

First-season growth and food of YOY pike (*Esox lucius*) are habitat specific within a lake

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ABSTRACT

Piscivorous fish are important predators in aquatic systems and as such they can have far-reaching effects on ecosystem composition and function. These effects depend on piscivore predation rates and behaviour, and recruitment of young-of-the-year fish into piscivory can hereby govern ecosystem properties. Growth and recruitment can differ between water bodies due to e.g. general productivity, but information on variation in juvenile growth and body condition between habitats within water bodies is scant. We here evaluate growth, body condition, food occurrence and stomach contents of an important piscivore, pike (*Esox lucius*), over the first growth season in two contrasting and spatially separated homogenous habitat types (emergent and submerged vegetation separated by 50 m of open sand) within the same lake. Individual size and body condition in pike were higher in the submerged vegetation early in the season, whereas by the end of their first summer pike were larger and in higher body condition in the emergent vegetation, in spite of occurrence of zooplankton, macro-invertebrates and fish prey being overall higher in the submerged vegetation. Pike showed habitat-specific patterns of macroinvertebrate consumption (higher in the submerged vegetation) and date-specific patterns of zooplankton (higher early in the season), macroinvertebrate (lower late in the season) and fish (higher later in the season) consumption that were not a result of occurrence of food types, as occurrence and consumption patterns did not match. We conclude that pike that hatched in the emergent vegetation habitat were larger towards the end of the season and, hence, these pike should have a higher survival probability and possibly contribute more to pike population density and predation at older ages, but also that submerged vegetation provides an alternative and added recruitment environment for pike in shallow lake ecosystems.

1. Introduction

Aquatic keystone predators at the top of the food chain (piscivorous fish) may have strong effects on the structure, function, and biodiversity of freshwater and coastal ecosystems (e.g. [Carpenter and Kitchell, 1993](#); [Hanley and La Pierre, 2015](#)). The effects of piscivores depend on their predation pressure on prey fish, and recruitment of piscivorous fish is particularly important as piscivores can regulate the recruitment and abundance of zooplanktivores with possible top-down trophic cascades and whole-system effects ([Carpenter et al., 1985](#)). Although it is well established that growth and recruitment patterns of aquatic predators may vary extensively between different water bodies (e.g. [Moslem-Aqdam et al., 2021](#)), less is known about how growth and body condition of first-year recruits may vary between the disparate habitat types

generally found within lakes.

The growth of young-of-the-year (YOY) fish often shows an intimate relationship with recruitment success in fish ([Chambers and Trippel, 1997](#); [Oele et al., 2018](#)). For example, mortality is size dependent and individual fish with higher growth often show higher survival than smaller conspecifics, partly because larger individuals are less vulnerable to gape-limited predators (e.g. [Hambright et al., 1991](#); [Nilsson and Brönmark, 2000](#)). Moreover, studies of growth rate have shown a considerable variability among individuals in natural populations ([Boel et al., 2018](#); [Cucherousset et al., 2009](#); [Mann and Beaumont, 1990](#)) and such differences in growth rates could lead to variation in survival and thereby recruitment, and food availability should be a key determinant of growth ([Boel et al., 2018](#); [Nunn et al., 2012](#)). Further, piscivores commonly undergo pronounced ontogenetic diet shifts, from

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zooplankton and macroinvertebrates to fish, during early life (e.g. Galorowicz et al., 2011; Persson and Brönmark, 2002; Skov and Nilsson, 2018), and the occurrence of these food types typically vary between different habitats (Hargeby et al., 1994; Marklund et al., 2001). However, whether within-lake variability in habitat-specific food occurrence and first-year growth have bearing for recruitment into piscivory remains elusive, despite obvious implications for management and conservation incentives.

The pike (*Esox lucius*) is an important piscivore in temperate freshwater systems with a potential for structuring freshwater food webs through cascading trophic interactions (Craig, 1996; Raat, 1988; Skov and Nilsson, 2018). Pike are gape-size limited predators that can catch and consume very large prey in relation to their own body size (Nilsson and Brönmark, 2000), but prefer to feed on smaller prey when given the choice (Juanes, 1994; Nilsson et al., 2000). They are highly dependent on vegetation for spawning, shelter and foraging, and YOY pike, specifically, depend heavily on vegetation for both foraging and predator avoidance (Casselman and Lewis, 1996; Craig, 1996; Skov and Nilsson, 2018). Submerged and emergent freshwater macrophytes are important in this context and both these vegetation types commonly co-occur in shallow lakes (Craig, 1996; O'Sullivan and Reynolds, 2005).

