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THE INFLUENCE OF TEMPERATURE DURING THE EMBRYONIC PERIOD ON LARVAL GROWTH AND DEVELOPMENT IN CARP, *CYPRINUS CARPIO* L., AND GRASS CARP, *CTENOPHARYNGODON IDELLA* (VAL.): THEORETICAL AND PRACTICAL ASPECTS

Michał Korwin-Kossakowski

Department of Pond Fisheries, The Stanisław Sakowicz Inland Fisheries Institute in Olsztyn, Poland

ABSTRACT. This work proposes modifications to the existing system for identifying the steps of embryonic and larval development in fish. The term "compensatory phase of development" is proposed for the phase from hatching to the first intake of food. Both the new designations of these steps and the new name of this phase do not require a declaration of whether the hatched individual is considered to be an embryo or a larva, something that has been, to date, a matter of dispute. Unification will allow for the wider use of the new nomenclature, and make easier the comparison of results. This work examines the influence of the thermal history during the embryonic period (temperatures of 20, 24, 28, and 32°C) on later development, growth, and survival of common carp, *Cyprinus carpio* L., and grass carp, *Ctenopharyngodon idella* (Val.) larvae, at a constant temperature of 23°C. It was confirmed that the optimal temperature ranges for the embryonic development of common carp and grass carp are higher than those currently applied widely in practice of 18-22°C and 21-26°C, respectively. Based on the evaluation of the development, growth, and survival of the larvae, it was determined that the optimal temperature for embryonic development is 26-28°C for the common carp and 32°C for the grass carp. It was confirmed that even a short-term increase in temperature from 20°C to 24°C during the compensatory phase has a positive influence on subsequent common carp larvae growth.

Key words: EMBRYO, LARVA, EARLY DEVELOPMENT, ONTOGENY, TEMPERATURE, COMMON CARP, GRASS CARP

1. INTRODUCTION

1.1. TYPOLOGICAL ISSUES REGARDING THE EMBRYONIC AND LARVAL DEVELOPMENT OF FISH

Early ontogenesis is divided by different authors into various periods, phases, or stages that do not always correspond to one another. The terminology applied in publications addressing fish development are very misleading, usually due to the

CORRESPONDING AUTHOR: Michał Korwin-Kossakowski, The Stanisław Sakowicz Inland Fisheries Institute in Olsztyn, Department of Pond Fisheries, Żabieniec, Główna 48, 05-500 Piaseczno, Poland, Tel./Fax: +48 (22) 7562088; e-mail: mkk@infish.com.pl

multiplicity of categories applied by various authors. As long as 60 year ago, Rass (1946) maintained that there was too much variation in the terminology used by researchers to describe the early ontogenesis of fish. By listing the terminology used by more than thirty authors, Rass concluded that the differences precluded any comparison of the subsequent developmental phases. Similar observations were made thirty years later by Snyder (1976), who found in the literature about sixty different terms describing the periods and phases of fish development between hatching and sexual maturity.

For many years, none of the terminology systems was recognized as the best. The greatest disparity regarded the hatching process, which is influenced by many factors, including temperature, oxygen concentration, and the chemical composition of water. The discussion of what the organism hatching from the egg is, whether an embryo or a larva, appeared again and again in reviews of the literature (Rass 1946, Kingsford 1988, Balon 1999, Peňáz 2001, Kamler 2002, Urho 2002), but unfortunately no consensus was reached. The hatched organism was referred to variably as follows: an embryo (Kryzhanovski 1949, Vasnecov et al. 1957, Peňáz 1973, Krupka 1988); an eleutheroembryo (Balon 1975a, b, Luczynski et al. 1988, Kucharczyk et al. 1997, Kujawa et al. 1997); a free embryo (Vasnecov 1948, Balon 1990, 1995a, b, 1999, 2002, Gozlan et al. 1999a, b, Pavlov 1999, Mercy et al. 2000, Peňáz 2001, Pinder et al. 2005); a prelarva (Rass 1946, Vasnecov 1948, Balon 1958a, Diaz et al. 2002a, b); a prolarva (Hubbs and Kampa 1946, Neudecker 1976); a protolarva (Snyder 1976, 1981, Potter and Potter 1981, Shireman and Smith 1983); a larva (Witkowski and Kokurewicz 1978, Araujo-Lima 1994, Marty et al. 1995, Winnicki and Korzelecka 1997, Kamler et al. 1998, Sanchez et al. 1999, Alami-Durante et al. 2000, Kamiński et al. 2006); or even a fry (Iwamatsu 2004).

With such diverse terminology in use, there are instances when authors themselves have used various terms over the years. For example, Balon, who has investigated early fish ontogenesis for over fifty years, has used various terms to refer to organisms between hatching and the beginning of exogenous feeding, as follows: prelarva (Balon 1958a, b); eleutheroembryo (Balon 1971, 1975a, b); eleutheroembryo and free embryo interchangeably (Balon 1984, 1985, 1989); and finally free embryo (Balon 1990, 1995a, b, 1999, 2002). Thus, terminology has come full circle from “Vasnecov to Vasnecov” since Vasnecov (1948) wrote noncommittally “...fish in this state are

referred to as prelarva or free embryos...”; this is evidence that he did not coin these terms. This same author in a later work (Vasnecov 1953) that discusses the saltation theory of development using *Abramis brama* (L.) as an example, describes the developmental steps consistently using the term “fish” to refer to individuals that have just hatched. A few years later, this author refers to such individuals interchangeably as embryos or larvae (Vasnecov et al. 1957).

Kingsford (1988) attempted to standardize the terminology used to refer to fish in the larval period. Based on the works of several authors, he compiled a list of terms applied to fish between hatching and the juvenile period, which included the following: eleutheroembryo (Balon 1975a); larva (Mansueti and Hardy 1967, Russell 1976); preflexion larva (Ahlstrom et al. 1976); protolarva (Snyder 1981). Prior to the juvenile period, the terms applied to individuals were as follows: pterygiolarva (Balon 1975a); postlarva (Russell 1976); pre-juvenile (Mansueti and Hardy 1967); postflexion larva (Ahlstrom et al. 1976); or metalarva (Snyder 1981). In turn, Fuiman (2002) identified four separate functioning parallel terminology systems proposed by Balon (1975a), Ahlstrom et al. (1976), Snyder (1976) and Hardy et al. (1978), the popularity of which was linked the particular researcher’s geographic region of origin.

As concluded by Kingsford (1988), in summation of an attempt to standardize terminology working at the Early Life History Section under the auspices of the American Fisheries Society, no single terminology system can be designated as superior to any other. In light of such difficulties, it is understandable that in order to avoid misunderstanding stemming from the various terminology systems used to describe individuals from hatch to the juvenile period, Kingsford and Choat (1985, 1986) applied the term “small fish”. This is an example of the consequence of the multitude of terms in use and a lack of standardized terminology that forces authors to resort to gross oversimplification in an attempt to be understood by all.

1.2. TEMPERATURE AS A FACTOR INFLUENCING DEVELOPMENT AND GROWTH

Early ontogeny is impacted by nearly all environmental factors, including temperature, oxygen content, salinity, pH, insolation, other biotic and anthropogenic factors (see reviews by Jones 2002, Kamler 2002, 2008), and even precipitation and winds that blow along coasts (Bergenius et al. 2005). Among these factors, temperature is

considered to be one of the more important, if not the most important, factors. Within a viable range, temperature plays a controlling role, beyond this range it is a lethal factor (for reviews see: Fry 1971, Brett 1979, Blaxter 1992, Kamler 1992, 2002). The influence of temperature on the development, growth, and survival of embryos and larvae has been confirmed by, among others, Vovk (1974), Mills (1980), Peňáz et al. (1983), Kucharczyk et al. (1997), Kujawa et al. (1997), Kamler et al. (1998), Hansen and Falk-Petersen (2001), Ojanguren and Braña (2003). The influence temperature has on meatbolism has also been described by Kamler and Kato (1983), Jaworski and Kamler (2002), and Finn and Rønnestad (2003).

As poikilotherms, fish react to temperature in a particular way. Individuals of the same age can develop at different rates depending on temperature. Thus, their calendar age is not reliable enough, especially in early ontogenesis when developmental changes occur rapidly. The possibility of determining precisely the developmental state of an organism at a given moment is significant from a cognitive point, but also for purely practical reasons. The development and growth of fish in early ontogenesis is a sensitive indicator of environmental quality, and changes in embryonic development are used increasingly for the evaluation of the harmfulness of pollution (Hollert et al. 2003, Hallare et al. 2005, Braunbeck and Lammer 2005, Braunbeck et al. 2005).

As temperature increases, the developmental rate and growth rate accellerate (Pepin 1991, Watanabe et al. 1995, Pepin et al. 1997, Vieira and Johnston 1999, Jordaan and Kling 2003, Kamiński et al. 2006). An example of this can be found in the study by Hutchinson and Hawkins (2004). While they reported that the length of *Pleuronectes flesus* L. during metamorphosis was the same at all of the experimental temperatures (7, 11, 15°C), they confirmed that it was achieved at different times, and the metamorphosis occurred earliest at the highest temperature. Thus, temperature not only shortens development, it also accelerates growth.

Blaxter (1992) reported that the incubation time from fertilization to hatching in fourteen freshwater and marine fish species was shortened at higher temperatures. Based on studies of numerous cold water and warm water species, this author maintains that, in most cases, smaller larvae hatch at higher temperatures. The same dependency was also reported by Kamler et al. (1998) for *Chondrostoma nasus* (L.), Hansen and Falk-Petersen (2001) for *Anarhichas minor* (Olafsen), Huuskonen et al. (2003) for *Salvelinus alpinus* (L.), Van Eenennaam et al. (2005) for *Acipenser*

medirostris (Ayres), and Kujawa et al. (2007) for *Rutilus rutilus* (L.). Although some species do produce larger larvae at higher temperatures (Alderdice and Forrester 1971, Pepin et al. 1997), this usually refers to the lower threshold of thermal tolerance. In species studied at low temperatures can also exhibit a dome-shaped dependency which is first positive and then negative (Chambers 1997, Galloway et al. 1998). Nevertheless, in order to describe the process precisely, many temperature levels must be applied and the studies must be performed within the appropriately wide temperature range (Kamler 2008).

There are different ways to explain the dependence of the size of hatched larvae on temperature. One of the simpler explanations is the one proposed by Blaxter (1992): at higher temperatures individuals less advanced in development have less tissue to divide. In review papers, Kamler (2008) reports a few other possible explanations. One of them involves the link between the smaller-sized larvae that hatch at higher temperatures and oxygen conditions. The author explains that in addition to the reduced availability of oxygen in the water, demand for it is higher due to, among other factors, increased locomotor and enzymatic activity. Obviously, worsening oxygen conditions hamper development (Kamler 1992) and accelerate hatching (Rombough 1988, Fuiman 2002).

The dependency between larval growth and temperature during yolk sac resorption is explained by Kamler (2008) as the mutual impact of and reaction to temperature of three significant life phenomena: developmental rate, growth rate, and metabolic rate. These mutual relations are linked by the fact that the developing organism has limited energy resources in its yolk, which can be apportioned variously. Based on comparisons of the corresponding Q_{10} temperature coefficients, Kamler concluded that developmental, growth, and metabolic rates increase with temperature, but not uniformly. She also hypothesizes that in most cases slower acceleration in development and growth is accompanied by greater metabolic acceleration, which, in effect, along with increased temperature, results in smaller- sized larvae. In turn, when the acceleration of development and growth are higher and that of metabolism is lower, at higher water temperatures the larvae are larger. When the values of the three Q_{10} temperature coefficients are clowse in value, then the larvae achieve similar sizes in different temperatures.

The dependencies of different life processes on the temperatures an organism experienced previously, otherwise known as the thermal history, has been described in many studies: development (Korwin-Kossakowski and Jezierska 1984, Galloway et al. 1998, Martell et al. 2005, 2006, Georgakopoulou et al. 2007), upper lethal temperature (Horoszewicz 1971, 1973, Lirski and Opuszyński 1988a) and lower lethal temperature (Lirski and Opuszyński 1988b). Even small changes in temperature permit eliciting the adaptation effect. Horoszewicz (1971) reported that increasing the adaptation temperature by a few degrees Celsius for six to 36 hours increased the upper lethal temperature in *R. rutilus* larvae. Even very short-term, specific types of adaptation such as repeating thermal stress lowers the reaction level in organisms as was observed in juvenile *Cyprinus carpio* L. by Tanck et al. (2000). The thermal history of parents prior to spawning has an impact on their progeny by influencing the optimal temperature for development (Zhukinski 1986), as well as eliciting differences in developmental rate (Goryunova 1971). Stroganov (1956), who studied the dependency of metabolism on temperature confirmed that there is a plateau (i.e., a range at which metabolism is less dependent on temperature) that includes the temperatures the fish experienced prior to measurements. This range is referred to by Stroganov as the adaptation zone of temperature, and this dependence was also confirmed in other poikilothermic organisms by Duncan and Klekowski (1975).

Temperature, which has a strong impact on most biological processes in poikilothermic organisms in particular and is an easy factor to regulate, could be a convenient and precise way to modify various life processes. The thermal history phenomenon, which has an impact on many subsequent life processes, has still not been studied comprehensively, especially with regard to the early ontogenesis of fish. The possibility of exploiting the short-term impact of temperature during egg incubation on the further development and growth of larvae of fish species produced on a large scale in hatcheries could be one way of optimizing procedures in aquaculture. This provides the foundation of the studies undertaken in the current work.

