with a fluorescent dye 3

to 5 days after hatching, in which the dye incorporates into the specific daily increment corresponding to the day of immersion [38]. Examination of dye incorporation into the otoliths revealed that daily increment counts matched the days post-hatching, although this was not explicitly detailed in the source study (Blabolil, *pers. comm.*). No further details on juvenile otoliths are known for the genus *Sander*, while a study confirmed the relationship between the otolith size and the body size in pikeperch [39]. Another study used otolith microchemistry in classifying walleye to known stocks and enabled estimates of persistence of individual stocks [40]. Sagittal otoliths of three adult pikeperch individuals are represented in the online AFORO database, Shape Analysis of Fish Otoliths; no records on otoliths of any juvenile pikeperch stage are available [41].

While prior studies established these multi-decade patterns in pikeperch intra-annual cohorts [13,20], this study delivers direct empirical evidence by analyzing daily otolith increments of extremely small pikeperch individuals collected in late-August 2023. Hence, the main aim of this study was to test the hypothesis that late-summer extremely small pikeperch individuals originate from an unknown hatching run. This would mean that the late-summer hatching is independent of the main, generally accepted, and literature-supported April-to-May spawning season. The daily otolith ring readings indeed revealed that extremely small pikeperch in the Lipno Reservoir hatched at the turn of July and August 2023.

2. Materials and Methods

The present study was carried out in the Lipno water reservoir, a shallow, eutrophic water body in South Bohemia (Czech Republic; altitude 720 m a.s.l.). The reservoir is located in the Bohemian Forest (Šumava in Czech), a low mountain range bordering Germany and Austria. The reservoir was constructed in the 1950s for hydropower generation, flood protection, flow augmentation, and recreational activities, including fisheries. It has a water volume of 306 million m³, a surface area of 46.5 km², a maximum depth of 22 m, and an average depth of 6.6 m [42].

We collected 89 individuals of extremely small and 380 normal fingerling age-0 pikeperch individuals during the night of 28 August to 29 August 2023 by night pelagic fry trawling (Table 1). Even the juvenile pikeperch individuals have a distinct morphology enabling their identification. The only theoretical possibility of misclassification is changing with the European perch. However, even here, there are powerful features like an elongated rostral head region, lower body height, much less pigmentation, and absence of lateral body stripes, particularly at this juvenile stage, pale body coloration, and much larger relative mouth size. Fish sampling has been performed with the use of a fixed-frame trawl with a mouth opening of 3 × 3 m as described in detail by [10]. The mesh size of the net used was 6 × 6 mm in the trawl main body and 4 × 4 mm at the cod-end, equipped with a funnel to prevent escape of captured fish. The trawl was towed 100 m behind a boat at a speed of 1 ms^{−1}. Trawling was performed in the pelagic area of the reservoir between the dam and town Černá v Pošumaví (upper, middle, and dam part according to [11]), 22 hauls approximately 600–650 m long each at the depth ranges 0–3 m, 5 hauls at 3–6 m, and 3 hauls at 6–9 m. The hauls were performed according to the bathymetry of the reservoir when the available shallow layers obviously dominated [42]. The trawl trajectory was measured by a GPS device, and the sampled volume of water was calculated. A random subsample of age-0 extremely small pikeperch individuals was immediately taken from the catch and frozen for later laboratory processing; the other individuals were anesthetized and subsequently preserved in a 4% formaldehyde solution.

Table 1. Summary table of pikeperch samples used in this study (sampled on 28 August 2023).

Intra-Annual Pikeperch Cohort	Count	Standard Length (mm)	Spawning	Age Estimation
Extremely small (ES)—total	89	13–38 (20.6 ± 4.81)	Summer	unknown
Subsample used for otolith analysis ¹	29	13–24 (19.1 ± 2.21)	Summer	19–29 days $\pm$ 7
Normal planktivorous fingerlings	380	40–76 (50.7 ± 4.03)	April/May	unknown
Piscivorous demersal individuals	39	93–160 (107.72 ± 18.86)	April/May	unknown

¹ Individuals at the lower part of the size range were selected to ensure they belonged to the ES cohort.

