Effects of temperature on the survival and development of the early life stages of northern pike (Esox lucius)

Emilie Réalis-Doyelle, Alain Pasquet, Pascal Fontaine, Fabrice Teletchea

Knowl. Manag. Aquat. Ecosyst. 2022, 423, 10
© E. Réalis-Doyelle *et al.*, Published by EDP Sciences 2022
https://doi.org/10.1051/kmae/2022007

www.kmae-journal.org

Knowledge & Management of Aquatic Ecosystems

Journal fully supported by Office français de la biodiversité

RESEARCH PAPER OPEN ACCESS

Effects of temperature on the survival and development of the early life stages of northern pike (*Esox lucius*)

Emilie Réalis-Doyelle[1,a], Alain Pasquet[2], Pascal Fontaine[1] and Fabrice Teletchea[1,*]

[1] University of Lorraine, UR AFPA, USC INRAE 340, Vandoeuvre-lès-Nancy, F-54506, France
[2] CNRS (National Center for the Scientific Research – France)

Received: 5 July 2021 / Accepted: 15 February 2022

Abstract – In the context of global change, the aim of this study was to investigate the effects of temperature on the survival rate and various variables (development time, morphometric measures, energy values) for both embryos and post-hatch stages until first food intake of northern pike (*Esox lucius*). We applied five constant temperatures (8, 10, 12, 14 and 16 °C) and their effects were analyzed during the entire endogenous feeding period at three stages: hatching, emergence and first food intake. Around 80,000 eggs from five females and five males were used. As expected, the development time was three times longer at 8 than at 16 °C. The survival rate of well-formed post-hatch stages at the end of the endogenous feeding period was similar between temperatures: 76% (10 °C), 73% (12 °C), 72% (14 °C), 72% (16 °C), except at 8 °C (70%). Also at 16 °C, post-hatch stages were larger and had the highest energy value when starting feeding exogenously. These results are in accordance with current models that predict an increase of the distribution area of northern pike in France in coming decades associated with climate change projections (1 to 5 °C increase by 2100 for France).

Keywords: Global warming / endogenous feeding period / egg / post-hatch stage / energy value / northern pike

1 Introduction

According to the report of the International Panel of climate change IPCC (2018), the average temperature at the Earth surface could rise between 0.5 and 5.5 °C during the coming decades. A recent synthesis shows that whatever the thermal range of the fish species considered, they will be affected by climate change (Myers *et al.*, 2017). In this context, an important scientific challenge is to try to predict how fish species could be impacted (Araùjo and Peterson, 2012).

The most commonly used model to predict the effect of climate change is the species distribution models or SDMs (Robinson *et al.*, 2017; McMahan *et al.*, 2020). Three types of data are generally considered, those related to species (presence/absence in a given area), environment (structure of rivers, physical and chemical parameters), and climate (temperature, precipitation, sunshine). Nevertheless, the potential role of phenotypic plasticity in the acclimation and adaptive potential of an organism to global change is not currently accounted for in prediction models (Vagner *et al.*, 2019).

In France, the modeling of the impact of global change on freshwater fish distribution was made by Buisson (2009) based on the presence/absence of 35 species sampled in more than 1000 stations in the last 30 years. This study forecasted that the effects of climate change could be rather positive during the next century (*e.g.*, 87% increase for chub, *Squalius cephalus*), except for cold-water species (*e.g.*, a 76% decrease for common trout, *Salmo trutta*). Northern pike (*Esox lucius* L. 1758), which is classified as "Vulnerable" (VU) in the French IUCN red list (2019) and Least Concern in the world IUCN red list, could increase its distribution area by 30% in France by the end of the century (Buisson, 2009).

Northern pike spawns from late February to March under optimal weather conditions, such as a temperature between 8 and 15 °C for France (Machniak, 1975; Dubé and Gravel, 1978), an increasing photoperiod (Bruslé and Quingnard, 2001), and flooding periods (Hennessey, 2011). After fertilization, the sticky eggs develop attached on vegetation or on other firm surfaces (Teletchea *et al.*, 2007; 2009a; Teletchea and Teletchea, 2020). After hatching, post-hatch stage remains attached to plants, and start swimming when their yolk reserves are exhausted (Teletchea and Teletchea, 2020).

For embryos, the thermal range is between 8 and 15 °C (Machniak, 1975; Dubé and Gravel, 1978) with lower lethal

[a]Present address: UMR CARTEL, INRAE/USMB, 74203 Thonon-Les-Bains Cedex, France
*Corresponding author: fabrice.teletchea@univ-lorraine.fr

temperature close to 3 °C while the upper limit was found to be 19 °C (Hassler, 1982). In addition, Lillelund (1966) observed a 50% decrease in 2–4 cell-stage survival at a temperature of 19.8 °C, and a 12% decrease in survival when temperature fluctuated daily between 15 and 20 °C for post-hatch stage. Hassler (1982) observed after a thermal shock (10–5 °C) during five hours applied 34 h after fertilization a 80% decrease in survival. This stage therefore appears very sensitive to temperature increased (Chauveheid and Billard, 1983). It is also well known that incubation time decreases when temperature rises (Teletchea *et al.*, 2009b); it varies from 36 and 43 days at 3 °C to 2.5 to 3.8 days at 18 °C for northern pike (Bondarenko *et al.*, 2015). For post-hatch stage, the maximal survival rate was obtained between 6 and 10 °C (Bondarenko *et al.*, 2015), the upper limit being 24 °C (Hassler, 1982). Bondarenko *et al.* (2015) also found that the total length at hatching decreased from 10.61 ± 0.37 mm at 10 °C to 9.21 ± 0.29 mm at 18 °C.

The present study aimed at evaluating the effects of five constant temperatures on the survival rate and the phenotypic plasticity of different traits, such as size (and other morphological parameters), developmental duration and energy value (yolk sac, body, and whole fish) of the early life stages of northern pike. Three key stages were studied: hatching, emergence, and first food intake. Based on these results, we discuss possible ecological consequences and predictions (Buisson, 2009) for both policymakers and aquatic biodiversity managers.

2 Materials and methods

2.1 Eggs

Local brood stock were sampled from the same pond (Neuf-Etang, 8 ha, Domaine de Lindre, Moselle, France), which were fed live prey (forage fish such as roach *Rutilus rutilus*, bleak *Alburnus alburnus*) throughout their life. Temperature in the Domaine de Lindre ponds varies between 8 and 12 °C between February and March. When sampled from the pond in mid-February, the water temperature was 12 °C and the oxygen concentration was 9.0 mg L^{-1}. Brood stock was then put in tanks at a constant temperature of 12 °C for artificial reproduction; offspring are also usually kept at 12 °C for up to 100 days. Thus, for this study we took 12 °C as our reference temperature for the rearing of early life stages. Five egg batches (approximately 500 g per batch by female) were obtained the same day (March 18, 2015 at 9:30 am) by stripping and artificial fertilization of oocytes of five females (mass of 2.87 ± 1.02 kg and total length of 75.4 ± 22 cm) with the sperm of five males (no information on the mass and total length). The average age of brood stock was four years. Females were anesthetized with an anesthetizing solution (0.1 mL L^{-1}) composed of 10% eugenol and 90% ethanol. After anaesthesia, oocytes were obtained by stripping. The milt of the males was obtained, after their euthanasia using an overdose of eugenol and ethanol, by grinding their gonads. Fertilization was carried out on site.

To avoid a male effect related to polyandry, the oocyte batch of each female was fertilized with the milt of one male to obtain five families. Just after fertilization, oocyte batch of each female from each family was transported in separate plastic bags with water supplied from the stocking earthen ponds and oxygen and put into polystyrene boxes to maintain the temperature close to 12 °C. Eggs were transferred to the University of Lorraine, in Nancy, the same day (about one hour by car). Upon arrival, eggs were treated with iodine solution (Romeiod, 20 ml L^{-1}) for 10 minutes to prevent stickiness and were washed three times with water from incubators at 12 °C.

The exact number of eggs used here was calculated at the end of the experiment by summing dead (collected and counted on a daily basis) and alive individuals. Overall, 79,129 eggs were used for all females: 14,264 (8 °C), 16,389 (10 °C), 18,381 (12 °C), 15,943 (14 °C), and 14,152 (16 °C).

2.2 Experimental conditions

The whole experiment was performed in a dedicated room with an air temperature fixed at 15 °C (these facilities are conforming to the French legislation with agreement number C54-547-18). Incubators were made by the company Lorraine Chaudronnerie Plastique (410 rue Henri Moissan 54710 Ludres) directed by M. Henrion (Réalis-Doyelle *et al.*, 2016). One incubator ($110 \times 64 \times 186$ cm) per temperature was used (five in total) with recirculating water systems. About 1/3 of the total volume of each incubator (90 L) was periodically renewed every two days. Each incubator contained nine separated trays ($45 \times 7 \times 12$ cm, these trays include rigid parts on the sides and a flexible lower part made of a synthetic material net with a 200 μm mesh). Eggs coming from the five females were mixed and then distributed within each of the nine trays of the five incubators. The initial number of eggs was $n = 1670 \pm 170$ eggs per tray.

