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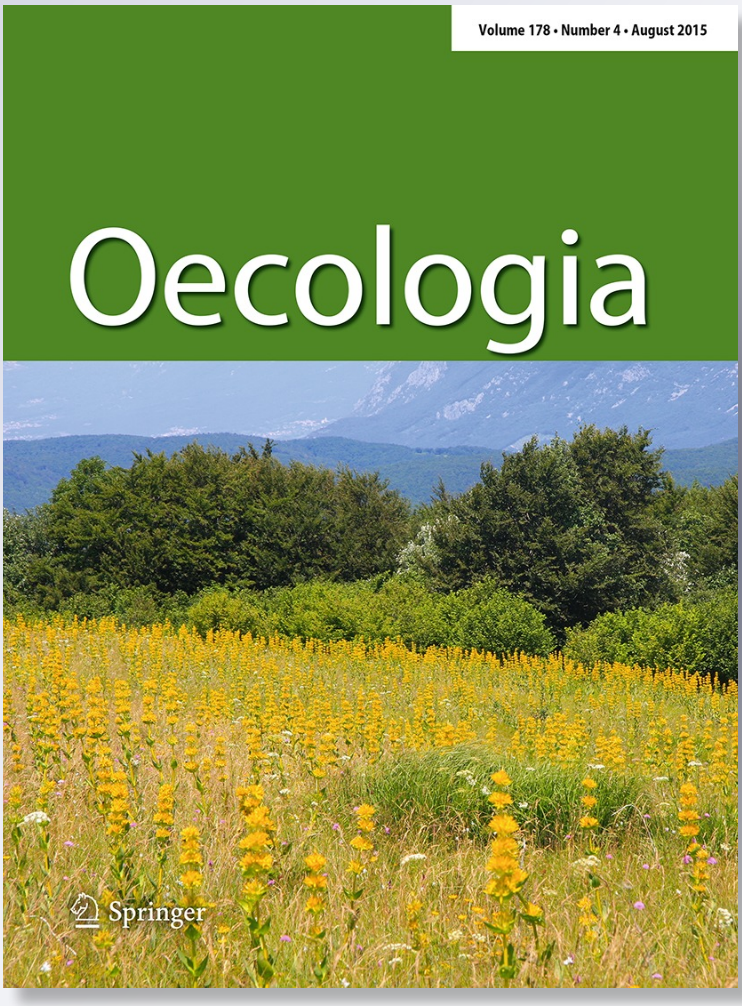

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HIGHLIGHTED STUDENT RESEARCH

Thermal and maternal environments shape the value of early hatching in a natural population of a strongly cannibalistic freshwater fish

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Abstract Hatching early in the season is often assumed to elevate fitness, particularly in cannibalistic fish in which size-dependent predation mortality is a major selective force. While the importance of the thermal environment for the growth of fish is undisputed, the relevance of maternal effects for offspring growth in the wild is largely unknown. Otoliths of 366 age-0 pike (*Esox lucius* L.) were sampled in a natural lake over three seasons. All offspring were assigned to more than 330 potential mothers using 16 informative microsatellites. We found temperature and past maternal environment (as represented by juvenile growth rate), but not female total length, to jointly contribute to explain within- and among-season size variation in juvenile pike. While there was no statistical evidence for maternal effects on offspring growth rate, fast female juvenile growth positively correlated with the offspring length in early summer. One mechanism could be related to fast-growing females spawning somewhat earlier in the season. However, the more likely mechanism emerging in our study was that fast-growing females could have been in better condition prior to spawning, in turn possibly producing higher numbers of high-quality eggs. Our study is among the few to reveal carry-over effects related to past maternal environments on offspring performance in a naturally reproducing fish stock. At the same time, our study underscores recent arguments that size-dependent maternal effects may not be expressed in the wild and that early hatching does not generally produce size advantages in light of stochastically varying temperature conditions.

Keywords Growing degree-day · Hatch date · Juvenile growth · Maternal effects · Northern pike

Introduction

Growth in fish is regulated by a range of physiological and ecological processes. Key physiological mechanisms include metabolism, food consumption rate and the energetic costs of foraging, food handling, digestion and excretion (Brett 1979; Brown et al. 2004). Ecologically, density-dependent (e.g., food competition) and density-independent (e.g., temperature fluctuations) factors are of fundamental importance for the growth of fishes in the wild (Lorenzen and Enberg 2002). Because survival in fish is positively size-dependent and often lowest during the larval and juvenile life stages (e.g., Sogard 1997), investigating the mechanisms causing growth variation in age-0 fish is important to understand recruitment dynamics (e.g., Miller et al. 1988). This is of particular interest in species that are regulated in the juvenile stage through size-dependent inter- and intra-cohort cannibalism.

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Recent research has (re)emphasized the relevance of the thermal environment in explaining substantial variation in juvenile size-at-age across several fish species of the temperate regions under natural conditions (Neuheimer and Taggart 2007; Venturelli et al. 2010a). Temperature determines the growth of all ectothermic animals in a non-linear and size-dependent fashion, either directly through its positive influence on metabolism and development rate (Brett 1979; Brown et al. 2004), or indirectly via the availability of food and the matching of predator and prey phenologies (Cushing 1990). By shaping both the abiotic and biotic environment the age-0 fish will experience, spawning and hence hatching time constitutes an important factor that affects an individual offspring's growth trajectory and subsequently fitness. Not surprisingly, strong selection on spawning date has been reported in various fish species (Schultz 1993; Einum and Fleming 2000). In cannibalistic freshwater fish, such as the North American centrarchids, early hatching has been reported to lead to growth advantages that are often maintained throughout the first season (Cargnelli and Gross 1996; Ludsin and DeVries 1997; Pine et al. 2000). However, this pattern has not been consistent across studies (e.g., Pine and Allen 2001; Peer et al. 2006). The divergent findings might be explained, at least in part, by stochastic environmental conditions (e.g., temperature during spawning and development time), which might disfavor early hatched offspring.

Not only the abiotic environment but also the conditions a ripening female has experienced prior to spawning (hereafter referred to as maternal environment) can affect hatching time and the amount of resources an embryo receives (Green 2008; Marshall et al. 2008; Hixon et al. 2014). Maternal effects are the non-genetic influence of the maternal phenotype on the offspring phenotype (Bernardo 1996). In fish, larger, older and better-conditioned females often invest more energy into the developing eggs and produce larger larvae with greater energy reserves, starvation resistance and swimming performance (Berkeley et al. 2004; Kamler 2005; Edeline et al. 2007; Marshall et al. 2008). Because most fisheries operate under positive size selection and heavily truncate the age and size structure towards younger spawners, the importance of size- or age-dependent maternal effects for population dynamics has been intensively discussed in recent years (Arlinghaus et al. 2010; Hsieh et al. 2010; Venturelli et al. 2010b; Hixon et al. 2014). However, limited empirical evidence about the relevance of size-dependent maternal effects on offspring performance under natural conditions exists (Heath and Blouw 1998; Marshall et al. 2008). The majority of studies were laboratory-based in which offspring of different-sized females were raised in a common environment. Maternal effects constitute adaptations to environmental variation (Marshall et al. 2010); therefore, studies that control for environmental variability have limited applicability to real-world conditions. Hixon et al. (2014) recently suggested to use parentage assignment methods to directly measure offspring development of differently sized (or aged) females in the wild and thereby contribute to answering the question on whether or not size-dependent maternal effects matter for recruitment.

Maternal effects have mostly been equated with size-dependent maternal influences in the fisheries literature. In this context, body size and condition at spawning integrates and represents the recent environment experienced by the adult female. However, the juvenile maternal environment of a future spawner may also affect offspring performance, but there is limited understanding of such effects in fish (Taborsky 2006a, b). Burton et al. (2013) recently found that female Atlantic salmon (*Salmo salar*) which grew fast early in life produced offspring that also grew faster under natural conditions. The opposite was reported by Taborsky (2006b) in a laboratory study in a cichlid species (*Simochromis pleurospilus*). Both studies used experimental crossings that circumvented natural mate choice. It thus remains unresolved whether and to what degree the early maternal environment results in fitness advantages of offspring in naturally reproducing fish populations.