In the laboratory, defrosted extremely small pikeperch individuals ($n = 29$) were measured for standard length with a precision of 0.5 mm. Their largest otoliths, i.e., both *sagittae* per individual, have been processed as described by [43]. Briefly, sagittal otoliths for age determination were extracted, cleaned from any attached tissues, and mounted on microscope slides using a thermoplastic mounting adhesive (CrystalBond 509 Clear Color produced by Electron Microscopy Sciences, Morgantown, PA, USA). The otoliths were viewed using an Olympus AX70 microscope (with $\times 200$ – $\times 600$ magnification) and photographed using a mounted camera. When it was necessary to improve the clarity of daily rings, the otoliths were ground with 400- and 600-grit sandpaper as described by [38]. Raw microphotographs were adjusted in terms of contrast and brightness to enable daily ring reading. An example of sagitta with daily rings is demonstrated in Figure 1c. Daily increments were counted by two independent readers in both the left and right sagittae (Figure 1). Using the sampling date and the averaged count of daily rings of each individual allowed for the estimation of its hatch day, and to aggregate the results by date. The approximate hatch dates had to take into account the knowledge gap in the timing of the first sagittal daily increment formation relative to hatching and the exogenous first feeding [35]. Hence, estimates of the hatch date were expressed as time intervals due to the absence of a fully validated pikeperch-specific daily increment protocol.

To contextualize the late-summer pikeperch hatching event, we plotted the daily temperature records of the Lipno Reservoir using data from the Vltava River Authority (Figure 2).

The standard length was recorded in the framework of the ichthyological survey for each fish used to determine the size structure. A total of 89 extremely small or dwarf individuals were measured together with fingerlings of the normal size, sometimes called ordinary fingerlings or planktivores ($n = 380$).

To visualize the outer morphology of otoliths (Figure 1d) used in this study, we have virtually extracted a single *sagitta* from a 3D model of an extremely small pikeperch head, sampled at the end of the August ichthyological survey of the Lipno Reservoir in 2023. The formalin-fixed juvenile pikeperch head was scanned with a laboratory-based μ CT system, GE Phoenix v|tome|x L 240 (GE Sensing & Inspection Technologies GmbH, Alzenau, Germany) in the CTLab at the Central European Institute of Technology (CEITEC) institute in Brno, Czech Republic. The head was stained with iodine to enhance contrast of soft tissues and fixed in a polypropylene conical tube with 0.5% agarose gel to prevent sample movement during the μ CT stage rotation. A total of 1600 projections were acquired; their relevant fraction was utilized to manually reconstruct the 3D model.

Statistical analyses have been performed by libraries of scripting languages, Python v3.16 (pandas, matplotlib, seaborn, scipy [44]). To statistically test bimodality in the length-frequency distribution of trawl-caught pikeperch individuals, we applied Hartigan's dip test using the `dip.test` function from the `dip.test` package and the excess mass test using the `modetest` function from the `multimode` package [45]. These computations and plotting were performed in the R software (v4.4.2) and ggplot2 [33].