In this study, we focus on habitat-specific recruitment of pike into piscivory by evaluating first-summer growth and diet of YOY pike in well-defined habitats characterized by a dominance of either submerged or emergent vegetation, separated by open sandy areas, within the same lake. We assume that habitat use in YOY is restricted to the specific habitats, i.e. that individual pike do not switch habitats, as earlier studies have shown limited movement and small home ranges (<15 m radial distance) in YOY pike (Cucherousset et al., 2009; Nyqvist et al., 2018). Moreover, YOY pike should avoid venturing across the open, sandy bottoms without vegetation where susceptibility to predation is much higher than in the more complex vegetated habitats (e.g. Savino and Stein, 1982). Accordingly, both small and large size classes of pike have been shown to display a preference for complex, vegetated habitats, and avoidance of open sand habitats (Eklöv, 1997). We evaluated a set of key characteristics of the first growth season recruitment process, including habitat-specific YOY pike body size, body condition and stomach content, as well as food occurrence in the two habitats.

2. Material and methods

2.1. Study site

The lake Krankesjön (55°42' N, 13°28' E, 3.4 km²), situated in southern Sweden, is a shallow (max depth 3 m), moderately eutrophic lake (Hargeby et al., 1994). There are two main vegetation habitats within the lake, where emergent vegetation (reed *Phragmites australis* and great fen-sedge *Cladium mariscus*) grows along the shoreline, and submerged vegetation (mainly stonewort *Chara* spp) grows offshore on the bottom of this shallow lake (Blindow et al., 2002). The vegetation in the stonewort beds (the submerged vegetation type) are dense and the architecture of stonewort creates a more complex habitat (Hargeby et al., 2004). The emergent vegetation habitat along the shoreline is about 10 m wide and ranges c. 0–1 m water depth. The submerged vegetation covers about 60% of the lake area at depths ranging c. 1–2 m. The two vegetation habitat types are separated by an approximately 50 m wide, unvegetated area with sandy bottom, and given the restricted home ranges of YOY pike (Cucherousset et al., 2009; Nyqvist et al., 2018) and that vegetation is crucial for foraging while avoiding predation (Eklöv, 1997; Jacobsen and Engström-Öst, 2018) this should minimize YOY pike movement between the two vegetated habitats.

Within each vegetation habitat type we sampled five 10 m transects, all perpendicular to the shoreline and starting c. 1 m outside the vegetation edge. On each transect we selected three points for sampling: 1) the outer end of the transect 1 m outside the vegetation, 2) 5 m in on the transect, within the vegetation, and 3) the inner end of the transect (i.e.

close to the shore at c. 0.3 m depth for emergent vegetation transects). We sampled the transect points in both habitats on four occasions during the first pike growth season, from June, when pike first become susceptible to capture by electrofishing, to September, after which decreasing temperatures restrict growth (Fey and Greszkiewicz, 2021). Sampling occurred on June 14th, July 6th, August 3rd and September 19th of 2005.

2.2. Fish sampling

Point-abundance-sampling electrofishing (10 s at each of the three sampling points of each transect, e.g. Perrow et al., 1996, LUGAB L1000 electrofishing gear, 1 kW, 600 V) was used to obtain proxies of habitat-specific prey fish densities, focusing on cyprinids as this is the dominant fish prey type in the lake. During each 10 s sampling, all stunned and visible fish were netted and retained. After fishing all points for all transects in one habitat we continued fishing along the transects in that habitat for YOY pike until 7–20 individuals were caught. All YOY pike were sacrificed (benzocaine overdose) and later measured for total length (TL, nearest mm) and weight (W, nearest 0.01 g). Pike condition was calculated as Fulton's K ($K = 100 \cdot W \cdot TL^{-3}$) (Nash et al., 2006). Stomachs from the pike were dissected and preserved in ethanol for later lab analyses of number of individual zooplankton and macroinvertebrates per stomach, as well as presence/absence of fish prey (only three individuals had more than one fish prey in their stomach). Ethical concerns on care and use of experimental animals were followed under permission (M14-04) from the Malmö/Lund Ethical Committee.

