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Variability of pikeperch *Sander lucioperca* (L. 1758) cohorts in early life history

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Abstract – Year to year fluctuations in 0+ fish cohort strength are a common phenomenon. Many factors can affect cohort strength during the fish's early life period. In this study, development of a 0+ pikeperch *Sander lucioperca* cohort in the pelagic zone was studied by trawling for 50 days from first larvae hatching, in two consecutive years. In 2007, an abundant *S. lucioperca* cohort collapsed suddenly soon after hatching. After the incident, slow-growing *S. lucioperca* prevailed in the catch. In 2008, the catch gradually increased during the whole study period because of prolonged hatching. Environmental factors differed mainly in a slower temperature increase, higher water level and higher zooplankton abundance in 2008 compared to 2007. Our study revealed that a strong 0+ *S. lucioperca* cohort at the time of hatching might not result in a strong *S. lucioperca* cohort in general.

Keywords: Growth / recruitment / temperature / water level / zooplankton

Résumé – Variabilité des cohortes de sandre *Sander lucioperca* (L. 1758) au début du cycle biologique. Les fluctuations d'une année à l'autre de la force des cohortes de poissons 0+ sont un phénomène courant. De nombreux facteurs peuvent influer sur la force de la cohorte au début de la vie du poisson. Dans cette étude, le développement d'une cohorte 0+ de sandres *Sander lucioperca* dans la zone pélagique a été étudié par chalutage pendant 50 jours à partir de l'éclosion des premières larves, pendant deux années consécutives. En 2007, une cohorte abondante de *S. lucioperca* s'est effondrée soudainement peu après son éclosion. Après l'incident, *S. lucioperca* à croissance lente a prévalu dans les prises. En 2008, les prises ont augmenté graduellement pendant toute la période d'étude en raison de l'éclosion prolongée. Les facteurs environnementaux différaient principalement par une augmentation plus lente de la température, un niveau d'eau plus élevé et une plus grande abondance du zooplancton en 2008 par rapport à 2007. Notre étude a révélé qu'une forte cohorte de *S. lucioperca* 0+ au moment de l'éclosion pourrait ne pas donner une forte cohorte de *S. lucioperca*.

Mots-clés : Croissance / recrutement / température / niveau d'eau / zooplancton

1 Introduction

The assessment of population recruitment is crucial for fisheries management to choose an optimal strategy to exploit and maintain natural resources (Jakobsen *et al.*, 2009). Many factors can determine the cohort strength of 0+ fishes and the importance of these can be dependent on the ontogenetic phase (Eklöv and Persson, 1995; Garvey and Stein, 1998; Hoxmeier *et al.*, 2006; Blabolil *et al.*, 2016). Based on early information on cohort development, fisheries managers can conduct effective actions (*e.g.* stocking, parental stock support, spawning and nursery habitat adjustment) to support the target populations (Cowx, 1994).

Fish monitoring in temperate waters is usually conducted in the summer (CEN, 2005; Jůza *et al.*, 2015). At this time, all fishes hatched in the spring are several months old, large enough for easy species identification, and occur in their preferred habitats (Jůza *et al.*, 2015). During early life, many fish species disperse in the pelagic zone where they can be monitored by hydroacoustics and netting (Čech *et al.*, 2005). Non-invasive hydroacoustics have a great potential in sampling large water volumes, but species determination is difficult or impossible (CEN, 2014). Quantitative monitoring in the pelagic zone utilising fixed-framed trawls was recently developed to obtain reliable data about 0+ fish cohorts

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(Jůza and Kubečka, 2007; Jůza *et al.*, 2010). Despite data collection being robust there is considerable variation in estimates of fish abundance (Jůza *et al.*, 2014). Measuring fish length is a common tool to determine growth. To follow cohort development precise ageing is necessary (Ralston and Williams, 1988; Campana, 2001).