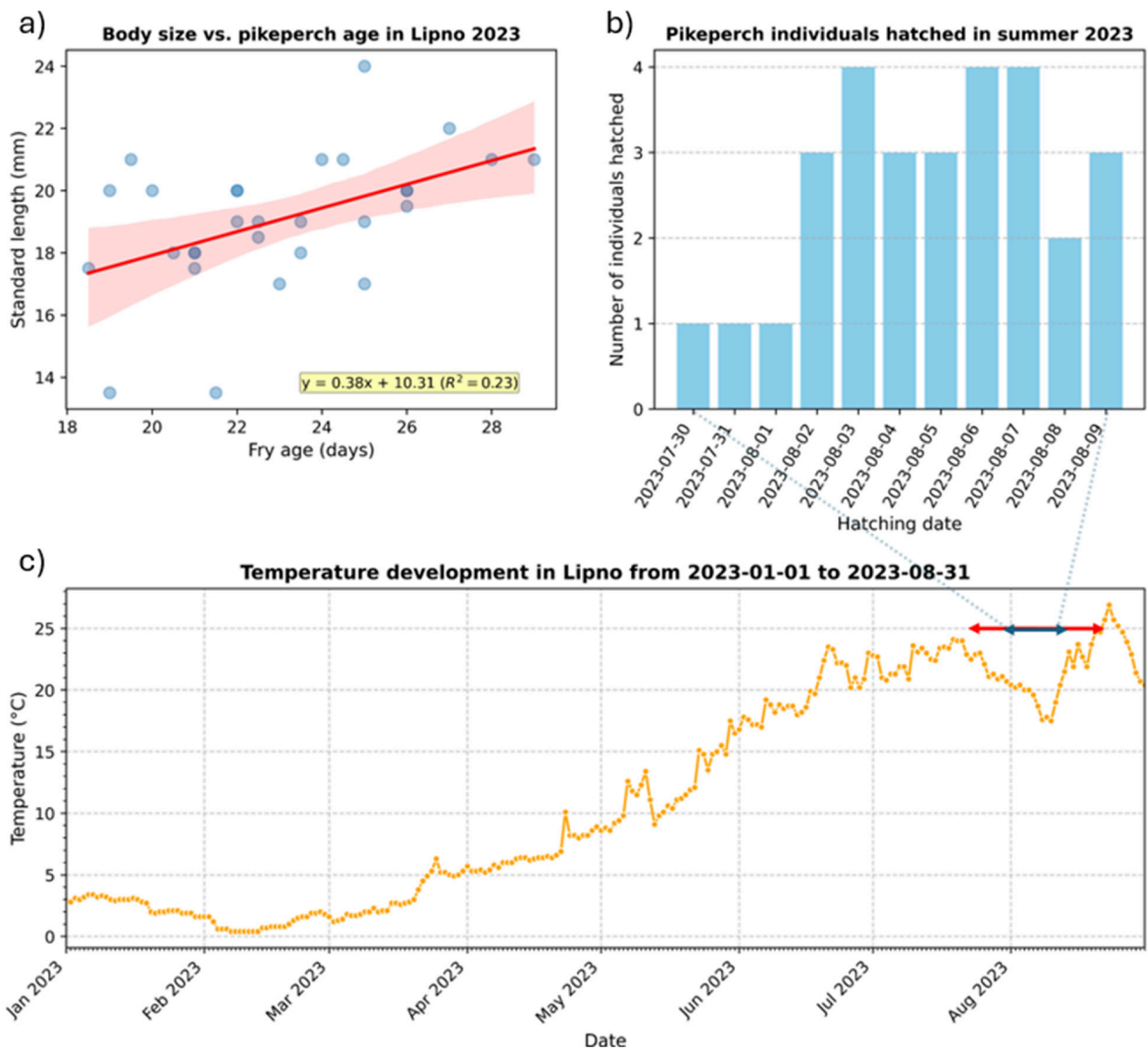


Figure 2. Overview of quantitative results for 29 pikeperch individuals originating from the summer hatching event in Lipno Reservoir sampled on 28 August 2023 (performed in Python). (a) Relationship between the standard length of extremely small pikeperch individuals and their average age in days; (b) extremely small pikeperch individuals aggregated according to their estimated hatch day based on daily otolith increments; (c) in-reservoir temperature records for the Lipno Reservoir, illustrating the thermal context of the summer-hatched pikeperch fraction recorded in this study (blue arrow). The red arrow delimits the time interval of the summer hatching event regarding the uncertainty in the first increment formation known in walleye.

The field sampling and experimental protocols used in this study were performed in accordance with the guidelines and permission from the Experimental Animal Welfare Commission under the Ministry of Environment of the Czech Republic (reference no. CZ 01679). The Experimental Animal Welfare Commission of the Biology Centre of the Czech Academy of Sciences approved the methods and ethics of the study.