2.3. Invertebrate and plant sampling

Invertebrate sampling was performed at the transect points the day after each fish sampling occasion (due to logistic time constraints). In the emergent vegetation habitat, invertebrates were sampled by enclosing vegetation (after being cut off at the water surface) in a net (20 cm in diameter, mesh size 20 µm) from above and cutting the vegetation 20 cm below the water surface. In the submerged vegetation habitat, invertebrates and vegetation were collected from the upper 20 cm of the macrophyte bed with a custom built pair-of-tongs-shaped sampler (1.3 m long rods) with sharp-edged metal cylinders (5.5 cm long and 10 cm in diameter), with sampling nets (mesh size 20 µm), facing each other at the end of the rods (Marklund, 2000). Vegetation was cut and sampled with associated invertebrates, and each sample was separated immediately upon collection, where invertebrates were preserved in alcohol and vegetation was placed in plastic bags. Macrophytes and invertebrates were sampled using different methods as the macrophyte types differ substantially in physical structure and no method works conveniently for both. Invertebrates were identified and counted in the lab, with zooplankton (mainly consisting of daphnids) and aquatic macroinvertebrates (*Asellus aquaticus*, Ephemeroptera, *Erythromma*, Chironomidae, Coleoptera) separated into two different categories to represent the ontogenetic diet changes in YOY pike. Plants were dried in 58 °C for two days and weighed (to nearest 0.01 g), and zooplankton and macroinvertebrate densities were calculated as number of individuals per g plant dry weight according to Marklund et al. (2001), as invertebrates are highly associated with vegetation structure in these habitats.

2.4. Statistical analysis

The dependent variables individual pike length (log₁₀), weight (log₁₀) and Fulton's condition factor (log₁₀) were compared between habitats (fixed factor) over the seasons (sampling date, fixed factor) in a general linear model (type III sums of squares) including the habitat×date interaction term. Proxies of habitat- and date-specific pike densities were not analysed as most point-abundance samplings did not catch any pike. The dependent variables number of zooplankton and

macroinvertebrates per pike stomach as well as per sample plant dry mass were analysed with a corresponding non-parametric two-way Scheirer-Ray-Hare model (Sokal and Rohlf, 1995) comparing habitats and dates as data did not meet distribution assumptions, even after transformations. The probability of pike stomachs containing YOY cyprinid prey was analysed with logistic regression with likelihood ratio backwards elimination from the full two-way habitat×date factorial design. Statistical analyses were performed in IBM SPSS 27 for Mac.

3. Results

The general linear models revealed significant habitat×date interaction terms for pike mean body sizes and conditions (Table 1, Fig. 1a-c). Early in the season (June-July) the pike in the submerged vegetation were comparably longer and heavier than pike in the emergent vegetation, while later in the season (August-September) pike in the emergent vegetation were longer and heavier than pike in the submerged vegetation (Fig. 1a-b). Pike body condition, quantified as Fulton's K,

Table 1

General linear model effects (upper panel) of factors habitat and date and their interaction term on pike individual total lengths (mm, log transformed), weight (g, log transformed) and Fulton's condition factor K (log transformed). The lower panel shows corresponding Scheirer-Ray-Hare (SRH) analyses of factorial effects on dependent variables number of zooplankton and macroinvertebrates per sample plant dry mass as well as pike stomach, along with numbers of young-of-the-year (YOY) cyprinids caught. Shapiro-Wilk (S-W) test p-values confirmed normality of model residuals ($p = 0.410$; $p = 0.266$; $p = 0.530$), and F-tests confirmed variance homogeneity ($F_{1,99} = 0.130$, $p = 0.719$; $F_{1,99} = 0.293$, $p = 0.589$; $F_{1,99} = 3.104$, $p = 0.081$) for log length, log weight and log Fulton's K, respectively. Significant effects are indicated in bold.

