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How climate change may affect the early life stages of one of the most common freshwater fish species worldwide: the common carp (*Cyprinus carpio*)

Emilie Réalis-Doyelle ^a, Alain Pasquet ^{a,b}, Pascal Fontaine ^a, Fabrice Teletchea ^a.

a : University of Lorraine, UR AFPA, USC INRA 340, Vandoeuvre-lès-Nancy, F-54506, France

b : CNRS (National center for the scientific research - France)

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Keywords

Climate change, early life stages, survival, morphometric parameters, energy value.

Abstract

The aim of the present study is to test the effects of temperature on the early life stages of one of the most common freshwater fish species worldwide, the common carp. About 16 000 eggs coming from 3-year old broodstock were randomly distributed into five incubators, one incubator by tested temperature (16, 18, 20, 22 and 24°C). Several parameters (survival and malformation rates, development time, morphometric parameters, and energy values) were studied at three key biological stages (hatching, emergence and first food intake). We found no significant impact of temperature on both survival and malformation rates. However, as expected, development time was three times longer at 16°C than at 24°C. At both 16°C and 24°C, the consumption of the yolk sac was highest; yet larvae were smaller at 16°C and largest at 24°C. Our results suggest that the early life stages of common carp developing at 22-24°C could survive better in the wild, which is in accordance with current models that predict a small change of the distribution area of the common carp in France, but probably an extension in Northern European regions, in the next decades consequently to climate change.

1. Introduction

Climate change is predicted to have major impacts on biodiversity at local, regional, and global scales (Heino et al., 2009). Freshwater ecosystems are very sensitive (Sala et al., 2000) as climate change is predicted to increase water temperature, decrease dissolved oxygen levels (Mooij et al., 2007), and lead to eutrophication (Schindler, 1997). In lotic systems, altered hydrologic regimes and increased groundwater temperature could also modify the quality of fish habitat (Ficke et al., 2007). These habitat changes may impact the distribution of fish species (Heino et al., 2009; Jeppesen et al., 2012). For example, Jeppesen et al. (2012) observed a strong dominance of eurythermal species, including common carp (*Cyprinus carpio*), shad (*Alosa alosa*), roach (*Rutilus rutilus*), and pikeperch (*Sander lucioperca*), in three European lakes that exhibited increased eutrophication due to elevated temperatures.

Common carp has a large distribution throughout France (Teletchea, 2011), Europe (Freyhof & Kottelat, 2008), and many other parts of the world (North America, Southern Africa, New Zealand, Australia and Asia) (FAO, 2013) where it has most often been introduced (Flajšhans & Hulata, 2006). The

large distribution of common carp could be explained by a wide tolerance towards environmental factors (Flajšhans & Hulata, 2006). Additionally, common carp is important for aquaculture and is one of the oldest domesticated species (Balon, 1995; Flajšhans & Hulata, 2006; Teletchea & Fontaine, 2014). However, despite its wide geographical distribution and strong environmental tolerance, common carp is classified as vulnerable in Europe, partly due to its hybridization with domesticated introduced stocks, and habitat modification by channelization and dams (Freyhof & Kottelat, 2008). Few studies have focused on the effect of temperature on the early life stages of common carp (Teletchea et al., 2007, 2009a). The lower lethal temperature for embryos was determined to be close to 10°C, while the upper limit was found at 33°C for carp living in Czech Republic (Peňáz et al., 1983; Geldhauser, 1995). In Europe, temperature used in hatcheries to incubate eggs ranged between 18 to 24°C (Woynarovich, 1962; Kamler & Malczewski, 1982; Korwin-Kossakowski, 2008). However, El-Hakim & El-Gamal (2009) observed no hatching at temperatures below 20°C for common carp in Egypt. The upper limit temperature for larvae was found close to 35°C in Czech Republic (Geldhauser, 1995). The incubation time

decreased when temperature increased: from 3.3 days (at 20°C) to 1.9 days (at 24°C) (Korwin-Kossakowski, 2008). The larvae from embryos incubated at higher temperatures were smaller at both hatching (5.7 mm at 20°C vs 5.1 mm at 32°C) and emergence (6.3 mm at 20°C vs 6.1 mm at 32°C) (Korwin-Kossakowski, 2008). In addition, Jezierska et al. (2000) observed a higher malformation rate (up to 22%) of hatching larvae when embryos were incubated at either 17°C or 26°C.

According to the literature, we anticipated that the survival rates of the early life stages of common carp will only be

slightly modified within the temperature range tested here (chosen according to the predicted modification of temperature in the coming decades). For the other parameters studied (malformation rate, morphometric parameters, energy values), it was, however, impossible to anticipate any specific trend according to the temperature tested, except a more rapid development with increasing temperature. The goal of this study was thus to provide a holistic evaluation of the different consequences of a modification of temperature on the early life stages of common carp at three key biological stages (hatching, emergence and first food intake).

2. Material and Methods

2.1. Animals and experimental conditions

Eggs were obtained on May 30, 2015, from 3-year old broodstock stocked in the pond of the Domaine de Lindre (Moselle, France). The temperature of the pond water was 20°C and the oxygen concentration was 9.0 mg L⁻¹. Oocytes obtained after stripping were fertilized with the milt of one male per female. Then, eggs of each female were transported in separated plastic bags with water coming from the stocking ponds and put into polystyrene boxes to maintain the temperature close to 20°C. Overall, about 16 000 eggs were collected and transferred to the University of Lorraine, in Nancy, the same day (about one hour by car).

The experiment was performed in a controlled temperature room (air ambient temperature maintained at 15°C, 16L/8D photoperiod, and light intensity of 100 Lux at the water surface). Five similar recirculating water systems (110 × 64 × 186 cm) were used as incubators at a flow rate of 4 m³ h⁻¹ with U.V.-sterilized. Each incubator contained nine separated racks (45 × 7 × 12 cm). Eggs from the three females were mixed to limit the inter-individual variability, and distributed within the nine racks of each of the five incubators; thus, all families were mixed in each rack of each incubator. After 24 hours, the temperature was modified from 20°C to one of the five experimental temperatures (16, 18, 20, 22, 24°C) with a 1°C incremental step per hour (Peterson & Martin-Robichaud, 1989; Réalis-Doyelle et al., 2016). These five temperatures were chosen according to global climate predictions, from 1 to 6°C (IPCC, 2014), as well as those for France only (1 to 5°C) taking into account possible local cooling (Field et al., 2014).