1.3. STUDY SUBJECT

The study subjects are two fish species from one family (cyprinid, Cyprinidae) that differ in reproductive biology: the common carp, *C. carpio*, and the grass carp, *Ctenopharyngodon idella* (Val.). Although they are warm water species, the grass carp

requires higher temperatures for proper development and growth. While the eggs of both species belong to the same group of polylecithal (Grodziński 1981) or oligolecithal (Peňáz 2001) eggs, they do differ in many respects. Common carp eggs are heavier, sticky, and are attach to plants during development, but the much larger grass carp eggs are free floating. According to the classification by Kryzhanovski (1949) that was modified by Balon (1975b), categorizing fish by the types of eggs they deposit, the common carp is a phytophil, while the grass carp is a pelagophil. Another difference is the time required for embryonic development; the common carp egg development rate is twofold slower than that of the grass carp. It is also noteworthy that the grass carp does not spawn naturally in Europe, and it is only reproduced in hatcheries here.

The choice of the common carp, the most widely cultivated species in Central European hatcheries, and the grass carp, the reproduction of which in Europe is only possible in hatcheries, is justified as study material. It was decided that they are suitable material for both study tasks, namely, the attempt to standardize the terminology applied to early fish ontogenesis, and to confirm the hypothesis that temperature during egg incubation can be used to modify growth during the larval period.

1.4. AIM OF THE STUDY

The first aim of this study was to attempt to standardize the terminology of early development that describes changes occurring in organisms. Based on studies of the development of common carp and grass carp and the relevant literature, the terminology was standardized and modifications are proposed that will allow for the normalization of differences and the dissemination their application.

The second aim of the study was to demonstrate that the thermal history during the embryonic period has a significant influence on further fish growth and development. Experiments conducted in three subsequent years at the Department of Pond Fisheries in Żabieniec, Inland Fisheries Institute in Olsztyn confirmed that it is possible to use egg incubation temperatures to modulate the growth rates of common carp and grass carp larvae. This work also presents an overview of current knowledge on the influence of temperature on the development and growth of fish.

In this text, references to the literature cited are made using the categories and terminology proposed in a given work, while the current author refers to individuals developing in eggs as embryos and individuals that have hatched as larvae.

2. MATERIALS AND METHODS

2.1. FISH AND REPRODUCTION CONDITIONS

The sex products used in the experiments were obtained from adult common carp and grass carp reared in ponds at the Experimental Fish Farm in Żabieniec. Reproduction was performed in the laboratories of the Department of Pond Fisheries in Żabieniec.

The sex products were obtained from fairly large, similarly sized spawners from each species in an attempt to eliminate the influence of age and size on quality of progeny (Korwin-Kossakowski 1989a, Huang et al. 1999, Keckeis et al. 2000). The common carp females used for reproduction weighed from 7 to 8 kg, while the males weighed from 5 to 8 kg. The grass carp weights were from 6 to 8 kg and from 5 to 7 kg, respectively. The sex products (eggs and milt) used came from single pairs of parents.

The females of both species were stimulated hormonally with carp pituitary extract (Argent, USA) administered in doses of 0.2-0.5 mg and 2.0-2.5 mg in the first and second injections, respectively. The males were administered with one dose of CPE 24 h prior to spawning at doses of 2.0 mg and 1.5 mg, respectively, for the common carp and grass carp. After being transported from the ponds, the common carp spawners were held for six days in concrete tanks at a water temperature of 18-20°C. Following the first hypophysis injection, the water temperature was increased to about 23°C. The second hypophysis injection occurred about 24 h following the first, and eggs were collected after another 24 h. Hypophysis injection in grass carp occurred approximately 20 h after they had been transported from the ponds. The water temperature in the concrete tanks was, at that time, about 23°C.

2.2. SCHEME OF EXPERIMENTS

In order to determine the influence of water temperature during egg incubation on subsequent growth and development of common carp and grass carp, it was decided that the development and growth of larvae hatched from embryos that had developed at various temperatures would be observed at one common temperature of 23°C. This temperature was within the range most frequently applied during larval cyprinid rearing (20-25°C, Wolnicki 2005). The embryonic and early larval development of both

species was examined at four temperatures: 20, 24, 28, 32°C. The course of the experiment in three subsequent years is presented in Table 1.

TABLE 1

Scheme of experiments with embryos and larvae of common carp and grass carp at different temperatures

Species	Experiment number	Temperature (°C)					14-day rearing (feed)
		20	24	28	32	20→24	
C. carpio	I	IC20	-	IC28	-	IC20-24	yes (AC)
	II	IIC20	IIC24	IIC28	IIC32	-	yes (AC)
	III	IIIC20	IIIC24	IIIC28	IIIC32	-	yes (AN)
	IV	IVC20	IVC24	IVC28	IVC32	-	no
C. idella	I	-	IG24*	-	IG32	-	yes (AC)
	II	IIG20	IIG24	IIG28	IIG32	-	yes AC)
	III	IIIG20	IIIG24	IIIG28	IIIG32	-	yes (AN)

Group designations include experiment number (I, II, III, IV), species name (C – common carp, G – grass carp), and egg incubation temperature. The designations used in the paper refer to group (e.g., IIC20), temperature variant (e.g., C20), or experiment (e.g., IIC). There were three replicates in each group: one for observing development and two for calculating survival and, after rearing, for measuring growth.

In group IC20-24, the water temperature was raised from 20 to 24°C after hatching.

In experiment IVC, following fertilization and removal of egg stickiness at temperatures of 22-23°C, the eggs were transferred immediately to the final temperatures. Results of this experiment were limited to determining survival following swim bladder inflation.

** In group IG24, two sub-groups of grass carp eggs from two sets of parents were studied simultaneously.*

AC – decapsulated Artemia cysts

AN – Artemia nauplii

The initial experiment material for rearing was swimming larvae with inflated posterior swim bladder chambers. Readiness for exogenous feeding was confirmed by delivering a portion of nauplii or decapsulated Artemia cysts to a sample of 50 larvae. When the first individuals began feeding, the remaining larvae were segregated into experimental groups and water temperatures began to be changed. The larvae from all the experimental groups were reared for 14 days, starting from the moment of the first exogenous feeding by the group (more than 50% of the individuals).

The fundamental criteria for evaluating the results of the study were: normality and length of development, growth of larvae with different thermal histories reared at a single, common temperature, and survival during the embryonic development period and after the 14-day rearing period. The normality of development is understood as the formation and growth of organs in the appropriate sequence and form that is typical of a given species.

2.3. TECHNICAL, PHYSICAL, AND CHEMICAL CONDITIONS

The eggs were incubated in a flow-through system. Deep-well waters, which were run through a mechanical filter, were directed to the retention tank, where they were heated (precision of the thermal regulation ± 0.2°C), oxygenated, and then filtered again. The water flowed gravitationally into the incubators. For the common carp these were Weiss jars with a volume of 0.3 dm^3 and 0.03 dm^3, and then round incubation sieves (20 cm diameter, 6 cm height, mesh bar length approximately 0.5 mm) that were placed in 20 dm^3 aquaria. Grass carp eggs were incubated in Weiss jars with a volume of 0.3 dm^3 and in Petri dishes 10 cm in diameter in incubation sieves. The water flow rate insured proper egg circulation in the jars and water flow around the eggs in the Petri dishes.

The larvae were reared in recirculation systems with a total volume of 900 dm^3. The system was comprised of a retention tank (400 dm^3), rearing tank (3 m in length, 300 dm^3) – which was the settling tank and water bath for the aquaria, and a biological filter (200 dm^3) with diatomite substrate (Kolman 1992), which also functioned as a mechanical filter. The water exchange rate in the system was about 0.7-1.0 dm^3 min^{-1}. The aquaria (20 dm^3 volume) stocked with fish were placed in rearing tanks and submerged to about three-fifths their height, which guaranteed sufficiently stable water temperature.

The water flow through the aquaria was 0.2-0.3 dm^3 min^{-1}. The chemical composition of the water, which was tested at intervals of a few days, did not fluctuate significantly and remained within the following ranges: pH 6.8-7.1; NO_2 – under 0.005 mg dm^{-3}; NO_3 – under 0.02 mg dm^{-3}; PO_4 – under 0.001 mg dm^{-3}; NH_4 – under 0.7 mg dm^{-3}; HCO_3 – under 150 mg dm^{-3}.

2.4. COMMON CARP EGG INCUBATION

The common carp eggs were fertilized in water at a temperature of 22-23°C. Egg stickiness was removed using methods commonly applied in hatcheries (Woynarovich 1962). After this procedure, the eggs were segregated into temperature variants (Table 1) and placed in Weiss jars. Then the water temperature was adjusted to the experimental temperature at a rate of 2-3°C per hour. Each temperature variant was comprised of one Weiss jar with a volume of 0.3 dm^3 containing eggs (the development of which was to be observed) and two jars with a volume of 0.03 dm^3 and containing portions of 350 to 600 eggs (experiments IC, IIIC, IVC). The exception was experiment IIC, in which survival was calculated based on samples of 200 eggs in each replication that

were incubated in Petri dishes placed on submerged sieves with water flowing around (as was done with the grass carp). Survival was calculated by counting unfertilized and dead eggs removed at the eye pigmentation stage, then hatched larvae, and finally larvae with inflated posterior swim bladder chambers. The hatched larvae swam out of the jars or Petri dishes to the sieves placed in the aquaria. After the swim bladders had inflated, the fish were moved to separate aquaria.

The IC20-24 experiment was based on increasing the temperature after hatching from 20 to 24°C at a rate of 2-3°C per hour. The aim of this was to test the effects of shortening the time between hatch and exogeneous feeding. Experiment IVC was conducted with eggs which, after removing stickiness, were immediately incubated in water at temperatures of 20, 24, 28, and 32°C.

2.5. GRASS CARP EGG INCUBATION

The grass carp eggs were fertilized in water at a temperature of 23°C, mixed for four minutes, and then divided into three replicates of each temperature variant (Table 1). The water temperature was increased by 2-3°C per hour to the experimental temperatures of 20, 24, 28, and 32°C. At each temperature variant, there was one Weiss jar with a volume of 0.3 dm^3 containing eggs for observing development and two portions of eggs numbering from 140 to 200 individuals (experiment IIG) and from 350 to 700 individuals (experiment IIIG). These eggs were used to calculate survival. They were placed in aquaria on Petri dishes that were on sieves bathed in the same water as those in the jars. During incubation, the unfertilized and dead eggs were counted, then hatched larvae and finally those with inflated posterior swim bladder chambers were counted. The hatching fish swam out of the jar or Petri dishes to the sieve. After swim bladder inflation, the larvae were moved to separate aquaria.

2.6. LARVAE REARING

Rearing aquaria of a volume of 20 dm^3 were stocked with larvae that were ready to begin exogenous feeding. The water temperature was raised or lowered by 2-3°C per hour until 23°C was obtained. The stocking density was 400 individuals. Rearing was conducted in three replicates for each group. One aquarium was used for development observations, and two aquaria for calculating the survival and growth of larvae. The larvae were fed six times daily (at 08:00, 10:00, 13:00, 16:00, 19:00, 22:00) with decapsulated

Artemia cysts (experiments I and II), at increasing daily rations of 1 g per aquarium at the start of rearing to 2.5 g in the final days of rearing, or ad libitum with freshly hatched Artemia nauplii (experiment III). Unconsumed food was removed successively. After the conclusion of the 14-day rearing period, samples numbering 50 individuals were taken and the remaining individuals were counted. In experiment IIG, the remaining individuals continued to be fed following the 14-day rearing period. On the final day of the experiment in group IIG20, which was 24 days following fertilization, a sample of 50 individuals was taken from each group, and the remaining individuals were counted.

2.7. OBSERVATION

The developing eggs were observed at intervals of five minutes from the moment of activation. Five eggs were collected for each observation. As development progressed and developmental steps lengthened, the intervals between observations were increased to 1 hour by the end of incubation. All morphological transformations occurring during embryonic and larval development that were visible in vivo were observed. The end of the larval period was designated as the moment of preanal fin folds disappearance.

The larvae were observed at the beginning (7 days) every 6 hours, and then for the next 7 days every 12 hours. Five larvae were collected for observation each time. They were anesthetized with MS-222. They were not returned to the rearing aquaria after observation, because the repeated administration of anesthetic can significantly retard the rate of development (Kimmel et al. 1995). The occurrence of a particular characteristic in three of the five individuals examined signaled the moment of occurrence of this characteristic, and this was the time recorded.

A Carl Zeiss Jena Citoval 2 stereo microscope coupled with a CCD camera was used for the observations. The eggs and larvae were photographed in a way that permitted subsequent measurements.

The following abbreviations to describe different stages are used in this work:

Fe – fertilization

BC – closure of the blastopore

EP – appearance of eye pigmentation

Ha – hatching

SB – inflated posterior swim bladder chamber

FF – beginning of exogenous feeding

2.8. MEASUREMENTS AND STATISTICS

The photographic images of the eggs were measured to about the nearest 3 pixels (0.07 mm). The larvae were weighed to the nearest 0.1 mg and measured (TL) to about the nearest 3 pixels (0.07 mm) from photographs made following hatching and after reaching the SB stage. At the end of rearing, the larvae were measured to the nearest 0.5 mm. The larvae were weighed about 10 hours after the last feeding, which minimized the impact of gut contents on body weight. The mean values of total length, body weight, and the condition coefficient were compared using Duncan's multiple range test. The relative growth rate (RGR) in common carp and grass carp was determined with the initial weights of 1.3 and 1.1 mg, respectively. Fish survival was normalized (Sokal and Rohlf 1969). Differences were accepted as significant at $P \leq 0.05$.

Development rate (V) was calculated with the equation:

$$V = \tau^{-1}$$

where τ is the time (days) from fertilization to the mass occurrence of a given developmental stage.

Linear regression was used to determine the dependency between developmental rate and the temperature applied:

$$V = a + bt$$

where t is the temperature.