	F	df	p	R ²
log length				0.864
habitat	0.567	1,93	0.453	
date	179.406	3,93	< 0.001	
habitat×date	6.887	3,93	< 0.001	
log weight				0.859
habitat	0.181	1,93	0.672	
date	170.650	3,93	< 0.001	
habitat×date	9.820	3,93	< 0.001	
log Fulton's K				0.441
habitat	3.248	1,93	0.075	
date	12.032	3,93	< 0.001	
habitat×date	8.120	3,93	< 0.001	
SRH χ^2 df p				
zooplankton per plant dry mass				
habitat	23.564	1	< 0.001	
date	13.171	3	< 0.01	
habitat×date	3.537	3	> 0.25	
zooplankton per stomach				
habitat	1.772	1	> 0.1	
date	21.746	3	< 0.001	
habitat×date	1.598	3	> 0.5	
macroinvertebrates per plant dry mass				
habitat	85.002	1	< 0.001	
date	3.139	3	> 0.25	
habitat×date	1.051	3	> 0.75	
macroinvertebrates per stomach				
habitat	148.520	1	< 0.001	
date	18.754	3	< 0.001	
habitat×date	3.942	3	> 0.25	
number of YOY cyprinids in habitat				
habitat	18.437	1	< 0.001	
date	5.129	3	> 0.1	
habitat×date	6.883	3	> 0.05	

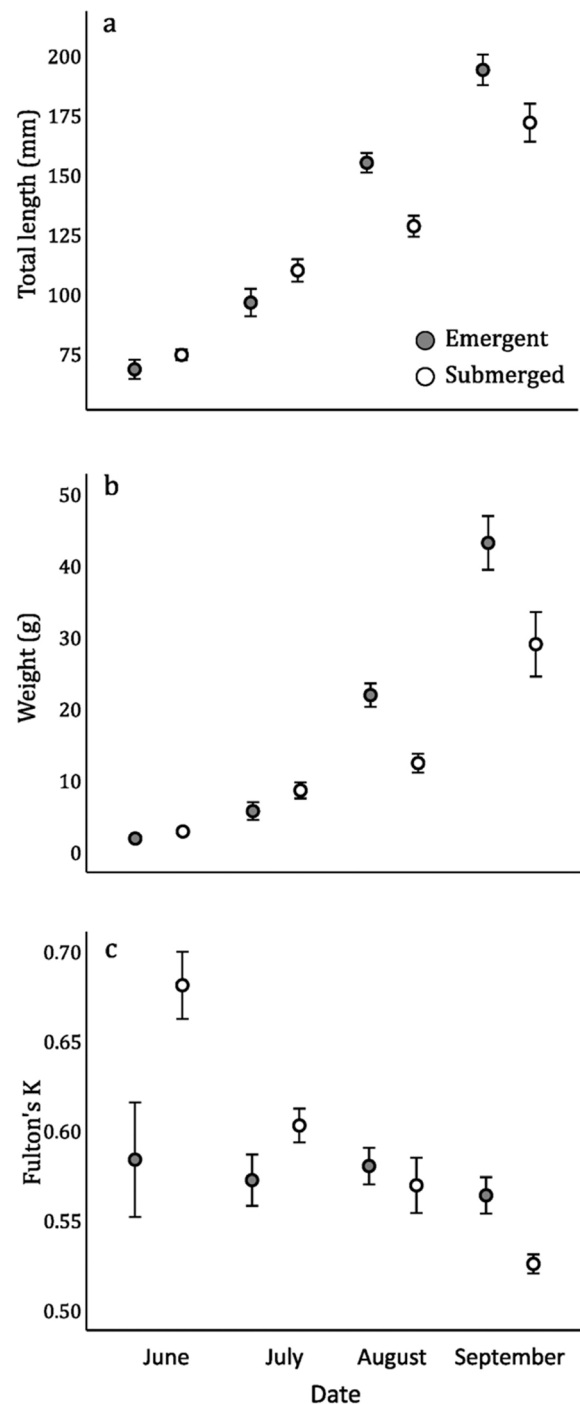


Fig. 1. Body growth (total length and weight) and condition developments (mean±SE) over the first growth season (months refer to June 14th, July 6th, August 3rd and September 19th of 2005) in young-of-the-year pike (*Esox lucius*) caught in emergent and submerged vegetation. Number of pike caught in emergent and submerged vegetation, respectively: June – 7 and 13, July – 10 and 15, August – 11 and 12, September – 20 and 13.

decreased over the season in the submerged vegetation, from a comparably high to a comparably low K, while the body condition of pike in the emergent vegetation habitat did not change over the season (significant interaction term in Table 1, Fig. 1c). The overall significant main effects of factor date on length and weight merely indicate that pike grew over their first summer, whereas there was no main effect of the habitat factor (Table 1, Fig. 1a-b).