2.2. Periods and biological stages studied

Three periods were defined throughout the endogenous feeding period: from fertilization to hatching (P1), from hatching to emergence (P2) and from emergence to first food intake (P3) when the yolk sac was absorbed. Hatching (H) was determined when at least 50% of larvae left the egg shell, emergence (EM) when at least 50% of larvae rose up and began swimming in the water column, and first food intake (FFI) when at least 50% of larvae started to feed exogenously (Kamler et al., 1998; Korwin-Kossakowski, 2008; Réalis-Doyelle et al., 2016). Artemia nauplii were given just after emergence twice a day at 9:00 a.m. and 2:00 p.m. (Wolnicki et al., 2009).

2.3. Parameters studied

2.3.1. Period duration

The total duration of the endogenous feeding period corresponds to the time between fertilization and first food intake (in days) for each temperature. The relative time (RT) of each period (P1, P2 and P3) was calculated as follows: $RT = \text{Number of days between two consecutive stages} / \text{total duration of the endogenous feeding period} \times 100$. The time between the first and the last hatched larvae was also studied to calculate the duration of the hatching period for each temperature (Ojanguren & Braña, 2003; Réalis-Doyelle et al., 2016).

2.3.2. Survival rate

Dead eggs and larvae were removed every day to avoid water pollution. Dead eggs were easily identified as they became white and opaque (FAO, 2013), while fertilized eggs were transparent and showed a clear cell division under a binocular microscope (OPTIKA microscope, PAS-10). Unfertilised eggs were removed from the analysis. Dead individuals were counted daily to calculate the survival rate (SR) for the entire experiment and at the end of each period as follows: $SR = 100 - (\text{number of dead individuals cumulated for the entire experiment or between two stages} / \text{number of individuals at the beginning of the experiment or the period considered} \times 100)$. Additionally, the daily survival rate (DSR) was calculated for each of the three periods (P1, P2 and P3) as follows: $DSR = (100 - (\text{number of dead individuals at day } n / \text{number of individuals at day } n-1 \times 100))$. Then, a mean was calculated per periods.

2.3.3. Malformation rate

Malformations were observed on larvae killed by an overdose of Ethyl 3-aminobenzoate methanosulfonate salt (MS-222, Tricaine), and were classified as either well-formed or malformed. Malformed larvae had visible malformations, including malformations of skeleton, head and yolk sac (Afonso et al., 2000; Holm et al., 2005; Jezierska et al., 2000; Lahnsteiner, 2012). The observations were performed on 54 live larvae per incubator ($n = 6$ per rack) sampled at the end of each period. The malformation rate (MF) was calculated as follows: $MF = \text{number of larvae malformed} / 54 \times 100$.

2.3.4. Morphometric parameters

The morphometric parameters analyzed were selected based on Lahnsteiner (2012) and Trabelsi et al. (2013). The measurements were performed on well-formed larvae only. All measures were done with a binocular (OPTIKA microscope, SZP-10) connected to a camera (MICROVISION Instruments, Lw1235C-GT1) with the Archimed software (MICROVISION Instruments 6.0.14). Three parameters were measured on larvae with a precision of 0.01 mm: total length (TL), height of the myotome (HM) and eye diameter (ED), and two on yolk sac: vertical and horizontal diameters. The yolk sac diameter (YSD) was then calculated by averaging these two (Trabelsi et al., 2013).

2.4. Energy value

The dry mass (0.001 mg) was obtained for 450 individuals per incubator (n = 50 per rack) at the three biological stages. Each sample was dried at 60°C for 72 hours. The dry mass was obtained after separating the yolk sac (MY) from the body tissue (MT) to obtain two separate analyses of energy values. Elemental analyses 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). Each sample (25 mg) was divided in two parts: one for carbon (C), hydrogen (H), nitrogen (N) and sulphur (S) analyses and the other to determine the total energy value. Each sample was analyzed in triplicates. The oxygen fraction (O, % dry matter) was then computed as follows: $O = 100 - (C + H + N + S)$. Energy 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 energy values: $[CV \text{ (J mg}^{-1}\text{)} = 0.004184 \times [88 \times \% C + 344 \times (\% H - 0.125 \times \% O) + 25 \times \% S]$ (Kamler et al., 1998). Individual energy value (EV Ind. J-1) was obtained by multiplying the energy value (CV, J-1 mg) by the dry mass (MT mg): $EV \text{ (J ind.}^{-1}\text{)} = CV \times MT$ (Kamler, 2002).

3. Results

3.1. Period duration

The total duration of the endogenous feeding period differed significantly with temperature ($X^2 = 18.9$; $p = 0.04$, d.f. = 4) and decreased exponentially with increasing temperature (Fig. 1).

The relative time of each period was significantly impacted by temperature ($X^2 = 249.6$, $p < 0.001$, d.f. = 12). The relative time of P1 was shorter (60%) for 16 and 24°C, and for P2, it was longer at 16°C (Fig. 2). The relative time of P3 was not different between temperatures, which ranged from 11% to 20% (Fig. 2). The duration of the hatching period decreased rapidly with increasing temperature (three days at 16°C, one day at 18, 20 and 22°C and less than 12 hours (9 am to 3 pm) at 24°C).

3.2. Influence of temperature on survival and malformation rates

3.2.1. Survival rate

There was no significant interaction between temperature and stage for the survival rates (GLM: $F_{1,8} = 0.8$, $p = 0.61$) and

2.5. Statistical analyses

Generalized Linear Models (GLM) were used to determine differences in survival rate, malformation rate, survival rate of well-formed larvae, total length of larvae, and energy value. In all analyses, temperature and stage were the fixed factors and racks (nested within temperature) were considered random factors (Réalis-Doyelle et al., 2016). The GLM was followed by a Tukey post hoc test to calculate pairwise differences between means. All parameters were expressed as mean \pm S.E. For development time, we compared the fitness of various models on the distribution by comparing their r^2 . The effect of temperature on the percentage of time between two consecutive stages was tested with a two-way frequency table analysis. All results were considered significant at the level of $p < 0.05$.

At hatching and emergence, a Principal Component Analysis (PCA) was used to investigate the relationships between the four morphometric parameters (ED, TL, HM, YSD) and masses (MT, MY). At first food intake, we investigated only the relations between four morphometric parameters and the tissue mass (MT). For all stages, the means of morphometric parameters and mass (from 6 larvae sampled per rack, 9 means per temperature) were calculated. PCA was followed by a hierarchical cluster analysis to identify groups of larvae sharing similar morphometric parameters. All statistical analyses were performed using the software Statistica (version 10).

survival rates were not significantly different between temperatures (GLM: $F_{1,4} = 2.2$, $p = 0.08$) and between stages (GLM: $F_{1,2} = 1.3$, $p = 0.27$). At the end of the endogenous feeding period, survival rates varied between 61% and 80% independently of the temperature (Fig. 3).