Northern pike (*Esox lucius* L., hereafter referred to as pike) is an iteroparous, strongly cannibalistic top predatory freshwater fish native to both North America and Eurasia. In pike, temperature has been found to not only affect egg and larval development rates (reviewed by Raat 1988) but also growth at all life stages (Casselman 1978; Bry et al. 1991, 1995; Vindenes et al. 2014). There is a strong selection pressure for fast juvenile growth in pike to outgrow gape-size-limited cannibals (Haugen et al. 2006, 2007). Although prey density, type of prey and density of pike in relation to prey availability will also control pike growth (Pierce et al. 2003; Edeline et al. 2007), the temperature sum experienced by individuals overwhelmingly explained the variability in juvenile pike growth up to a total length of around 70 mm in experimental ponds (Bry et al. 1991). This is in line with a meta-analysis of Rypel (2012) who found that temperature (e.g., growing degree-days, GDD) explained a large fraction of variation in size-at-age (age-1–age-3) across 119 pike populations. Overall, through its joint influence on egg and larval development as well as growth of age-0 pike, water temperature strongly drives pike recruitment (Edeline et al. 2008; Paxton et al. 2009).

In the mesothermal pike, the length and timing of the annual spawning period is primarily driven by temperature (Raat 1988). There are some indications of size-dependent spawning time, with older and larger fish spawning somewhat earlier in the season (Sukhanova 1979; Pagel 2009). Research has also reported positive relationships between the age or size of female pike and egg size (Lindroth 1946; Murry et al. 2008), the energy content of larvae and larval survival under laboratory and experimental pond conditions (Arlinghaus et al. 2010; Kotakorpi et al. 2013). It could thus be hypothesized that offspring released by larger female pike in the wild may not only benefit from a larger size at hatching but also from a longer growing period. Moreover, the early environment experienced by the females themselves may affect their own offsprings' growth similar to the case in Atlantic salmon (Burton et al. 2013). The objective of our study was to examine how both the thermal and maternal environments shape the value of early hatching under natural conditions using pike as a model species of a strongly cannibalistic fish species.

Materials and methods

Study area

The study was conducted at Kleiner Döllnsee located 80 km northeast of Berlin, Germany (52°59′32.1″N, 13°34′46.5″E). It is an isolated, small (25 ha), dimictic and mesotrophic natural lake (total phosphorus concentration at spring overturn of 27 µg L^{-1} in 2011). The lake has a mean depth of 4.1 m, a maximum depth of 7.8 m, and the littoral is covered by dense reed belts. During the study years, 2008–2010, submerged macrophytes occurred in water depths down to 4.5 m, and covered in total about 10 ha (Kobler et al. 2009). In 2008, the pike density in the lake was estimated by mark–recapture methods as 22.6 fish ha^{-1} age-3 and older (95 % confidence interval: 19.6–26.4 fish ha^{-1}), which amounted to 54.3 fish age-3 and older per vegetated ha overgrown by macrophytes (Pagel 2009).

Sampling of age-0 pike

Age-0 pike were sampled during early summer in three consecutive years. In 2008, the sampling period lasted 14 days (1–19 July 2008) and was conducted 4 weeks later than in the two subsequent years 2009 (10 days, 8–19 June 2009) and 2010 (9 days, 8–22 June 2010). A battery-powered DC electro-fishing unit (Type EFGI 4000, 4 KW, 40 cm diameter ring anode; Bretschneider Spezialelektronik, Chemnitz, Germany) was used to sample age-0 pike within the reeds and above submerged macrophytes. Catch-per-unit-effort (CPUE) was estimated during the first electro-fishing event in each year by counting the number of age-0 pike caught per 100-m sampling stretches ($n = 6$). To minimize sampling bias, the electro-fishing equipment and the team of fishers were kept identical over the years. The entire shoreline was fished on each sampling day. However, to increase sample size, some areas of the lake known to host age-0 pike were non-randomly sampled with higher intensities at the end of each sampling period within each year. Pike were measured (total length) using a digital calliper with a precision of ±0.01 mm and weighed with a precision of ±0.01 g (ED2201; Sartorius, Germany). All fish were frozen at −20 °C for further preparation of otoliths.

Otolith extraction, preparation and analysis

Both lapilli were removed, cleaned and mounted to microscope slides. After mounting, otoliths were dried in an oven for 12 h at 55 °C. Due to the relatively old age of age-0 pike, some grinding of the otolith surface was necessary to reveal daily increments. All slides were then viewed at ×40 and ×100 magnification. Daily increments were counted three times per otolith by one person. To reduce the risk of counting errors, all otoliths were blind-counted in random order with at least 4 weeks between each count. If the six counts per fish (or up to three counts if one otolith was available) agreed within 10 % from the mean, we averaged them for further analysis (Ludsin and DeVries 1997). In total, otoliths from $n = 62$ age-0 pike were excluded because the individual counts differed by more than 10 %.

For the calculation of individual hatch date, 2 days were added to the mean daily ring count following the otolith validation study of daily ring formation by Wang and Eckmann (1992). The individual hatch date was estimated by subtracting the mean daily ring count from the date of capture (expressed in calendar day). For the calculation of individual spawning date, the non-linear temperature dependency of development duration from fertilization to hatch was considered following an empirical relationship reported by Lillelund (1966) as summarized in Fig. 9 in Raat (1988). To that end, for each developmental day prior to the hatch date, the percent contribution to the temperature-dependent total development time (total degree-days) was calculated. The spawning date was then derived by summing the daily proportions until 100 % of needed degree-days were reached. Finally, the mean daily growth rate (DGR) from hatching until sampling date was calculated as:

$$\mathrm{DGR} = (\mathrm{TL_C} - \mathrm{TL_H})/\mathrm{age},$$

where $\mathrm{TL_C}$ is the total length (mm) at capture, $\mathrm{TL_H}$ is the total length (mm) at hatch (assumed to be 9 mm following Billard 1996), and age (days) is the mean daily ring count (+2 days). We were unable to consider potentially varying size-at-hatching from offspring spawned by differently sized or aged females (Kotakorpi et al. 2013).

Water temperature

Water temperature was measured continuously during intervals of 15 min for all three sampling years between 15

March (calendar day 75) and 23 June (calendar day 175). Water temperature in 2008 was measured using a YSI-Multi-Parameter-Sensor (YSI 6600; Yellow Springs, OH, USA), which was located in a water depth of 1.5 m near the reed belt. In the two subsequent years, water temperature was measured using 11 (2009) and 5 (2010) temperature loggers placed in 1.5-m-deep water near the reed belt (Hobo StowAway TidbiT v.2). Variability in water temperature between locations was less than 0.25 °C per day. Therefore, mean daily temperatures measured by the loggers were pooled for further analyses. Unfortunately, due to malfunction, the YSI-sensor did not record water temperatures between 23 June and 19 July in 2008. To impute missing values, a linear regression model following Matuszek and Shuter (1996) was developed using average air temperatures of the preceding days combined with a time function, which was based on daily air and water temperature measurements between 4 April and 19 June of all 3 years. The following model achieved the lowest Akaike's information criterion ($\mathrm{AIC_c}$) value and hence received the greatest statistical support of all models that were tested (for details, see Online Resource 1):

$$W_\mathrm{T} = -22.562 + 0.850(T_{10}) + 0.377(Y\mathrm{DAY}) - 0.001(Y\mathrm{DAY})^2,$$

where W_T is the daily water temperature (°C), T_{10} is the 10-day air temperature mean and *Y*DAY is the calendar day of the year.