After 1 h of their arrival at the laboratory, *i.e.* around five hours after fertilization, the temperature was modified from 12 °C to the experimental temperatures targeted with a 1 °C incremental step per hour (Peterson and Martin-Robichaud, 1989; Réalis-Doyelle *et al.*, 2016). Five temperatures (8, 10, 12, 14, 16 °C) were tested according to IPPC (2018) predictions.

The temperature was monitored by two different systems, via a probe integrated into the water heating/cooling system, and manually by a probe (ODEON, accuracy range for the probe is 0.1 °C). To maintain temperature, each incubator was equipped with an individual thermostat allowing the water temperature to be varied from 1 to 28 °C. Temperatures were obtained using a chiller with a power of 550W (no storage tank). If a difference of ±0.5 °C occurred, the system regulated the temperature. In addition, to ensure optimum temperature maintenance, the rearing tanks were covered with a removable transparent PETG cover. This system also has an integrated UV lamp (16W) for the regulation of the microbial load.

Oxygenation of the water was ensured by means of a cascade to the filtration tank (Réalis *et al.*, 2016). Water was circulated by a pump integrated into the incubators (flow rate of 4 m^3 h^{-1}). Five luminous lights (LED bulbs) were installed above each incubator, with the possibility to control the light intensity (45 and 450 lux). The photoperiod was 16 hours' light/8 hours' dark throughout experiment. Light intensity was 100 lux at the water surface of each incubator.

Water quality (ammonia, nitrite and pH) was checked twice per week. Total ammonia and nitrite concentrations in each incubator were kept below 0.05 and 0.01 mg L^{-1} respectively and pH remained at 8 ± 0.4.

2.3 Events and periods studied

Three events (hatching, emergence and first food intake) were analysed when 50% of the individuals passing to the next developmental stage was determined by visual observation. These events delimitate three periods: P1 from fertilization to hatching (post-hatch stage left the eggshell); P2 from hatching to emergence (post-hatch stage began swimming in the water column), and P3 from emergence to first food intake (ffi): onset of exogenous feeding when the yolk sac was completely consumed). *Artemia nauplii* were given just after emergence twice a day (8:00 a.m and 2:00 p.m) and the ffi was determined when at least 50% of post-hatch stages started feeding by direct observation. For each incubator, random samples of embryos and post-hatch stages were checked every 1 h between 8 a.m and 6 p.m.

The total duration of the endogenous feeding period was defined as the time from fertilization to the onset of external feeding. The relative time (RT) of each period (P1, P2, and P3) was calculated as follows: RT = Number of days between two consecutive stages × 100/ total duration of the endogenous feeding period (days).

2.4 Parameters studied

2.4.1 Survival rate

The unfertilized eggs were not taken into account as dead; they were removed from the analysis. The unfertilized eggs were easily identified as they became white and opaque (within 24H) (Bondarenko *et al.*, 2015) In addition, following these 24 hours, we took a sample in order to determine the fertilization rate and then determine the real morality rate, the result obtained was 98%. Dead eggs and post-hatch stages were removed daily and counted per tray and temperature.

The survival rate (SR) for the entire experiment (from fertilization to first food intake) and at each period was calculated as follows: [SR = 100 − (Number of dead individuals cumulated over a period of time × 100) / Number of viable eggs at the beginning of the studied period of time]. Dead individuals (embryos or post-hatch stages) were counted every day to calculate the daily survival rate (DSR, in percentage) for each of the three periods (P1, P2, and P3) as follows: [DSR = (Number of dead individuals cumulated over a period / Number of days within this period) × 100 / Total number of viable eggs].

2.4.2 Malformation rate

Post-hatch stages were classified as either well-formed or malformed. The observations were performed under a binocular microscope (OPTIKA microscope, SZP-10) equipped with a camera (MICROVISION Instruments, Lw1235C-GT1). We randomly sampled 54 post-hatch stages (six post-hatch stages per tray, temperature and stage), which represent about 10% of the total population. Malformed post-hatch stages had visible malformations defined as structural abnormalities of the body (Boglione *et al.*, 2013; De Clercq *et al.*, 2017) such as axial deviations (lordosis, kyphosis and scoliosis) (Holm *et al.*, 2005; Jezierska *et al.*, 2009; Lahnsteiner, 2012). The malformation rate (MF) was calculated as follows: MF = Number of malformed post-hatch stage X 100/54. Subsequently, all post-hatch stages were photographed and were not used for measurements.

2.5 Morphometric and morpho-anatomical parameters

Post-hatch stages were euthanized by an overdose of Ethyl 3-aminobenzoate methanesulfonate salt (MS-222, Tricaine). The morphological parameters analyzed were selected based on Osse and Van den Boogaart (1995), Trabelsi *et al.* (2012), and Lahnsteiner (2012). The morphometric measurements were performed on well-formed post-hatch stages only per temperature and per stage ($n = 6$ per tray). All images were taken with a binocular (OPTIKA microscope, SZP-10) connected to a camera (MICROVISION Instruments, Lw1235C-GT1). All measurements were obtained by processing the images with the Archimed software (MICROVISION Instruments 6.0.14). Four parameters were measured (precision of 0.01 mm): total length (TL), which is the distance between the snout to the tip of the tail; height of the myotome (HM) corresponding to the distance perpendicular to the body axis between the anus and the base of the dorsal fin, and eye diameter (ED) obtained as the mean of the maximum and minimum diameter of the eye orbit, and height (HSV) and length (LSV) of the yolk sac (Fig. 1). The diameter of the yolk sac (YSD) was then calculated by averaging these two measures (Trabelsi-Zouari, 2011).

2.6 Dry mass and Energy value

The dry mass (0.01 mg) was obtained for 27 post-hatch stages per incubator ($n = 3$ per tray, representing 5% of the population) at the three developmental stages (hatching, emergence and first food intake; $n = 405$ samples). For each post-hatch stage, the yolk sac and tissue were first separated, dried at 60 °C for 72 hours, and then weighed using a Denver Instrument S-114 balance (with a precision of 0.01 mg). This allowed obtaining the separate mass of the yolk and tissue (MY and TM, respectively), as well as the energetic values of each by elemental analysis. The total energetic value of post-hatch stage tissue was obtained by combining the values of the yolk and tissue.

Elemental analyses, carbon (C), hydrogen (H), nitrogen (N) and sulfur (S), were performed using a Flash EA 1112 (ThermoFinnigan 2003) elemental analyzer at the Laboratory of Physical Measures (LMP) at the University of Montpellier 2 (France). The oxygen fraction (O% of dry matter) was computed as follows: $O = 100\text{-}(C+H+N+S)$. Caloric values (J mg^{-1} dry mass) were computed from C, H, O and S fractions (% dry matter). The following formula was used to calculate the caloric values: $[CV\ (\mathrm{J\,mg^{-1}}) = 0.004184 \times [88 \times \%\ C + 344 \times (\%\ H - 0.125 \times \%O) + 25 \times \%S]$ (Kamler *et al.*, 1998).

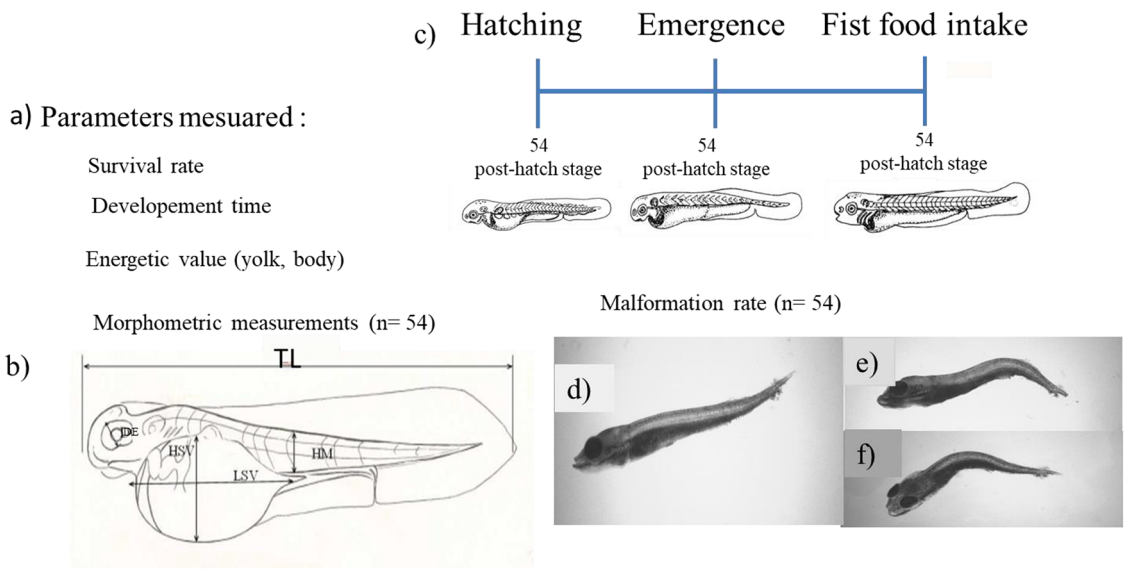

Fig. 1. Schematic Northern pike larval or post-hatch stages showing morphometrics parameters: TL: total length, HM: height of the myotome, ED: eye diameter, HSV: height of the sac yolk, LSV: yolk sac length (Trabelsi, 2011). Malformation rate (a) normal phenotype, (b) and (c) malformed phenotype.