There was a strong interaction between temperature and stage (GLM: $F_{1,8} = 7.1$, $p < 0.001$) for the mean daily survival rate (DSR). It was the lowest during P1 at 20°C compared to the other temperatures (Table 1). For each temperature, a high number of dead individuals were observed between two and six days post fertilization according to the temperature tested: at six days at 16°C (number of dead embryos per hatchery, $n = 52$), at three days at 18°C ($n = 109$), at three days at 20°C ($n = 61$), at two days at 22°C ($n = 146$) and at one day at 24°C ($n = 164$). For P2, the mean daily survival rate was the lowest at 24°C compared to other temperatures (Table 1). For P3, it was the highest compared to P1 and P2, and no significant difference was found between temperatures (Table 1).

3.2.2. Malformation rate

Malformations were observed on the vertebral column only. The malformation rate was less than 3% for all stages and temperatures. Malformation rate did not differ between temperatures (GLM: $F_{1,4} = 2.3$, $p = 0.07$), but differed between stages (GLM: $F_{1,2} = 9.5$, $p < 0.001$) (Fig. 4(a)).

3.2.3. Survival rate of well-formed larvae

The survival rate of well-formed larvae ranged from 60 to 80% at the end of the endogenous feeding period; yet no significant effect was found either for the interaction between temperature and stage (GLM: $F_{1,8} = 0.7$, $p = 0.68$) or temperature (GLM: $F_{1,4} = 2.2$, $p = 0.08$) and stage (GLM: $F_{1,2} = 0.8$, $p = 0.43$) (Fig. 4(b)).

3.3. Morphometric parameters

There was a significant interaction between temperature and stage (GLM: $F_{1,8} = 6.2$, $p < 0.001$). At hatching, larvae ranged from 6.54 ± 0.18 mm at 16°C to 7.20 ± 0.32 mm at 20°C. At emergence, TL ranged from 7.23 ± 0.34 mm at 16°C to 7.65 ± 0.26 mm at 24°C and at first food intake between 7.40 ± 0.33 mm at 16°C to 7.90 ± 0.23 mm at 24°C (Fig. 5).

At hatching, the first two axes of the PCA explained 65% of the total variance (Fig. 6 (a)). The first axis (42%) was correlated with four parameters: ED ($r = 0.86$), TL ($r = 0.85$), YSD ($r = 0.81$) and HM ($r = 0.56$). The second axis explained 23% of the total variance and was correlated with mass: MT ($r = 0.82$) and MY ($r = 0.80$). At emergence, the first two axes of the PCA explained 53% of the total variance (Fig. 6 (b)). The first axis (34%) was correlated with ED ($r = -0.90$), TL ($r = -0.86$) and MT ($r = -0.47$). The second axis explained 19% of the variance and was correlated with HM ($r = 0.76$), YSD ($r = 0.56$) and MY ($r = 0.49$). At first food intake, the first two axes of the PCA explained 77% of the total variance (Fig. 6 (c)). The first axis (54%) was correlated positively with TL ($r = -0.83$), ED ($r =$

4. Discussion

As expected, this study highlighted that temperature had not significant effects on survival rate during the entire endogenous feeding period of common carp. The malformation rate was also similar between the five tested temperatures. However, temperature had significant effects on development time, larval size, and energy value of both yolk sac and larval tissue. Development time was three times longer at 16°C than at 24°C. At both 16°C and 24°C, the consumption of the yolk sac was more important than at the three other temperatures. Larvae were smaller at 16°C throughout the endogenous feeding period compared to the other temperatures. In contrast, the larvae were the largest at 24°C at the end of the endogenous feeding period.

4.1. Influence of temperature on the early life stages

4.1.1. Incubation period

The mean daily survival rate was lower during incubation (P1) compared to the two other periods, except at 24°C, where it was lower during P2. This lower mean daily survival rate during

0.90), and HM ($r = 0.62$). The second axis explained 23% of the total variance and was correlated with MT ($r = 0.75$). At each stage, the larvae at 16°C were the smallest with the smallest yolk sac and the lowest tissue mass. Two other clusters were found at the three stages that were different between hatching and emergence and first food intake. At hatching, the second cluster (22°C) was characterized by larvae with a medium size, a medium yolk sac diameter and the highest yolk sac mass. The third cluster (18, 20, 24°C) was characterized by the longest larvae with the highest mass of tissue. At both emergence and first food intake, the second cluster (18, 20, 22°C) was characterized by larvae with a medium yolk sac diameter and mass. The third cluster (24°C) was characterized by the longest larvae with the highest mass of tissue.

3.4. Energy value

The interaction between temperature and stage was significant (GLM: $F_{1,8} = 12.3$, $p < 0.001$) on the energy value of the whole individual. At hatching, the total energy value was not different between temperatures (Fig. 7 (a)). At emergence, the total energy value was the highest at 20 and 22°C (Fig. 7 (a)).

The interaction between temperature and stage was significant for the tissue only (GLM: $F_{1,8} = 12.0$, $p < 0.0001$). At hatching, the energy value of the tissue was not different between temperatures (Fig. 7 (b)). At emergence, it was the highest at 20 and 22°C (Fig. 7 (b)).

No interaction between temperature and stage was found for the energy value of the yolk sac ($F_{1,8} = 0.8$, $p = 0.49$ respectively), but temperature influenced the yolk sac energy value (GLM: $F_{1,4} = 8.1$, $p < 0.001$), as well as the stage (GLM: $F_{1,2} = 54.7$, $p < 0.001$). At hatching, the yolk sac energy value was the lowest at 16 and 24°C and the highest at 18 and 22°C, and at emergence, it was the highest at 22°C (Fig. 7 (c)).

incubation was also observed in salmonids (Milla et al., 2011; Réalis-Doyelle et al., 2016) and suggested that the early phase of development (gastrulation), in which cell differentiation predominates over growth, may be more sensitive to either mechanical perturbations (Milla et al., 2011) or unfavorable thermal conditions (Peterson et al., 1977; Ojanguren & Braña, 2003; Korwin-Kossakowski, 2008; Réalis-Doyelle et al., 2016).

Incubation time strongly decreased with increasing temperature, which is a well-known phenomenon for fish species (Peñáz et al., 1983; Rombough, 1997; Kamler, 2002; Teletchea et al., 2009b; Teletchea & Fontaine, 2011). Indeed, over 90% of the variation in embryo ontogenetic rate is controlled by temperature (Kamler, 2002), and depends also on the egg diameter as larger eggs take much time to incubate than smaller ones at the same temperature (Pauly & Pullin, 1988; Rombough, 1997). In the present study, egg diameters were 2.38 ± 0.11 mm, which are slightly higher than those generally described in the literature, from 1.7 up to 2.2 mm (Woyanovich, 1962; Kamler & Malczewski, 1982; Peñáz et al., 1983; Linhart et al., 1995).