Daily water temperature data were used to calculate the daily growing degree-days ($\mathrm{GDD}_{\mathrm{day}\ n}$) for all days n (McMaster and Wilhelm 1997):

$$\mathrm{GDD}_{\mathrm{day\ n}} = [(T_\mathrm{MAX} + T_\mathrm{MIN})/2] - T_\mathrm{BASE},$$

where T_MAX and T_MIN are the daily maximum and minimum water temperatures, respectively, and T_BASE is the water temperature (5 °C) below which growth of pike ceases (Casselman 1996). If $(T_\mathrm{MAX} + T_\mathrm{MIN})/2$ was $< T_\mathrm{BASE}$, the $\mathrm{GDD}_{\mathrm{day}\ n}$ was assigned a value of 0. The accumulated GDDs experienced by each offspring were the sum of all daily $\mathrm{GDD}_{\mathrm{day}\ n}$ from hatching date (0) to sampling (capture) date (k) as:

$$\mathrm{GDD} = \sum_{n=0}^{k} \mathrm{GDD}_{\mathrm{day}\ n}.$$

Sampling of adult pike and parentage assignment

To determine the spawning stock as completely as possible, adult pike of all age classes were sampled on 108 different events (days) between November 2007 and October 2010. The same electro-fishing unit was used as described before. In addition, rod and reel angling was conducted each year on multiple occasions to catch pike in the pelagic zone and above submerged macrophyte beds of the lake. In total, 1619 juvenile and adult pike (age-1 and older) were caught over the 3 years of which 485 were recaptures (30 %). Pike were anesthetized using clove oil in a dosage of 0.4 ml clove oil-ethanol emulsion (1:9)/L (Zaikov et al. 2008). After anaesthesia, pike were measured to the nearest mm and weighted with a precision of ±1.0 g (ED2201; Sartorius). A minimum of seven scales per fish was taken for analysis of age and growth. An external sex determination was conducted by examination of genital papilla (Casselman 1974). Every captured pike (TL > 150 mm) was then tagged with individually numbered passive integrated transponder tags (Trovan, Electronic Identification Systems, Germany) and released near their capture point.

Maternal analysis and female traits

Microsatellite-based parentage assignment was applied to determine the mothers of the age-0 pike sampled over the course of 3 years (for details, see Online Resource 2). Only females age-2 and older were considered in the parentage assignment because females tend to become fully mature then (Pagel 2009). We focused on female pike because it is generally believed that maternal influences due to nutritional provisioning of the eggs are more important than paternal effects because sperm contain virtually no extranuclear material (Bernardo 1996).

Four female traits were included in the analysis as potential predictor variables of offspring growth performance. These included female total length (mm), female age (years) and the juvenile growth rate of the females in the first and in the second year of life (mm year^{-1}). An attempt was made to assign these traits to all potential females of a given spawning stock in 2008, 2009 and 2010, respectively. Female length at spawning was determined by back-calculation for individuals recaptured after the spawning period. Some individuals ($n = 21$) with successfully assigned offspring sampled in the years 2008 and 2009 were not recaptured later. For these fish, the length in the following spawning year was unknown. To approximate the likely length at spawning, the length was forward estimated using a regression of length at catch and recapture of 170 female pike to control for sex-dependent growth rates in the study lake (Pagel 2009). Female length at recapture (y) was modeled as a function of total length at first capture (x_1), the time elapsed (days) between both events (x_2) and the interaction term ($x_1 \times x_2$). Recapture time varied between 226 and 1400 days. The model [$y = -1.066 + 0.998(x_1) + 0.026(x_2) - 0.0003(x_1 \times x_2)$] explained 89.9 % of variability in total length at recapture ($F_{1,166} = 500.454$, $P = 0.015$). The parameter estimates were then used to estimate the female length at the next spawning season for the mentioned 21 fish that had contributed at least one offspring using 1 May as reference date. In general, over 3 years, we identified 118 females with at least one offspring in early summer. Of the 304 age-0 pike used in the otolith analysis, 179

(58.9 %) individuals were successfully assigned to a female ($n = 54$ in 2008, $n = 59$ in 2009 and $n = 66$ in 2010).

Three scales per fish were used to determine age and growth of females. Distances between the annuli and the scale centre were measured anterior to the scale center for each growth year (Quick Scope, Mitutoyo, Japan). Back-calculation of length-at-age was conducted for every pike age-1 and older using the Fraser-Lee equation based on the scale-proportional hypothesis (reviewed by Francis 1990):

$$L_{\mathrm{i}} = c + [(L_{\mathrm{c}} - c)/S_{\mathrm{c}}] \times S_{\mathrm{i}},$$

where L_{i} is the estimated length at age i, L_{c} is the length of fish at first capture, S_{c} is the diameter of the scale at capture and S_{i} is the scale measurement at annulus i. The constant c is the y-intercept in the linear body length-scale diameter regression. Overall, age estimates were found to be reliable and rather precise as revealed by a scale age validation exercise (for details, see Online Resource 3).

Statistical analyses

Analysis of variance (ANOVA) was used to compare the mean number of age-0 pike per 100-m stretches between sampling years (followed by Tukey's HSD post hoc test for homogeneous variances) to study whether recruitment varied among seasons. The effect of hatching date (coded from day 1 to day 21 within each hatching period) and GDD on mean DGRs (mm day^{-1}) and total length (mm) in early summer (July in 2008 and June in 2009 and 2010) was analyzed by general linear models (GLM). The first model included sampling year as a fixed factor and hatching date as a covariate as well as the interaction term to analyze whether the effect of hatching date on growth and size of age-0 pike was similar in all three study years. To account for the different lengths of the sampling periods within and across the 3 years, the age (in days) of each individual offspring was included as an additional covariate in the first calendar-based model. To analyze whether GDD as a measure of temperature sum experienced by the age-0 pike provided a better model compared to the calendar-based model (Neuheimer and Taggart 2007), a second set of models substituted hatch date for GDD. For each model, different measures of the goodness of fit [adjusted r^2, corrected Akaike's information criterion ($\mathrm{AIC_c}$)] were estimated. Bias-corrected $\mathrm{AIC_c}$ was calculated as follows (Hurvich and Tsai 1989):

$$\mathrm{AIC_c} = -\mathrm{LL} + 2K + \frac{2K(K+1)}{N-K-1},$$

where LL is the log-likelihood value obtained from the maximum likelihood estimation, K is the number of estimated parameters, and N is sample size. The model yielding the smallest $\mathrm{AIC_c}$ value in a given set of models is considered the best one (Burnham and Anderson 1998). All models were ranked by calculating the delta (Δ_{i}) $\mathrm{AIC_c}$ (models with a $\Delta\mathrm{AIC_c} < 2$ were considered to be equivalent) and the probability (Akaike weights, w) that any given model in the set of j models is the best (Anderson 2008):

$$w_i = \frac{\mathrm{e}^{-0.5\Delta i}}{\sum_{j=1}^{J} \mathrm{e}^{-0.5\Delta i}}.$$

To aid in interpretation, the relationship between the dependent variables and hatch date as well as GDD was also visualized for each year. To that end, the total length for all age-0 pike with known age was projected forward or backward to the same reference time (19 July in 2008, 19 June in 2009/2010) using the mean DGR for each fish. In this context, linear growth of age-0 pike was assumed as documented under experimental conditions (Bry et al. 1991).

The effect of maternal traits on dependent variables was tested in separate models because these traits were only available for a subset (58.9 %) of age-0 pike. The best temperature model (calendar day- or GDD-based) according to $\Delta\mathrm{AIC_c}$ was chosen to test the additional influence of maternal effects against the temperature-only model as the null model. Linear mixed-effect models (LME) were fitted, in which maternal identity was included as a random variable to control for non-independence of siblings for females with multiple offspring (up to four offspring per female and year). Due to high linear correlation between female size and age ($r = 0.882$, $P < 0.001$, $n = 131$), age and length were tested independently. The total length of female pike ranged between 211 and 857 mm (the age ranged between 2 and 11 years). Quadratic effects of either size or age were also included to test for reproductive senescence of very large or exceptionally old females (possible non-linear dome-shaped effect), as suspected by Eslinger et al. (2010) for the congeneric muskellunge (*Esox masquinongy*) and Kotakorpi et al. (2013) for pike. In addition, the isolated influence of juvenile growth rate of females as well as in interaction with maternal age/size on offspring growth was investigated. To determine the joint impact of thermal environment in combination with maternal traits on offspring growth, the interaction term of maternal traits with GDD was also included. Again, different measures of the goodness of fit were estimated ($\mathrm{AIC_c}$, $\Delta\mathrm{AIC_c}$ and w) to rank models. In addition, we visualized predicted values and the 95 % confidence intervals from the LME model with the highest statistical support. Finally, we analyzed the effect of maternal traits on hatch date to detect any trends of a size-, age- or growth-dependent spawning timing. All LME models included sampling year as a fixed factor, maternal identity as a random variable, and the female trait under investigation as a covariate. We also included the interaction term with year to analyze whether the effect of female age, size or juvenile growth rate on hatch date of age-0 pike was consistent over years. Again, all models were ranked by different measures of goodness as mentioned before. Statistical significance for all tests was set at $P \leq 0.05$. Analyses were conducted in R statistical software v.2.15.2 (R Development Core Team 2011) using the packages "arm" (v.1.6-10; Gelman et al. 2013) and "lme4" (v.1.0-5; Bates et al. 2013).