In the early larval phase, fishes are highly sensitive to environmental factors (Bone and Moore, 2008). Critical bottlenecks in cohort development can be either of short duration or long-lasting and can deplete fish energetic reserves (Moberg and Mench, 2000). The first important period determining cohort strength is spawning which can be affected by external stimuli such as photoperiod, temperature and availability of appropriate substrata (Balon, 1975; Morgan, 2008). After spawning, hatching and larval development are temperature dependent (Čech *et al.*, 2012). At high temperatures, larvae can hatch earlier, however, a longer time at the egg stage in colder conditions can improve fish development (Wood and McDonald, 1997). The first bottleneck after hatching is switching to exogenous feeding, when adequate food in type and quantity have to be present (Rao, 2003). At high temperatures, fishes have a higher metabolic rate compared to cold conditions and fish starvation is more likely due to high demands on the available food (Pepin, 1991).

In this study, pikeperch *Sander lucioperca* (L. 1758) was used as a model species. *Sander lucioperca* is a commercially valuable and a game fish, native to eastern Europe and western Asia and introduced to other European, Asian and north African countries (Specziár and Turcsányi, 2017; FAO, 2018). In natural water bodies, *S. lucioperca* is a top-predator and therefore it is used in many biomanipulative projects to reduce zooplanktivorous species and increase water quality (Wysujack *et al.*, 2002; Blabolil *et al.*, 2016). At most localities, *S. lucioperca* spawns in spring when the temperature increases to 8 °C. Males create nests as depressions in the bottom substrata that they clean from sediments often containing vegetation. After the eggs are spawned, they protect them until the larvae hatch (Lappalainen *et al.*, 2003). The larvae move into the pelagic zone and in late summer large individuals migrate into the littoral zone (Frankiewicz *et al.*, 1996; Specziár, 2005).

The aim of this study was to monitor the development of 0+ *S. lucioperca* cohorts from hatching for *c.* 50 days in two consecutive years using quantitative trawling in the lacustrine part of the Rímov Reservoir. In particular, we asked the following questions: Does the whole *S. lucioperca* cohort appear at the same time in the pelagic zone? Do the larvae and juveniles grow continuously during the study period? Is 0+ *S. lucioperca* growth the same in different years?

2 Materials and methods

2.1 Study site

The study was conducted in the Rímov Reservoir (Fig. 1). The reservoir (maximum depth 45 m, average depth 16 m, surface area 210 ha, volume 33.1×10^6 m^3) was built on the Malše River in 1978 for drinking water storage, flood control and hydroelectric power generation. The river is the main inflow with the long-term annual average water flow varying from 2.8 to 7.0 m^3 s^{-1}. The reservoir is dimictic with well-developed thermal stratification during the summer. A longitudinal gradient of productivity is developed and total phosphorus and chlorophyll-*a* concentrations are highest at the tributary and decrease downstream towards the dam (Sed'a and Devetter, 2000). The largest part of the reservoir in terms of volume (56%) and significant area (32%) is the mesotrophic lacustrine part (Fig. 1b), which has homogenous conditions. In the reservoir a long-term biomanipulation project has been conducted and predatory fishes have been propagated since 1985 (Ríha *et al.*, 2009). Despite the presence of a viable *S. lucioperca* population, natural recruitment is highly variable between years (Blabolil *et al.*, 2016).

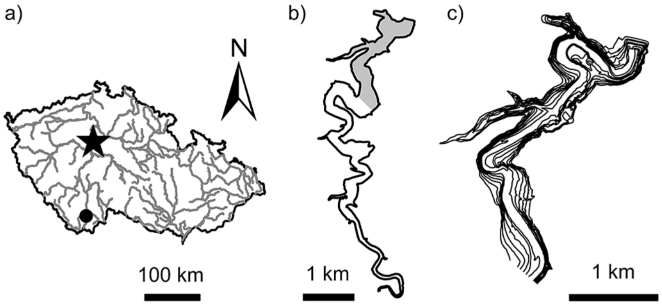

Fig. 1. (a) Location of the Římov Reservoir (black circle) and Prague (star symbol) within the Czech Republic. (b) Map of the Římov Reservoir with the lacustrine part (grey area) and (c) bathymetric map of the area with lines in 5 m intervals.