Based on the calculated linear regression, the threshold temperature (i.e. the temperature of so-called biological zero) was calculated – the temperature at which embryonic development is theoretically arrested (Kamler 1992):

$$t_0 = -a/b$$

and also the effective day-degrees ($D°_{eff}$)

$$D°_{eff} = \tau \cdot t_{eff} = b^{-1}$$

where the effective temperature is

$$t_{eff} = t - t_0$$

In order to confirm how many times the biological process rate (in this case development) increases theoretically with temperature increases of 10°C, temperature coefficient Q_{10}, which had already been applied to developmental rate V (Kamler 2002), was calculated according to the following equation:

$$Q_{10dev} = (V_2/V_1)^{10/(t2-t1)}$$

where V_1 – developmental rate at the lower (t_1) of two temperatures; V_2 – developmental rate at a higher temperature (t_2).

The relative growth rate (RGR – % body weight on the day; Ricker 1975, Myszkowski 1997), used to identify increases in body weight, was calculated using the following equation:

$$RGR = 100\ (e^G - 1)$$

The values of parameter G were calculated according to the following equation:

$$G = (\ln M_n - \ln M_0)\ n^{-1}$$

where: n – experiment length in days; M_0 and M_n – respective body weight (mg) on day 0 and body weight (mg) on day n.

Condition coefficient K was calculated with the following equation:

$$K = 10^2 \cdot M \cdot TL^{-3}$$

where: M – body weight (mg); TL – total length (mm).

In order to compare the three different parameters which comprised the results of the study (development, growth, survival) the Average Quality Ratings (AQR) method was used and the quality indicator q (Kolman 1975) was calculated with the following equation:

$$q = (v_m - v_{min})/(v_{max} - v_{min})$$

where: v_m – measured value; v_{min} – minimum value; v_{max} – maximum value. The quality indicator is presented as the mean of three indicators calculated for the survival, weight, and developmental rate. Higher indicator values mean better quality.

3. RESULTS

3.1. DEVELOPMENT – CLASSIFICATION

The embryonic and early larval periods were divided into phases, and these were further divided into steps (Fig. 1). The steps division applied was a modification of the system by Peňáz (2001). The term "larva" is used however for hatched individuals, and the typology of Peňáz is modified by the addition of the compensatory development phase, which is proposed in the current work, as well as double names for the steps that occur in this phase (Table 2). It was confirmed that the stages designated were possible to identify in repeated observations of the studied common carp and grass carp individuals.

TABLE 2

Comparison of the distribution of developmental steps in common carp and grass carp within the hierarchy of developmental periods and phases

	C. carpio	*C. idella*
PERIOD	EMBRYO	
Phase	Cleavage	
Step	E1 – Activation	E1 – Activation
	E2 – Cleavage	E2 – Cleavage
	E3 – Blastulation	E3 – Blastulation
	E4 – Gastrulation	E4 – Gastrulation
Phase	Embryo	
Step	E5 – Organogenesis	E5 – Organogenesis
	E6 – Active movement	E6 – Active movement
	E7 – Pigmentation	E7 – Hatching
	E8 – Hatching	
PERIOD	LARVA	
Phase	Compensatory development	
Step	E9/L0 – Swim bladder inflation	E8/L0 – Pigmentation and lower jaw formation
		E9/L01 – Swim bladder inflation
Phase	Finfold larva/Preflexion	
Step	L1 – Mixed feeding	L1 – Mixed feeding
	L2 – Exogenous feeding	L2 – Exogenous feeding
Phase	Finformed larva/Flexion and Postflexion	
Step	L3-L6 – Subsequent larval development	L3-L6 – Subsequent larval development

Development stages observed: E1 – fertilization, blastodisc; E2 – 2, 4, 8, 16, 32 blastomeres, early morula, late morula; E3 – high blastula, sphere blastula; E4 – early gastrula (about 1/3 of a sphere), late gastrula (about ½ of a sphere), blastopore closure; E5 – tail bud, 3 somites, 10 somites, 15 somites; E6 – separation of the caudal section, first embryonic movement, heart beating, colourless blood visible; E7 – eye pigmentation, duct of Cuvier visible, blood pigmentation, melanophores near the back; E8 – egg envelopes weakens from effects of chorionase and intensified embryonic movements, onset of hatching (first individuals), 50% of individuals hatched; E8/L0 – beginning of eye pigmentation, duct of Cuvier visible, blood pigmentation, melanophores on head and trunk; E9/L0 and E9/L01– swim bladder walls visible – not inflated, swim bladder inflation begins (first individuals), swim bladder inflated in 50% of individuals; L1 – initiation of exogenous feeding (first specimens), food visible in 50% of individuals.

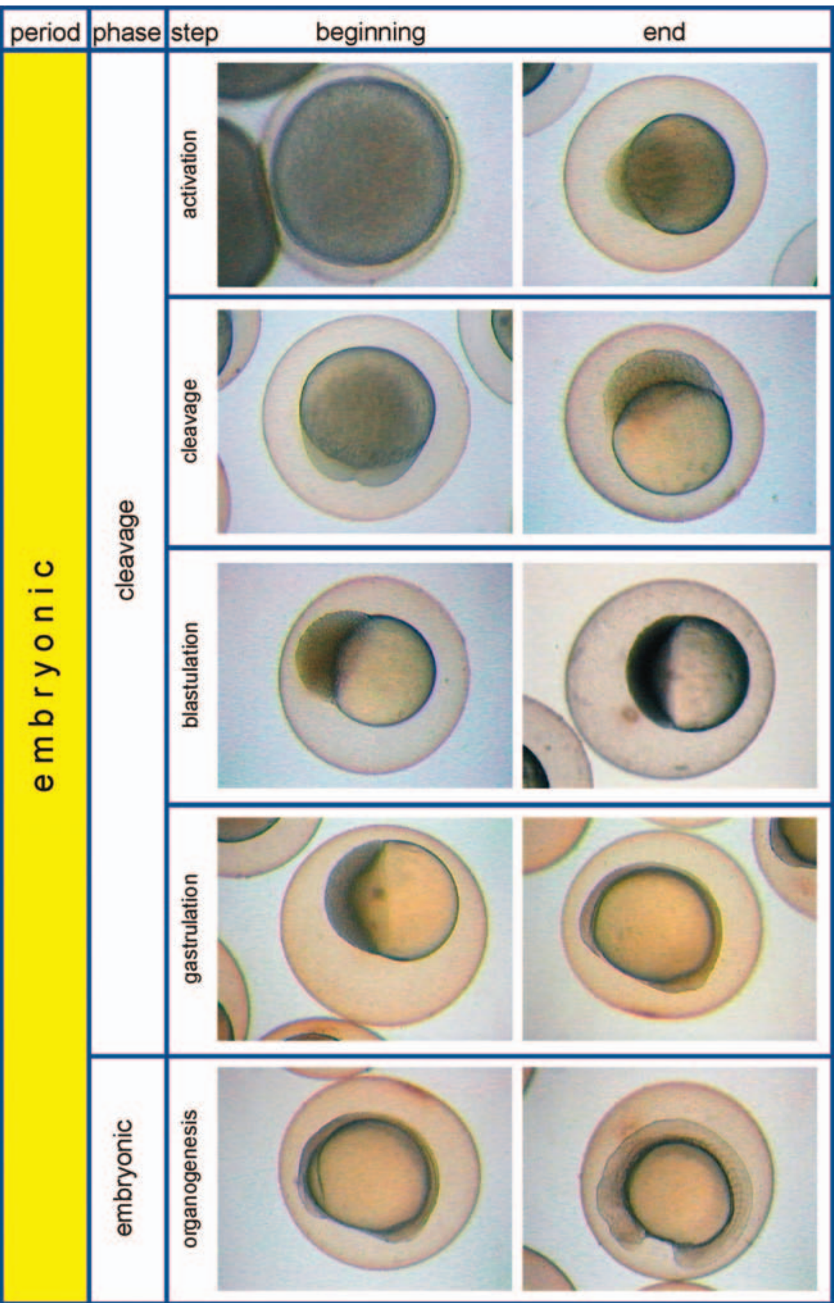
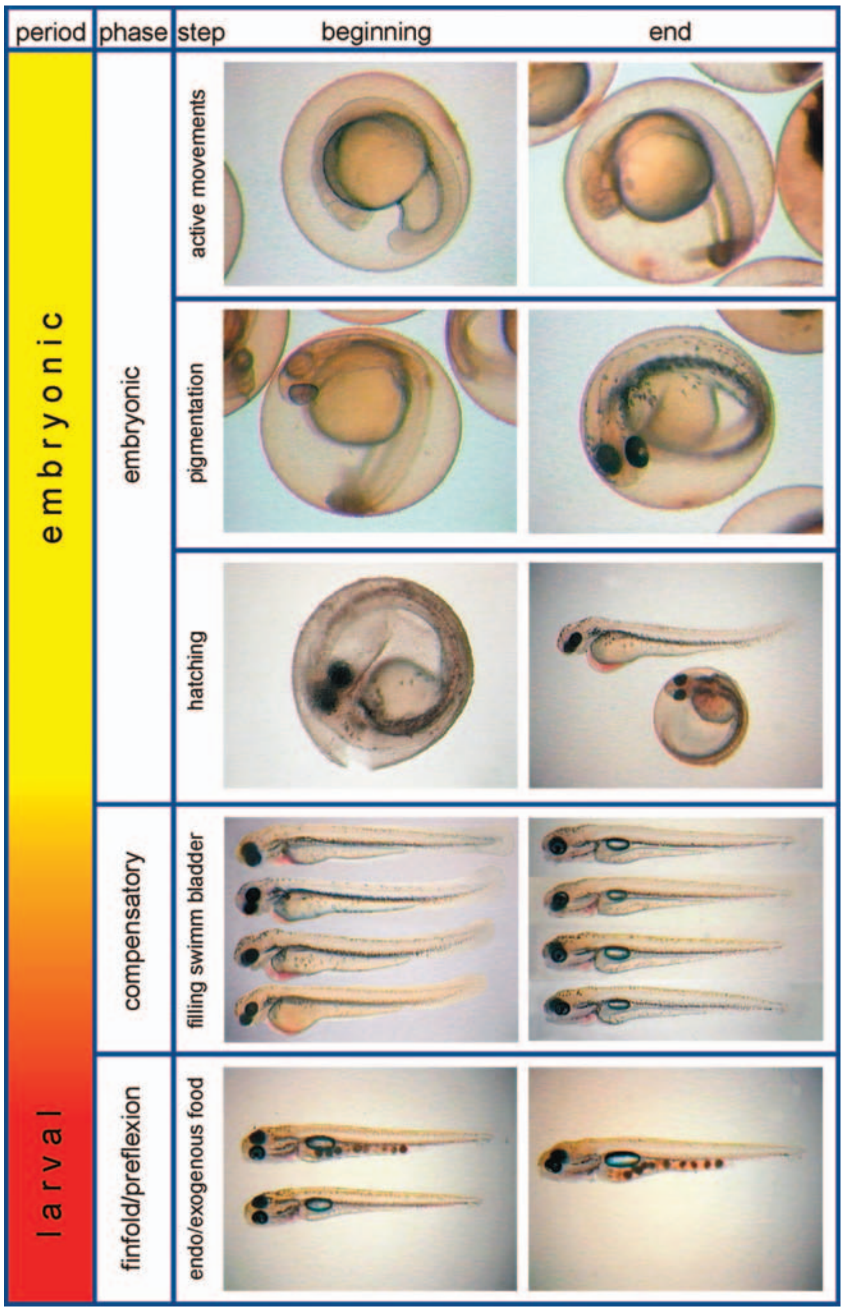


Fig. 1. An illustration of the transition between embryo and larva using a hierarchical division into periods, phases, and steps using common carp as an example.



cont. Fig. 1. Photographs of four larvae in the compensatory development phase: from the top 20, 24, 28, 32°C.

3.2. INFLUENCE OF TEMPERATURE

3.2.1. DEVELOPMENT

The time of development (τ, days) of common carp was shortened at higher temperatures, and this phenomena was noted in all four of the developmental stages compared (Table 3). The differences between the low and high temperatures were substantial. The influence of temperature on development time was the highest up to the hatching stage (Ha): in experiments IIC and IIIC the acceleration of hatching between the temperatures of 20°C and 32°C was threefold.

TABLE 3

Influence of temperature on the moment when certain development stages are achieved by common carp and on the value of temperature coefficient Q_{10}

	Eye pigment (EP)		Hatching (Ha)		Inflation of posterior swim bladder chamber (SB)		First exogenous feeding (FF)	
Group	τ (days)	Q_{10}	τ (days)	Q_{10}	τ (days)	Q_{10}	τ (days)	Q_{10}
IC20	1.81		3.29		3.79		5.63	
IC28	0.90	2.39	1.92	1.96	2.72	1.51	3.13	2.08
IIC20	2.06		4.69		6.48		7.06	
IIC24	1.35	2.88	2.56	4.54	4.48	2.52	5.27	2.07
IIC28	1.02	2.02	2.02	1.81	2.90	2.97	3.65	2.51
IIC32	0.90	1.37	1.52	2.04	2.48	1.48	3.23	1.35
IIIC20	2.04		4.54		6.00		7.00	
IIIC24	1.46	2.31	2.79	3.38	4.38	2.20	5.08	2.23
IIIC28	1.08	2.12	1.92	2.55	2.75	3.20	3.25	3.06
IIIC32	0.96	1.34	1.54	1.74	2.38	1.44	2.83	1.41

Coefficient Q_{10} was calculated for adjacent temperature variants, in experiment IC $t_2 - t_1 = 8°C$, and in experiments IIC and IIIC $t_2 - t_1 = 4°C$.

The temperature coefficient Q_{10} in both embryonic stages (EP and Ha) was the highest at the 20-24°C temperature difference; it decreased, however, at the higher temperatures differences of 24-28°C and 28-32°C. During the larval period, the maximum Q_{10} value moved toward the higher temperatures. During the stages of the inflation of the posterior swim bladder chamber (SB), as well the first exogenous feeding (FF), the Q_{10} coefficient value was the highest at the temperature difference of 24-28°C.