Prey numbers were significantly higher in the submerged vegetation

habitat as compared to the emergent vegetation for zooplankton, macroinvertebrates and YOY cyprinids alike (Table 1, Fig. 2a-c). The number of zooplankton was also different between sampling occasions over the summer season (Table 1, Fig. 2a). There were no significant habitat×date interaction terms for prey numbers (Table 1).

Pike stomach contents of zooplankton, macroinvertebrates and YOY

cyprinids were all significantly different between sampling dates (Table 1, Fig. 2d-f, final logistic model on fish prey occurrence contained a significant effect of sampling date: Wald $\chi^2=9.361$, $df=3$, $p=0.025$, whereas factor habitat, $p=0.930$, and the habitat×date interaction term, $p=0.584$, were sequentially removed from the previous models). Number of zooplankton in stomach contents was high at the June

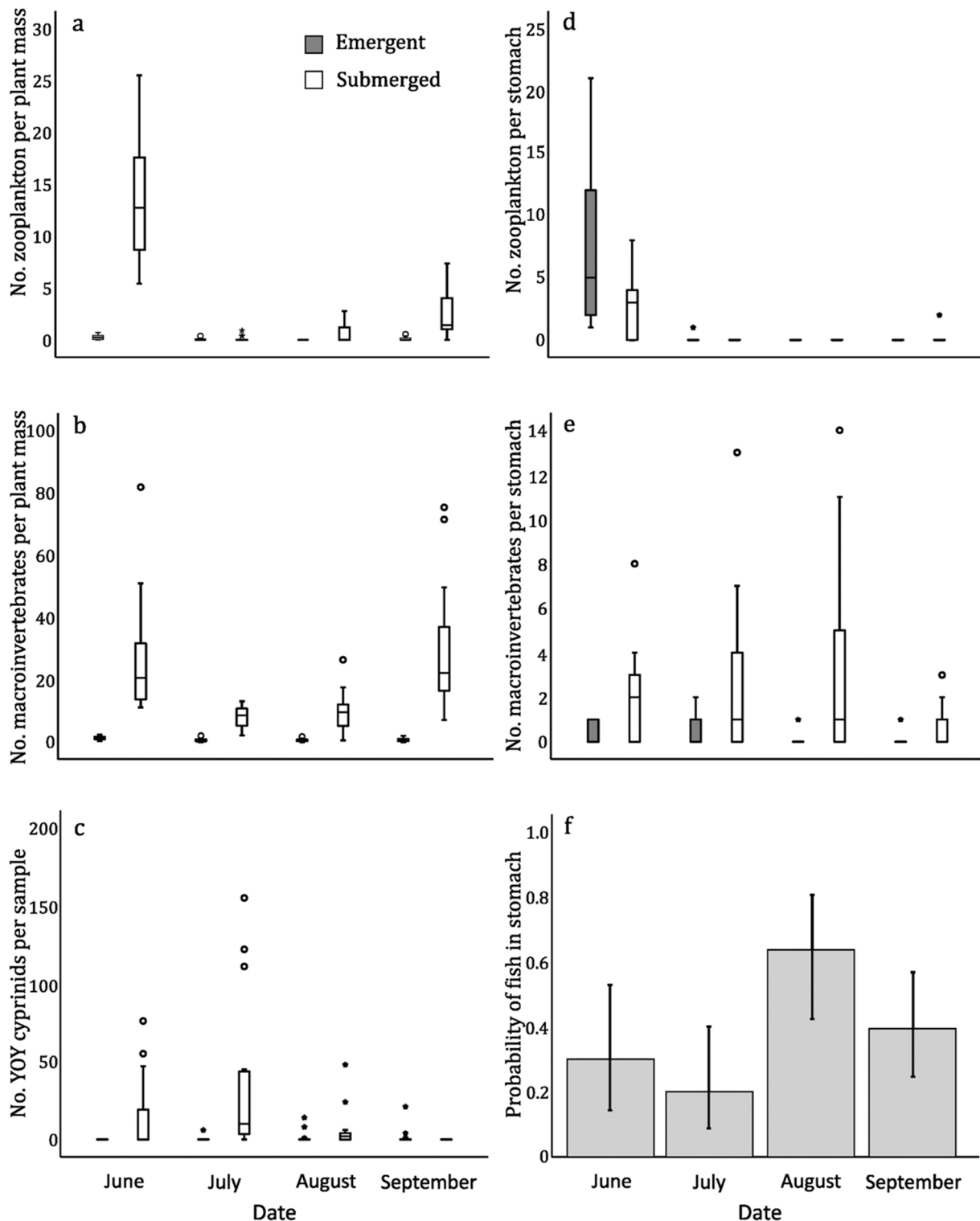


Fig. 2. Habitat-specific (emergent and submerged vegetation) food occurrence and prey occurrence in pike (*Esox lucius*) stomachs over the first growth season (months refer to June 14th, July 6th, August 3rd and September 19th of 2005 for c-f, and the respective days after for a-b) in young-of-the-year pike. Fig. 2a-e are box plots and Fig. 2 f the estimated probabilities from logistic regression \pm 95%CI. To enhance readability, the y axes in Figs. 2a and 2b are adjusted to not show high extreme values. Fig. 2a has one extreme of 86.4, and Fig. 2b has one extreme of 195.45, both from the June samples from submerged vegetation.

sampling, but negligible during the rest of the season (Fig. 2d), macroinvertebrates were least represented in the diet from the September sampling (Fig. 2e), and probability of YOY cyprinid prey in pike stomachs was higher from the August sampling (Fig. 2f). The number of macroinvertebrates in pike stomachs was also affected by the habitat factor, where pike in the submerged vegetation habitat consumed more macroinvertebrates (Fig. 2e).

4. Discussion

We found that seasonal patterns of YOY pike growth (length and weight) and body condition (Fulton's K) differed between the two habitat types over the first summer growth season. Early in the season (June–July), pike in the submerged vegetation habitat were larger and had a relatively higher body condition than pike in the emergent vegetation. In August and September, these patterns were reversed, such that pike in the emergent vegetation were larger and had higher body condition by the end of the season. This shift in relative body condition between habitats was driven by a gradual decrease in body condition of pike in the submerged vegetation, while body condition remained constant in pike from the emergent vegetation.