Individual energy value (EV Ind. J^{-1}) was obtained by multiplying the calorific value (CV J^{-1} mg) by the dry mass (TM mg): EV (J ind.$^{-1}$) = CV × TM, as described in Kamler (2002).

2.7 Statistical analyses

The normality of the distributions (Kolmogorov–Smirnov test) and the homogeneity of variances (Levene's *F* test) were tested. Generalized Linear Models (GLMM) were used to determine differences in survival rate, daily mortality rate, malformation rate, survival rate of well-formed post-hatch stage, total length, and energy value. In all analyses, temperature and stage were the fixed factors and trays (nested within temperature) were considered as random factor; The GLMM was followed by a post-hoc Tukey test to calculate pairwise differences, when the interaction between factors was not significant. All parameters were expressed as mean ± S.D. For development time, we used an exponential model. The effect of temperature on the percentage of time between two consecutive stages was tested with a log linear model. All results were considered significant at the level of $p < 0.05$.

A Principal Component Analysis (PCA) was used at both hatching and emergence to investigate the relationships between the six morphometric parameters and body mass. For first food intake, because the yolk sac was exhausted, we treated four morphometric parameters: eye diameter (ED), total length (TL), height of the myotome (HM) and tissue mass (TM). For all stages, the means of morphometric parameters and mass (6 post-hatch stages sampled per tray that gave 54 means per temperature and per stage) were calculated. PCA was followed by a hierarchical cluster analysis (Euclidian distance) to identify groups of post-hatch stage sharing similar morphometric characteristics. All statistical analyses were performed using the software Statistica (version 10).

3 Results

3.1 Development duration

The total duration of the endogenous feeding period differed significantly between temperatures ($X^2 = 28.0$, $p < 0.05$). It decreased exponentially with increasing temperature (Fig. 2). Relative duration time was significantly impacted by temperature ($X^2 = 92.8$, $p < 0.001$) but not by stages ($X^2 = 8.4$, $p = 0.74$). The relative duration of the period P1 was similar between temperatures: between 45% and 52% (Fig. 3). However, the temperature had an effect on the two other periods P2 was the shortest at 12, 14 and 16 °C and inversely P3 was the longest for these three temperatures, compared with 8 and 10 °C (Fig. 3).

3.2 Survival rate

During incubation, an important peak of mortality was observed between three and eight days post-fertilisation according to the temperature tested (Fig. 4): three days at 16 °C (number of dead embryos, $n = 107 \pm 10$ per tray), and at three days at 14 °C ($n = 156 \pm 29$ per tray), six days at 12 °C ($n = 180 \pm 40$ per tray), seven days at 10 °C ($n = 87 \pm 24$ per tray), and eight days at 8 °C ($n = 132 \pm 38$ per tray). The survival rates differed significantly between temperatures ($F_{1,4} = 122.53$, $p < 0.0001$) and stages ($F_{1,2} = 3.29$, $p < 0.0001$), and were also influenced by the interaction between temperatures and stages ($F_{1,8} = 3.4$, $p = 0.002$). There was no effect of trays ($F_{1,35} = 0.86$, $p = 0.64$). The survival rate at the end of the endogenous feeding period was between 70% and 75% for all temperatures (Fig. 4).

The daily mortality rate (in percentage) during each of the three studied time periods (P1, P2, P3) was significantly different between temperatures ($F_{1,4} = 18.8$, $p < 0.0001$) and

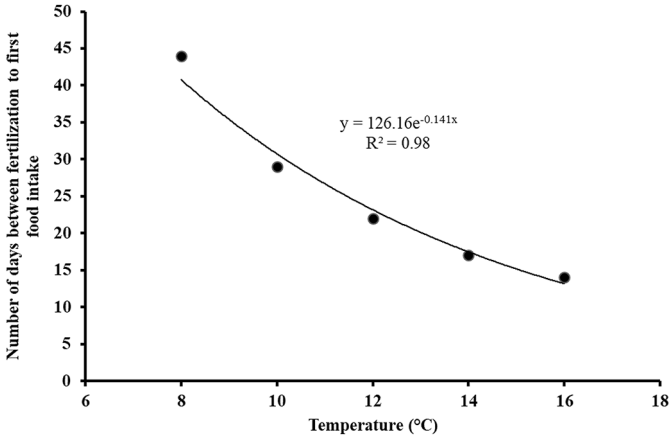

Fig. 2. Effect of temperature on time between fertilization to first food intake (in days). The indicated model was exponential and R^2 indicates the correlation between temperature and duration in days. Each point represents one value per temperature.

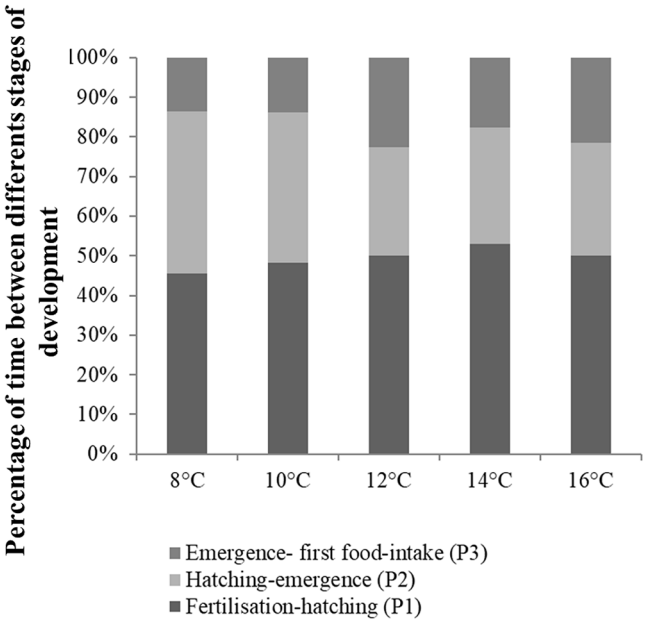

Fig. 3. Effect of temperature on number of days during each period. (P1: from fertilization to hatching; P2 from hatching to emergence; P3 from emergence to first food intake). Only one value was used per temperature because we summed the number of days for each temperature

stages ($F_{1,2}=353.8$, $p < 0.0001$), and was also influenced by the interaction between temperatures and stages ($F_{1,8} = 8.1$, $p < 0.0001$). There was no effect of trays ($F_{1,35}=0.9$, $p=0.49$). The daily mortality rate was the highest for P1 compared to the other periods and at 16 °C compared to the other temperatures (Tab. 1). No difference was found between temperatures for P2 and P3 (Tab. 1).

3.3 Malformation rate

The malformation rate was less than 4% for all stages and temperatures. The rare malformations observed were

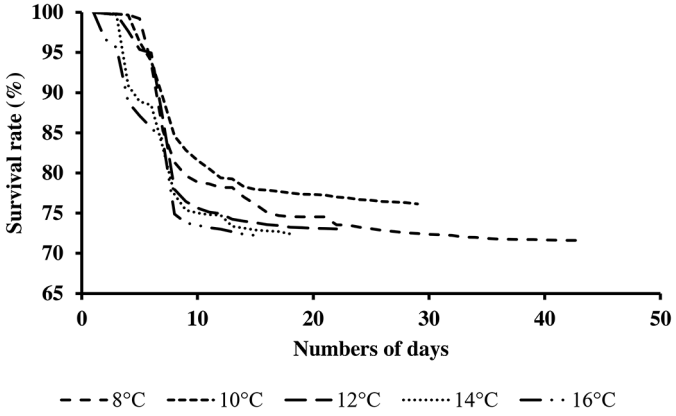

Fig. 4. Effect of temperature on survival rate (%). Only one value was used per temperature.

whole body curvatures. The malformation rate was influenced by the interaction between temperatures and stages ($F_{1,8}=410.5$, $p < 0.0001$). There was no effect of trays ($F_{1,35}=0.9$, $p=0.48$). The percentage of malformed post-hatch stages was highest at 16 °C at hatching compared to other temperatures (Fig. 5a).

3.4 Survival rate of well-formed post-hatch stage

The survival rate of well-formed post-hatch stages was significantly influenced by the interaction between temperatures and stages ($F_{1,8}=4.8$, $p < 0.0001$). There was no effect of trays ($F_{1,35}=1.0$, $p=0.48$) (Fig. 5b). For the three stages, the survival rate was the lowest at 8 °C and highest at 10 °C compared to the three other temperatures (Fig. 5b).

3.5 Total length

The total length was significantly influenced by the interaction between temperatures and stages ($F_{1,8}=12.2$, $p < 0.0001$). There was no effect of trays ($F_{1,35}=1.1$, $p=0.33$). Post-hatch stages were the smallest at 8 °C at hatching and at 16 °C at emergence (Fig. 6). At first food intake, the longest post-hatch stages were in the 16 °C group (Fig. 6).