To determine the influence of temperature on the embryonic and larval development rate (V) of common carp, combined linear regression was calculated for both experiments and included the groups studied at four temperatures (Table 4). The development intervals

analyzed were from fertilization to hatching (Fe-Ha), from fertilization to inflation of the posterior chamber of the swim bladder (Fe-SB), and from fertilization to the first exogenous feeding (Fe-FF). The value of b, which describes the influence of temperature on developmental rate, decreased as the length of the studied development interval increased. Similarly, regression indicated that the biological zero t_0 values also decreased.

TABLE 4

Results of linear regression of the growth rate of common carp at four temperatures and the calculated temperature of the biological zero (t_0) and the number of effective day-degrees ($D°_{eff}$)

V = a +bt	Df	a	b	r^2	P	t_0	$D°_{eff}$
Fe-Ha	6	-0.5004	0.03610	0.995	0.000000	13.86	27.70
Fe-SB	6	-0.2853	0.02205	0.972	0.000007	12.94	45.35
Fe-FF	6	-0.1928	0.01662	0.971	0.00006	11.60	60.17

t – temperature (°C), Df – degrees of freedom (n-2), r^2 – determination coefficient, P – confidence level.

The development time (τ) of grass carp also decreased at higher temperatures (Table 5). The decrease in development time between the highest and lowest temperatures studied was in excess of 2.5-fold. Eye pigmentation did not appear until after hatching. In group IIIG20 the swim bladders of the larvae did not inflate. Although they survived for 19 days, they were unable to feed and their development was halted.

TABLE 5

Influence of temperature on the moment when certain development stages are achieved by grass carp and on the value of temperature coefficient Q_{10}

	Blastopore closure (BC)		Hatching (Ha)		Eye pigment (EP)		Inflation of posterior swim bladder chamber (SB)		First exogenous feeding (FF)	
Group	τ (days)	Q_{10}	τ (days)	Q_{10}	τ (days)	Q_{10}	τ (days)	Q_{10}	τ (days)	Q_{10}
IG24	0.40		1.25		4.67		6.75		8.29	
IG32	0.29	1.49	0.63	2.35	2.00	2.88	2.54	3.39	3.08	3.44
IIG20	0.58		1.75		5.46		7.96		10.08	
IIG24	0.44	1.99	1.17	2.74	3.29	3.55	4.96	3.26	7.08	2.42
IIG28	0.33	2.05	0.79	2.67	2.63	1.75	3.29	2.79	4.96	2.44
IIG32	0.29	1.38	0.67	1.51	1.92	2.20	2.46	2.07	3.29	2.78
IIIG20	-	-	1.75		-	-	stages not attained			
IIIG24	-	-	1.04	3.67	-	-	4.50		5.50	
IIIG28	-	-	0.83	1.76	-	-	3.13	2.48	4.50	1.65
IIIG32	-	-	0.63	1.99	-	-	2.46	1.83	3.50	1.87

Coefficient Q_{10} was calculated for adjacent temperature variants, in experiment IG $t_2 - t_1 = 8°C$, and experiments IIG and IIIG $t_2 - t_1 = 4°C$. In experiment IIIG, it was only calculated for the key stages Ha, SB, and FF. (-) in cells of the BC and EP columns means no measurements were taken.

There were no great differences in temperature coefficient Q_{10} in grass carp, although the range of changes was different in experiments IIG and IIIG (Table 5).

Linear regression for the development rate (V) of grass carp was calculated together for experiments IIG and IIIG and included the groups studied at four temperatures (Table 6). Similarly to carp, the developmental intervals of Fe-Ha, Fe-SB, and Fe-FF were analyzed. The value of b decreased as the length of the studied development interval increased. The biological zero t_0 values were the lowest in the embryonic period (Fe-Ha), and were higher for the longer development intervals.

TABLE 6

Results of linear regression of the growth rate of grass carp at four temperatures and the calculated temperature of the biological zero (t_0) and the number of effective day-degrees ($D°_{eff}$)

V = a +bt	Df	a	b	r^2	P	t_0	$D°_{eff}$
Fe-Ha	6	-1.038	0.08082	0.988	0.000001	12.84	12.37
Fe-SB	5	-0.3538	0.02374	0.994	0.000001	14.90	42.12
Fe-FF	5	-0.2273	0.01610	0.951	0.0002	14.12	62.11

t – temperature (°C), Df – degrees of freedom (n-2), r^2 – determination coefficient, P – confidence level.

3.2.2. GROWTH

The dependence of the length of the common carp hatched larvae on incubation temperature was distinct and statistically significant, and the hatched larvae were shorter in length at higher temperatures (Table 7). This difference decreased during the compensatory development phase. During this time, the larvae still fed only endogenously. The dependence of hatching grass carp size on temperature was typical; smaller individuals hatched at higher temperatures (Table 8). Hatching grass carp larvae were smaller than common carp in the same stage.

TABLE 7

Influence of temperature on the length (TL, mm) of common carp larvae in the first key developmental stages

Group	Ha	SB
IIC20	5.71^{a} (2.63)	6.31^{a} (1.93)
IIC24	5.46^{b} (2.04)	6.19^{ab} (4.47)
IIC28	5.34^{c} (2.89)	6.04^{b} (4.30)
IIC32	5.14^{d} (1.94)	6.15^{ab} (2.97)

Egg diameter after swelling was 1.9 mm, and yolk diameter was 1.3 mm (n=10). Data in columns with different letter indexes differ significantly ($P \leq 0.05$), n=10. Coefficient of variation in parentheses (CV).

TABLE 8

Influence of temperature on the length (TL, mm) of grass carp larvae in the first key developmental stages

Group	Ha	SB
IIG20	5.08^{a} (6.50)	6.79^{a} (2.65)
IIG24	4.87^{b} (1.85)	6.62^{b} (2.87)
IIG28	4.80^{b} (1.67)	6.68^{ab} (1.80)
IIG32	4.61^{c} (2.60)	6.72^{ab} (1.93)

Egg diameter after swelling was 3.4 mm, and yolk diameter was 1.2 mm (n=10). Data in columns with different letter indexes differ significantly (P ≤ 0.05), n=10. Coefficient of variation in parentheses (CV).

The final size of common carp larvae reared at the temperature of 23°C is presented in Table 9. The larvae that had been incubated at temperatures of 24°C and 28°C were longer and heavier than those that had been incubated at temperatures of 20°C and 32°C. The larvae from experiment IIC had the lowest weight in all temperature variants (but at a similar length) than in experiments IC and IIIC. The larvae from group IC20-24 grew significantly faster than those from group IC20.

TABLE 9

Comparison of size, condition coefficient (K), relative growth rate of body weight and survival of common carp larvae with different thermal history of incubation after 14 days of rearing at a temperature of 23°C

Group	TL (mm)	W (mg)	K	RGR (% d^{-1})	Survival (%)
IC20	18.12^{c} (7.0)	108.08^{c} (20.0)	1.80^{c} (6.7)	37.13	99.88^{a}
IC28	21.19^{a} (6.7)	178.69^{a} (23.1)	1.84^{b} (7.1)	42.14	99.38^{a}
IC20-24	19.52^{b} (4.9)	141.57^{b} (16.9)	1.89^{a} (6.3)	39.80	99.25^{a}
IIC20	18.69^{b} (4.4)	83.43^{b} (15.3)	1.27^{c} (5.5)	34.62	99.75^{a}
IIC24	19.18^{a} (5.1)	92.85^{a} (17.4)	1.30^{b} (5.4)	35.65	99.00^{ab}
IIC28	19.17^{a} (5.1)	95.72^{a} (16.8)	1.35^{a} (5.9)	35.94	97.38^{bc}
IIC32	18.58^{b} (5.1)	85.68^{b} (17.2)	1.32^{b} (6.1)	34.87	96.38^{c}
IIIC20	18.24^{bc} (5.9)	103.56^{c} (17.3)	1.69^{c} (4.7)	36.71	99.38^{a}
IIIC24	19.10^{a} (4.9)	119.61^{a} (15.0)	1.71^{bc} (5.3)	38.13	99.25^{a}
IIIC28	18.48^{b} (8.7)	112.95^{b} (24.3)	1.74^{a} (7.5)	37.56	99.50^{a}
IIIC32	18.13^{c} (6.1)	103.64^{c} (18.3)	1.72^{ab} (5.8)	36.72	99.38^{a}

Data in columns with different letter indexes (within one year) differ significantly at a level of P ≤ 0.05; TL, W and K, n=100; survival, n=800. Coefficient of variation in parentheses (CV).

During the rearing of grass carp (Table 10), the longest and heaviest larvae came from the groups incubated at a temperature of 32°C. The greatest differences in size among the

subsequent temperature variants was between groups IIG20 and IIG24. The relative growth rate of grass carp in all the experiments was lower than in the common carp.

TABLE 10

Comparison of sizes, condition coefficient (K), relative growth rate of body weight and survival of grass carp larvae with different thermal history of incubation after 14 days of rearing at a temperature of 23°C

Group	TL (mm)	W (mg)	K	RGR (% d^{-1})	Survival (%)
IG24	18.56^{b} (7.0)	65.63^{b} (22.9)	1.01^{b} (6.9)	33.92	97.00^{a}
IG32	19.15^{a} (5.4)	77.75^{a} (18.0)	1.10^{a} (8.2)	35.55	94.50^{a}
IG24# *	17.20^{c} (9.4)	57.04^{c} (31.2)	1.09^{a} (10.1)	32.58	95.50^{a}
IIG20	13.69^{c} (11.5)	27.72^{c} (37.8)	1.02^{d} (9.8)	25.92	58.25^{b}
IIG24	16.34^{a} (6.3)	47.68^{b} (21.0)	1.08^{c} (6.5)	30.90	95.13^{a}
IIG28	15.88^{b} (8.1)	49.30^{b} (25.4)	1.21^{a} (12.4)	31.21	95.50^{a}
IIG32	16.56^{a} (10.3)	53.41^{a} (28.0)	1.16^{b} (7.8)	31.96	99.50^{a}
IIIG20**	-	-	-	-	-
IIIG24	19.92^{b} (5.8)	83.61^{a} (15.0)	1.05^{a} (6.7)	36.25	93.88^{a}
IIIG28	19.96^{b} (6.4)	84.13^{a} (17.0)	1.05^{a} (8.6)	36.31	94.75^{a}
IIIG32	20.41^{a} (5.3)	84.23^{a} (18.7)	0.98^{b} (8.2)	36.33	94.13^{a}

Data in columns with different letter indexes (within one year) differ significantly at a level of $P \leq 0.05$; TL, W and K, n=100; survival, n=800. Coefficient of variation in parentheses (CV).
** - group IG24# are the progeny of different pairs of parents than those of the other two groups.*
*** - the larvae from group IIIG20 died without having inflated their swim bladders.*

The sizes of grass carp larvae in all of the groups on the final day of rearing of the last group (IIG20; day 24 of the experiment) are presented in Table 11. The differences among all the groups were statistically significant ($P < 0.05$).

TABLE 11

Comparison of size and condition coefficient (K) of grass carp larvae in group IIG20 on the final day of rearing (24th day of the experiment)

Group	TL (mm)	W (mg)	K	Survival* (%)
IIG20	13.69^{d} (11.5)	27.72^{d} (37.8)	1.02^{b} (9.8)	58.25^{b}
IIG24	18.51^{c} (6.9)	63.45^{c} (24.3)	0.99^{c} (13.1)	95.13^{a}
IIG28	20.48^{b} (10.4)	95.81^{b} (31.0)	1.08^{a} (10.2)	95.50^{a}
IIG32	21.19^{a} (12.2)	105.99^{a} (45.9)	1.04^{b} (12.5)	99.50^{a}

Data in columns with different letter indexes differ significantly at a level of $P \leq 0.05$; TL, W and K, n=100; survival, n=800. Coefficient of variation in parentheses (CV).
** - survival in these groups was the same as in the 14-day rearing period, with mortality during rearing only noted at the beginning of exogenous feeding.*

3.2.3. SURVIVAL

The survival of the developing common carp was high in all experiments. The cumulative survival from the embryonic period and during rearing did not fall below 80% in any group and exceeded 85% in most groups (Table 12). Survival was determined for the first time at the appearance of eye pigmentation (EP), and it indicated the number of eggs fertilized. Survival at this stage in experiments IC and IIIC did not differ significantly among the temperature variants. In experiment IIC it was more varied, but it equalized after hatching (Ha). A significant difference occurred only in the final survival of experiment IIC, while that in groups IIC24 and IIC28 did not differ significantly ($P > 0.05$).

TABLE 12

Cumulative survival of embryos and larvae of common carp with different thermal history of incubation at key developmental stages

Group	n	Survival (%)				
		EP	Ha	SB	FF	after 14 days of rearing
IC20	756	92.84^{a}	-	89.16^{a}	-	89.05^{a}
IC28	882	91.31^{a}	-	88.60^{a}	-	88.07^{a}
IIC20	400	97.50^{a}	92.00^{a}	90.00^{a}	-	89.78^{a}
IIC24	400	93.75^{b}	91.50^{a}	87.50^{ab}	-	86.63^{ab}
IIC28	400	90.00^{b}	89.00^{a}	88.00^{ab}	-	85.69^{b}
IIC32	400	93.25^{b}	92.50^{a}	83.50^{b}	-	80.47^{c}
IIIC20	888	87.25^{c}	86.69^{a}	85.68^{b}	85.11^{b}	84.58^{a}
IIIC24	912	89.25^{bc}	88.70^{a}	87.60^{ab}	87.05^{ab}	86.40^{a}
IIIC28	1176	90.05^{ab}	89.45^{a}	88.77^{a}	88.34^{a}	87.90^{a}
IIIC32	1020	90.18^{a}	89.50^{a}	88.81^{a}	88.41^{a}	87.86^{a}

Data in columns with different letter indexes (within one year) differ significantly at a level of $P \leq 0.05$; after 14 days of rearing, n=800

The survival of grass carp during embryonic development was generally lower than that of common carp (Table 13). The highest mortality was noted either in the cleavage phase (experiment IIIG) or in the compensatory development phase (experiment IIG). The lowest final survival was noted at the temperature of 20°C. Higher mortality at this temperature occurred after hatching (group IIIG20), when the larvae had non-inflated swim bladders, and after exogenous feeding had begun (group IIG20). Survival during rearing was high in all groups (above 93%; Table 10) and did not differ significantly, with the exception of group IIG20, in which survival was significantly lower.