4.1.2. Hatching

At hatching, no significant impact of temperature on survival rates was found. The overall survival rates (comprised between 62-79% in the present study) are similar (45-80%) to those reported by Peñáz et al. (1983); yet lower than those (89-92%) described by Korwin-Kossakowski (2008) for the same temperature range. However, El-Hakim & El-Gamal (2009) observed no hatching at temperatures below 20°C and the survival rate of newly hatching larvae was only 38% at 24°C for carp in Egypt. These differences in survival rates at hatching, particularly between European and Egyptian populations, might reflect local adaptations of thermal tolerance between populations living at different latitudes (Réalis-Doyelle et al., 2016). In addition, we found very low rates of malformed larvae (less than 3% in all temperatures tested), which are close to the values (from 3 up to 10%) observed at 20°C by Jezierska et al. (2000). Yet, when temperature was lower than 17°C or higher than 25°C (not tested here), the malformation rates were higher (up to 22%), including mainly yolk sac malformations or edema, and vertebral abnormalities (Jezierska et al. 2000). At last, the hatching period duration strongly decreased according to increasing temperature, which confirmed earlier results on common carp (from 43 hours at 17.5°C to 6.5 hours at 24.3°C, Korwin-Kossakowski, 2008), and more generally in other species (e.g., Réalis-Doyelle et al., 2016). Therefore, the optimal limits (higher survival rate combined with a low malformation rate) for the embryonic development of common carp populations could be between 18-24°C; yet probably with significant local adaptations in thermal optimum.

At hatching, larval size was not different between temperatures, except at 16°C where larvae were the smallest (6.54 ± 0.18 mm). Similar results were already described in common carp between 24 and 30°C (El-Hakim & El-Gamal, 2009). However, there exist a variety of responses of larval size at hatching to incubation temperature between species, e.g., a decrease of size with increasing temperature has been observed (Kamler, 2008). Kamler (2008) tentatively proposed six possible mechanisms that could explain such different responses between species, among which the most likely is that most studies (as the present study) did not analyse a sufficiently large range of temperatures to demonstrate the effects in full and may lead to truncated shape of relationship between larval size and incubation temperature.

The different larval sizes at hatching for embryos incubated at similar temperatures may be partly explained by egg size as it is well-known that larval size at hatching is strongly linked to egg diameter (Miller et al., 1988; Pepin, 1991; Teletchea & Fontaine, 2010), that itself depends on the age and female size

(Hulata et al., 1974). Yet, the difference in body weight of females (1.5-2 kg) used in the study of El-Hakim & El-Gamal (2009) compared to those in the present study (2.26 ± 0.48 kg) did not seem to be sufficient to explain such strong differences in larval size at hatching, and thus remain partly unexplained.

The energy value of yolk sac was lowest at hatching at both 16°C and 24°C. At 16°C, the protracted development time could have led to an over-consumption of the yolk sac and thus left less energy for new tissues (Ojanguren & Braña, 2003). At 24°C, it might be due to an increase of metabolism that could also have left less energy to create new tissues (Jaworski & Kamler, 2002; Kamler, 2008). A similar result was found in a previous study at higher temperature for common nase *Chondrostoma nasus* (Kamler et al., 1998).

4.2. Possible ecological consequences of climate change

Common carp is one of the most common freshwater fish species in metropolitan France (Poulet et al., 2011) and in many other parts of the world (other European countries, North America, Southern Africa, New Zealand, Australia and Asia) (Freyhof & Kottelat, 2008; FAO, 2013). Compared to the recently introduced species that display the most impressive colonization and population growth in France, such as asp (*Aspius aspius*), carp did not show an expansion pattern in the past decades in this country, probably because 20 years ago it had already colonized its potential habitats (Poulet et al., 2011). The present results confirm that warmer water temperatures favor the early life stages of common carp and thus the possible geographical expansion of this species in the coming decades, particularly where warming will occur during June to July corresponding to the spawning months of this species (Herzig & Winkler, 1986; Flajšhans & Hulata, 2006). Indeed, at higher temperatures, the survival rate was high with a low malformation rate and larvae were longer with a higher energy value at the end of the endogenous feeding period, particularly when compared to larvae at 16°C. These larger larvae are expected to be less vulnerable to predation (Miller et al., 1988; Fuiman, 1994). Predation by copepods is indeed higher when carp are smaller (Ludwig, 1999; Frimpong & Lochman, 2005; Kumar et al., 2012). Additionally, larger larvae are more resistant to starvation (Wolnicki & Opuszynski, 1988; Fuiman, 2002) and this could therefore influence the point of no return, which corresponds to the moment when the individual will die due to irreversible starvation (Kai et al., 2012). This is particularly crucial for carp as larvae are not very resistant to starvation; only a few days after hatching at a water temperature of 20-22°C (Peñáz et al., 1983).

5. Conclusion

In conclusion, temperature had no significant impact on the survival rate during the endogenous feeding period of common carp; yet morphological variables and energy values were different, particularly at 16 and 24°C. At higher temperatures, larvae were longer and had a higher energy value. Conversely, at the lowest temperature (16°C), larvae were smaller, had

lower energy value, mainly due to a much longer developmental time. Our results are in accordance with current models that predict a small change of the distribution area of the common carp in France, but probably an extension in Northern European regions, in the next decades consequently to climate change.

Table 1. Effect of temperature on the mean daily survival rate of common carp (in percentage ± S.E) for three periods P1, P2, and P3

	16°C	18°C	20°C	22°C	24°C
P1	96.44 ± 1.25	94.23 ± 2.71ac	91.83 ± 1.70α	96.03 ± 1.70α	93.20 ± 2.28ac
P2	98.54 ± 0.59a	99.34 ± 1.61a	99.85 ± 0.23a	99.96 ± 0.05a	92.20 ± 4.30b
P3	99.76 ± 0.01a	99.09 ± 0.06a	99.55 ± 0.02a	99.97 ± 10.3a	99.48 ± 0.08a

P1 from fertilization to hatching, P2 from hatching to emergence, P3 from emergence to first food intake. Mean (±S.D). Differences obtained by X2 are considered significant at P<0.05. The same letter indicates no significant difference among temperatures in each of the three periods