Results

Over the three study years, 366 age-0 pike were collected. Mean number of age-0 pike per 100 m sampling stretches was similar across years as revealed by electrofishing (ANOVA: $F_{2,15} = 0.855$, $P = 0.433$). Mean (±SD) CPUE was 2.33 ± 1.03 fish/100 m^{-1} in 2008, 2.17 ± 1.94 in 2009 and 3.50 ± 2.43 in 2010. From hatch to early summer (July in 2008, June in 2009 and 2010), mean (±SD) DGR of 304 age-0 pike with readable otoliths varied across years and was 1.22 ± 0.21 mm day^{-1} in 2008 ($n = 66$), 0.89 ± 0.13 mm day^{-1} in 2009 ($n = 104$), and 0.88 ± 0.11 mm day^{-1} in 2010 ($n = 134$). Similarly, the total length at the reference time (19 July in 2008, 19 June in 2009 and 2010) varied across years and was on average (±SD) 108.3 ± 16.6 mm in 2008, 72.2 ± 8.2 mm in 2009 and 59.4 ± 6.7 mm in 2010.

Water temperature and distribution of spawning and hatch dates

The temporal succession of the mean daily water temperature differed between the three study years (Fig. 1). At the beginning of April (calendar day 95), the water temperature in 2008 was 3.4 °C cooler than in 2009 and 1.6 °C cooler than in 2010. The year 2009 was also characterized by a particularly warm spring and overall more stable temperature conditions, while 2008 exhibited a prolonged cool spring, followed by a short period of rapid warming and a rather stable warm summer period. In 2008 and 2009, the spawning of pike occurred at water temperatures ranging between 5 and 15 °C, while in 2010 it occurred at much more contracted temperature range between 8 and 15 °C. The estimated spawning times for offspring that survived varied among years and ranged from 26 March to 2 May in 2008 (37 days), 14 March to 17 April in 2009 (35 days) and 3 April to 1 May in 2010 (29 days). By contrast, the duration of the hatching period (of survived age-0 pike) was identical in all years lasting about 3 weeks (21–22 days; Fig. 2). However, in line with variation in spawning time the initiation of hatching varied across years. In 2008 and 2010, hatching occurred between mid-April and the first week of May. By contrast, in 2009, hatching started at the beginning of April. In 2008, the hatching of pike larvae occurred at water temperatures ranging between 8.1 and 17.3 °C, while in 2009 and 2010, it occurred at much more contracted temperature range between 10.2 and 14.6 °C, and 9.9 and 12.8 °C.

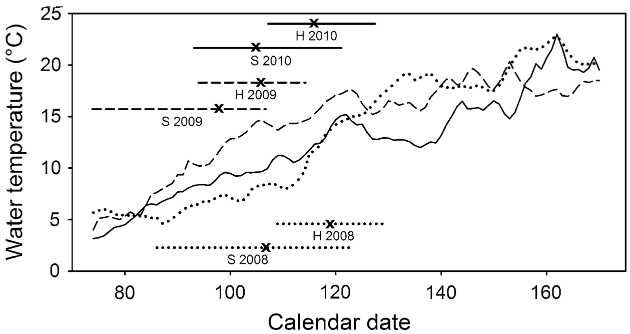

Fig. 1 Temporal succession of mean daily water temperature (°C) in Kleiner Döllnsee measured between 15 March (calendar day 75 in 2008 and 74 in 2009/2010) and 19 June (calendar day 171 in 2008 and 170 in 2009/2010) in 2008 (*dotted line*), 2009 (*dashed line*) and 2010 (*solid line*). Marks (*X*) represent the mid-points (50 % of the total) of the spawning (*S*) and hatching periods (*H*)

Influence of hatch date and temperature on length and growth of age-0 pike

The effect of hatch date on age-0 pike total length in early summer with age as a covariate explained 80.2 % (adjusted r^2) of the variation ($\text{AIC}_\text{c} = 2190.159$). A significant interaction between hatch date and year was present ($F_{2,301} = 4.061$, $P = 0.018$; Online Resource 4a). While hatch date exhibited no relationship to total length at the chosen reference date in 2008, indicating that later-hatched fish achieved on average similar lengths as early-hatched fish (Fig. 3a), early-hatched individuals exhibited greater total lengths by mid-June in both 2009 and 2010 (Fig. 3b, c). Using GDD as a predictor variable instead of hatch date and offspring age achieved a similar explanatory power in terms of total length of age-0 pike as the described calendar-day model (adjusted $r^2 = 0.809$; Online Resource 4b). Based on the AIC_c value ($\text{AIC}_\text{c} = 2177.344$), however, the GDD model constituted a by far better fit to the data compared to the calendar-based model ($\Delta\text{AIC}_\text{c} = 12.825$). The significant interaction between GDD and year remained (Online Resource 4b), indicating that the effect of GDD on age-0 pike length varied between years. GDD had no relationship with total length in early summer in 2008 (Fig. 4a), while positive relationships were present in 2009 and 2010 (Fig. 4b, c).

A GLM with year as a fixed factor and hatch date as a covariate explained 52.1 % (adjusted r^2) of the variance

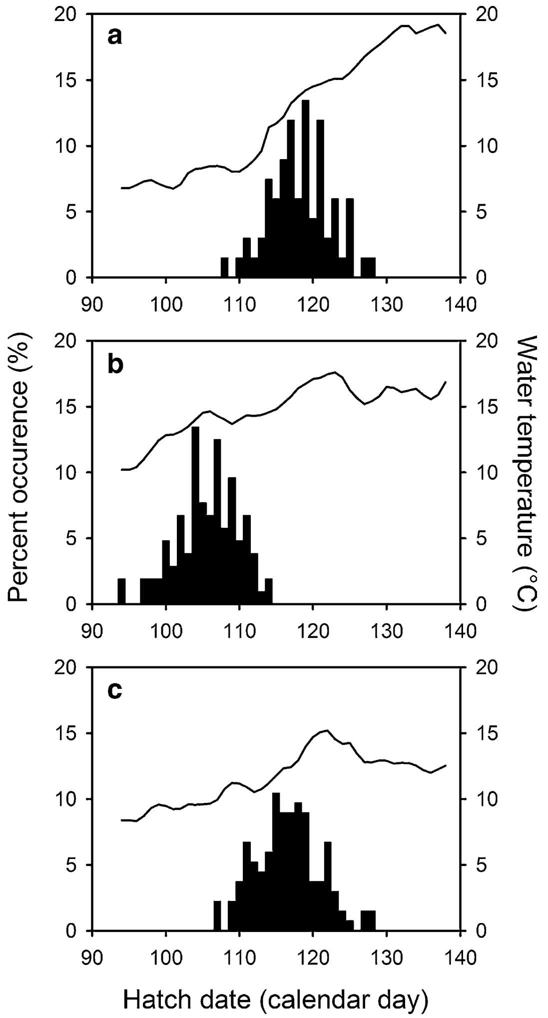

Fig. 2 Frequency distributions of hatching dates (*bars*) of age-0 pike (*Esox lucius*) in Kleiner Döllnsee in **a** 2008 ($n = 66$), **b** 2009 ($n = 104$), and **c** 2010 $n = 134$). In addition, the mean daily water temperatures (*solid line*), measured between 5 April (calendar day 96 in 2008 and 95 in 2009–2010) and 18 May (calendar day 139 in 2008 and 138 in 2009–2010), are presented in each panel

in mean DGRs ($\text{AIC}_c = -338.380$) of age-0 pike (Online Resource 4c). Again, a significant interaction effect between hatch date and year was present ($F_{2,301} = 14.631$, $P < 0.001$). In 2008 and 2010, the later-hatched individuals showed higher DGRs (Fig. 3d, f). The opposite was true in 2009, when earlier-hatched individuals had higher DGRs (Fig. 3e). Using GDD as a predictor variable instead of hatch date achieved a somewhat greater explanatory power of variation in DGRs of age-0 pike, and the model fitted substantially better (adjusted $r^2 = 0.579$; $\text{AIC}_c = -377.600$; $\Delta\text{AIC}_c = 39.220$; Online Resource 4d). The significant interaction of GDD and year remained ($F_{2,301} = 35.787$, $P < 0.001$), and while increasing GDD was associated with reduced DGR in 2008 (Fig. 4d), positive relationships between GDD and DGR were present in 2009 and 2010 (Fig. 4e, f).