TABLE 13

Cumulative survival of embryos and larvae of grass carp with different thermal history of incubation at key developmental stages

Group	n	Survival (%)			
		BC	Ha	SB	after 14 days of rearing
IIG20	344	-	87.80[a]	66.88[a]	38.96[b]
IIG24	302	-	86.10[a]	65.56[a]	62.36[a]
IIG28	368	-	82.07[ab]	63.58[a]	60.72[a]
IIG32	388	-	77.88[b]	64.46[a]	64.14[a]
IIIG20	730	68.49[c]	66.86[b]	0	0
IIIG24	962	73.39[b]	72.66[a]	70.89[a]	66.55[a]
IIIG28	886	67.71[c]	67.71[b]	63.63[b]	60.29[b]
IIIG32	894	75.61[a]	75.61[a]	72.93[a]	68.64[a]

Data in columns with different letter indexes (within one year) differ significantly at a level of $P \leq 0.05$; after 14 days of rearing, n=800

Survival to the inflated swim bladder stage (SB) of the larvae from experiment IV, in which common carp eggs were placed directly into the incubation temperature (Table 1), was 76.6, 80.0, 64.2, and 0% at the corresponding temperatures of 20, 24, 28, and 32°C. Sudden changes in temperature from 22 to 28°C lowered survival by 12.4 and 15.8% in comparison with groups IVC20 and IVC24°C, where the temperature change was 2°C. Changes in temperature of 10°C (group IVC32) led to the deaths of all the individuals studied.

4. DISCUSSION

4.1. METHODOLOGICAL ISSUES

4.1.1. NUMBER OF PARENTS

There are two ways to decide on the number of parents whose progeny are used in an experiment. Mixing sex products averages parental effects. Results such as growth rate, metabolism, or resistance to toxins are then less burdened by parental effect and are, thus, more representative of a given species. However, in studies of development, where each individual within an observed group is a "result", comparing the progeny of several parents increases the variability of these results, i.e. the time to the appearance of subsequent observed characters. Decreasing the variability of results also facilitates

comparing development among the temperatures studied. The progeny of single females were used in development studies by Peňáz (1973) of *Barbus barbus* (L.), Tatarko (1977a) and Alami-Durante et al. (2000) of *C. carpio*, Kamler et al. (1998) of *Ch. nasus*, Vagelli (1999) of *Pterapogon kauderni* (Koumans), Arvedlund et al. (2000) of *Amphiprion melanopus* (Bleeker), Geffen (2002) of *Clupea harengus* L., Sado and Kimura (2002b) of *Candidia barbatus* (Regan), Browman et al. (2003) of *Gadus morhua* L., and Sund and Falk-Petersen (2005) of *A. minor*.

Parental effects can originate from either one of the parents. Paternal effect is usually related to the sperm density and motility (Kołdras and Mejza 1983, Linhart et al. 1997, 2005); however, some studies have indicated that the effects of fertilization can also stem from the sperm enzyme level (AspAT and AP; Glogowski et al. 1997), or even from the sperm velocity (Gage et al. 2004).

Egg size is the primary factor dependent on parental impact, and it originates from the age, size, and fecundity of the female (Bonisławska et al. 2000, Keckeis et al. 2000, Kamler 2005). The dependence of egg size, but also of the length of incubation, larval size, and resistance to starvation on the size of females from the same age class, was confirmed by Huang et al. (1999) in *Acanthopagrus schlegeli* (Bleeker). The dependence of the development of progeny on egg size has also been described by, among other authors, Moodie et al. (1989) in *Sander vitreus* (Mitchill), and Einum (2003) in *Salmo salar* L. *S. vitreus* larvae hatched from larger eggs grew faster, and their survival rate was higher. The maternal effect on the survival of larvae was also confirmed by Huuskonen et al. (2003) in *S. alpinus*. Saillant et al. (2001) reported that, in addition to quantity, yolk quality also impacted larval growth. Kokurewicz (1970) reported variation in embryonic growth rate in *Tinca tinca* (L.) depending on the origin of the parents. Parental effect was also notable in the reaction to temperature: 15°C, which was the lethal temperature for several groups of tench, was sufficient (80% hatched) for the proper development of embryos from other parents.

An interesting dependency was reported by Fox et al. (2003) with regard to *Pleuronectes platessa* L.; namely, that embryonic development in the largest and smallest eggs at 6°C lasted four days longer than that in eggs of medium size. This comprised about 20% of the entire embryonic period. These same authors confirmed that embryonic development varied slightly in each group of eggs. Resistance to long-term starvation is linked with egg size and especially with yolk quantity, which was confirmed in

studies by Słomińska et al. (1995) of *Coregonus albula* (L.), Keckeis et al. (2000) of *Ch. nasus*, and by Tamada and Iwata (2005) of *Rhinogobius* sp.

Berkeley et al. (2004) emphasized that there is a very high dependency between growth rate as well as the survival of *Sebastes melanops* Girard larvae and female age; this was due to the larger lipid droplet in the yolk sac in the progeny of older females. The primary ingredient, triacylglycerol, is the main energy source for freshly-hatched larvae (Norton et al. 2001). Egg size increases with female age to a certain point, but it begins to decrease in older fish (Kamler 1992) and this dependence is linked more to egg weight than diameter. After reaching a certain age, which is different in each species, fish begin to exhibit signs of aging (Peňáz 2001). Wolnicki (unpubl. data) observed weight loss, limited appetite, and apathy in six-year-old *Ch. nasus* females. Aging leads to lower weight, which, after age, is the second most important non-genetic internal factor influencing egg quality (Kamler 1992).

The comparison of the sizes of grass carp larvae from various pairs of parents (this work, groups IG24 and IG24$^{\#}$; Table 10) confirmed that they differed significantly in both length and weight after 14 days of rearing under identical conditions. The range of temperature tolerance can also depend on parental factors as was exemplified in the different survival rates noted in groups IIG20 and IIIG20 (Table 13). Therefore, the use for subsequent reproduction of females of similar size and age, and in the case of each experiment the eggs of a single female, permitted minimizing the number of factors other than temperature that can influence embryonic and larval development and growth of common carp and grass carp.

4.1.2. SAMPLE SIZE

The development studies described in this work were performed on samples of five specimens that were collected as frequently as possible. The time intervals applied during the observations of the embryos, which ranged from 5 minutes at the beginning of development to 1 hour in the final phase, were frequent enough to allow noting precisely when a particular change in development occurred. The simultaneous observation of five individuals made it possible to conduct the observations in a relatively short period of time, and all the larvae recovered from the anesthetic without difficulty. Samples of 5 larvae were also used in development and growth studies by Fuiman et al. (1998) of *Brevoortia tyrannus* (Latrobe) and *Sciaenops ocellatus* (L.), by Arvedlund et

al. (2000) of *A. melanopus*, and by Reynalte-Tataje et al. (2004) of *Brycon orbignyanus* (Val.). In a study of the early development of *P. kauderni*, Vagelli (1999) collected three to four embryos at 24 hour intervals, while Humphrey et al. (2003) studied the development of *Melanotaenia splendida splendida* (Peters) with samples of 5 eggs, and used 10 larvae for growth measurements. The methods applied in the current study and those of the various authors cited utilize microscopes coupled with cameras, which ensures that the measurements are precise and can be done in the shortest possible time. Thanks to the recorded images, uncertainties can be clarified by comparing these images with those from previous stages.

The images made following hatching and after the posterior swim bladder chamber had inflated permitted measuring to approximately the nearest 3 pixels at a total length (TL) of 240-250 pixels. If the larvae at this point measured, for example 5.4 mm, the precision of the measurements was about 0.07 mm (1.22% of TL). The length variation coefficient of the larvae examined was exceptionally low, for example, the range of this value in common carp measured after hatching was from 1.94-2.89% (Table 7), which does not deviate much from the standard measurement error. With such high measurement precision and such little variation, the number of 10 individuals measured per sample was sufficient for the comparisons presented in Tables 7 and 8.

4.1.3. INCUBATION CONDITIONS

In Siberian rivers the large, light eggs of the pelagophil grass carp (3.4 mm, Table 8), rise through the water column during development, and this buoyancy is an adaptation to natural environmental conditions (Gorbach 1972, Antalfi and Tölg 1975). During incubation in hatcheries, large Weiss jars are required, otherwise the eggs float out of them at even very low water flow rates. Since the eggs would have floated out of jars with a volume of 0.03 dm^3, it was decided to incubate the eggs in Petri dishes; the guarantee of success was to ensure that there was water movement inside the dishes.

The comparison of egg incubation with various circulation systems indicated that they had no impact on subsequent growth (Korwin-Kossakowski 1988a) or on larval development (Fox et al. 2003). The application of two different methods for incubating common carp eggs (in Weiss jars and Petri dishes) had no impact on the results. Survival rates at the hatching stage were similar in experiment IIC (Petri dishes) and IIIC

(Weiss jars), and in these two experiments the differences in survival between the groups was not statistically significant (Table 12).

4.1.4. GROWTH INDICATORS

In order to calculate the relative growth rate (RGR), it is necessary to have data regarding the initial body weight. Since the larvae used in all the experiments were not weighed at the beginning of the 14-day rearing period, an arbitrarily chosen initial body weight was applied for each species. In order to determine what this means for the final results, calculations were performed using the grass carp from experiment IIG; the impact of initial larval body weight on the value of the RGR was calculated for three hypothetical, but also confirmed, initial weights. The initial weights used were 1.1, 1.2, and 1.3 mg as well as one common final weight of 48 g that was obtained after 14 days of rearing. Three values of RGR were calculated at 31.85, 30.96, and 30.15% d^{-1}. The difference of 0.1 mg, which is about 10% of the initial body weight, meant that, effectively, the differences in weight gain were 1 percentage point per day; this value is small enough that applying a single, common larval body weight is permissible. The final value applied, which was twice or even threefold larger (and was close to that noted with common carp), did not alter the level of these differences. Standardized initial weights of cyprinid larvae were used in comparisons of RGR by Wolnicki (2005). Moreover, Jaworski and Kamler (2002) as well as Kamler (2008) confirmed that initial size has only a slight impact on calculating the specific growth rate (SGR).

4.2. ISSUES IN EARLY ONTOGENESIS

4.2.1. DEVELOPMENTAL TYPOLOGY

"Biological phenomena do exist regardless of what humans think about them" (Kovač and Copp 1999). What can be added to this statement is that these phenomena also exist regardless of what the observer calls them. However, in reporting information and aiming for it to be universally understood, it is significant whether or not the observer refers to the organism correctly.

The desire to be well understood and to disseminate knowledge clearly and uniformly appear to be sufficiently good rationalization for the attempts that have been made over the years to standardize the typology of early fish development. The lack of a definite standard is not the only problem. Hatching, which is a key transitional environ-

mental change for fish, not only provokes differences in opinion that are the root of the typological chaos, but also stormy discussions (Balon 1999, 2004, Peňáz 2001, Kamler 2002, Urho 2002).

Depending on the theory one accepts, fish development occurs either as a series of "leaps" or as a continual process. The saltation development theory created by Vasnecov (1946, 1948, 1953), which was later expanded by Kryzhanovski et al. (1953), and then further developed by Balon (1971, 1984, 1985, 1990), maintains that ontogenesis is a series of steps occurring one after the next. These are comprised of quantitative changes in development and growth separated by moments of qualitative transition (the "leaps"), when the altered cells, tissues, or organs are prepared to take on a new function. This theory is exceptionally interesting and is excellent in explaining the succession of organs and the functions of the developing organism. Distinguishing between two subsequent steps can be difficult sometimes, especially when the examined specimens simultaneously exhibit meristic and biometric characters that are typical of two steps (Kamler et al. 1990, Kamler 2002). Confirming the continuity or saltation of early ontogenesis can depend on the number and the frequency of observations of developmental processes (Gorodilov 1996).

Works on early fish ontogenesis often divide development into hierarchical levels. Numerous stages that represent separate phenomena are grouped into steps. Several steps make a phase, a developmental interval, the name of it describes the situation the organism is in at a given moment, for example, the cleavage or embryonic phases. Phases are grouped into periods, and the names of these indicate the developmental form of the fish (i.e., embryo, larva, juvenile, adult, or senescent). The division of phases, steps and stages is significant almost exclusively to the embryonic and larval periods since these are when numerous quality developmental transformations that comprise morphogenesis occur. Growth in subsequent periods does not require the application of more precise divisions, and these are not usually found in the literature. To date, there is no set standard in developmental terminology, which is why there are differences in early ontogenesis hierarchy and descriptions. The terms applied usually depend on a particular author's convictions, convenience or preferences. Table 14 presents examples of the various divisions used by authors to describe embryonic and larval development.

Let's create, for practical purposes, a definition of "stage": *Stage is a specific state of organism, which can be named, described and repeatedly identified in other individuals*. The number of stages described within a certain step of development usually depends on the precision and ability of the observer, and also stems largely from the frequency of observations. This is true especially of the cleavage phase when changes occur so rapidly that frequent observations are essential for the identification of subsequent stages. For example, the first divisions into two, four, and eight blastomeres were noted in grass carp held at a temperature of 24°C at intervals of 10 to 20 minutes, while hatching began about 17 hours after the blastopore had closed at the end of the cleavage phase (group IIG24, Table 5). Thus, the use of numerous stages selected and then described in a manner allowing each observer to identify them objectively, increases the possibility that any observer will, even with less frequent observations, be able to identify a given stage.