3.6 Morpho-anatomical changes

At hatching, the two first PCA axes explained 75% of the total variance (Fig. 7a). The first axis (55% of the variance) was correlated with four morpho-anatomical parameters: TL ($r=0.92$), HM ($r=0.79$), ED ($r=0.78$), and TM ($r=-0.88$). The second axis explained 20% of the total variance and was correlated with MY ($r=-0.79$), and YSD ($r=-0.61$). Two clusters were identified by the hierarchical cluster analysis, based on larval size and tissue mass (Fig. 7a). This analysis separated post-hatch stage at the lowest temperature (8 °C) which were the smallest individuals with the smallest yolk sac and highest tissue mass, separated from the other four other temperatures (10, 12, 14, 16 °C) that grouped longer and bigger post-hatch stages.

Table 1. Effect of temperature on daily mortality rate for each period. (P1: from fertilization to hatching; P2 from hatching to emergence; P3 from emergence to first food intake). Differences obtained by the post-hoc Tuckey test were considered significant at $P < 0.05$. The same letter indicates no significant difference between temperatures in each of the three stages.

	P1	P2	P3
8 °C	1.64 ± 0.65^{a}	0.22 ± 0.07^{a}	0.03 ± 10^{-3a}
10 °C	1.53 ± 0.41^{a}	0.12 ± 0.04^{a}	0.11 ± 0.05^{a}
12 °C	2.29 ± 0.57^{b}	0.29 ± 0.07^{a}	0.04 ± 10^{-3a}
14 °C	2.74 ± 0.78^{b}	0.45 ± 0.26^{a}	0.12 ± 10^{-3a}
16 °C	3.58 ± 1.10^{c}	0.43 ± 0.15^{a}	0.41 ± 0.16^{a}

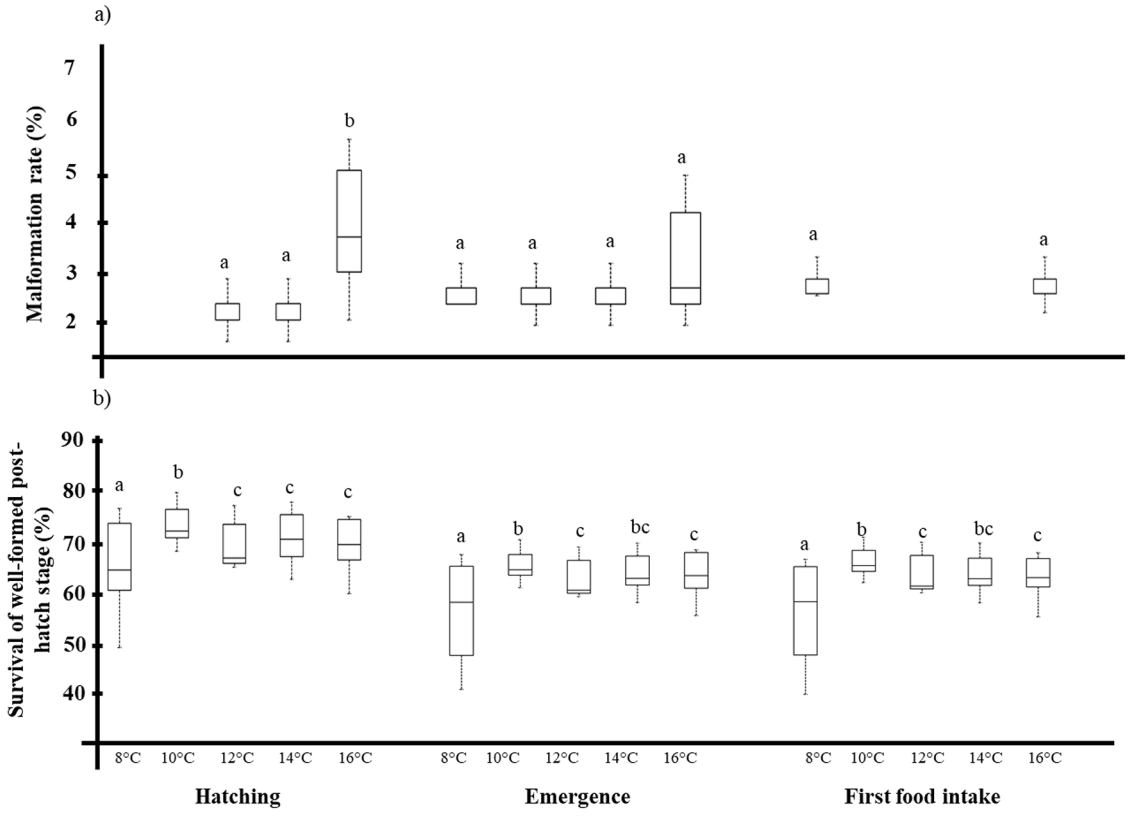

Fig. 5. Effect of temperature on (a) malformation rate, and (b) survival rate of well-formed individuals compared between different developmental post-hatch stages. Mean (±S.D.). Significant differences obtained by X^2 are indicated by different letters ($P < 0.05$).

At emergence, the two first PCA axes explained 73% of the total variance (Fig. 7b). The first axis (47% of the variance) was correlated with four morpho-anatomical parameters: TL ($r = 0.75$), HM ($r = 0.86$), ED ($r = 0.90$), and with MY ($r = -0.80$). The second axis explained 26% of the variance and was principally correlated with YSD ($r = 0.83$) and TM ($r = -0.81$). Two clusters were identified based on larval size and tissue mass (Fig. 7b). This analysis separated the highest temperature (16 °C) corresponding to the smallest individuals with the highest yolk sac mass, separated from the other temperatures (8, 10, 12, 14 °C) that grouped the longest post-hatch stages with the smallest yolk sac.

At first food intake, the two first PCA axes explained 77% of the total variance (Fig. 7c). The first axis (54% of the total variance) was correlated positively with three morpho-anatomical parameters: TL ($r = 0.88$), HM ($r = 0.77$), and with ED ($r = 0.80$). The second axis explained 23% of the total variance and was correlated with TM ($r = 0.92$). Three main clusters were identified. This analysis separated post-hatch stages at 16 °C from fish at 10 °C displaying an average body mass from the other three temperatures (8, 12 and 14 °C) that regrouped post-hatch stages with lower body masses.

3.7 Energy value

The energy value of whole post-hatch stages was significantly influenced by the interaction between temperatures and stages ($F_{1,8} = 3.8$, $p < 0.0001$). There was no effect of trays ($F_{1,35} = 5.0$, $p = 0.94$). For all stages, the total energy

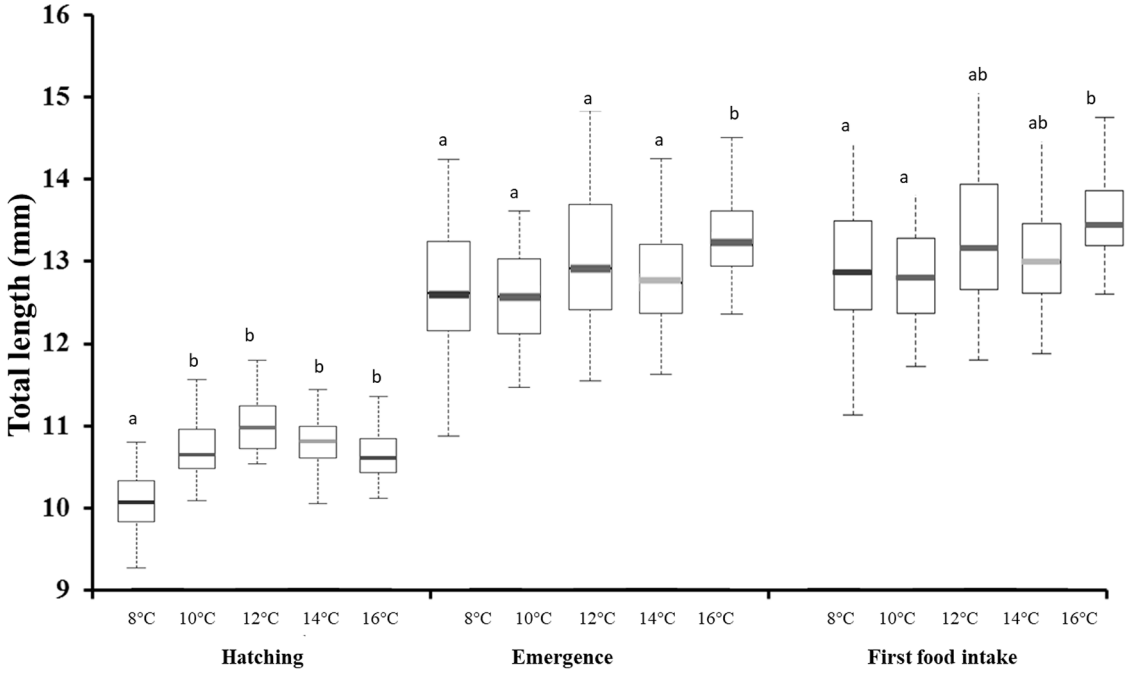

Fig. 6. Effect of temperature on total length at hatching, emergence and first food intake on total length. Mean (±S.D.). Significant difference between temperatures in each of the three stages are indicated by differents letters ($P < 0.05$).