3. Results

The sagittal otoliths analyzed in this study already had the flattened morphology (Figure 1). Analysis of their daily increments revealed the average age of sampled extremely

small pikeperch individuals ($n = 29$) as ranging from 18 to 29 days (with standard deviation $SD = 1.9$ and coefficient of variation $CV = 8.23\%$). Since these individuals were sampled on 28 August, they hatched between 30 July and 9 August 2023, provided that the first increment forms during the hatching, as observed in a pikeperch population in Czechia. Regarding the uncertainty in the timing of the first increment formation reported for walleye, the hatch date should be ± 7 days (Figure 2). Their standard length was in the range of 13.5–24 mm. The SL was positively, although weakly, related to the age of the extremely small pikeperch individuals (Figure 2; $R^2 = 0.23$). This pattern is in accordance with the size structure of the extremely small pikeperch individuals (Figure 3), where the gradually hatched extremely small individuals form the group with the largest size, but still do not overlap with the normal-sized pelagic individuals hatched in the spring spawning season.

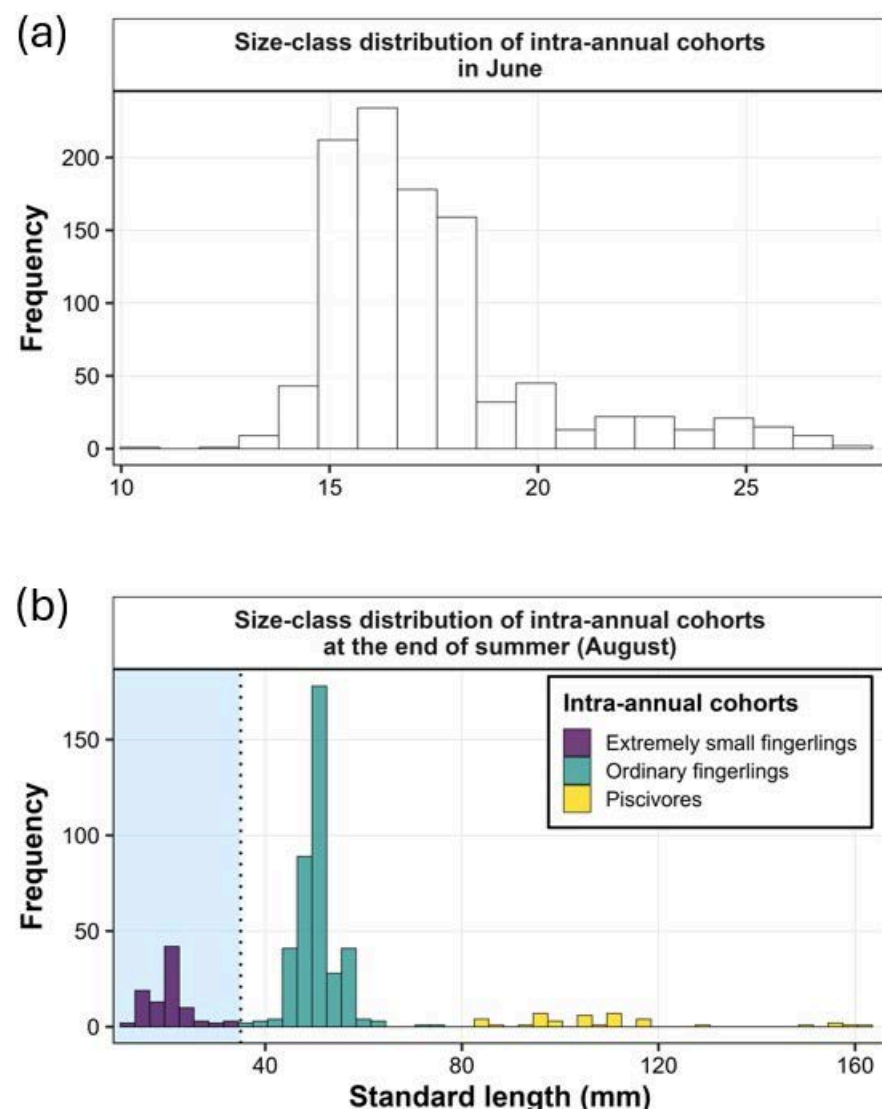


Figure 3. Graphic summary of pikeperch hatching in the Lipno water reservoir in 2023 (performed in R). (a) Visualization of the standard length of pikeperch hatched during the generally accepted spring hatching; (b) the size structure of all YOY pikeperch individuals originating from both hatching events, caught by night pelagic trawling and multimesh gillnets of the regular ichthyological survey at the end of August 2023, more details in [20].