Influences of maternal environment on hatch date, length and growth of age-0 pike

The inclusion of maternal variables in addition to the thermal environment improved model fit in terms of explaining variation in total length of age-0 pike in early summer (Table 1), but the random effect of maternal identity had no significant influence on offspring total length. Note the significant and positive bivariate correlations between adult female length and female juvenile growth in the first ($r = 0.278$, $P = 0.001$, $n = 131$) and second year of life ($r = 0.506$, $P < 0.001$, $n = 129$). In addition, we found a positive correlation between a female's juvenile growth in the first and second year of life ($r = 0.382$, $P < 0.001$, $n = 114$). The best predicting maternal variable for explaining variation in total length of age-0 pike in early summer was the female's juvenile growth rate in the second year, which was present in all top three models (Table 1). Although not statistically significant ($P = 0.190$) when judged against a conservative P value of 0.05, inclusion of a female's juvenile growth rate in the GDD model resulted in the lowest AIC_c value and hence the model with the greatest statistical support of all (Table 1). Also the juvenile growth rate in the first year of life was relevant as revealed by its inclusion in the second best ranked model for predicting total length of age-0 pike. When judging direction by the sign of estimated parameters, female juvenile growth in the second year of life had a positive effect on total length of age-0 pike in early summer in all three study years (Online Resource 4e). However, a model with an interaction of juvenile growth rate in the second year of life and GDD received a nearly equal statistical support (model 3, $\Delta\text{AIC}_c = 1.875$; Table 1), and this model also retained the previously elaborated interaction of GDD and year. Visualizing the year-specific effect of a female's juvenile growth rate and GDD on total length of age-0 pike in early summer based on model 1 in Table 1 showed that the size of age-0 pike was larger when a large temperature sum (GDD) was experienced by offspring released by females that grew fast during the juvenile stage (second year of life) in all study years (Fig. 5). Differences among study years (i.e., the interaction effect) were related to the slope of the effect of maternal juvenile growth on total length of their offspring but did not reverse the direction. While the female's juvenile growth rate influenced length of offspring positively, neither the actual size at spawning nor the female's age influenced offspring size. There was also no evidence for an aging effect as models with squared terms performed substantially worse compared to the best models for both size and age (Table 1).

Modeling the offspring's hatching dates as a function of maternal traits also revealed that female juvenile growth in the second year of life was the best predicting maternal

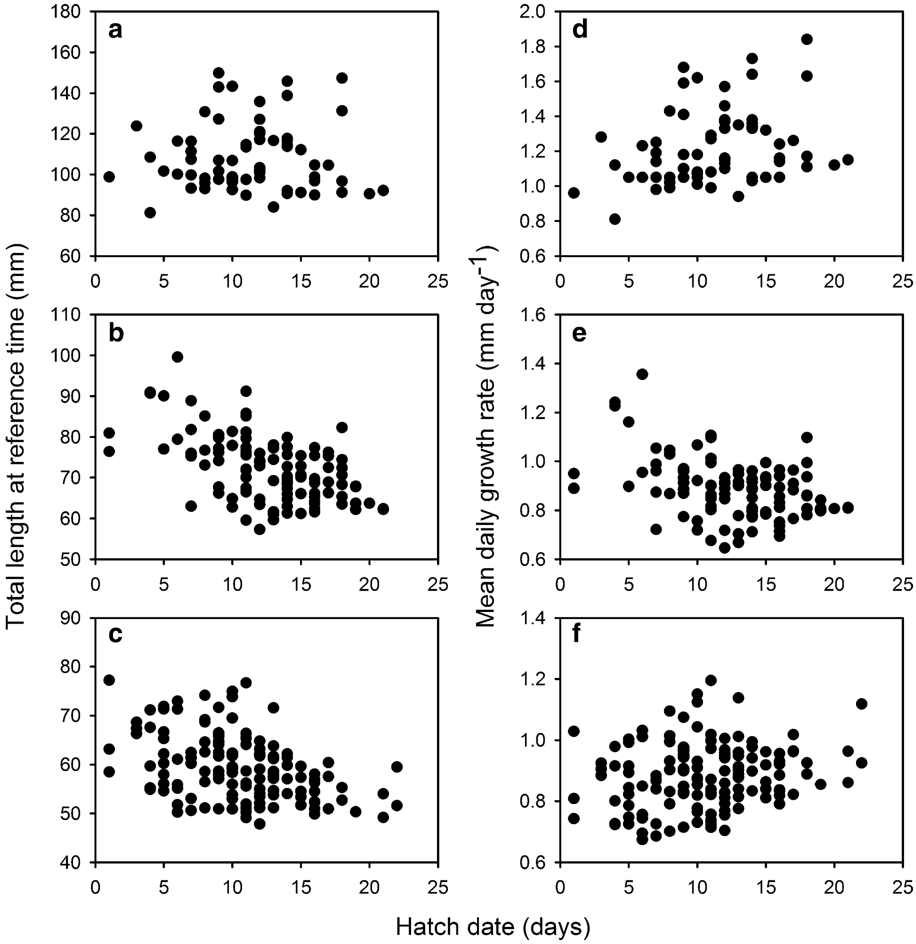

Fig. 3 Descriptive analyses of total length at reference time (mm, **a**–**c**) and mean daily growth rate (mm day^{-1}, **d**–**f**) in relation to hatch date (days) for age-0 pike in Kleiner Döllnsee in the year 2008 (**a**, **d**, $n = 66$), 2009 (**b**, **e**, $n = 104$) and 2010 (**c**, **f**, $n = 134$). Hatch date 0 represents the day before the first hatch in each year occurred. Reference time was 19 July in 2008 and 19 June in 2009 and 2010. Note the different scales in the various panels

variable (Table 2). Although not significant at a conservative P value of 0.05 ($P = 0.124$), offspring released by fast-growing females tended to hatch somewhat earlier in all three study years (Online Resource 4g). Similarly to the results mentioned before, female total length and age were not significant in systematically explaining hatching dates of age-0 pike (Table 2). Overall, a female's past performance in terms of juvenile growth exerted substantially more maternal influence on offspring performance (in terms of total length in early summer) than the female's current size or age. In terms of predicting the mean DGRs of age-0 offspring, total length of females was the best-predicting maternal variable, but its inclusion resulted in a model that was equally parsimonious compared to the simpler temperature-only model (Online Resource 4h). This was also true for other models that either included total length (or age) of female pike as a main and a quadratic term or an interaction of female length and GDD, indicating that there was no size- (or age-) dependent maternal effect on age-0 pike growth rate in the wild. However, when judging directional influence by the sign of estimated parameters, female length had a positive effect on mean DGRs of age-0 pike in all three study years (Online Resource 4f), which was, however, not statistically significant ($P = 0.591$).