2.2 Fish sampling and processing

The 0+ fishes were collected on 1, 11, 21, 31 May and 12 June in 2007 and 24 April, 1, 5, 26 May and 5, 11, June in 2008. Fish sampling was done using a fixed-frame trawl with a mouth opening of 0.5 × 2 m in April and early May followed by 2 × 2 m opening in late May and July, a mesh size of 1 × 1.35 mm, with a collecting bucket at the end of the net (Jůza *et al.*, 2010). The trawl was towed 100 m behind a boat at a speed of 1 m s^{-1}. Trawling was performed in the pelagic (0–2 m depth) at a maximum distance of 1.5 km from the dam before the meandering part of the reservoir (Fig. 1b). The trawling was conducted at night with the exception of 12 June in 2007 and 26 May in 2008 when the sampling was done during the day. The trawl trajectory was measured by a GPS device and the sampled volume was calculated. A random subsample of 0+ *S. lucioperca* was immediately taken from the catch and frozen for laboratory processing, the other fishes were anaesthetized, and subsequently preserved in 4% formaldehyde solution.

In the laboratory, defrosted *S. lucioperca* were measured for standard length (L_S) with precision of 0.5 mm, sagittae otoliths for age determination were extracted, cleaned from any attached tissues and mounted on microscope slides using thermoplastic glue (Crystalbond 509 clear). The otoliths were viewed using an Olympus AX70 microscope (×200–600 magnification). When necessary to improve clarity, the otoliths were ground with a sandpaper of 400 and 600 grit (Blabolil *et al.*, 2018). The formaldehyde-fixed fishes were identified to species and *S. lucioperca* were counted and measured as for the defrosted sample.