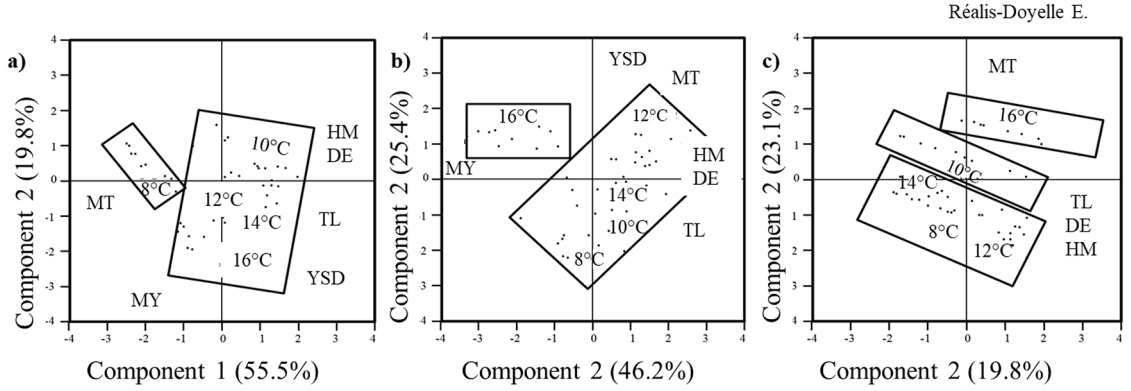

Fig. 7. Principal component analysis performed with six morphometric parameters measured on northern pike (a) at hatching, (b) at emergence, (c) at first food intake (TL= total length, HM= height of myotome, ED= eye diameter, TM= dry wet tissue, MY= dry wet yolk sac, and YSD= yolk sac diameter).

value was highest at 16 °C. At emergence, the total energy value was lowest at 8 °C (Fig. 8a).

The energy value of the body only ($J.ind^{-1}$) was significantly different between temperatures and stages ($F_{1,8} = 8.9$, $p < 0.0001$). There was no effect of trays ($F_{1,35} = 1.3$, $p = 0.13$). At hatching, the body only energy value was lowest at 12 °C and highest at 8 and 10 °C. At emergence, the body only energy value was lowest at 8 °C and highest at 16 °C. At first food intake, the body only energy value was highest at 16 °C (Fig. 8b).

The yolk sac energy value ($J.ind^{-1}$) was significantly different between temperatures and stages ($F_{1,8} = 8.1$, $p < 0.0001$). There was no effect of trays ($F_{1,35} = 0.9$, $p = 0.52$). At hatching, the energy value of the yolk sac was lowest at 8 and 10 °C and highest at 16 °C. At emergence, the yolk sac energy value was not different between temperatures (Fig. 8c).

4 Discussion

4.1 Effect of temperature on the early life stages

4.1.1 Embryological period

This study highlights that the daily mortality rate was higher during the embryological period compared to the two other periods. This phenomenon was also observed in other species suggesting that the earliest ontogenetic stages between fertilization and hatching, in which cell fate determination predominates over growth, may be more sensitive to

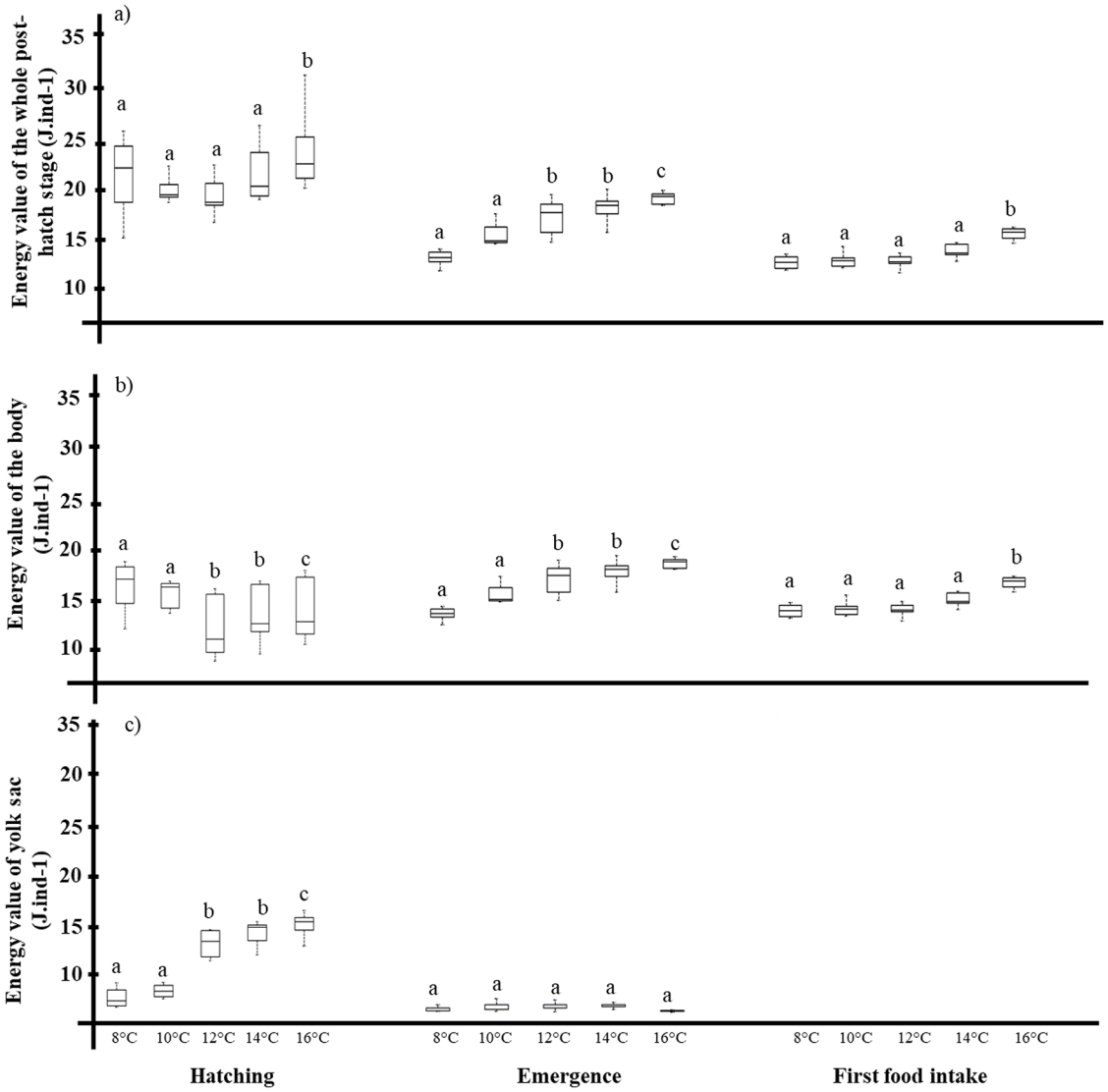

Fig. 8. Effect of temperature on energy value (J.ind^{-1}) at each stage of development (a) for whole post-hatch stage (b), for body only, and (c) for yolk sac (data are mean ±S.D.). Differences obtained by post hoc (test Tukey) are considered significant at $P < 0.05$.

unfavourable thermal conditions (Boglione *et al.*, 2013; Dionısio *et al.*, 2012; Takle *et al.*, 2005; De Clercq *et al.*, 2017). In addition, as expected (Kamler, 2002; Teletchea and Fontaine, 2010), the incubation duration strongly decreased when temperature increased, as already described for northern pike (Billard, 1996), as well as many other species, among which bream *Abramis brama* (Kucharczyk *et al.*, 1997), brown trout *Salmo trutta* (Lahnsteiner, 2012, Ojanguren and Braña, 2003; Réalis-Doyelle *et al.*, 2016), pikeperch *Sander lucioperca* (Ott *et al.*, 2012), and burbot *Lota lota maculosa* (Barron *et al.*, 2012).

4.1.2 Hatching

At hatching, post-hatch stages were not strongly affected by temperature, except at 8 °C where the survival rate was lower, the total length was smallest and fish displayed lowest energy; the highest malformation rate was obtained at 16 °C. Bondarenko *et al.* (2015) found a similar pattern of survival at hatching for northern pike with 56% (at 6 °C) *vs* 65% (at 10 °C). Previous studies found an optimum temperature between 6 and 10 °C for northern pike in the Czech Republic (Bondarenko *et al.*, 2015) or below 12 °C in St. Lawrence River (Cooper, 2000; Farrell *et al.*, 2006). These differences of optimum temperature might reflect local adaptation (Berggren *et al.*, 2016), particularly when comparing populations living in different environments (Sunde *et al.*, 2019) or at different latitudes (France, Czech Republic or Canada). Such local adaptations were highlighted for Eurasian perch (*Perca fluviatilis*) with differences in growth and survival rates between several populations (*i.e.* Belgian, Finnish, French, and Italian) corresponding to genetically differentiated groups (Toomey *et al.*, 2019, 2020, 2021).