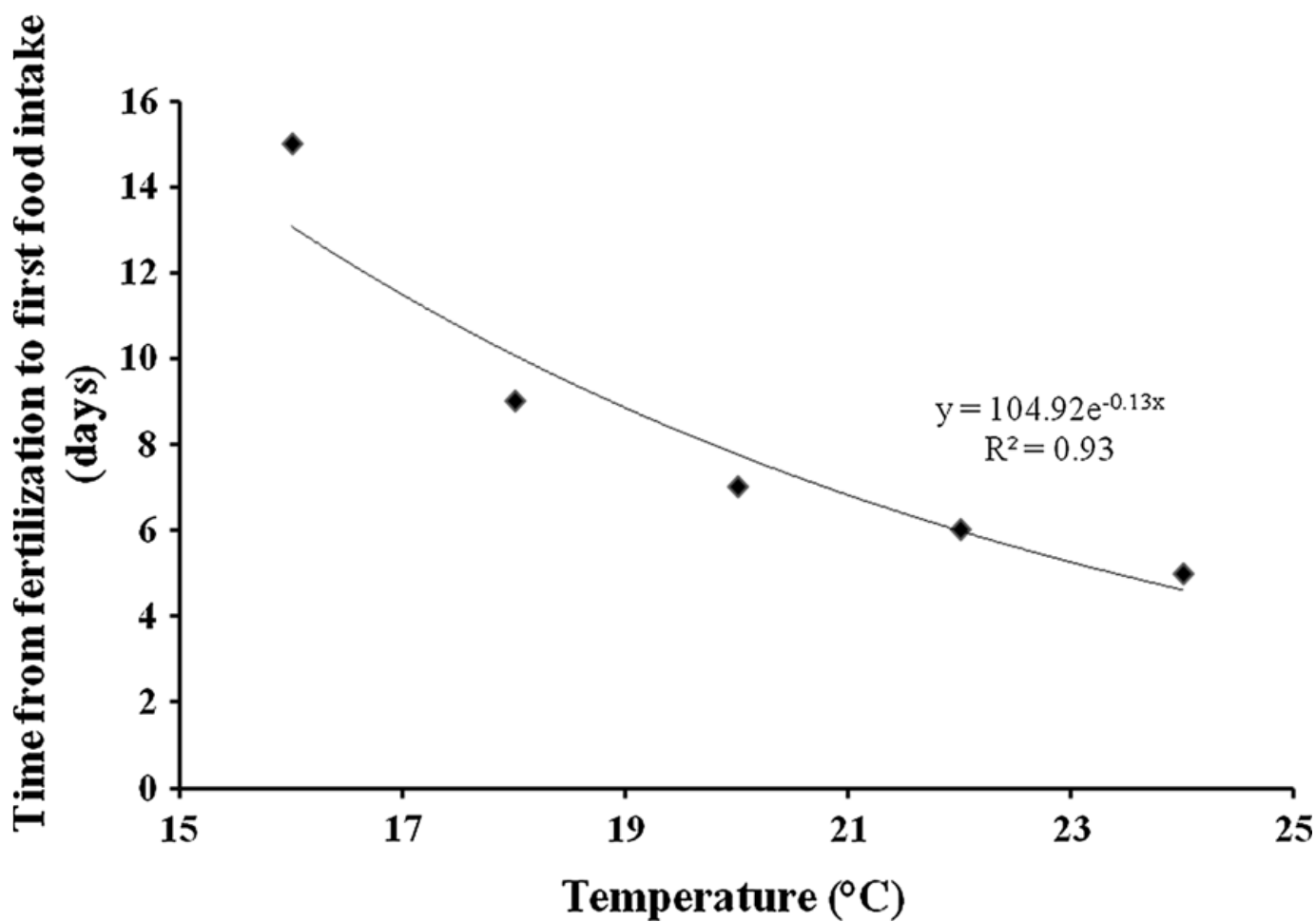


Figure 1. Effect of temperature on the duration between fertilization and first food intake (in days) in common carp

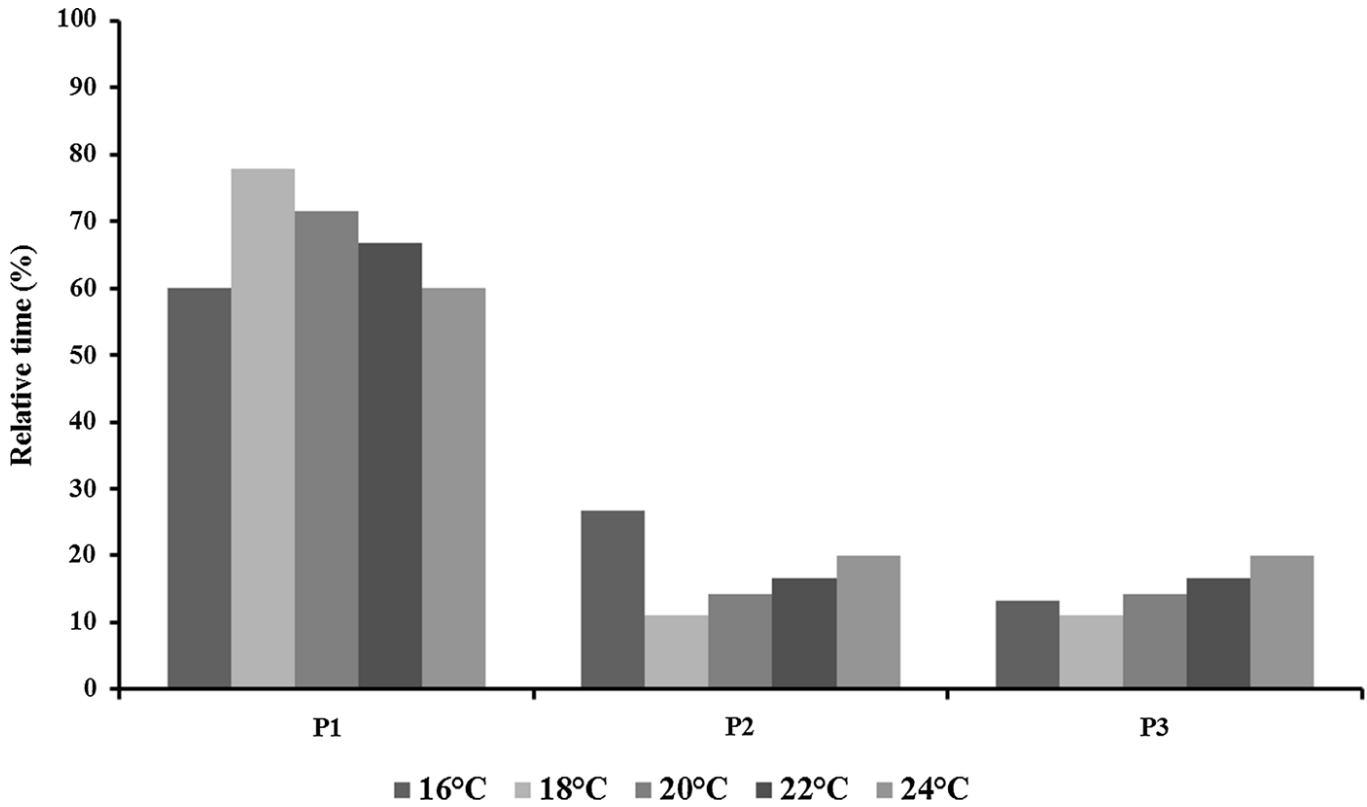


Figure 2. Effect of temperature on the relative time of the three successive periods P1, P2, and P3 in common carp. (P1: from fertilization to hatching; P2: from hatching to emergence; P3: from emergence to first food intake).