As individual body size and condition are likely to affect survival in fish, this suggests that pike in the emergent vegetation could approach their first autumn with a better opportunity of surviving and contributing to future pike population density. From this perspective, the emergent vegetation habitat may be viewed as a more productive and, hence, important habitat for pike growth and subsequent recruitment. This, however, relies on our assumptions that YOY pike remain stationary in a given habitat type. Studies on movement strategies in YOY pike indicate a sedentary life style as they move only short daily distances (6–8 m) and have small home ranges with less than 15 m average radial distance (Cucherousset et al., 2009; Nyqvist et al., 2018). Switching between habitats would also mean leaving the safety of the vegetated habitat and swimming across the 50 m wide sandy, unvegetated bottoms separating the two habitat types. Accordingly, pike have been shown to avoid sandy, open habitat in habitat preference assessments (Eklöv, 1997).

Differences in growth and body condition in pike from the two habitats could not be explained by differences in food occurrence alone. In YOY pike, individuals undergo size-dependent and ontogenetic diet shifts early in life, from zooplankton, to macroinvertebrates and fish prey (Craig, 1996; Raat, 1988; Skov and Nilsson, 2018). Because of this, we expected foraging and growth opportunities to be influenced by the habitat-specific occurrences of suitable prey types. At about 120 mm body length, a majority of YOY pike switch to a piscivorous diet (probability of piscivory reaches 0.5 at about 120 mm total length in pike, Skov and Nilsson, 2007). This suggest that a switch to piscivory occurred in mid-July in the studied pike, between the second and third sampling event. Our sampling revealed that all three prey types – zooplankton, macroinvertebrates and YOY cyprinids – were consistently more abundant in the submerged vegetation than in the emergent vegetation, where all prey types remained at low densities throughout the season. In the submerged vegetation habitat, YOY pike grew better and had higher body condition early (June–July) in the season. This is consistent with the observed higher occurrence of zooplankton and macroinvertebrate prey at this time of the year when most YOY pike have not yet reached sizes that allow for piscivory (Skov and Nilsson, 2007). However, despite the higher occurrence of zooplankton prey in the submerged vegetation at the first sampling occasion, pike stomachs from the submerged vegetation habitat contained comparably fewer zooplankton than pike stomachs from the emergent vegetation. This suggests that prey occurrence was not a major driver of pike stomach contents in this system. Similarly, we find that occurrence of macroinvertebrates in the habitats did not mirror occurrence of macroinvertebrates in pike stomachs, although the occurrence of macroinvertebrates in stomachs is higher for pike from the submerged