Discussion

We found temperature and past maternal environment to jointly determine age-0 pike growth performance in a non-exploited pike stock under natural conditions. The overall positive influence of temperature on age-0 pike growth agreed well with reports from natural (Rypel 2012; Vindenes et al. 2014) and pond-held pike populations (Bry et al. 1991). However, earlier hatching and a corresponding large temperature sum accumulated led to larger total length of age-0 pike in early summer in only 2 of the 3 years. Two temperature-related phenomena might have contributed to the observed effects—one related to effects on growth and one related to development issues. In relation to the former, the exceptional year 2008 was characterized by an prolonged cool spring and by the widest spread of temperatures experienced by early- and late-hatched individuals of all study years (between 8.1 and 17.3 °C; Fig. 2). This resulted in early-hatched fish developing

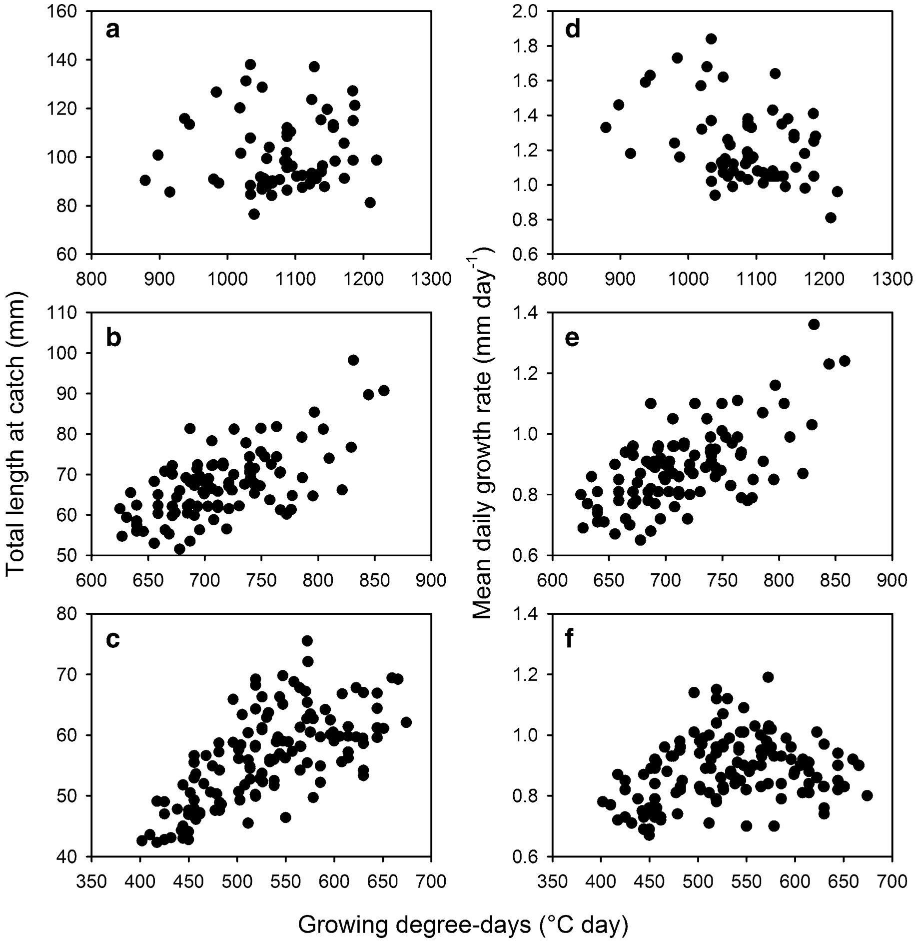

Fig. 4 Descriptive analyses of total length in early summer (mm, **a**–**c**) and mean daily growth rate (mm day^{-1}, **d**–**f**) in relation to growing degree-days (DGG, °C day) for age-0 pike in Kleiner Döllnsee in the year 2008 (**a**, **d**, $n = 66$), 2009 (**b**, **e**, $n = 104$) and 2010 (**c**, **f**, $n = 134$). Note the different scales in the various panels

under cool temperature regimes far from the optimal growth temperature in juvenile pike (22–23 °C; Casselman 1978). Hokanson et al. (1973) found that growth of newly-hatched larvae was negligible below 7 °C, a period that was very pronounced in the spring of 2008 and affected the early hatchlings. Correspondingly, late-hatched pike larvae in 2008 grew particularly well when the water had rapidly warmed, and the relationship between hatch date and DGR had the greatest positive slope in this year (Fig. 3d). Related to the development hypothesis, exposure to extreme temperatures (e.g., outside a range of 5.8–21 °C; Lillelund 1966) and rapid thermal changes (e.g., from 10 to 5 °C within 34 h; Hassler 1970) during the development from fertilization to hatch has been found to reduce hatching rates and lead to greater occurrence of deformed larvae at hatch, which might also affect post hatch growth (Lillelund 1966). However, such patterns probably did not contribute to the specific growth patterns found in 2008 because low temperatures near or below 5 °C at the onset of spawning were also observed in 2009.

The lack of positive relationship between GDD and body length in 2008 (Fig. 4a) was noteworthy, which was in contrast to among-population comparisons in other temperate fish species in which GDD had a consistent and positive effect on growth of juveniles (Neuheimer and Taggart 2007; Venturelli et al. 2010a). In addition to the already mentioned contribution of the particularly prolonged period of cool water in the spring of 2008, the lack of correlation among total length of age-0 pike and GDD in 2008 could potentially be explained by density- and resource-dependent factors. Density-dependent growth has been documented for pike (Pierce et al. 2003; Edeline et al. 2007), which can be caused by direct food limitation (Lorenzen and Enberg 2002), or through interference competition, antagonistic behavioral interactions and social stress (Nilsson 2006; Edeline et al. 2010). However, time series analysis from Lake Windermere (UK) revealed that adult pike growth was less influenced by density fluctuations compared to interannual temperature variation (Edeline et al. 2007; Haugen et al. 2007). Moreover, Wright and Giles (1987) did not detect a relationship between pike fry growth rates and fry density in pond enclosure experiments. In our study, the CPUE of age-0 pike was statistically similar across years. Hence, density-dependence in growth can be likely excluded as having substantially affected size variation of age-0 pike in relation to hatch

Table 1 Model summary of linear mixed-effect models explaining variation in total length (mm) of age-0 pike in early summer

Model: total length in early summer	*n*	K	AIC$_c$	ΔAIC$_c$	*W*$_i$
1. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FJG2} + \beta_4\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	**175**	**9**	**1295.202**	**0**	**45.869**
2. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FJG1} + \beta_4\text{FJG2} + \beta_5\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	**175**	**10**	**1296.952**	**1.751**	**19.116**
3. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FJG2} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FJG2} \times \text{GDD} + a_i + \varepsilon_i$	**175**	**10**	**1297.076**	**1.875**	**17.966**
4. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{FJG2} + \beta_5\text{Y} \times \text{GDD} + \beta_6\text{FT} \times \text{FJG2} + a_i + \varepsilon_i$	175	11	1298.021	2.819	11.206
5. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{FJG2} + \beta_5\text{Y} \times \text{GDD} + \beta_6\text{FA} \times \text{FJG2} + a_i + \varepsilon_i$	175	11	1299.374	4.172	5.697
6. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FA}^2 \times \text{GDD} + a_i + \varepsilon_i$	177	10	1309.698	14.496	0.033
7. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	177	9	1309.870	14.668	0.030
8. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FJG1} + \beta_4\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	177	9	1310.060	14.858	0.027
9. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{FA}^2 + \beta_5\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	177	10	1310.297	15.095	0.024
10. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FA} \times \text{GDD} + a_i + \varepsilon_i$	177	10	1311.880	16.678	0.011
11. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FJG1} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FJG1} \times \text{GDD} + a_i + \varepsilon_i$	177	10	1312.019	16.817	0.010
12. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{FJG1} + \beta_5\text{Y} \times \text{GDD} + \beta_6\text{FT} \times \text{FJG1} + a_i + \varepsilon_i$	177	11	1312.986	17.784	0.006
13. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FA} + \beta_4\text{FJG1} + \beta_5\text{Y} \times \text{GDD} + \beta_6\text{FA} \times \text{FJG1} + a_i + \varepsilon_i$	177	11	1313.350	18.148	0.005
14. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	179	8	1321.311	26.109	<0.001
15. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	179	9	1323.086	27.866	<0.001
16. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{FT}^2 + \beta_5\text{Y} \times \text{GDD} + a_i + \varepsilon_i$	179	10	1324.154	28.952	<0.001
17. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FT}^2 \times \text{GDD} + a_i + \varepsilon_i$	179	10	1324.746	29.544	<0.001
18. $\beta_0 + \beta_1\text{Y} + \beta_2\text{GDD} + \beta_3\text{FT} + \beta_4\text{Y} \times \text{GDD} + \beta_5\text{FT} \times \text{GDD} + a_i + \varepsilon_i$	179	10	1325.309	30.107	<0.001
19. $\beta_0 + \beta_1\text{Y} + \beta_2\text{H} + \beta_3\text{A} + \beta_4\text{Y} \times \text{H} + a_i + \varepsilon_i$	179	9	1327.921	32.719	<0.001
20. $\beta_0 + \beta_1\text{Y} + a_i + \varepsilon_i$	179	5	1342.685	47.483	<0.001