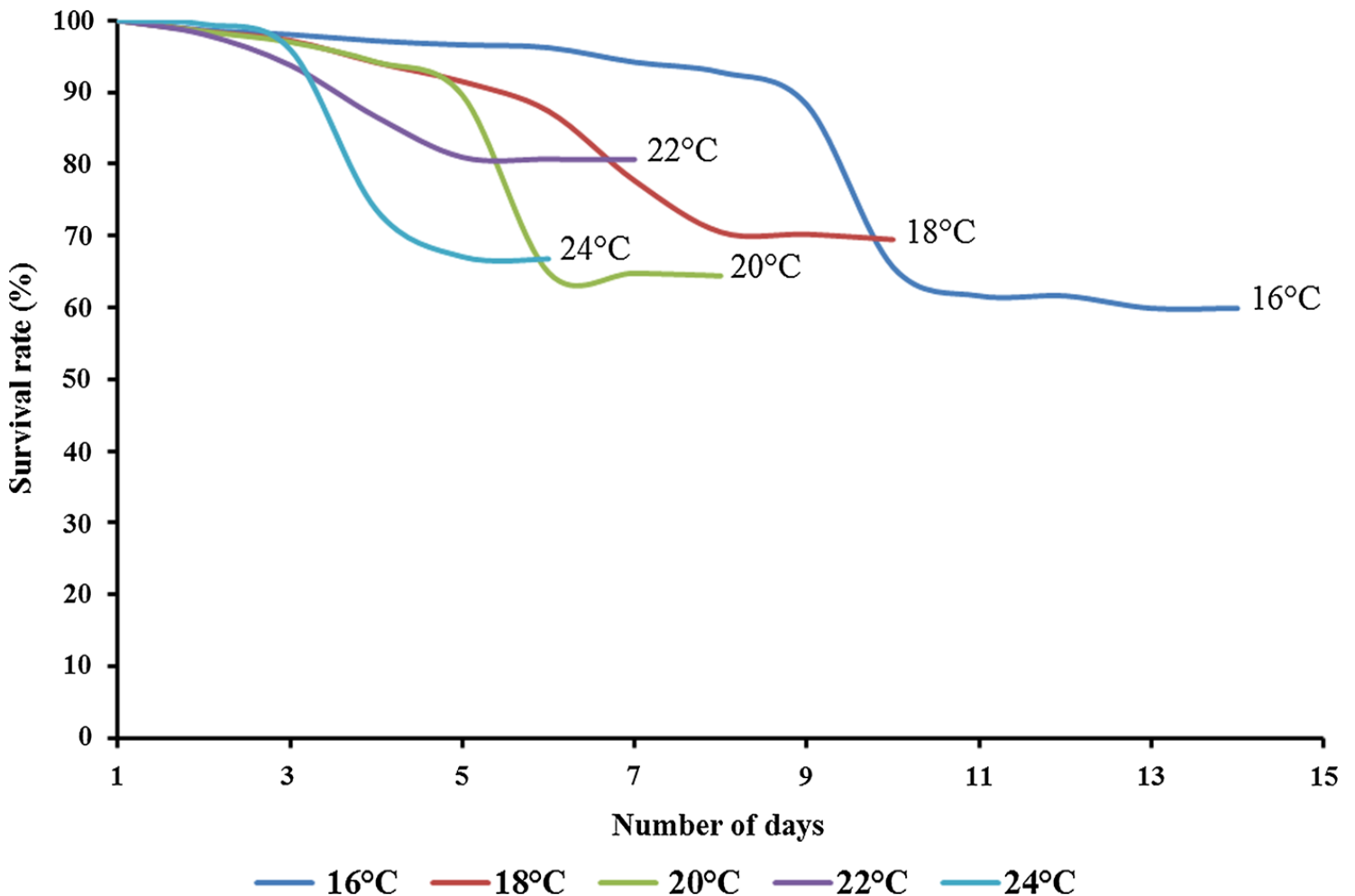


Figure 3. Effect of temperature on survival rate (SR) of common carp during the endogenous feeding period. The number of days was the number of days between fertilization and first food intake