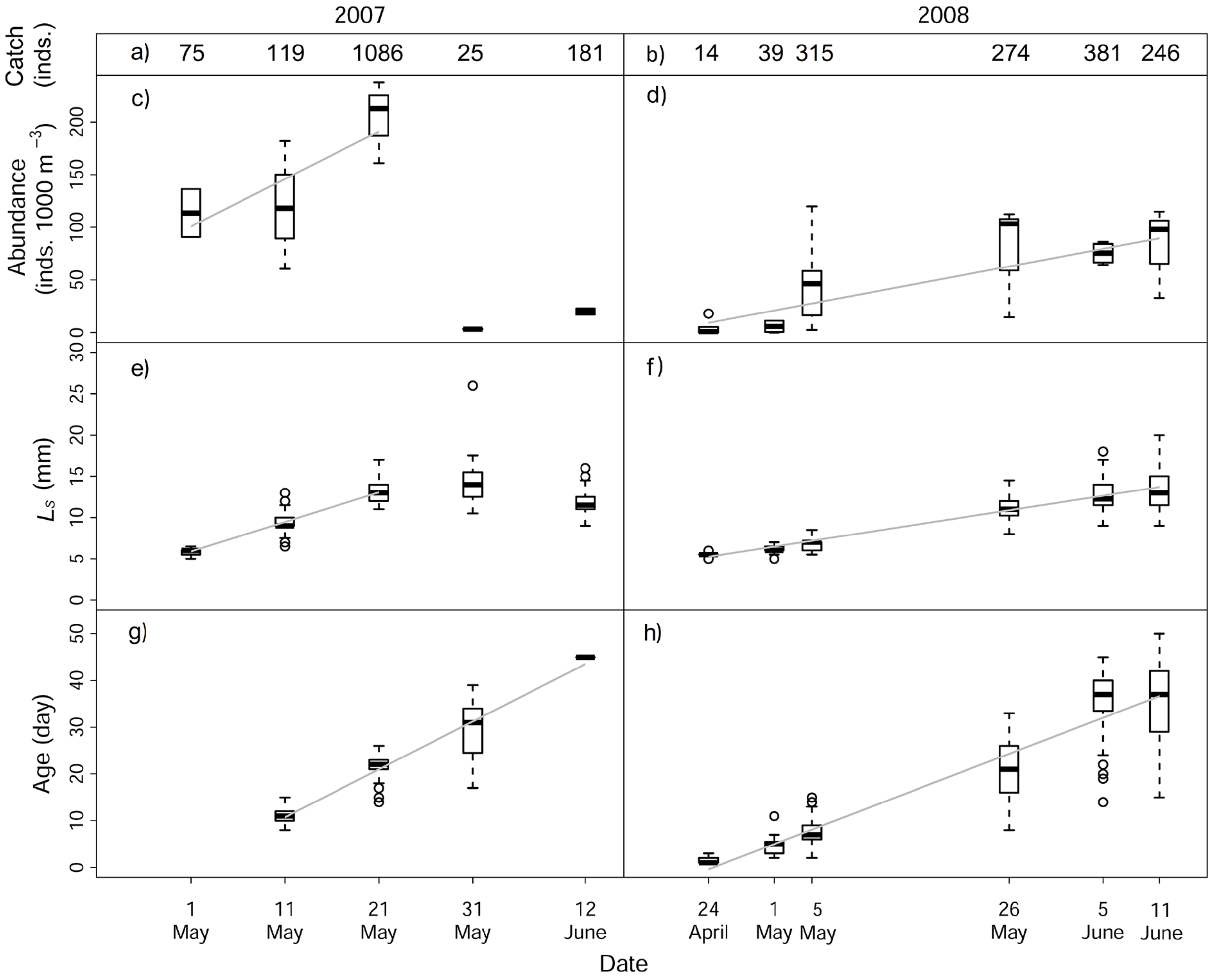

Fig. 2. Individual characteristics: (a), (b) catch, (c), (d) abundance, (e), (f) standard length (L_S), and (g), (h) age, of 0+ *Sander lucioperca* trawl catches in the Římov Reservoir in (a), (c), (e), (g) 2007 and (b), (d), (f), (h) 2008. Grey lines indicate linear relationship between observed values and sampling time. Median values (thick lines), upper and lower quartiles (boxes), maximum and minimum values (whiskers), and outliers (dots) are shown.

2.3 Environmental data

Water temperature (°C, at 1 m depth) and water level (m above the Baltic sea level) were measured every day at 0700 hours from the sampling tower located 80 m from the dam by the Vltava River Authority. Zooplankton were sampled during the daytime at 3 week intervals (25 April, 16 May and 6 June in 2007 and 23 April, 14 May and 4 June in 2008) by vertical hauls from the bottom to the surface with a 200 µm Apstein plankton net from a boat at the deepest part of the reservoir located 250 m from the dam. This was part of long-term monitoring programme of the reservoir. The samples were anaesthetised using chloroform and sorted into Copepoda and Cladocera (adults and copepodites). The zooplankton abundance was expressed as individuals per 0.01 m^2.

2.4 Data analyses

The *S. lucioperca* catch was expressed as individuals captured per 1000 m^3 of water sampled. The trends in 0+ *S. lucioperca* abundance, size, age and growth were tested by linear regression, where for direct comparison, the 24 April was set as day 1 for both years (the first sampling day in 2008). The data in the text are expressed as mean ± S.D. All statistical analyses were performed in R 3.4.2 (R Developement Core Team, 2018).

3 Results

The total 0+ *S. lucioperca* catch and sampled water volumes were 1486 individuals and 23,898 m^3 in 2017 and 1269 individuals and 29,192 m^3 in 2008 (Fig. 2a, b). The standardised 0+ *S. lucioperca* catch at similar times in both years was different (Fig. 2c, d). In 2007, the 0+ *S. lucioperca* catch was 113.63 ± 32.14 individuals 1000 m^{-3} on 1 May and increased up to 203.87 ± 39.19 individuals 1000 m^{-3} on 21 May, followed by sudden drop by two orders on 31 May and stayed low until the end of the study period (Fig. 2c). In 2008, the 0+ *S. lucioperca* catch was low 4.24 ± 7.15 individuals 1000 m^{-3} on 24 April and the average catch increased gradually by *c.* 1.68 individuals day^{-1} (slope of linear regression, $P < 0.01$) during the study period to 82.00 ± 43.28 individuals 1000 m^{-3} on 11 June (Fig. 2d).