The malformation rate was low (<4%) for all temperatures. These results were similar to those obtained previously for northern pike: 2% (at 6, 18 and 21 °C) by Hassler (1982)

and 6% (at 10 °C) by Bondarenko *et al.* (2015). The size at hatching was smaller for the two extreme temperatures tested. Similar results were already described in northern pike between 3 and 18 °C (Bondarenko *et al.*, (2015) as well as for other species (Kamler *et al.*, 1998; Martell *et al.*, 2005; Kaminski *et al.*, 2006). The decrease of size at extreme temperatures might be due to a less efficient use of the yolk reserves (Bondarenko *et al.*, 2015). This hypothesis seems confirmed by the fact that at hatching, post-hatch stage at 8 °C had an energy value (whole larva) lower than at the other temperatures (Fig. 8). The extended incubation time could lead to an over-consumption of the yolk sac (Ojanguren and Braña, 2003). The second hypothesis would be a less efficient use of the energetic reserves beyond the optimum growth range (Bondarenko *et al.*, 2015). Moreover, at 8 °C, the hatching period was longer than at other temperatures (7 days at 8 °C *vs* 1 day at the other temperatures). This difference could lead to a much higher energy value heterogeneity. Trabelsi *et al.* (2016) showed within the same cohort a difference for biochemical and energy value (yolk sac and body) between early, middle and late hatching post-hatch stages. They found a better efficiency of yolk conversion in terms of energy for early and mid-hatched compared to the late hatched post-hatch stage. At 8 °C, the size and energy differences might result from diverse incubation times between early and late hatching post-hatch stages. These differences of size and energy could increase intra cohort cannibalism (Baras *et al.*, 2011; Barron *et al.*, 2012).

4.1.3 Emergence

At emergence, post-hatch stages were moderately impacted by temperature. No impact was observed for survival rate, except at 8 °C where it was significantly lower and fish had lower energy; the highest malformation rate and energy value were obtained for post hatch-stage at 16 °C. This increased growth between hatching and emergence for post-hatch stages at 16 °C might be explained by a compensatory growth (Korwin-Kossakowski, 2008). This phase would allow a smaller and perhaps less developed hatched fish to catch up with other individuals with an average size just prior to the onset of exogenous feeding (Kamler, 2008). This compensatory growth has already been observed for northern pike (Trabelsi *et al.*, 2012, 2016) as well as other species such as Atlantic cod (*Gadus morhua*) (Jordaan *et al.*, 2005) and common carp (*Cyprinus carpio*) (Korwin-Kossakowski, 2008). It is the result of an accelerated development for a very short period after hatching. At emergence, post-hatch stages reared at 16 °C had the highest energy value. During the endogenous feeding period, growth rate is related to the quantity and quality of the yolk and the metabolic capacity of the post-hatch stage to effectively use their yolk sac (Cavalli *et al.*, 1997). Increasing the efficiency of yolk utilisation is possible if the cost of protein synthesis is reduced or if energy is reallocated from maintenance functions to growth (Wieser *et al.*, 1992). Therefore, post-hatch stages at 16 °C, which had the highest energy value, are probably due to the better use of their vitelline reserve to create new tissues (Kaminski *et al.*, 2006; Kamler, 2008). In contrast, for the pike reared at 8 °C, the energy in the yolk sac was used less efficiently for tissue and more for both respiration and maintenance, and consequently could explain the smaller size at emergence (Pepin, 1991; Jaworski and Kamler, 2002).

4.2 Possible ecological consequences

The survival rate of well-formed post-hatch stages at the end of the endogenous feeding period was impacted by temperature, ranging from 60% (at 8 °C) to 75% (10 °C); at 8 °C, post-hatch stages were also the smallest with the lowest energy value. At 16 °C, 70% of post-hatch stages were well-formed, were the longest, and they showed the highest energy content. Post-hatch stages reared at higher temperatures could have an advantage during dispersion, reducing the exposure to predation and unfavorable environmental conditions, and a better access to food resources. In contrast, at 8 °C, post-hatch stages could be disadvantaged because they were the smallest and had a lower energy value. Previous studies showed that during the dispersal phase, smaller post-hatch stages have to move over relatively greater distances to acquire resources while larger post-hatch stages disperse less (Skov and Koed, 2004; Kobler *et al.*, 2009). The dispersal phase of small post-hatch stages could also be due to social stress (Edeline *et al.*, 2010), such as avoiding or reducing the risk of cannibalistic attacks and intimidation interference with conspecifics (Nilsson, 2004). Laboratory experiments on pike have also shown that more social stress increases energetic costs and induces growth depression (Edeline *et al.*, 2010). In addition, the time to reach first food intake stage was strongly reduced when temperature increased, so post-hatch stage developing at higher temperatures could potentially reduce their exposure time to predators or to unfavorable environmental conditions, which are important sources of mortality in nature (Houde, 1989; O'Connor *et al.*, 2009).

In addition, the temperatures during embryonic development can continue to shape the phenotype of organisms beyond the incubation period, via developmental plasticity. Georga and Koumoundouros (2010) showed morphological changes in adult zebrafish to be due to different incubation temperatures, including fish shape and position of anal, caudal and dorsal fins, as well as gill covers and lower jaws. Durtsche *et al.* (2021) also suggest an onset of the plastic response to temperature during the embryonic period allowing the adult to better cope with subsequent temperature variations. One possible future study would be to investigate the mechanism underlying the plastic response via trait variations (Toomey *et al.*, 2019, 2020, 2021) and molecular techniques (Sunde *et al.*, 2019; Massey and Hutchings, 2020) in order to predict how populations will be affected by natural and anthropogenic environmental variability (Oomen and Hutchings, 2015).

If post-hatch stages are unable to feed exogenously before the exhaustion of their yolk reserves, they could die from starvation, known as the Point of No Return (Dou *et al.*, 2005). Yet, post-hatch stage may still survive by using energy normally dedicated to growth, swimming and predation (Kamler, 1992; Dou *et al.*, 2002, 2005), but this would ultimately affect growth, making these post-hatch stage more vulnerable to predation (Miller *et al.*, 1988). Important differences in development time to reach the first food intake (Fig. 2) could reduce the "window of opportunity" for post-hatch stages to find appropriate prey, a phenomenon known as

"match-mismatch" (Rahel *et al.*, 1996; Gustafsson *et al.*, 2010). For instance, a change in zooplankton and fish communities has affected the growth of juvenile pikeperch (*Sander lucioperca*) in Lake Võrtsjärv (Ginter, 2012). Growth decreased by 1.5 times when prey (large cladocerans and smelt: *Osmerus eperlanus eperlanus m. spirinchus* (Pallas)) were less abundant (Ginter, 2012). In addition, it was shown that the collapse of the prey population (smelt) was triggered in lakes Võrtsjärv and Peipsi (in central Estonia) by an increase in water temperature (Kangur *et al.*, 2002). Ginter (2012) concluded that it is very likely that global warming has influenced the recruitment of pikeperch juveniles because of its impact on their potential prey. Nevertheless, other studies on northern pike in Sweden and Norway, where a strong decline of the populations occurred, concluded that the "match-mismatch" phenomenon alone could not explain the decline in recruitment (Leggett and Deblois, 1994; Nilsson *et al.*, 2004; Kallasvuo *et al.*, 2010).

4.3 Implications for management and responses to environmental change

Our results suggested that higher water temperatures favour the survival and development of early life stages of pike and thus could favour the increase of its distribution area in France in the coming decades (Buisson, 2009). Conversely, local cooling could also have significant consequences on the early life stages of pike (in the present study, survival rate was lower), which has become an important model species in both ecology and evolution (Forsman *et al.*, 2015). Individuals, populations and species could have various strategies to acclimate (Ghalambor *et al.*, 2006) or adapt (Burger *et al.*, 2005) to novel conditions, or to disperse to habitats with more suitable conditions, which might result in range shifts and expansions. For instance, Tibblin *et al.* (2016) showed that pike could adjust its time of spawning between years to ensure that its embryos and post-hatch stages develop when temperature conditions are most favourable. Here, our results demonstrated the sensitivity to temperature of a local French pike population (only 5 families); the species showed also a high plasticity to temperature and salinity variations (Sunde *et al.*, 2018, 2019), which varies between families (female/male pairs) (Sunde *et al.*, 2019). Sunde *et al.* (2019) concluded that those plasticity and genetic variation could be key to resilience and long-term survival in the face of global change.

Kallasvuo *et al.* (2010) proposed that recruitment is also influenced by several other abiotic factors such as water level fluctuations during the spawning season, causing temporary drying out of suitable spawning areas and habitats for the early life stages in lakes and rivers. It seems that the main obstacle for the future recruitment of pike in France will therefore probably not be the increasing water temperature itself, but more likely the negative effect of the increasing water temperature on macrophytes present in the shallows (Casselman and Lewis, 1996; Kallasvuo *et al.*, 2010). This cover of macrophytes is crucial for two main reasons: i) at hatching, post-hatch stages are stuck on submerged wetland plants in shallows near riverbank habitats where spawning took place (Casselman and Lewis, 1996), ii) it increases zooplankton density (cladocerans and cyclopoid copepods) known to be the most important prey for early exogenous feeding pike (Telesh, 2004). In France, the main factor affecting pike recruitment was the degradation of the water flow regime (Denys et al., 2014; Keith et al., 2020) . Thus, floodable areas should be better taken into account in order to preserve the breeding and rearing areas for pike.