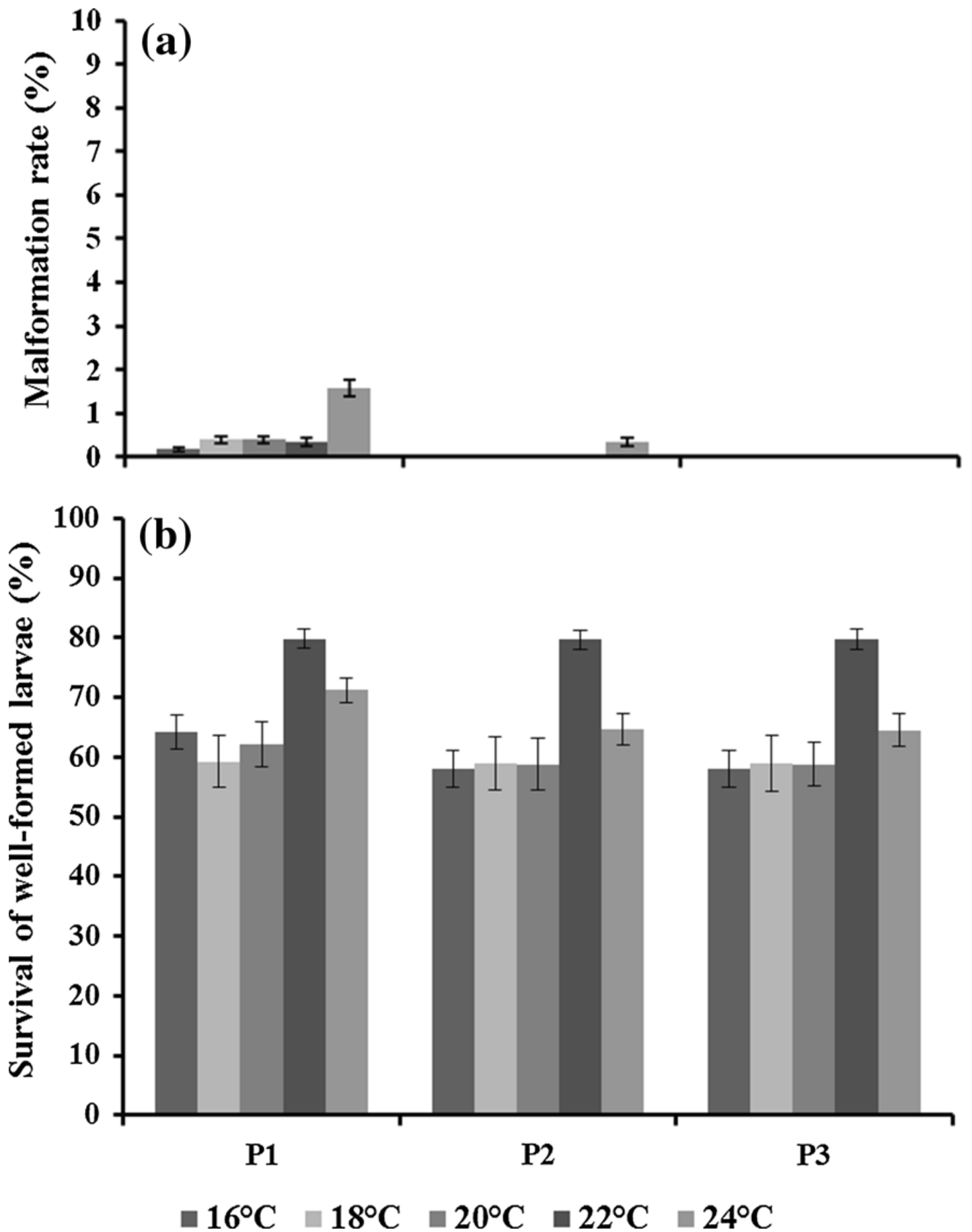


Figure 4. Effect of temperature on (a) the malformation rate, and (b) the survival rate of well-formed larvae calculated at three biological stages (hatching, emergence, and first food intake) for common carp. Data are mean \pm S.E. Differences obtained by X² are considered significant at $P < 0.05$. The same letter indicates no significant difference between temperatures in each of the three stages

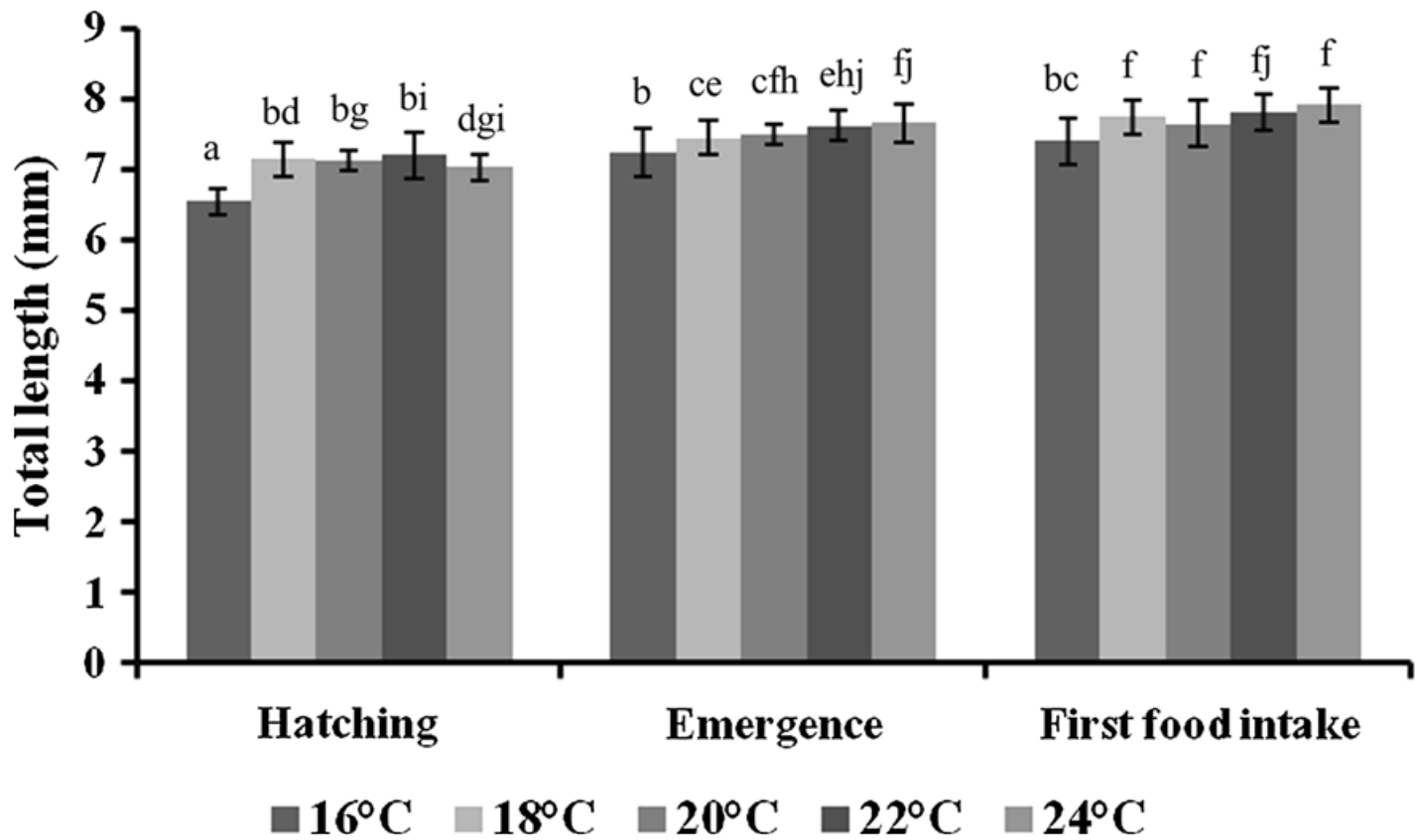


Figure 5. Effect of temperature on total length for common carp at hatching, emergence, and first food intake. Data are mean \pm S.E. Differences obtained by Tuckey post hoc are considered significant at $P < 0.05$. The same letter indicates no significant difference between temperatures and stages