TABLE 14

Hierarchy of divisions of embryonic and larval development according to different authors

Authors	Phase	Step	Stage
Vasnecov et al. (1957), Korwin-Kossakowski and Jezierska (1984)	-	LN	-
Peňáz (1973)	D	-	N
Peňáz (1981, 1982)	-	N+D	-
Kryzhanovski et al. (1953), Gozlan and Copp (2005)	-	LN+D	-
Balon (1958a, b, 1985)	D	LN	-
Gozlan et al. (1999a), Killeen et al. (1999), Kawamura and Uehara (2005)	D	N+D	-
Kováč (2000)	D	LN+D	-
Peňáz (1974), Krupka (1988)	-	-	N
Peňáz et al. (1983)	-	D	D
Neudecker (1976), Witkowski and Kokurewicz (1978), Sado and Kimura (2002a, b), Falk-Petersen and Hansen (2003)*	-	-	D
Tavolga (1949)			N!
Kimmel et al. (1995), Gorodilov (1996), Hill and Johnston (1997), Iwamatsu (2004)	-	-	D!

N – numerical name, LN – letter-numerical name, D – descriptive name, ! – precise stage description
** – stages are described; however, the names of some refer only to embryo size*

Since the divisions are to serve informational purposes, it is of the utmost importance to describe precisely the stages that are the most detailed states of organism development. Unambiguously described stages should be both the basis for and the reference point of comparisons of the early ontogenesis in a given species under various

conditions. With interspecific comparisons it is more prudent to use the key stages, such as hatching or swim bladder inflation. Some stages occur at different moments during the ontogenesis of different species, and comparing these can lead to erroneous conclusions. Examples of this include the appearance of eye and body pigmentation; in common carp it occurs in the third embryonic step while in grass carp it occurs in the first step following hatching (Table 2).

In order for the names of stages to fulfill their investigative function, they should reflect precisely the phenomenon they refer to, for example, "two blastomeres" or "blastula". Obviously, the moment at which a character (or the precisely described elements of a character) appears should be given as the time at which a given stage is achieved. This is significant in that the process of the formation of an organ or character lasts for a certain period, while a stage, which should not describe a period of time (Kryzhanovski et al. 1953, Balon 1975a, 1984, 1989), should be the reflection of a moment.

Precisely identifying and describing the numerous subsequent stages provides the foundation for making detailed comparisons of development rate. One example of the appropriate presentation of developmental stages can be found in the work by Kimmel et al. (1995). Although these authors employed atypical terminology by using the term "period" to refer to time intervals that generally correspond to phases, their work does describe developmental changes in *Danio rerio* (Hamilton) very precisely based on numerous stages. Their division and description of stages was used as the model for the ZFIN project (The Zebrafish Information Network), which is the largest existing data base that includes genetics, genomics, and the development of a single species (Sprague et al. 2001). This division, which is considered to be highly precise, is also applied to describe the embryonic development of other species such as *C. harengus* (Hill and Johnston 1997), or *G. morhua* (Hall et al. 2004). On principle, Kimmel et al. (1995) decided to apply descriptive names to the stages and not numerals or only age, and this renders comparisons easier.

Studies of developmental changes, which are essentially basic biological studies, also have practical applications. The detailed and definitive descriptions of the embryonic developmental stages of *D. rerio* and the subsequent design of optimal incubation technology permitted developing standard toxicity tests (DIN 38415-6, 2003). These permit testing the toxicity of various chemical compounds, as well as pollution levels of water

and sediments by evaluating embryonic development (in earlier standards evaluation was based on fish larva development) of this species in reference to model development as described by Kimmel et al. (1995). This method has been applied successfully in practice (Hollert et al. 2003, Braunbeck et al. 2005, Hallare et al. 2005). The application of these standards is also recommended by the Organization for Economic Co-operation and Development (OECD) based on the work of Braunbeck and Lammer (2005).

The embryonic period is generally divided into two phases: cleavage and embryonic. These two names are the most common, they are also always qualified as being part of the embryonic period. This changes at the moment of hatching, when the term "embryo" is then used alternately with the term "larva". The first phase of development after hatching, which is the root of disagreement, is discussed in a separate subsection (4.2.3). Further development is divided in many ways.

One of the oldest systems for classifying development after hatching uses the terms "protopterygiolarva" and "pterygiolarva", which were published by Rass (1946), and then later used for a many years by Balon (1958a, b, 1975a). Richards (1976) accused Balon of introducing complicated names citing these old terms "protopterygiolarva" and "pterygiolarva", but he did not mention the term "eleutheroembryo" introduced by Balon. This term is nearly synonymous with "free embryo", and both of them mean an embryo that is free from the egg envelopes. Balon (1975a), who introduced the term "eleutheroembryo" based on the Greek word *eleutheros* meaning free, began himself, at a certain point to use the term "free embryo", which had been in use in the literature for many years (Vasnecov 1948, Gozlan et al. 1999a, b, Pavlov 1999, Mercy et al. 2000, Peňáz 2001, Pinder et al. 2005), initially interchangeably with "eleutheroembryo". Abandoning the use of the term "eleutheroembryo" was well advised and served the interests of simplifying terminology. As reported by Kamler (2002) and Urho (2002), this word never came into widespread use and is noted in the literature on early fish development only rarely; however, it is still used even today (e.g., Bennett et al. 2007). A similar simplification was to discontinue the use of the term "protopterygiolarva" in favor of "finfold larva" and the term "pterygiolarva" in favor of "finformed larva" (Balon 1984, 1985, 1990, 2002). The term "finfold larva", has been in use for many years to describe the phase following "yolk-sac larva" (Mansueti 1958 cited in Fay et al.1983, Hardy et al. 1978, Ulanowicz et al. 1982, Secor and Houde 1995); however, these authors refer to the next developmental phase as "post-finfold". The term "finformed"

was probably introduced by Balon (1984) in response to his justified reservations concerning the use of terms with the prefixes “pre-” and “post-” (Balon 1975a, 1979) and is still in current use (Saitoh 1990, Easton and Orth 1992, Kováč 1994, 2000, Gozlan et al. 1999b, Nunn et al. 2007).

Researchers of marine fish use the more common and fairly simple division of the larval period beginning after hatching and based on changes in the shape of the notochord. It divides larvae into the phases of “yolk-sac”, “preflexion”, “flexion”, and “postflexion”. This classification has been in use for years and essentially remains unchanged (Ahlstrom et al. 1976, Kendall et al. 1984, Neira et al. 1998, Aceves-Medina et al. 2003, Machinandiarena et al. 2003, Takemura et al. 2004). It is also sometimes used with freshwater fish (Sado and Kimura 2002a, b). Seen sometimes as not precise enough, this system was expanded by, among others, De Forest and Busby (2006), who divided the “flexion” phase into three additional early, middle, and late flexion phases. Classification based on the notochord flexion is also applied at the Ichthyoplankton Information System data base created by the Alaska Fisheries Science Center (IIS, AFSC). It should be emphasized here that this system also uses the term “stage” in a fully different meaning that refers to time interval that reflect functional phase.

The system proposed by Snyder (1976, 1981) for dividing development after hatching into the protolarval, mezolarval, and metalarval phases is used less frequently (Potter and Potter 1981, Shireman and Smith 1983). In a more recent work (Snyder and Muth 2004), the author himself attempts to join his system with the most widely used classification by Ahlstrom et al. (1976) that separates the larval period into the yolk-sac, preflexion, flexion, and postflexion larval phases, asserting that the systems are not competitive but rather complementary.

Thus, in the contemporary literature there are five systems, that have been in simultaneous use for many years, that divide early larval fish development into phases. Two of the most common and widely encountered were created by Ahlstrom (1976) and Balon (1984):

- yolk-sac larva, preflexion larva, flexion larva, and postflexion larva (Ahlstrom et al. 1976, Kendall et al. 1984, Neira et al. 1998, Sado i Kimura 2002a, b, Aceves-Medina et al. 2003, Machinandiarena et al. 2003, Takemura et al. 2004);

- free embryo, finfold larva, and finformed larva (Balon 1984, Saitoh 1990, Easton and Orth 1992, Kováč 1994, 2000, Gozlan et al. 1999b, Nunn et al. 2007).

The three following classification systems are noted less frequently:

- yolk-sac larva, finfold larva, and post-finfold larva (Mansueti 1958 cited in Fay et al.1983, Hardy et al. 1978, Ulanowicz et al. 1982, Mooij 1989, Secor and Houde 1995);
- protolarva, mesolarva, and metalarva (Snyder 1976, 1981, Potter and Potter 1981, Shireman and Smith 1983);
- lecithotrophic larva, lecithoexotrophic larva, and exotrophic larva (Deplano et al. 1991a, b, Aguilera et al. 2002, Mendoza et al. 2002, Firat et al. 2005, Korkut et al. 2006).

The older classifications introduced by Balon (1971) were as follows:

- eleutheroembryo, protopterygiolarva, and pterygiolarva; while this system is usually no longer noted in its entirety, the term "eleutheroembryo" is seen sometimes (Falkowski et al. 1988, Luczynski et al. 1988, Kucharczyk et al. 1997, Kujawa et al. 1997, Braunbeck and Lammer 2005).

Such significant variation in terminology could also be the root of difficulties in the exchange of information and misunderstandings especially among researchers investigating freshwater and marine fish, which is something Houde (1975) recognized long ago. Since it has been impossible to date to unify developmental terminology, it would be prudent to concentrate on simplifying the precise and definitive presentation of research results. As Balon (1979) and Urho (2002) asserted, nomenclature is not as significant as clear definitions and comprehension of what a given term means and the phenomenon it describes. Thus, to ensure that reported findings will be understood unequivocally, the phenomena that are the foundation of developmental studies should be stages described in detail and in the greatest number possible.

4.2.2. HATCHING – EMBRYO OR LARVA?

When does an embryo become a larva? Are newly-hatched individuals still embryos, or are they already larvae? How far does development have to progress before an embryo can be called a larva? These issues regarding the typology of known developmental states

that have been described in some detail by numerous authors, are related to the problem Lem (1983) referred to quite jocularly as the "baldness paradox"[1], which he made reference to during some very serious discussions on the limits of autoevolution.

Hatching is the most drastic environmental change a fish endures during ontogenesis. This phenomenon is also affected by nearly every environmental factor. Temperature can either accelerate or retard embryonic development; it influences the development and the activity of the hatching glands; it influences metabolism and, thus, oxygen demand as well as the oxygen content in the water (Kamler 1992, 2002, Kamler et al. 1998). The pH and chemical composition of the water also influence the hatching date (for a review of the literature see Jezierska 1988, Jezierska and Witeska 2001), by accelerating, retarding, or lengthening the process, similarly to the pesticides or insecticides applied in agriculture (Mercy et al. 2000, Gonzáles-Doncel et al. 2003).

As reported by Fuiman (2002), under natural conditions, hatching occurs when the embryo attains a size at which its oxygen demand can no longer be met by transmembrane diffusion or the perivitelline fluid. Lower oxygen content in the water, and, thus, in the perivitelline fluid, causes the increase of chorionase secretion, which permits quicker hatching (Rothbard 1981, Shireman and Smith 1983). The *C. carpio* larvae that had hatched earlier as a consequence of slower water flow, continued to develop normally, and their swim bladders were inflated at the same time as those in fish that had hatched without assistance (Korwin-Kossakowski 1988b). Fuiman (2002) described accelerated hatching resulting from a lack of oxygen as an adaptive phenomenon that prevents asphyxiation and helps the hatched larvae find water that is better oxygenated. This same author also maintains that hatching can be delayed if there is excess oxygen.

Hatching is the result of the combined effects of hatching enzymes and the mechanical tearing of the egg envelopes by the embryo. The production and activity of hatching enzymes depends on, among other factors, temperature, insolation, and water pH, as well as from the oxygen content (Rechulicz 2001, Fuiman 2002, Ostaszewska 2002a). However, the development rate of the embryo, and this includes the timing of the

[1]The citation reads as follows: "It is at this point in autoevolution that we have the 'baldness paradox'. While losing one hair does not result in baldness, it is impossible to determine just how many hairs must be lost for one to be bald. Changing one gene for another does not change the progeny into an alien species, but it is impossible to pinpoint just when a new species is created".

appearance of the hatching glands, is dependent on environmental conditions, and has a significantly greater impact on the timing of hatching than do either the production or activity of the enzymes (Fuiman 2002).

The issue of whether a hatched individual is an embryo (Balon 1999, Peňáz 2001) or a larva (Kamler 2002, Urho 2002) has been discussed repeatedly, but no binding standard has been adopted. Each side remains true to their own convictions. Some researchers refer to the hatched organism as an embryo (Kryzhanovski 1949, Kryzhanovski et al. 1953, Peňáz 1973, 1974, Balon 1975a, 1989, 1990, Peňáz et al. 1983, Krupka 1988, Luczynski et al. 1988, Gozlan et al. 1999a, b, Pavlov 1999, Kováč 2000), while other refer to it as a larva (Hubbs 1943, Tatarko 1977b, Witkowski i Kokurewicz 1978, Araujo-Lima 1994, Winnicki and Korzelecka 1997, Jezierska et al. 2000, Kamler 2002, Urho 2002, Faria et al. 2002, Takemura et al. 2004). Some authors, like Vasnecov et al. (1957), have referred to hatched individuals interchangeably as “embryos” and “larvae” within the same paper.