The size structure of both extremely small and normal-sized pikeperch fingerlings when taken together shows a non-overlapping bimodal distribution (Figure 3). Both

methods of bimodality testing, i.e., Hartigan's dip test using the `dip.test` function and the excess mass test using the `modetest` function, strongly rejected unimodality (Hartigan's dip test: $D = 0.054$, $p < 0.001$; excess mass test: statistic = 0.096, $p < 0.001$). This confirms the bimodal size distribution within the pikeperch YOY population also quantitatively. The normal-sized planktivorous pikeperch individuals were more abundant than the extremely small individuals (Figure 3). Quantitatively, this situation is in accordance with the Scenario II described by [20] based on the ichthyological surveys of the Lipno Reservoir since 2003. Besides the year 2023 investigated in this study, a quantitatively similar situation with normal-sized pikeperch fingerlings heavily outnumbering the extremely small individuals also occurred in years 2008 and 2019 [20].

The aforementioned results, combined with numerous other studies listed earlier, enable us to establish a second hatching event of pikeperch in a single year. The second hatching event is clearly separated by more than two months from the generally known main spring (April to May) hatching season in the Lipno Reservoir (Figure 3).

4. Discussion

Occurrence of extremely small, i.e., late-hatched, pikeperch individuals co-existing with other intra-annual pikeperch cohort(s) and differing in body size was also recorded in other water reservoirs like Švihov (also known as Želivka; 2009) and Slapy (2004) in the Czech Republic and in two reservoirs in the Netherlands (2008), all reported by [9]. Such a late-hatched pikeperch intra-annual cohort was later also recorded in the water reservoir Římov (Jůza and Kubečka, *pers. comm.*). On the other hand, the absence of the late-hatched pikeperch individuals in the Lipno Reservoir was proved in the years 2003 and 2010, when the comparable sampling effort was performed, as in the years after [46]. Hence, the situation described in the Lipno Reservoir by this study is not specific only for this single site and sampling year 2023, and can be potentially extended. A factor that has substantially contributed to repeated identification of the late-hatched pikeperch intra-annual cohort is the unusually high sampling effort, including night trawling with a small mesh size of nets used [10].

Daily rings used here to estimate the hatching time of the ES pikeperch individuals represent a well-established tool in freshwater fish biology and aquaculture [35] as well as specifically in percid fish [36], including pikeperch [47]. The weak relationship between the standard length of extremely small pikeperch individuals and their average age in days (Figure 2) suggests that factors other than age determine their growth. The temperature can belong to environmental factors driving the body size in the ES pikeperch individuals hatched at the turn of July and August [48].

The following scenarios, based on intrinsic biological factors, may potentially explain the unusual occurrence of the late-hatched pikeperch individuals in the Lipno Reservoir:

1. Size- and age-dependent timing of spawning is known in pikeperch. Namely, individuals of different age and body size spawn at slightly different times: the oldest and the largest ones spawn first, whereas the younger and smaller ones spawn later [2]. This scenario could only be considered if there were a broad range of individuals of different ages and body sizes, resulting in non-overlapping spawning events, followed by non-overlapping hatching. Increasing temperatures during late spring and early summer would mean that later-laid eggs and later-hatched individuals experience higher incubation temperatures. The higher temperature would accelerate ontogeny and increase their chances of catching up with earlier laid and hatched conspecifics. This could blur the initial time difference between the early- and the late-hatched pikeperch individuals. Therefore, only a more substantial time difference (like two

months between late May and late July) itself could explain the origin of the extremely small intra-annual cohort of pikeperch.