In 2007, the growth of 0+ *S. lucioperca* was linear from 1 May 5.88 ± 0.39 mm L_S to 21 May 13.04 ± 1.36 mm L_S ($y = 0.36x + 3.02$, $P < 0.01$) followed by the occurrence of 0+ *S. lucioperca* of similar or smaller size (Fig. 2e). In 2008, the 0+ year growth was continuous during the whole study period from 5.61 ± 0.17 to 13.73 ± 2.44 mm L_S ($y = 0.18x + 5.02$; $P < 0.01$, Fig. 2f).

Sagittae otoliths were extracted and age determined from 0+ *S. lucioperca* from all sampling campaigns with the exception of 1 May 2007. The total number of read sagittae otoliths was 316 and 799 in 2007 and 2008. The range of *S. lucioperca* ages in 2007 was from 11.24 ± 1.31 days on 11 May to 45 days (only one individual) on 12 June (Fig. 2g) and in 2008 from 1.43 ± 0.86 days on 24 April to 35.56 ± 7.65 days on 11 July (Fig. 2h). The linear regressions between *S. lucioperca* age and the sampling dates were very significant: $y = 1.05x - 8.26$; $P < 0.01$ in 2007 and $y = 0.76x - 0.77$, $P < 0.01$ in 2008 (Fig. 2g, h). The S.D. of 0+ *S. lucioperca* age was not dependent on the sampling day in 2007 ($P > 0.05$), but significantly increased with the date of sampling in 2008 ($y = 0.13x + 1.05$, $P < 0.05$).

The relationship between 0+ *S. lucioperca* L_S at given age in 2007 was divided into two parts. By 21 May, the growth was faster in the first ($y = 0.45x + 4.62$; $P < 0.01$) than during the second part ($y = 0.32x + 5.04$, $P < 0.01$; Fig. 3a). In 2008, the relationship was the same during the whole study period ($y = 0.26x + 5.09$, $P < 0.01$; Fig. 3b).

In both years temperature increased during the study period (Fig. 4a). The spring was warmer in 2007 compared to 2008 when a more rapid temperature increase was observed (slopes of linear regressions 0.18 and 0.24 in 2007 and 2008). The water level was on average 1.37 m higher in 2008 compared to 2007 and stable in the study period (Fig. 4a). During the study periods, the abundance of Cladocera and Copepoda decreased in 2007 compared to increased abundance of Cladocera and peaking abundance of Copepoda in the middle of May in 2008 (Fig. 4b).