Models are highlighted in bold because ΔAIC$_c$ is less than 2

Y year, *H* hatch date (days), *A* age of age-0 pike (days), *GDD* growing degree-days (°C day), *FA* female age (years), *FA*^{2} female age squared (years^2), *FT* female size (mm), *FT*^{2} female size squared (mm^2), *FJG1* female juvenile growth in the first year (mm year^{-1}), *FJG2* female juvenile growth in the second year (mm year^{-1}), β_0 intercept, a_i random intercept (maternal identity), ε_i error term, *n* total number of observations, *K* number of parameters, *AIC$_c$* corrected Akaike`s information criterion, *ΔAIC$_c$* delta AIC$_c$, w_i Akaike weight

date. However, it should be noted that the CPUE values of age-0 pike were related to the month of July in 2008, while the CPUE assessment in 2009 and 2010 took place in June. The CPUE values in 2008 were not adjusted for natural losses that most likely happened from June to July, and hence the age-0 pike density in June of 2008 was probably greater than reported, potentially contributing to density-dependent growth depression in the 2008 cohort.

While density may not be the most important factor, it is possible that other ecological factors, in particular food availability, co-varied with the particular temperature conditions of 2008, potentially contributing to the decoupling of GDD and within-season growth. It is, for example, possible that the warming pattern in 2008 resulted in a mismatch of predator and prey (Cushing 1990). Under low resource levels, smaller individuals are often superior in exploitative competition (Persson 1985). This might have promoted higher DGRs of initially smaller, late-hatched individuals leading to size convergence in 2008 (Huss et al. 2008). Irrespective of the exact mechanism, one key message of our study is that the benefits of early hatching are strongly moderated by the prevailing temperature conditions. Hence, there is no consistent benefit to be expected of early hatching on body length in early summer in pike, similar to reports in other cannibalistic fish species (Pine and Allen 2001; Peer et al. 2006).

In addition to temperature influences on age-0 pike growth, a main finding of our study was the presence of early growth-dependent maternal effects on the performance of age-0 pike in the wild. In particular, as revealed by the best-ranked models, we found that the past ecological environment of mothers affected the current fitness of their offspring (using length in early summer as a fitness surrogate). Inclusion of a female's early growth rate produced models that were substantially more supported than temperature-only models, which we interpret as evidence of the presence of a growth-related maternal effect. By contrast, and in conflict with initial expectations, neither female size nor female age as a measure of the current ecological environment exerted a significant influence on offspring performance. Although female size was the best-predicting maternal variable of age-0 pike mean DGRs, its inclusion resulted in a model that was not better compared to a temperature-only model. We interpret this finding as lack of a size-dependent maternal effect on offspring growth rate in the unexploited population of pike in Kleiner

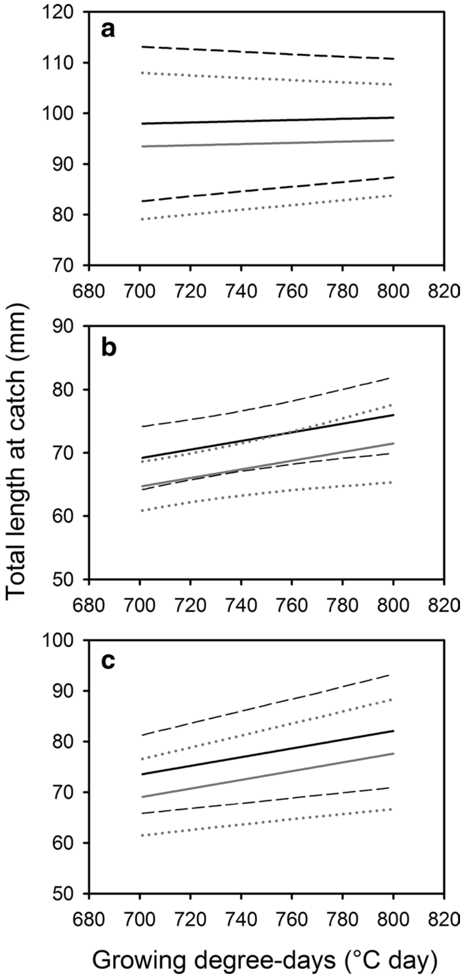

Fig. 5 The relationship between growing degree-days (DGG, °C day) and the total length (mm) in early summer for age-0 pike in Kleiner Döllnsee in **a** 2008, **b** 2009, and **c** 2010. The *solid* and *dashed/dotted lines* are the predicted values and 95 % confidence intervals from the linear mixed-effect model 1 (Table 1). *Black* and *gray lines* refer to predictions for fast (201.3 mm year^{-1}) and slow (63.6 mm year^{-1}) female juvenile growth in the second year of life. The values represent the maximum and minimum values obtained from the whole dataset independent of the year

Döllnsee. This is a noteworthy finding given the convincing laboratory-based evidence for size- and age-dependent maternal effects on egg and larval traits (e.g., size) in pike (Arlinghaus et al. 2010). However, Kotakorpi et al. (2013) recently noted that size-dependent maternal effects were expressed more strongly in exploited pike populations in which the per capita food availability is elevated compared to unexploited pike populations, supporting the theoretical argument that the manifestation of size-dependent maternal effects is dependent on the environment (Marshall et al. 2010). Kleiner Döllnsee constitutes an unexploited pike population at carrying capacity, and the spawning stock is resource-limited as evidenced by extremely low growth rates of adult fish (Pagel 2009). Such ecological conditions may hamper the expression of size-dependent maternal effects on offspring phenotypes, and we thus predict that size-dependent maternal effects will gain in importance as pike populations become exploited or otherwise better nutritioned.

The lack of size-dependent maternal effects on offspring growth rate in pike agreed with laboratory work on a range of fish species showing that size-dependent maternal effects rarely have lasting effects beyond the larval life stages (Heath and Blouw 1998). Marshall et al. (2010) theorized that size-dependent maternal effects in fish should not lead to differential fitness in the wild because they may be adaptations to varying environments. Accordingly, size-dependent maternal effects should be particularly pronounced when assessed under controlled environmental conditions and be much less prevalent in nature. Findings in pike fully agree with these considerations as size- (or age-) dependent maternal effects were pronounced in controlled studies in tanks and ponds (Arlinghaus et al. 2010; Kotakorpi et al. 2013), while no such effects on the growth of pike juveniles were present in the wild.