2. A hypothetical case that pikeperch could be a so far unnoticed facultative batch spawner that usually spawns only once in a season in colder climates. Water warming may allow the underlying genetic capacity for batch spawning to be expressed, leading to the appearance of a seeming switch from total, or determinate, spawning. Batch (or fractional, portional) spawning is defined as spawning more than once during a spawning season, as opposed to spawning only once in a relatively short period, and is widespread among fishes [49]. Facultative batch spawning allows for a more even distribution of reproductive investment and increases the chances of encountering favorable conditions for larval survival [50].
3. A prolonged period of spawning and hatching might be a candidate factor potentially explaining the unusual occurrence of the late-hatched pikeperch individuals. The prolonged spawning period may improve the survival rate of the offspring since it increases the chances that at least some fraction of larvae will hatch at an optimum period [2]. This phenomenon belongs to bet-hedging evolutionary strategies, explaining how maternal effects can contribute to coping with environmental uncertainty and can increase offspring survival rate by reducing early-life competition [51,52]. However, the prolonged spawning itself would not have resulted in so distinct size classes of the normal fingerlings and the extremely small individuals as repeatedly described by [13,20]. The clearly bimodal size structure indicates that a second spawning runs independently of the spring spawning season (Figure 3).
4. Spatial heterogeneity and thermal gradients may also contribute to the explanation of the occurrence of late-hatched pikeperch individuals. Pikeperch in the Lipno Reservoir typically spawn at depths of 1.5–5 m (Kubečka unpublished observation). Hence, it is unlikely to undertake extensive upstream migrations into fast-flowing tributaries, where spawning grounds near tributary confluences are subject to different thermal regimes. Inflows from tributaries often maintain lower temperatures well into the spring due to thermal inertia from catchment areas. Consequently, pikeperch spawning in these inflow-affected zones may initiate reproduction significantly later than conspecifics inhabiting the warmer, sheltered bays of the main reservoir. This spatial asynchrony, driven by localized cooling from tributaries rather than riverine migration per se, would result in a distinct, later-hatching cohort appearing in the reservoir. Another so far unknown possibility would be delayed spawning and slower embryonal development in larger depths of the reservoir [19].

A probable combination of several of the aforementioned scenarios might have resulted in the situation in the Lipno Reservoir described in this study. Namely, eggs of the pikeperch individuals hatched at the turn of July and August must have been laid by parents that spawn only in the summer season (scenarios 1 and 3) or by parents that spawn in both spawning seasons as (facultative) batch spawners (scenario 2). Moreover, spatial heterogeneity resulting in thermal gradients and the availability of suitable spawning substrates likely influenced the timing of spawning readiness.

A combination of several of the aforementioned scenarios with an influence of the ongoing climate change and the consequent water warming could be another direction of potential explanations. The role of climate change and water warming aligns with the observation of the late-hatched pikeperch individuals for the Czech Republic and for the Netherlands [9]. Hence, it can be hypothesized that the occurrence of the late-hatched pikeperch is linked to water warming, as already extensively discussed by [13]. Fish physiological processes largely depend on the environmental temperature and photoperiod [53]. Therefore, the warming water approaches the temperature optimum known for pikeperch,

which in turn may impact reproductive behavior and its phenology. One such impact expected in the future may be that the warming water prolongs the summer season, whereby even the late-hatched individuals could survive the winter.

Pikeperch and generally species of the genus *Sander* (syn. *Stizostedion*) are supposed to respond to climate change by shifts in their reproductive phenology [54]; however, their response cannot be simply generalized for their entire area of Holarctic distribution with a wide gradient of temperature and photoperiod conditions [2,19]. Pikeperch have been shown to benefit from the warmer waters in terms of individual growth rates in central-European water reservoir(s) [16] as well as in the northernmost part of the Finnish coast (Bothnian Bay) [55]. On the other hand, no such response to water warming was identified in pikeperch of two lakes in the Netherlands [56]. Besides temperature itself, latitude and precipitation seasonality, together with zooplankton availability, are crucial for walleye [57,58]. Therefore, more factors are obviously involved in pikeperch reproductive phenology and for the subsequent fry survival.