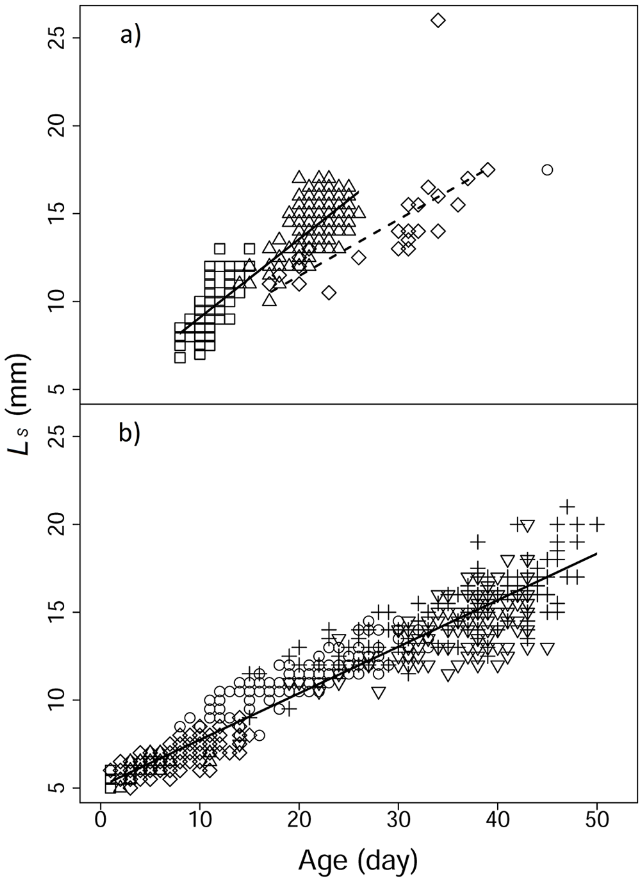

Fig. 3. Relationships between *Sander lucioperca* standard length (L_S) at age in (a) 2007 (square 11 May, triangle 21May, rhombus 31 May and circle 12 June) and (b) 2008 (square 24 April, triangle 1 May, rhombus 5 May, circle 26 May, inverted triangle 5 June and cross 11 June). Black lines indicate linear relationship between L_S and age. The sampling period in 2007 is divided into two parts, to 21 May and later. In the second part, the largest 0+ *S. lucioperca* (outlier) was omitted from the regression.

4 Discussion

The development of a cohort is a complex process affected by many factors acting at different times (Jakobsen *et al.*, 2009). The identification of the exact timing of a cohort bottleneck including changes in environmental variables is rare (Jůza *et al.*, 2014). The present study was fortunate in the timing of sampling in two consecutive years with significantly different development of 0+ *S. lucioperca* cohorts.

The greatest volume and depth of deep reservoirs is the lacustrine zone close to the dams. During the early larval and juvenile period *S. lucioperca* occur in the pelagic zone (Frankiewicz *et al.*, 1996; Specziár, 2005), that can be quantitatively sampled by trawling (Jůza and Kubečka, 2007; Jůza *et al.*, 2010). During the night, 0+ *S. lucioperca* occur mainly in layers close to the surface (Čech *et al.*, 2005), but in the day some fish can migrate into deep layers (Čech *et al.*, 2007; Jůza *et al.*, 2015). In this study, the pelagic layer was sampled during the day on 12 June in 2007 and 26 May in 2008. Therefore the reported catches at these two times should be interpreted as minimal. The littoral zone represents a minor part of deep reservoirs, and due to water level fluctuations the macrophyte dominated littoral is usually poorly developed and the pelagic zone begins close to the shore (Krolová et al., 2012).

In both years, the sampling began at the time of *S. lucioperca* hatching and their occurrence in the pelagic zone. Despite the fact that data on the parental stock were not collected, a previous study indicated that adult densities were low. Poaching was suggested to be the main reason for low abundance of *S. lucioperca* populations, even in drinking water storage reservoirs (such as the Římov Reservoir) where all public entry is officially prohibited (Vašek *et al.*, 2013). Similarly, predator pressure was not the reason for the sudden drop of the *S. lucioperca* cohort in 2007. The main predator of larvae and juvenile fish was the European perch *Perca fluviatilis* L., 1758 (Dörner *et al.*, 1999). They prefer benthic habitats and their abundance in the Římov Reservoir is low (Prchalová *et al.*, 2009; Říha *et al.*, 2009).

The main influence on the 0+ cohorts' development is temperature as it affects other processes (*e.g.* stratification and growth of poikilothermic organisms) in a waterbody. The optimal temperature for *S. lucioperca* growth is relatively high,