We found clear evidence for a so far unknown, alternative maternal effect. Females that grew fast when young produced larger offspring in early summer. We suspect a resource-oriented mechanism associated with early growth performance of females, which carries over to offspring performance later in life. Because growth rates of females in the first and second year of juvenile life were positively correlated with adult size, fast-growing females either exhibited an intrinsically greater growth capacity or achieved greater resource intake levels, which probably led to an improved condition at spawning. It has been shown in a variety of fish species, including in part in pike (Edeline et al. 2007), that fast-growing individuals tend to spawn earlier, produce more and better quality eggs (Jonsson et al. 1996; Morita et al. 1999), and overall invest more into gonads compared to slow-growing fish. In line with these observations, we found that offspring from pike females with fast juvenile growth hatched somewhat earlier in the season across the three study years. Hence, the larger lengths of offspring emerging from fast-growing females can be explained, at least in part, by the longer growing season. More likely, however, are effects of good condition of fast-growing females on the quality of gonads produced because the relationship of female juvenile growth rate and early spawning was only modest (Online Resource 4g), and GDD should have captured most of the effect of a slightly longer growth period. Indeed, a model with an interaction term of juvenile growth in the second year of life and GDD did not improve model fit, indicating that other factors than simply a higher GDD experienced by earlier-hatched fish released by fast-growing females must have been present

Table 2 Model summary of the linear mixed-effect models explaining variation in hatch date (days)

Model: hatch date~	n	K	AIC$_\text{c}$	ΔAIC$_\text{c}$	W_i
1. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG2} + a_\text{i} + \varepsilon_\text{i}$	**175**	**6**	**1006.283**	**0**	**72.518**
2. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG2} + \beta_3\text{Y} \times \text{FJG2} + a_\text{i} + \varepsilon_\text{i}$	175	8	1010.259	3.976	9.930
3. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG2} + \beta_3\text{FA} + \beta_4\text{FJG2} \times \text{FA} + a_\text{i} + \varepsilon_\text{i}$	175	8	1010.539	4.256	8.633
4. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG2} + \beta_3\text{FT} + \beta_4\text{FJG2} \times \text{FT} + a_\text{i} + \varepsilon_\text{i}$	175	8	1010.542	4.259	8.620
5. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG1} + a_\text{i} + \varepsilon_\text{i}$	177	6	1019.435	13.125	0.101
6. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FA} + a_\text{i} + \varepsilon_\text{i}$	177	6	1019.902	13.619	0.080
7. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FA} + \beta_3\text{FA}^2 + a_\text{i} + \varepsilon_\text{i}$	177	7	1021.168	14.885	0.042
8. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FA} + \beta_3\text{Y} \times \text{FA} + a_\text{i} + \varepsilon_\text{i}$	177	8	1021.740	15.457	0.032
9. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG1} + \beta_3\text{Y} \times \text{FJG1} + a_\text{i} + \varepsilon_\text{i}$	177	8	1023.109	16.826	0.016
10. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG1} + \beta_3\text{FT} + \beta_4\text{FJG1} \times \text{FT} + a_\text{i} + \varepsilon_\text{i}$	177	8	1023.527	17.244	0.013
11. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FJG1} + \beta_3\text{FA} + \beta_4\text{FJG1} \times \text{FA} + a_\text{i} + \varepsilon_\text{i}$	177	8	1023.623	17.340	0.012
12. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FT} + a_\text{i} + \varepsilon_\text{i}$	179	6	1029.668	23.385	0.001
13. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FT} + \beta_3\text{FT}^2 + a_\text{i} + \varepsilon_\text{i}$	179	7	1031.275	24.992	<0.001
14. $\beta_0 + \beta_1\text{Y} + \beta_2\text{FT} + \beta_3\text{Y} \times \text{FT} + a_\text{i} + \varepsilon_\text{i}$	179	8	1031.655	25.372	<0.001

Model is highlighted in bold because ΔAIC$_\text{c}$ is less than 2

Y year, *FA* female age (years), *FA*^{2} female age squared (years^2), *FT* female size (mm), *FT*^{2} female size squared (mm^2), *FJG1* female juvenile growth in the first year (mm year^{-1}), *FJG2* female juvenile growth in the second year (mm year^{-1}), β_0 intercept, a_i random intercept (maternal identity), ε_i error term, *n* total number of observations, *K* number of parameters, *AIC$_c$* corrected Akaike`s information criterion, *ΔAIC$_c$* delta AIC$_\text{c}$, w_i Akaike weight

(model 3, Table 1). In contrast to Burton et al. (2013) in Atlantic salmon, we did not find a relationship between female juvenile growth and offspring growth rate, which reduces the probability of a genetic growth effect transferred from fast-growing females to their young. In light of these arguments, we interpret our finding as evidence for a growth- and condition-dependent maternal effect by spawning females on offspring performance in a natural pike population unrelated to size or age at spawning.

It is likely that fast juvenile growth by female pike is related to a bold and risk-averse behavioral type (aka personality). In juvenile pike, avoiding predation by cannibals is a major selective force (Nilsson 2006; Haugen et al. 2006, 2007). Hence, pike that grow fast early in life are forced to take more risks to secure resources while trading off elevated mortality risk (Stamps 2007). There is an emerging literature of consistent behavioral differences in fish, including pike (Kobler et al. 2009; Nyqvist et al. 2012). Kobler et al. (2009) found that three behavioral types of pike co-occurred in Kleiner Döllnsee, and the more active habitat opportunists also showed an elevated lifetime growth pattern, which encompassed females with fast early growth rates. Laboratory-based studies have also reported a relationship between behavioral types and metabolism and the size of eyes as an important sensory organ for the visual predator pike (McGhee et al. 2013). Although the link between personality and growth has not been confirmed in juvenile pike under laboratory conditions (Nyqvist et al. 2012), we found a relationship between female juvenile growth and adult body size, suggesting either an intrinsically greater growth capacity or consistently greater food resource acquisition of faster-growing females compared to slower-growing ones. We therefore assume that the fast juvenile growth rate is a surrogate variable for individuals that forage more and are more risk prone, potentially securing and ingesting more resources, which in turn could improve condition, fecundity, and egg quality, in addition to a tendency for early spawning. All these factors likely contributed to the longer offspring sizes emerging from fish hatched by females that grew fast when they were young. In line with earlier work (Taborsky 2006a, b; Burton et al. 2013), our results suggest that early experience has implications for subsequent adult reproductive performance, maybe by affecting the development of specialized skills and traits important not only for early life but also for adult performance.

Influences by the thermal and maternal environment on body size and growth are ecologically of importance because even small differences in size of age-0 pike are sufficient to affect mortality caused by inter- and intra-cohort cannibalism (Bry et al. 1991). Ecologically, larger body size results in improved size-dependent competitive abilities (Hühn et al. 2014) and the opportunity to undergo size-dependent diet shifts earlier during ontogeny (Huss et al. 2008), which lower size-dependent winter mortality (Haugen et al. 2007). Pike fry become cannibalistic at about a total length of 70 mm (Bry et al. 1995), and the earlier onset of cannibalism by larger-sized individuals will result in a growth advantage (Giles et al. 1986). Because fast early growth is positively related to survival in pike

(Haugen et al. 2006, 2007), differential survival of offspring in relation to hatch timing and growth-related maternal effects may also result in selection on spawning time and correlated female traits. However, because spring temperature varies stochastically, our study implies that there is unlikely a consistent benefit of early spawning and hatching in pike.

Our study has some limitations worth mentioning. Firstly, hatching dates were only estimated for those age-0 pike that survived until sampling in June or July. As size-selective mortality for pike is particularly high during the first weeks of life (Bry et al. 1995; Hühn et al. 2014), sampling designs of this type may not account for the full range of observed hatching dates. Secondly, it would have been worthwhile to measure resource availabilities (e.g., zooplankton density) at a high temporal resolution to better explain growth variation within seasons of early- and late-hatched age-0 pike. Finally, due to the study design, it was impossible to include more maternal traits that might have influenced offspring performance. Future work in natural populations might do better by estimating as many individual traits as close as possible to the spawning period, including, of course, condition.

Notwithstanding these limitations, the present work has shown that temperature and growth-related maternal effects jointly matter for affecting the size of age-0 pike in the first weeks of life and that the particular thermal environment in spring will moderate whether or not hatching early pays off. In contrast to expectations emerging from laboratory studies, we found no evidence for size- or age-dependent maternal effects to affect growth rate and size attained of age-0 pike in an unexploited natural population. Because spring temperature will vary stochastically among years, selection pressures on hatch dates in pike will also vary, in turn maintaining a spread of spawning times in the population to serve as bet-hedging strategy to buffer against unpredictable environmental fluctuations. In addition, it was recently found in Kleiner Döllnsee that fast-growing females are more vulnerable to angling than slow-growing females (Pieterek 2014). Hence, recreational fishing may selectively remove fast-growing females which not only tend to spawn earlier but also produce fitter offspring similar to the case in largemouth bass (*Micropterus salmoides*) (Sutter et al. 2012). Thus, our study underscores the need for paying attention to the trait-selective removal of pike (and other species), which is why management by harvest slots seems to be a superior strategy to classical minimum-length limits in this species (Gwinn et al. 2015; Matsumura et al. 2011).

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