vegetation habitat. The weak links between prey occurrence and pike diet could be partly due to habitat complexity or sampling methods. A higher habitat complexity, here provided by submerged stonewort vegetation as compared to emergent reed and fen-sedge vegetation, may alter foraging success and thereby diet composition, as habitat complexity is known to affect foraging success in fish (e.g. Crowder and Cooper, 1982; Eklöv 1997). Also, the vegetation and invertebrates were sampled with different methods in the two habitats the day after electrofishing, with possible consequences for quantitative results on food-type occurrences and temporal availability to pike. Later in the season (August and onward), when pike sizes to a greater extent allow for a piscivorous diet, pike were larger in the emergent vegetation habitat. However, attributing this size difference to piscivory cannot be corroborated by our data. The occurrence of YOY cyprinid prey was relatively low in our samples from both habitats, and there was no difference between habitats in the probability of finding fish prey in pike stomachs. As our point-abundance sampling of pike in the two habitats did not suffice for estimation of relative CPUE pike densities over the season, we can unfortunately not exclude density-dependent effects on pike growth and body-condition development. It is possible that e.g. mortality from predation and/or starvation differ between the habitats, affecting pike densities, making intracohort competition differently strong in the two habitats, which could contribute to the presented results. The specific links between habitat-specific prey-type occurrences, diet composition and YOY pike growth deserve further attention, preferably with higher temporal resolution in sampling and consideration of possible density-dependent effects.

We conclude that first-season growth and food occurrence of YOY pike can be habitat specific within lakes, and that pike in the emergent vegetation habitat are larger and have a higher body condition later in the first growth season. Although this end-of-season size difference cannot be mechanistically explained by our data on prey occurrence and stomach contents, we suggest the emerging vegetation habitat may be more productive for recruitment of one-year-old pike, ameliorated by habitat-specific individual growth and body-condition development in YOY pike. It still remains elusive how and why YOY pike distribute in the two vegetation-type habitats at the start of the growing season, after adult spawning. However, pike have been shown to exhibit both natal-site and spawning-site fidelity (Miller et al., 2011). Coupled with limited opportunity for dispersal between habitat types for juveniles, parental habitat selection for spawning may have large implications for within-lake habitat distribution of YOY pike. Hence, to more thoroughly understand the mechanisms and consequences of habitat-specific YOY pike growth and recruitment, studies into possible differential spawning and site fidelity (Miller et al., 2011), along with potential maternal (Vindenes et al., 2016), density (Hühn et al., 2014) or microclimate (Bry et al., 1991) effects, should help explain both recruitment and possible selective effects (Hargeby et al., 2004) of the two vegetation-type habitats. Such future endeavours should also be evaluated in multiple independent systems to consider possible lake-specific patterns and processes. Regardless, both our study habitats did produce and contain YOY pike and thereby both contribute to recruitment, and should be conserved to act as important spawning and recruitment habitats for pike.

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CRedit authorship contribution statement

Anders Nilsson: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Project administration, Visualization, **Lynn Ranåker:** Conceptualization, Methodology, Formal analysis, Investigation, Project administration, Visualization, **Kaj Hulthén:**

Conceptualization, Formal analysis. **Viktor Nilsson-Örtman**: Conceptualization. **Christer Brönmark**: Conceptualization, Resources, **Jakob Brodersen**: Conceptualization, Methodology, Formal analysis, Investigation, Project administration, Resources, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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