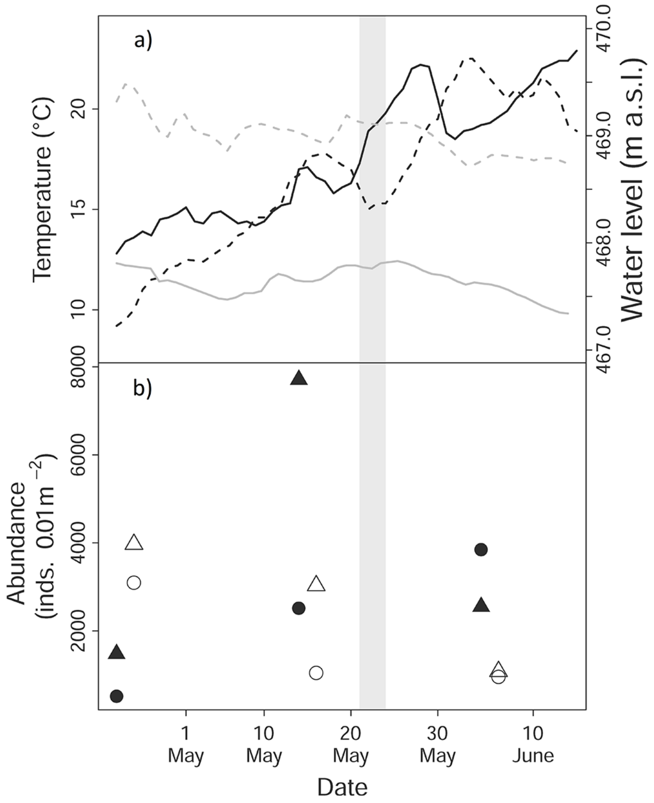

Fig. 4. (a) Temperature (continuous black line in 2007 and dashed in 2008), and water level (continuous grey line in 2007 and dashed in 2008) and (b) abundance of Cladocera (circles) and Copepoda (triangles) in 2007 (empty symbols) and 2008 (black symbols) during the 0+ *Sander lucioperca* sampling period. The grey bar indicates the period of 0+ *S. lucioperca* cohort collapse in 2007.

28–30 °C (Hokanson, 1977; Wang *et al.*, 2009) and many previous studies reported a positive relationship between *S. lucioperca* cohort strength and temperature (Lehtonen *et al.*, 1996; Kjellman *et al.*, 2003; Heikinheimo *et al.*, 2014). The spring temperature increase stimulates *S. lucioperca* to spawn and a higher temperature reduces the time to hatching (Lappalainen *et al.*, 2003; Löffler *et al.*, 2008). The warm spring in 2007 stimulated *S. lucioperca* to spawn, shortened the time before hatching and therefore many fish occurred at a similar time in the reservoir. The short time for development at the egg stage results in smaller larvae which have higher mortality (Löffler *et al.*, 2008). The 0+ *S. lucioperca* catch gradually increased in 2007 only until the middle of May. In 2008, the warming was slower and the 0+ *S. lucioperca* abundance increased during the whole study period suggesting prolonged hatching.

The 0+ *S. lucioperca* showed their fastest growth during the first period in 2007 and the slowest in 2008. The fastest growth corresponds to the observation of growth of 0.45 mm day^{-1} in a shallow pond with high 0+ *S. lucioperca* density and the artificial addition of zooplankton (Peterka *et al.*, 2003). In ponds with lower 0+ *S. lucioperca* densities, the growth was 1.05–0.90 mm day^{-1} (Peterka *et al.*, 2003). The same authors reported 0+ *S. lucioperca* growth in 1993 in the reservoir to be only 0.19 mm day^{-1}, but they commented that the observation was an artefact due to the prolonged spawning period in the reservoir (Peterka *et al.*, 2003). The observation in 2008 supports this explanation because of similar growth (0.18 mm day^{-1}) and age determination. A more reliable growth rate of 0.23 mm day^{-1} was provided by Ljunggren (2002) from cultured *S. lucioperca* in Sweden, a value close to the 0.26 mm day^{-1} calculated for L_S at the age in our study in 2008. In a laboratory experiment, Löffler *et al.* (2008) demonstrated temperature dependent growth (mean 13.0 ± 1.1 and 21.8 ± 2.1 mm total length at 15.5 and 18.0 °C after 40 days).

Sander lucioperca larvae switch to exogenous feeding at 5-6 mm L_S at an age of 8 days (Peterka *et al.*, 2003; Löffler *et al.*, 2008). High zooplankton abundance (>585 prey l^{-1}) should be present at the time of the switch and later on can be lower (Ljunggren, 2002). The first food are Copepoda followed by Cladocera (Peterka *et al.*, 2003; Specziár, 2005; Kratochvíl *et al.*, 2010). The zooplankton data collected during the spring in 3 weeks, at the time of fast changes in the zooplankton community (Sommer *et al.*, 2012), were insufficient for development of a predictive model. Although the whole water column was sampled, approximately 90% of the crustacean zooplankton in the Římov Reservoir is concentrated in the epilimnetic layer without any vertical diurnal migration (Seďa 1989, Seďa *et al.*, 2007) and therefore the zooplankton density data can suggest the processes driving 0+ *S. lucioperca* cohorts.