Both hatching and the initiation of exogenous feeding are crucial changes that delineate the active life of larvae from the “passive form” of embryo life. Hatching is the greatest ontogenetic transition (Fuiman 2002); it exposes the organism to a wholly new environment, and allows for both full locomotor activity and an increase of a metabolic rate (Kamler and Kato 1983, Kamler 1992, Kamler et al. 1995). In turn, the initiation of exogenous feeding is the start of individual energy independence. According to Balon (1989), a larva is an individual that has begun exogenous feeding, which refers to the ingestion and digestion of external food. The start of exogenous feeding can be however artificially postponed by withholding feed. Thus, Peňáz (2001) widened the definition of the transition from embryo to larva to include individuals that were capable of exogenous feeding. This means, however, that in order to classify an individual as a larva, it must have a fully formed, functioning digestive tract, and the confirmation of this requires detailed inspection. Peňáz (2001) and Urho (2002) reviewed arguments of other reserchers who referred to hatched individuals as either embryos or larvae. Both authors ultimately maintain their original positions.

Prior to engaging in a discussion of whether a freshly hatched organism is an embryo or a larva, it is worthwhile considering the purpose this term will serve. Studies of early ontogenesis require the use of standard terminology that fully describes the state of development of the organism in question, but it must be one that is also com-

prehensible by all. Proponents of the two theories present convincing arguments, but each contends that different aspects of development are more important. The time of hatching, the state of development of the newly-hatched individual, as well as the moment when exogenous feeding begins are all influenced by internal factors (characters related to species, egg size, parental effect), as well as both physical and chemical external ones. Both of these phenomena are equally suitable, or equally unsuitable, to serve as the border between subsequent periods of development.

Similar reservations are also encountered when attempting to determine precisely the moment between larval and juvenile period. Characters signaling metamorphosis can be morphological, physiological, ecological, or even behavioral (Hensel 1999, Pavlov 1999, Vilizzi and Walker 1999, Peňáz 2001, Fuiman 2002, Urho 2002), and even today it has yet to be established which is the decisive one. This is also why for some purposes such as calculating ontogenetic index O_L (Fuiman 1994, Fuiman et al. 1998), based on specimen length during metamorphosis, certain characters are chosen that enable objectively confirming the developmental stage in a given species; these include the formation of rays or the disappearance of the fin folds. Some authors, including Ditty et al. (2003), apply a score system to describe the developmental state of a chosen morphological character, and individuals are identified as reaching metamorphose when a determined score level is achieved. Despite a certain incongruity in applying "practical" considerations, it is actually those that, in certain situations, are the decisive factors in using one name rather than the other.

Larval age, developmental rate, and growth rate must all have points of reference in time. One moment that is possible to confirm or calculate, and the one that is most readily used, is hatching. As a key stage, it is used as point "0" in calculations of developmental or growth rates, while larval age is most frequently recorded as "days post hatching" (Adriaens and Verraes 1997, 1998, Alami-Durante et al. 2000, Arvedlund et al. 2000, Humphrey et al. 2003, Trotter et al. 2003, Sala et al. 2005, Geffen et al. 2006, King et al. 2006, Kowalska et al. 2006). Vasnecov was the father of the developmental saltation theory, but he remained undecided about what to call individuals after hatching (Vasnecov 1948, 1953, 1957); however, in explaining his theory he described the developmental steps of *A. brama*, beginning with step A (the first following hatching) which he chose as the key transitional one. It is much more difficult to determine when an organism has achieved the state of development that permits exogenous feeding.

Despite the lack of categorical biological indications, hatching was chosen at the reference point, and it is more frequently used as the border between the embryonic and larval periods. Hatching is the most important environmental transition in the life of a young organism, while the resulting locomotory independence is the most important behavioral transition.

4.2.3. COMPENSATORY DEVELOPMENT PHASE

The primary tasks of the hatched organism are to develop respiration structures and the ability to swim independently and then to be able to capture and digest food. This means that the larvae have to inflate their swim bladders with gas, and then begin exogenous feeding. The developmental advancement of the hatching organism depends on the fish species, and the water temperature, pH, and chemical composition. Thus, the time interval following hatching is the most difficult one in the life history of fish. Individuals that are poor swimmers are an easy target for predators, and even slight morphological imperfections or variations in the typical environmental conditions render swim bladder inflation and exogenous feeding difficult or even impossible (Kindschi and Barrows 1994, Korwin-Kossakowski 1988c, 1989b, Ostaszewska et al. 1999). Regardless of development advancement at hatching, which can be highly variable, the goals the individual must achieve are always the same; it must be fully capable of locomotor and feeding independence. The size of the larvae of one species can differ at the moment of hatching, but this is largely equalized by the end of endogenous feeding. It has been noted when the individuals that hatched at higher water temperatures were larger (*Eopsetta jordani* (Lockington) – Alderdice and Forrester 1971), or smaller (*Ch. nasus* – Kamler et al. 1998, *Melanogrammus aeglefinus* (L.) – Martell et al. 2005, *E. percnurus* – Kamiński et al. 2006). In the current study, the differences between the length of larvae hatching at different temperatures decreased twofold in common carp and nearly twofold in grass carp during the resorption of the yolk sac (until the inflation of the posterior chamber of the swim bladder). The equalization of size prior to the initiation of exogenous feeding is significant since it provides larvae reared at various temperatures a more equal chance during the first feeding attempts (Kamler 2008).

Figure 1 presents the transition of common carp from the embryonic to the larval period. Photos that show the hierarchical divisions of phases and stages give a graphic illustration useful for the placement of the compensatory development phase.

Depending on environmental conditions and species, hatching individuals are in various states of developmental advancement. The hatched individuals of common carp that had been in various temperatures were of different lengths (Table 7) and in different states of development. Higher water temperatures during development resulted in larger yolk sacs at hatching, less developed jaws, gills, heart and circulatory system and heads that were bent downward. After hatching, all of the individuals had to develop to the stage that permitted exogenous feeding; thus, their mouths, esophagus, and digestive tracts had to develop to a sufficient degree. They also had to inflate the posterior chamber of their swim bladders. The time from hatching, through to the inflation of the swim bladder and then to the first exogenous feeding, is one of "equalizing" or "compensing" chances; in other words, the achievement by all individuals of a developmental state that provides them with the locomot or and energetic independence required for further life.

As mentioned previously, the fundamental difference between the most commonly applied developmental classifications in fish (section 4.2.1) consider hatched individuals to be either embryos (according to Balon 1984) or larvae (according to Ahlstrom 1976). The time from hatching to beginning of exogenous feeding is usually referred to as the "free embryo phase" or the "yolk-sac larva phase". Using the name of this phase requires a declaration from the researcher whether the hatched organism is still considered to be an embryo, or if it is already a larva. This phase is a time interval when, regardless of developmental advancement and following a dramatic change of environment, the individual must attain a state that permits it to live a fully active and independent life. Taking into consideration all of these phenomena, the term "compensatory development phase" is proposed. It explains the current state of the organism without specifying if it is an embryo or a larva. Thus, the embryonic phase ends with hatching, and the hatched individual undergoes a phase of compensatory development, during which it is most susceptible to disadvantageous environmental conditions and predation. The compensatory development phase ends with the initiation of exogenous feeding, which results in much accelerated growth and, in effect, decreasing danger of predation. The author considers that shortening the compensatory development phase, in addition to growth and survival, is one of the important indicators that should guide the choice of optimal incubation temperature.

4.2.4. INTERMEDIATE STAGES – COMMON TYPOLOGY

The use in papers on developmental studies of the terms “free embryo” or “yolk-sac larva” to describe individuals between hatching and the first exogenous feeding has created a nomenclature problem that remains unsolved till today. The discussion to date (Balon 1999, Peňáz 2001, Kamler 2002, Urho 2002) has hinged primarily on the presentation of individual convictions and attempts to impose them on others rather than on the search for common ground. The concept of applying a common typology will have to be based on a change in the approach to this problem.

The basis of the proposed modification is the division into steps, which has been applied for a long time (Kryzhanovski et al. 1953, Lange et al. 1974) and is well known and widely used (Kovač 2000, Keckeis et al. 2001, Peňáz 2001, Pinder and Gozlan 2004). Proponents of this term are generally advocates of the saltation development theory. This classification is still viable and is currently used successfully in descriptions of developmental biology (Löffler et al. 2008), as well as for other research aims, including dividing caught larva samples according to age criteria (Nunn et al. 2007). The steps of embryonic period in this classification are referred to as E1 to E9, while the steps of the larval period are referred to as L1 to L6. Hatching occurs at step E7, E8, or E9, depending on the species and environmental conditions, and the first larval step (L1) begins with exogenous feeding (Peňáz 2001).

Figure 2 presents common carp (a) and grass carp (b) development based on a few key stages. The upper arrows indicate the transition from the embryonic to the larval periods according to the division by Ahlstrom (1976), while the lower arrows refer to the division by Balon (1984). This means that an individual in the compensatory development phase (Ha-FF) is considered to correspond to the “yolk-sac larva” or the “free embryo”, respectively. Since eye pigmentation (EP) occurs in these two species at different moments (Table 2), the compensatory development phase is comprised only of one stage (E9) in common carp or by two (E8 and E9) in grass carp. According to the division into steps that is applied, hatched individuals are classified as embryos (E), but not until they have begun exogenous feeding (FF) are they classified as larvae (L). This may not be acceptable to those who use the term “larva” to refer to individuals that have just hatched. The solution proposed in the current work is to use a double description in the compensatory development phase. In the case of common carp, this designation is E9/L0, while for grass carp these designations are E8/L0 and E9/L01. Additional

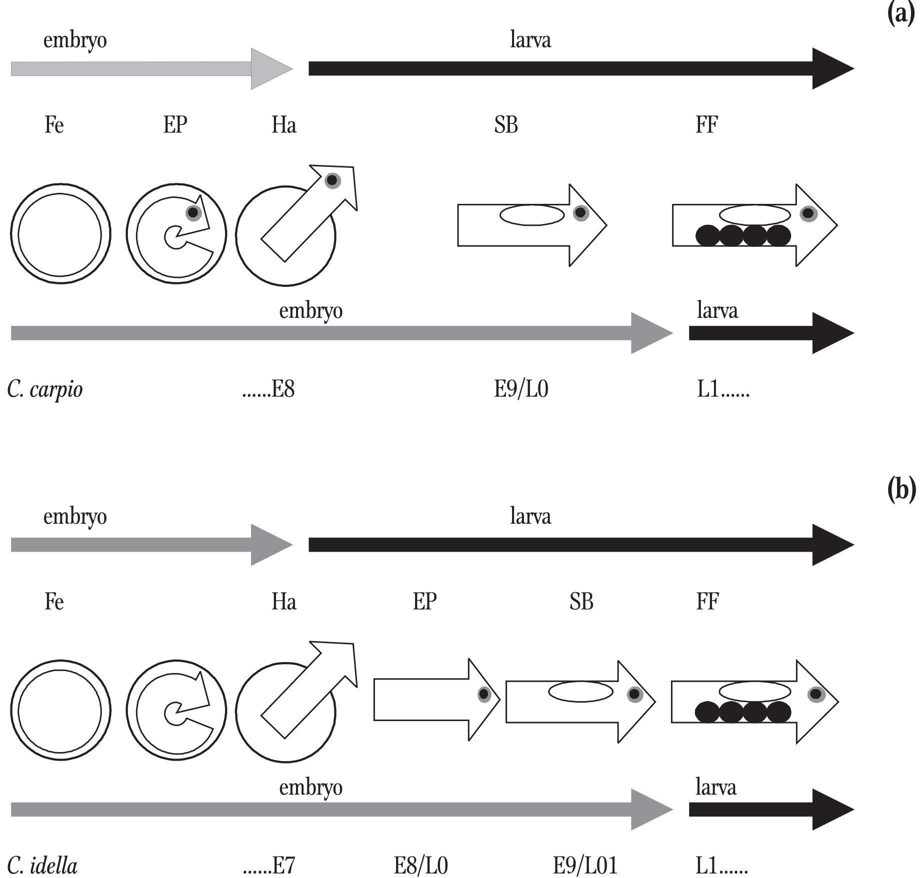


Fig. 2. An explanation of modifications to the system of divisions into steps based on the development of common carp and grass carp. a – common carp, b – grass carp; transition from the embryonic to the larval periods: upper arrows according to Ahlstrom (1976), lower arrows according to Balon (1984); E – embryonic stages; L – larval stages; E/L – modified names for stages of the compensatory development phase.

larval designations (L0 and L01) do not affect those applied to date (E1-E9 and L1-L6), but only supplement them. Table 15 presents the modified system of division into steps for common carp and grass carp. Accepting the new approach into the older divisions would provide a chance for the implementation of a common typology. The use by all researchers of the same symbols would be a small price to pay for allowing much better communication among researchers investigating the early ontogeny of fish.

TABLE 15

Connection of the modified system of division into steps of common carp and grass carp with two of the most frequently applied typological systems

Phases	Steps		Key stages	Name of individual	
	C. carpio	*C. idella*		Ahlstrom (1976)	Balon (1984)
Cleavage	E1	E1	Fe	embryo	embryo
	E2	E2			
	E3	E3			
	E4	E4			
Embryo	E5	E5			
	E6	E6			
	E7				
	E8	E7	Ha		
Compensatory development		E8/L0		yolk-sac larva	free embryo
	E9/L0	E9/L01	SB		
*	L1	L1	FF	preflexion larva	finfold larva
*	L2	L2			
*	L3	L3		flexion larva	finformed larva
*	L4	L4			
*	L5	L5		postflexion larva	
*	L6	L6			

** - Names of larval phases used to date, according to names of individuals, for example, preflexion larva phase (Ahlstrom 1976) or finfold larva phase (Balon 1984), etc.*

4.3. INTERSPECIFIC DEVELOPMENTAL DIFFERENCES BETWEEN COMMON CARP AND GRASS CARP

Kryzhanovski (1949), one of the pioneer researchers of the early ontogenesis of fish, maintained that during the embryonic period the most significant factors for the survival of the eggs were predation and oxygen conditions. Comparisons of the early development of common carp and grass carp, as species that differ in how they deposit their eggs (Kryzhanovski 1949, Balon 1975b), confirm the adaptations these species have made to both the protection of eggs from predators and varied oxygen conditions.