In conclusion, this study showed that the survival rate of well-formed post-hatch stages at end of endogenous feeding period (around 70%) was not strongly impacted by temperatures, except at 8 °C (60%). At higher temperatures, first-feeding post-hatch stages are larger and have the highest energy value, which could be better for recruitment. This result is in accordance with current models that predict an increase of the distribution area of pike in France in the coming decades due to climate warming.

Ethics

This study was carried out in strict accordance with recommendations contained in the Guide for the Care and Use of Laboratory Animals and with the French legislation [on animal experimentation] (agreement number: C54-547-18). The protocol was approved by the Committee on the Ethics of Animal Experiments of the University of Lorraine (Directive 499 2010/63/EU). All efforts were made to minimize suffering.

Acknowledgments. We thank Hammani Vincent for his help during the experimental work. The project was funded by ONEMA (National Agency for Water and Aquatic Environments).

References

Araùjo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93: 1527–1539.

Baras E, Raynaud T, Slembrouck J, Caruso D, Cochet C, Legendre M. 2011. Interactions between temperature and size on the growth, size heterogeneity, mortality and cannibalism in cultured post-hatch stage and juveniles of the Asian catfish, *Pangasianodon hypophthalmus* (Sauvage). *Aquac Res* 42: 260–276.

Barron J, Jensen N, Anders P, Egan J, Ireland S, Cain K. 2012. Effects of temperature on the intensive culture performance of larval and juvenile North American burbot (*Lota lota maculosa*). *Aquaculture* 365: 67–73.

Berggren H, Nordahl O, Tibblin P, Larsson P, Forsman A. 2016. Testing for local adaptation to spawning habitat in sympatric subpopulations of pike by reciprocal translocation of embryos. *PLoS One* 11: e0154488

Billard R. 1996. Reproduction of pike: gametogenesis, gamete biology and early development. *Fish Fish* 19: 13–43.

Boglione C, Gisbert E, Gavaia P, *et al.* 2013. Skeletal anomalies in reared European fish larvae and juveniles. Part 2: Main typologies, occurrences and causative factors. *Rev Aquac* 5: S121– S167.

Bondarenko V, Drozd B, Policar T. 2015. Effect of water temperature on egg incubation time and quality of newly hatched larvae of northern pike (*Esox lucius* L., 1758). *J Appl Ichthyol* 31: 45–50.

Bruslé J, Quingnard JP. 2001. Biologie des poissons d'eau douce européens. Collection aquaculture-pisciculture.

Buisson L. 2009. Des rivières françaises et changement climatique: impacts sur la distribution des espèces et incertitudes des projections. Thèse de doctorat de l'université de Toulouse. 282 p. http://ethesis.inp-toulouse.fr/archive/00000946/01/buisson.pdf.

Casselman JM, Lewis CA. 1996. Habitat requirements of northern pike (*Esox lucius*). *Can J Fish Aquat Sci* 53: 161–174.

Cavalli RO, Scardua MP, Wasielesky WJ. 1997. Reproductive performance of different Sized Wild and Pond-reared *Penaeus paulensis* Females. *J World Aquac Soc* 28: 215–300.

Chauveheid A, Billard R. 1983. Incubation and hatching of pike eggs and larval yolk resorption. INRA.

Cooper J. 2000. Comparative development and ecology of northern pike *Esox lucius* and *muskellunge E. masquinongy* eggs and larvae post-hatch stage in the upper St. Lawrence River and the implications of changes in historical spawning habitat. State University of New York, College of Environmental Science and Forestry, Syracuse.

De Clercq A, Perrott MR, Davie PS, Preece MA, Huysseune A, Witten PE. 2017. The external phenotype-skeleton link in post-hatch farmed Chinook salmon (*Oncorhynchus tshawytscha*). *J Fish Dis* 41: 511–527.

Denys GP, Dettai A, Persat H, Hautecœur M, Keith P. 2014. Morphological and molecular evidence of three species of pikes Esox spp. (*Actinopterygii, Esocidae*) in France, including the description of a new species. *C. R. Biologies* 337: 521–534.

Dionısio GC, Campos C, Valente MP, Conceicao LEC, Cancela ML, Gavaia PJ. 2012. Effect of egg incubation temperature on the occurrence of skeletal deformities in *Solea senegalensis*. *J Appl Ichthyol* 28: 471–476.

Dou S, Masuda R, Tanaka M, Tsukamoto K. 2002. Feeding resumption, morphological changes and mortality during starvation in Japanese flounder larvae. *J Fish Biol* 60: 1363–1380.

Dou SZ, Masuda R, Tanaka M, Tsukamoto K. 2005. Effects of temperature and delayed initial feeding on the survival and growth of Japanese flounder larvae. *J Fish Biol* 66: 362–377.

Dubé J, Gravel Y. 1978. Plan pilote d'aménagement intégré des ressources biologiques du territoire de la frayère du ruisseau Saint-Jean, comté de Châteauguay, Québec, p 52.

Durtsche RD, Jonsson B, Greenberg LA. 2021. Thermal conditions during embryogenesis influence metabolic rates of juvenile brown trout *Salmo trutta*. *Ecosphere* 12: e03374.

Edeline E, Haugen TO, Weltzien FA, *et al.* 2010. Body downsizing caused by non-consumptive social stress severely depresses population growth rate. *Proc R Soc B* 277: 843–851.

Farrell JM, Mead JV, Murry BA. 2006. Protracted spawning of St. Lawrence River northern pike (*Esox lucius*): simulated effects on survival, growth, and production. *Ecol Freshw Fish* 15: 169–179.

Forsman A, Tibblin P, Berggren H, Nordahl O, Koch-Schmidt P, Larsson P. 2015. Pike *Esox lucius* as an emerging model organism for studies in ecology and evolutionary biology: a review. *J Fish Biol* 87: 472–9.

Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr Comp Biol* 1: 5–17.

Georga I, Koumoundouros G. 2010. Thermally induced plasticity of body shape in adult zebrafish *Danio rerio* (Hamilton, 1822). *J Morphol* 271: 1319–1327.

Ginter K. 2012. The diet of juvenile pikeperch *Sander lucioperca* in lakes Peipsi and Võrtsjärv: relations between long-term changes in the fish communities and food resources in large shallow lakes. These de doctorat: Doctoral Committee for Agricultural and Environmental Sciences of the Estonian University of Life Sciences has accepted the thesis for the defense of the degree of Doctor of Philosophy in Hydrobiology.

Gustafsson P, Bergman E, Greenumbererg LA. 2010. Functional response and size-dependent foraging on aquatic and terrestrial prey by brown trout (*Salmo trutta* L.). *Ecol Freshw Fish* 19: 170–177.

Hassler TJ. 1982. Effect of temperature on survival of northern pike embryos and yolk-sac larvae. *Freshwater Fish Culture In The United States* 4: 174–178.

Hennessey S. 2011. *Esox lucius*: Northern pike. *Aquatic Invasion Ecology Fall*. FISH 423.

Holm J, Palace V, Siwik P, *et al.* 2005. Developmental effects of bioaccumulated selenium in eggs and Frye of two salmonid species. *Environ Toxicol Chem* 24: 2373–2381.

Houde ED. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish Bull* 87: 471–495.

IPCC, 2018.: Summary for Policymakers. In: Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte V, Zhai P, Pörtner HO, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, and Waterfield T (eds.)].

Jaworski A, Kamler E. 2002. Development of a bioenergetics model for fish embryos and post-hatch stage during the yolk feeding period. *J Fish Biol* 60: 785–809.

Jezierska B, Ługowska K, Witeska M. 2009. The effects of heavy metals on embryonic development of fish (a review). *Fish Physiol Biochem* 35: 625–640.

Jordaan A, Hayhurst E, Kling J. 2005. The influence of temperature on the stage at hatch of laboratory reared *Gadus morhua* and implications for comparisons of length and morphology. *J Fish Biol* 68: 7–24.

Kallasvuo M, Salonen M, Lappalainen A. 2010. Does the zooplankton prey availability limit the larval habitats of pike in the Baltic Sea? *Estuar Coast Shelf Sci* 86: 148–156.

Kaminski R, Kamler E, Korwin-Kossakowski M, Myszkowski L, Wolnicki J. 2006. Effects of different incubation temperatures on the yolk-feeding stage of *Eupallasella percnurus* (Pallas). *J Fish Biol* 68: 1077–1090.

Kamler E, Keckeis H, Bauer-Nemeschkal E. 1998. Temperature-induced changes of survival, development and yolk partitioning in *Chondrostoma nasus*. *J Fish Biol* 53: 658–682.

Kamler E. 1992. Early life history of fish: An energetics approach. *Fish Fish Ser* 4, ed. Pitcher TJ. 267p.