Since the extremely small pikeperch is one of the main drivers of YOY pikeperch [20], it cannot be excluded that the late-hatched pikeperch secondarily serve to feed up the conspecifics in a similar way as trophic eggs do. Trophic eggs are known in fish, sharks, and coelacanths [53,59], and their function is not reproduction but nutrition, since they are usually unfertilised eggs. Observations in captivity, i.e., when fish are fed *ad libitum*, suggest that the provisioning of trophic eggs is widespread among species within the most species-rich lineage of the genus *Channa* [59]. It was also hypothesized that trophic eggs contributed to the large adaptive radiation found in the *Channa gachua* group [59]. Although the provisioning of trophic eggs is rare in fish, no other function of the late-hatched pikeperch can be found for the time being, since these individuals have only a little chance to survive their first winter [20]. A parallel situation can be seen in the opportunistic feeding of pikeperch on smelt (*Osmerus eperlanus*) in Estonia and the Netherlands [60,61]. In these cases, smelt serve to feed up the YOY pikeperch similarly to the late-hatched conspecifics in the Lipno Reservoir.

The exact knowledge on early-life ecology of pikeperch is crucial for ichthyology and fishery management, because the late-hatched individuals can occur in extreme abundances and have a positive influence on the early-hatched conspecifics [14,20]. In this way, the overall recruitment success can be modulated by the availability of this additional source of prey. The additional pikeperch spawning can also have further implications for filet quality [62]. Finally, should climate change lead to a prolonged summer, even the late-hatched individuals might have a chance to switch to piscivory before the onset of winter and to survive the first winter. This would have important implications for pikeperch recruitment and stocking management.

Given its complex ontogeny during the first year of life and its growing importance in aquaculture and fisheries management, pikeperch is positioned to become a novel model species for temperate freshwater biology, complementing established laboratory models like zebrafish (*Danio rerio*). The median time of evolutionary divergence between the genera *Sander* and *Danio* is 224 million years (supported by 35 scientific publications; [63]). Due to its significant divergence from the cyprinid model species zebrafish, pikeperch is an excellent model for central European eco-physiological studies, particularly regarding the impact of climate change and human activity on freshwater ecosystems. It has been established that the brain neuroanatomy of perciform species differs from that of zebrafish [64]. Hence, neurophysiological and general physiological differences can be expected across the teleost phylogeny, which would justify pikeperch as the novel model species. The complex knowledge on Lipno pikeperch obtained during the last decades has been recently accom-

panied by transcriptomics studies focusing on the transition of planktivorous pikeperch to piscivory [65,66], thus providing further types of resources.

Regarding the fact of how demanding detailed ichthyological surveys are, the following steps appear as feasible and potentially highly informative to provide more data on pikeperch spawning and hatching in lakes and reservoirs:

1. Size structure based on the June fry trawling samples combined with data on daily otoliths would represent a suitable comparison between the generally known April/May-hatched pikeperch and the here presented data on the end-of-August late-hatched pikeperch individuals.
2. Employing and monitoring of artificial pikeperch nests could elucidate the length, depth, and dynamics of the spawning season as described by [67] and shed light on the availability of suitable spawning substrate.
3. A population genetic analysis of June and August fry will assess whether the two spawning events are utilized by the same parents or by distinct groups.
4. An anatomic analysis of female ovaria and male testes after the first period of the spring spawning and/or before the period of the expected second spawning run, i.e., during July. This would test two potential situations: whether the same females spawn twice a year (when the second batch would be ripening after the first spawning) or whether the late spawners skip the spring spawning and spawn only in the summer spawning period.

Finally, this study has several limitations. While our results demonstrate an additional summer spawning event, we could not identify its underlying mechanisms or precisely determine the age of the extremely small pikeperch analyzed here.

5. Conclusions

Analysis of daily otolith increments in extremely small pikeperch individuals from Lipno Reservoir sampled during late August 2023 resolved the long-standing question regarding their origin as late-hatched. Although the study by Lappalainen et al. (2003) [19] remains the key reference for the reproduction biology of this species, our study suggests a need to update our understanding of pikeperch reproduction. Specifically, the observed flexibility in spawning time indicates that the species is more ecologically plastic than previously documented and thought. While one crucial question has been answered, more questions have arisen, particularly regarding the intrinsic biological factors leading to the additional hatching. Our four above-proposed scenarios remain untested hypotheses for downstream research. Similarly, it should be determined how climate change could further reshape the reproductive strategies of freshwater predators.

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Abbreviations

The following abbreviations are used in this manuscript:

ES	Extremely small
SL	Standard length (without tail)
YOY	Young-of-year

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