The first fast growing 0+ *S. lucioperca* group in 2007 matched the time of high zooplankton abundance, but later on, the cohort suddenly collapsed at the time of rapid temperature increase. After this period, only slower growing individuals were captured and at the same time the zooplankton abundance decreased. The mismatch in timing of the high zooplankton-abundance period is similar to one described by Persson and Brönmark (2008) in the Swedish Lake Ringsjön and by Wysujack *et al.* (2002) in the German Lake Feldberger Haussee. In the Římov Reservoir fish migration to the littoral zone is highly improbable because the zone occupies only a limited part of the reservoir (Blabolil *et al.*, 2016) and migration to deeper layers is mainly conducted during the day (Jůza *et al.*, 2010). Previous studies demonstrated no statistical significant size selectivity (Jůza *et al.*, 2010, 2012) with *S. lucioperca* catches of up to 40 mm L_S (Čech *et al.*, 2007). Therefore although the present study is based on only the uppermost pelagic layer, it reflects the representative part of 0+ *S. lucioperca* cohorts. The possibility that some fast growing (usually piscivorous, independent of zooplankton density) *S. lucioperca* could escape sampling, however, could not be excluded as the largest individuals were not captured and it is very rare that the largest individuals suffer the highest mortality during early ontogeny.

The 0+ *S. lucioperca* catch increased in 2008 and the growth was continuous suggesting gradual supplement of newly hatched fish, resulting in a higher 0+ *S. lucioperca* catch at the end of the study period. Moreover, in the three zooplankton samples of the 2008 period the abundance of Cladocera increased and the abundance of Copepoda peaked during the first half of May. Therefore a significant part of *S. lucioperca* larvae abundance matched the most suitable period of switching between food sources in 2008.

Water level should be considered when comparing cohort development. Water level in 2008 was more than 1 m higher than in 2007. When the water level is high, adult phytophilous

S. lucioperca have more suitable habitats with flooded terrestrial vegetation for their nests (Dimitrieva, 1973). There is a chance that the availability of suitable substrata stimulates more fish to spawn than when water levels are low.

This study focused on 0+ *S. lucioperca* cohorts. The collapse in 2007 might be one of the results of intraspecific competition. In the Římov Reservoir, 0+ *S. lucioperca* (5-10% of catch 0+ fishes) is usually present with ruffe *Gymnocephalus cernua* (L., 1758) (0-5%) and much more abundant 0+ *P. fluviatilis* (90–95%) in May followed by 0+ fish density increase by newly hatched cyprinids represented by the main species in the reservoir bream *Abramis brama* (L., 1758), bleak *Alburnus alburnus* (L., 1758) and roach *Rutilus rutilus* (L., 1758) in June, when cyprinids dominate (>90%) in the pelagic community (Jůza *et al.*, 2010, 2014). All these species can compete with 0+ *S. lucioperca* for food sources.

The sampling interval could be more frequent than *c.* 10 days that we carried out to better capture the timing of cohort collapse or development. The data series in 2008 is not complete because the samples taken in 15 May were spoiled by incorrect storage. The study period of *c.* 50 days seemed to be sufficient. A previous study (Blabolil *et al.*, 2016) dealing with 0+ *S. lucioperca* cohorts at the end of summer, found the cohort in 2008 to be much stronger than in 2007 and therefore supporting our observation.

Intensive sampling can reveal short term fatal periods in development of a 0+ *S. lucioperca* cohort. Quantitative sampling in the pelagic zone can provide robust abundance estimates and captured fish can be used for other analyses. Daily estimates of age can provide valuable insights into fish growth. Routine monitoring of environmental parameters performed by water authorities may provide useful background data for interpretation of scientific observations. In this study, the cohorts were clearly determined early after hatching. The results provide valuable insights that can guide further research, help fisheries managers and broaden knowledge on *S. lucioperca* early life history.

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