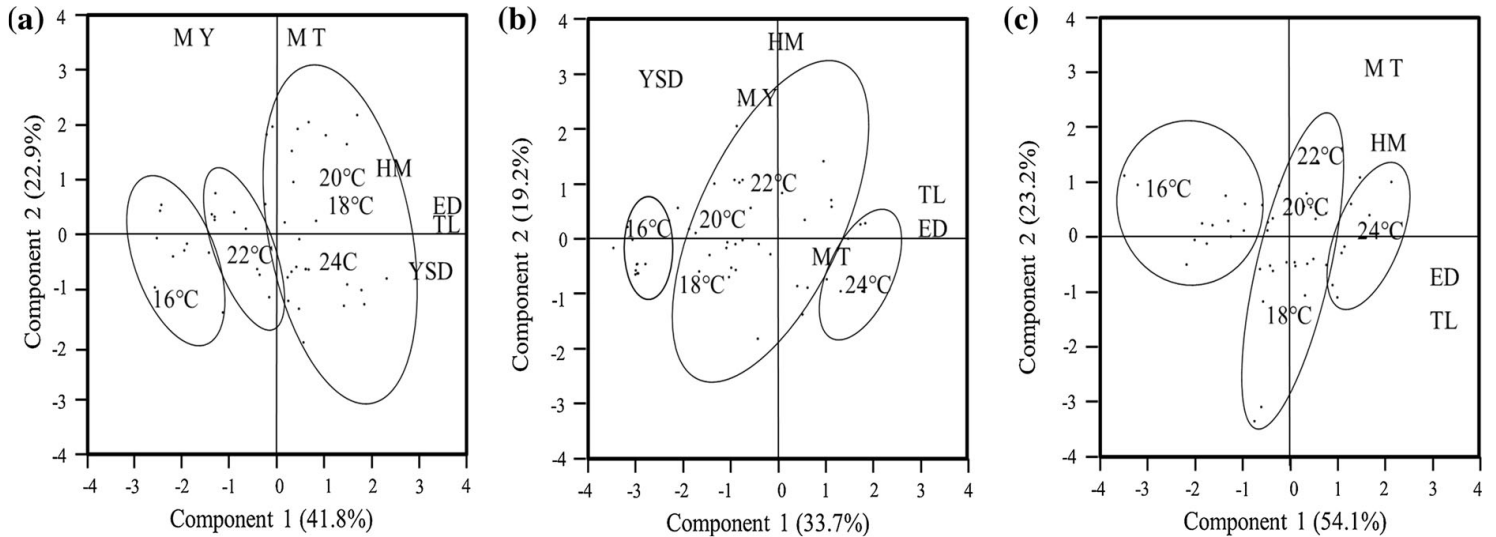


Figure 6. Principal component analysis performed with six morphometric parameters measured on common carp (a) at hatching, (b) at emergence, (c) at first food intake. TL total length, HM height of the myotom, ED eye diameter, MT mass of the larval tissue, MY mass of the yolk sac, and YSD yolk sac diameter)

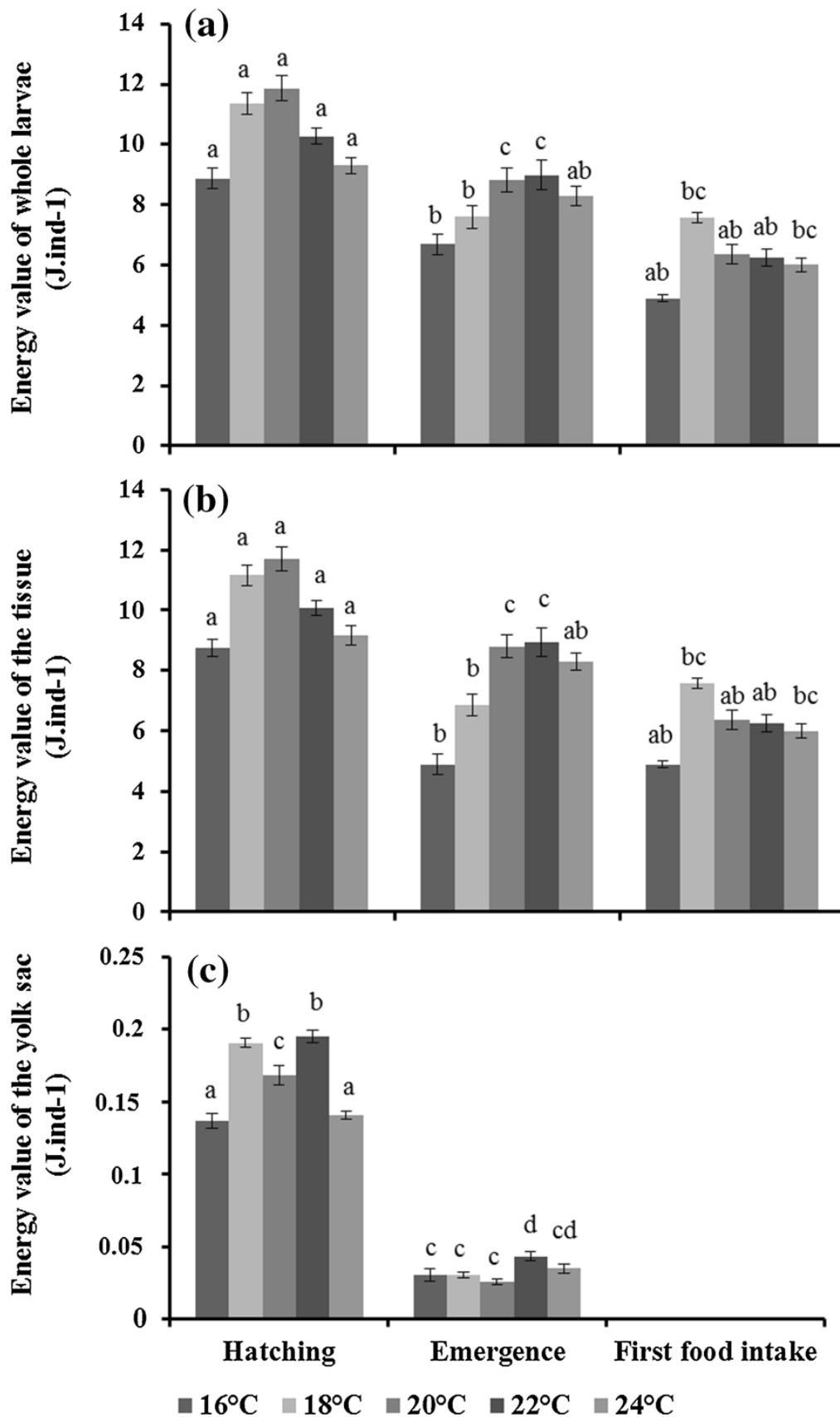


Figure 7. Effect of temperature on the energetic value at each stage of development (a) for global energetic value (whole larvae), (b) for energetic value of the larval tissue, (c) for energetic value of the yolk sac only (data are mean \pm S.E). Differences obtained by Tukey post hoc are considered significant at $P < 0.05$. The same letter indicates no significant difference between temperatures in each of the three stages

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