Kamler E. 2002. Ontogeny of yolk-feeding fish: an ecological perspective. *Rev Fish Biol Fish* 12: 79–103.

Kamler E. 2008. Ressource allocation in yolk-feeding fish. *Rev Fish Biol Fish* 18: 143–200.

Keith P, Poulet N, Denys G, Changeux T, Feunteun É, Persat H, 2020. Les Poissons d'eau douce de France. Deuxième édition. Muséum national d'Histoire naturelle; Biotope,: 704 p.

Kangur K, Milius A, Mols T, Laugaste R, Haberman J. 2002. Lake Peipsi: Changes in nutrient elements and plankton communities in the last decade. *Aquac Ecosyst Health* 5: 363–377.

Kobler A, Klefoth T, Mehner T, Arlinghaus R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia* 161: 837–847.

Korwin-Kossakowski KM. 2008. The influence of temperature during the embryonic period on larval growth and development in carp, *Cyprinus carpio* L., and grass carp, *Ctenopharyngodon idella*: Theorical and pratical aspect. *Arc Pol Fish* 16: 231–316.

Kucharczyk D, Luczynski M, Kujawa R, Czerkies P. 1997. Effect of temperature on embryonic and larval development of bream (*Abramis brama* L.). *Aquat Sci* 59: 214–224.

Lahnsteiner F. 2012. Thermotolerance of brown trout, *Salmo trutta*, gametes and embryos to increased water temperatures. *J Appl Ichthyol* 28: 745–751.

Leggett WC, Deblois E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth J Sea Res* 32: 119–134.

Lillelund VK. 1966. Versuche zur erbrutung der Eier vom Hecht, *Exos lucius* L., in Abhängigkeit von Temperatur und Licht. *Arch Fisher* 17: 95–113.

Machniak K. 1975. The effects of hydroelectric development on the biology of northern fishes. A literature review and bibliography Canadian Fisheries Marine Service p68.

Martell D, Kieffer J, Trippel E. 2005. Effects of temperature during early life history on embryonic and larval development and growth in haddock. *J Fish Biol* 66: 1558–1575.

Massey M, Hutchings J. 2020. Thermal variability during ectotherm egg incubation: a synthesis and framework. *J Exp Zool* 1–13.

McMahan C, Fuentes-Montejo C, Ginger L, Carrasco JC, Chakrabarty P, Matamoros W. 2020. Climate change models predict decreases in the range of a microendemic freshwater fish in Honduras. *Sci Rep* 10: 12693.

Miller TJ, Crowder LB, Rice JA, Marschall EA. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can J Fish Aquat Sci* 45: 1657–1670.

Myers BJE, Lynch AJ, Bunnell DB, *et al.* 2017. Global synthesis of the documented and projected effects of climate change on inland fishes. *Rev Fish Biol Fish* 27: 339–361.

Nilsson J, Andersson J, Karås P, Sandstrom O. 2004. Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden. *Boreal Environ Res* 9: 295–306.

O'Connor MI, Bruno JF, Gaines SD, *et al.* 2009. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *PNAS* 23: 104–4.

Ojanguren AF, Braña F. 2003. Thermal dependence of embryonic growth and development in brown trout. *J Fish Biol* 62: 580–590.

Oomen RA, Hutchings JA. 2015. Genetic variability in reaction norms in fishes. *Environ Rev* 23: 353–366.

Osse JW, Van den Boogaart JGM. 1995. Fish larvae, development, allometric growth, and the aquatic environment. *ICES Mar Sei Symp* 201: 21–34.

Ott A, Loffler J, Ahnelt H, Keckeis H. 2012. Early development of the postcranial skeleton of the pikeperch *Sander lucioperca* (Teleostei: Percidae) relating to developmental stages and growth. *J Morph* 273: 894–908.

Pepin P. 1991. The effect of temperature and size on development and mortality rates of the pelagic early life history stages of marine fish. *Can J Fish Aquat Sci* 48: 503–518.

Peterson RH, Martin-Robichaud DJ. 1989. First feeding of Atlantic Salmon (*Salmo solar* L.) fry as influenced by temperature regime. *Aquaculture* 78: 35–53.

Rahel F, Keleher C, Anderson J. 1996. Potential habitat loss and population fragmentation for cold water fish in the North platte river drainage of the rocky mountains: response to climate warming. *J Oceanol Limnol* 41: 1116–1123.

Réalis-Doyelle E, Pasquet A, De Charleroy D, Fontaine P, Teletchea F. 2016. Strong effects of temperature on the early life stages of a cold stenothermal fish species, brown trout (*Salmo trutta* L.). *PLoS ONE* e0155487.

Robinson N, Nelson W, Costello M, Sutherland J, Lundquist C. 2017. A systematic review of marine-based species distribution models (SDMs) with Recommendations for Best Practice. *Front Mar Sci*.

Skov C, Koed A. 2004. Habitat use of 0+year pike in experimental ponds in relation to cannibalism, zooplankton, water transparency, and habitat complexity. *J Fish Biol* 64: 448–459.

Sunde J, Larsson P, Forsman A. 2019. Adaptations of early development to local spawning temperature in anadromous populations of pike (*Esox lucius*). *Bmc Evol Biol* 19: 148.

Sunde J, Tamario C, Tibblin P, Larsson P, Forsman A. 2018. Variation in salinity tolerance between and within anadromous subpopulations of pike (*Esox lucius*). *Sci Rep* 8: 22.

Takle H, Baeverfjord G, Lunde M, Kolstad K, Andersen Ø. 2005. The effect of heat and cold exposure on HSP70 expression and development of deformities during embryogenesis of Atlantic salmon (*Salmo salar*). *Aquaculture* 249: 515–524.

Telesh IV. 2004. Plankton of the Baltic estuarine ecosystems with emphasis on Neva Estuary: a review of present knowledge and research perspectives. *Mar Poll Bull* 49: 206–219.

Teletchea F, Fontaine P. 2010. Comparison of early life-stage strategies in temperate freshwater fish species: trade-offs are directed towards first feeding of larvae in spring and early summer. *J Fish Biol* 77: 257–278.

Teletchea F, Fostier A, Le Bail PY, Jalabert B, Gardeur JN, Fontaine P. 2007. STOREFISH: A new database dedicated to the reproduction of temperate freshwater teleost fishes. *Cybium* 31: 237–245.

Teletchea F, Fostier A, Kamler E, *et al.* 2009a. Comparative analysis of reproductive traits in 65 freshwater fish species: application to the domestication of new fish species. *Rev Fish Biol Fish* 19: 403–430.

Teletchea F, Gardeur JN, Kamler E, Fontaine P. 2009b. The relationship of oocyte diameter and incubation temperature to incubation time in temperate freshwater fish species. *J Fish Biol* 74: 652–668.

Teletchea S, Teletchea F. 2020. STOREFISH 2.0: a database on the reproductive strategies of teleost fishes. Database, doi:10.1093/database/baaa095

Trabelsi A, Gardeur JN, Teletchea F, Brun-Bellut J, Fontaine P. 2012. Hatching time effect on the intra-spawning larval morphology and growth in Northern pike (*Esox lucius*). *Aquac Res* 44: 657–666.

Trabelsi A, Jaworski A, Kamler E, *et al.* 2016. The effect of hatching time on the bioenergetics of northern pike (*Esox lucius*) post-hatch stage from a single egg batch during the endogenous feeding period. *Fish Physiol Biochem* 42: 593–606.

Trabelsi-Zouari A. 2011. Effet intra-ponte du moment d'éclosion sur la morphologie, la croissance et l'efficience métabolique des larves de brochet *Esox lucius* et de carpe commune *Cyprinus carpio*. PhD dissertation, Nancy 1.

Tibblin P, Forsman A, Borger T, Larsson P. 2016. Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike. *J Anim Ecol* 85: 136–45.

Toomey L, Lecocq T, Pasquet A, Fontaine P. 2021. Finding a rare gem: Identification of a wild biological unit with high potential for European perch larviculture. *Aquaculture*, 530: 1–8.

Toomey L, Dellicour S, Vanina T, *et al.* 2020. Getting off the right foot: Integration of spatial distribution of genetic variability for aquaculture development and regulations, the European perch case *Aquaculture* 521 (734981), 1–11.

Toomey L, Bláha M, Mauduit E, *et al.* 2019. When behavioural geographic differentiation matters: inter-populational comparison of aggressiveness and group structure in the European perch. *Aquaculture International, European Percid Fish Culture (Online)*, pp. 1–15.

Vagner M, Zambonino-Infante J-L, Mazurais D. 2019. Fish facing global change: are early stages the lifeline? *Marine Environmental Research* 147: 159–178.

Wieser W, Laich A, Medgyesy N. 1992. Energy allocation and yield and cost of growth in young *Esox Lucius* and *Coregonus Lavaretus* (Teleostei): Influence of species, prey type and body size body size. *J Exp Biol* 169: 165–179.

Cite this article as: Réalis-Doyelle E, Pasquet A, Fontaine P, Teletchea F. 2022. Effects of temperature on the survival and development of the early life stages of northern pike (*Esox lucius*). *Knowl. Manag. Aquat. Ecosyst.*, 423, 10.