Figure 3 presents the comparison of the length of time common carp and grass carp need to develop at three key stages:

- hatching (Ha) – drastic environmental change;
- inflating the posterior chamber of the swim bladder with gas (SB) – the beginning of active swimming;
- ingesting the first food (FF) – the beginning of feeding independence.

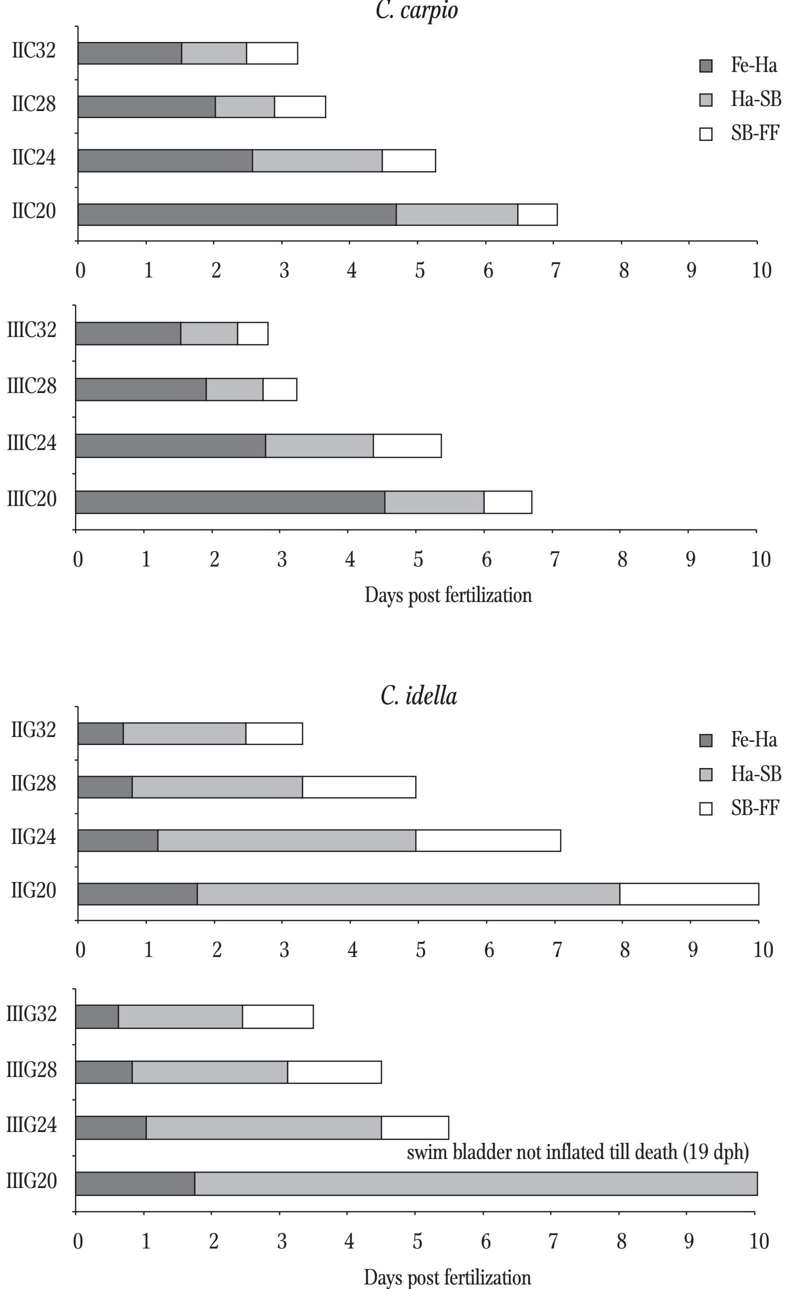


Fig. 3. Comparison of the time when the following key stages are achieved: hatching (Ha), inflation of the posterior chamber of the swim bladder (SB), first exogenous feeding (FF) in the development of common carp and grass carp at temperatures of 20, 24, 28 and 32°C. Data from tables 3 and 5.

The first and fundamental difference between the development of these two species is the period of time required for embryonic development in the egg. At all temperatures this period was more or less two and a half times longer in common carp than in grass carp. In turn, the compensatory development phase was half as long in common carp than it was in grass carp. These differences were undoubtedly responses to the environmental conditions under which the early development of these two species occurs. It is worth remembering that the incubation of the common carp and grass carp eggs under laboratory conditions differs substantially from natural ones. Under natural conditions, common carp eggs develop in places that are not readily noted by predators. After hatching, the larvae become more susceptible to predation, which is why the compensatory development phase is so relatively short. This sequence of developmental changes does not pose many problems (except removing stickiness from the eggs) either during incubation or during maintaining the larvae in the hatchery. The most difficult time interval, which is from hatching to the inflation of the swim bladder, does not last too long.

It is different with the grass carp. Following a very short embryonic period in the egg, there is a long phase of compensatory development. The time interval during which the larvae cannot swim independently is nearly three times longer than the embryonic period. Grass carp spawn in fast flowing rivers (Gorbach 1972, Fischer and Lyakhnovich 1973, Antalfi and Tölg 1975). One of the adaptations to this environment is the large perivitelline space that protects the embryo (Balon 1975b, Andrade-Talmelli et al. 2001) and increases the buoyancy of the egg. Immediately following spawning, the eggs disperse and are carried on water currents finally reaching shallow flood plains. Although the grass carp eggs are very light, even in waters flowing at speeds of 0.5-1 m s^{-1} they are generally found in the mid to lower layers of the water current (Nezdoli and Mitrofanov 1975). Under these conditions, it is more advantageous to hatch quickly, since, when the eggs reach the floodplains they all sink to the bottom. The hatched larvae attach themselves to vegetation and their wide distribution ensures higher survival. These adaptations to the natural environment pose difficulties under hatchery conditions. During the long compensatory development phase, and especially from hatching to swim bladder inflation, the mortality of the larvae can increase.

As mentioned in the introduction, the eggs of common carp and grass carp differ significantly in size. According to Kamler (2005), larger eggs are generally encountered in cold water fish, and such eggs usually produce larger larvae (Fuiman 2002). Egg size is also positively correlated with the length of the embryonic period (Fuiman 2002, Kamler 2005). Kendall et al. (1984) and Chambers (1997) maintained that pelagic eggs are generally smaller than those that sink to the bottom. The size of eggs, understood as the exterior dimensions, is not as significant to the further development of the organism as is the size and quality of the yolk (Balon 1999). Similarly, Fuiman (2002) emphasizes that egg size has more to do with weight than diameter, due to the rather large perivitelline space in pelagic eggs. The eggs of common carp and grass carp examined differed significantly in external size (1.9 and 3.4 mm, respectively), but differed less with regard to yolk size (1.3 and 1.2 mm, respectively). The freshly hatched larvae of the common carp were only slightly larger than those of grass carp. This corresponded to yolk size rather than to overall egg size (compare Tables 7 and 8). Thus, the significant difference in egg sizes, which stems from the size of the perivitelline space and not the yolk, are linked to adaptations of life strategy and the location of their development in the natural environment.

The primary difference in the course of common carp and grass carp development, in addition to the time of development, was the moment when pigmentation appeared. The appearance of eye pigmentation is a practical sign of continuing development, and indicates in many commercially reared species that incubation had been conducted properly. Survival is usually calculated at this stage, which provides information on the fertilization success. In grass carp, pigmentation does not appear until after hatching, and darkening of the eyes occurs just before the occurrence of pigmentation in the blood.

Differences in the timing of the appearance of pigmentation in the body result from adaptations to the varied environmental conditions in which the eggs of these species develop. In common carp, which develop in sticky, sinking eggs, pigments such as hemoglobin and myoglobin appear relatively early, which is primarily related to the poor oxygen conditions near the bottom. In common carp development, the beating of the heart and then the coloring of the blood occurs, regardless of the temperature, shortly after the embryo begins moving (Table 2). As reported by Kamler et al. (1974), when hemoglobin is being formed, there were indications that common carp embryos had greater oxygen requirements. Kamler et al. (1995) also confirmed that in embryos

of *T. tinca* significant increases in oxygen demand occurred prior to hatching; the authors explained this as the result of increased activity at this time. The situation with pelagic eggs is different since they develop in better oxygen conditions. With such eggs, including those of the grass carp (Gorbach 1972, Antalfi and Tölg 1975), the development of respiratory structures and pigments happens much later (Kryzhanovski 1949, Balon 1975b). As Rombough (1988) reported, pelagic embryos also have relatively less developed surface capillary systems, even though freshly hatched grass carp breathe only through the skin (Tatarko 1977b).

The second reason grass carp blood becomes pigmented later is to reduce visibility, which helps to protect them from predators (Kryzhanovski 1949, Balon 1975b, Rombough 1988). The pelagic eggs of grass carp float in the water column, and as long as they are invisible the embryos have a better chance of survival. The transparent, colorless embryos in large, thin, transparent envelopes are nearly invisible in the water. The pigmentation of common carp embryos that are fastened to vegetation does not put them in danger, but pigmentation in the drifting grass carp eggs would make them much easier targets for predators.

Another reason for different pigmentation times stems from the egg sizes of the investigated species. The common carp eggs examined attained a diameter of about 1.9 mm, while the freshly-hatched larvae measured from 5.14 to 5.71 mm (Table 7), which means that the embryo had to develop and grow in a curled position. Body movements become visible practically from the separation of the tail section (Matlak 1980, Korzelecka 1999), which was also observed in the current study (Table 2). Shortly following this, eye and then blood pigmentation occur in the embryos. The increased oxygen demand, due to the intensified activity, requires the creation of a system that is more advanced than just diffusion through the body covering, although this will remain the primary form of breathing for some time to come (Rombough 1988). The appearance of hemoglobin in the blood permits increasing the efficiency of the oxygen delivery. Additional help is provided by the embryo’s fin movements; the primary task of which is to mix the perivitelline fluid to accelerate oxygen diffusion (Korzelecka 1999). Active organisms require increasing amounts of oxygen, and frequent changes in position by the curled embryo also helps to promote symmetrical development (Sroczyński, personal comm.). Following hatching, the pectoral fin movements of common carp lar-

vae also assist breathing (Tatarko 1977b) by increasing the flow of water caused by the movements of the gill covers.

Just how important it is to have the possibility of movement was confirmed in common carp (Korwin-Kossakowski 1996). Eggs that are rinsed in a tannin solution longer than normal swell less, and so they were smaller and the embryos later did not have enough space to move. These eggs produced significantly more hatched larvae with spinal curvature (lordosis, kifosis). These defects can probably be attributed to the inability of the developing embryos to freely shift position within the egg. Growth is also stimulated by the opportunity to move; for example, *Oncorhynchus mykiss* (Walbaum) embryos that had no egg envelopes grew faster (Ciuhandu et al. 2005).

Thus, the bigger is an embryo, the more frequent and of greater amplitude are its movements (Matlak 1980), and oxygen demand increases (Kamler et al. 1974). The larger egg size of the grass carp offers decidedly more space, and the nearly straightened out embryo moves far less than does the common carp embryo. Oxygen diffusion from the water to perivitelline fluid is also easier. The eggs of grass carp have thinner envelopes that do those of common carp, and the thickness of the egg envelopes determines what kind of oxygen barrier there is (Fuiman 2002). A large perivitelline space is a warehouse for oxygen, and is practical in places where there are high fluctuations in oxygen content in the water. The oxygen stored during the day in the perivitelline fluid is later used at night when oxygen concentrations in the water decrease.

The sequence in which organs appear and their rates of development are dependent on the life strategy of a given species. Timmermans (1987) pointed out, for example, that freshly hatched Cichlidae larvae, which are incubated in the mother's mouth, have very weakly developed muscles, while their sensory organs and digestive tracts are more advanced. Conversely, just after hatching the muscles of free-swimming common carp larvae are much more developed than their digestive tracts.

Thus, the length of time required for development, the moment hatching occurs, and the moment pigment appears in both of the species examined are intrinsically linked with their environmental conditions during the embryonic and larval periods. These adaptations, however, do not necessarily have to be advantageous under the conditions of artificial incubation. The compensatory development phase, the length of which depends on the adaptation of a given species to natural living conditions, is a time interval during which poorly developed and weakly moving larvae can experience

the most difficulty under the industrial conditions of hatcheries. In situations where incubation differs significantly from natural conditions, it might be advantageous to shorten embryonic development and some larval development of these fish while simultaneously accelerating their growth.

4.4. INFLUENCE OF TEMPERATURE ON DEVELOPMENT

The temperature range tolerated by developing common carp embryos under natural conditions is 12.5-30°C (Keiz 1959, Kokurewicz 1971, Wojda 2006). At temperatures above 32.5°C the eggs die (Wojda 2006), and the optimal temperature sum in natural spawning grounds in day-degrees is 95°D, which refers to a temperature of 19°C. The temperatures applied in hatcheries for the incubation of common carp and grass carp eggs are presented in Table 16.

TABLE 16

Ranges of temperature used for incubation of common carp and grass carp eggs in hatcheries

Species	Temperature (°C)	Source
C. carpio	25-28	Rothbard and Yaron (1995)
	23	Horvath et al. (1992)
	22-24	Albrecht (1986)
	20-25	Ouyang Hai (1991)
	19-20	Kwiatkowski (unpublished data) – hatchery in Żabieniec, Poland
	18-20	Guziur et al. (2003)
C. idella	23-25	Adamek (unpublished data) – hatchery in Gołysz, Poland
	22.5-25.5	Vovk (1974)
	22-28	Jähnichen (1986), Zhong et al. (1991)
	22-25	Kokurewicz 1971, Antalfi and Tölg (1975)
	22-23	Romanenko et al. (1988)
	21-26	Fedorenko and Fraser (1978)
	21-25	Shireman and Smith (1983)
	18-19	Fischer and Lyakhnovich (1973) (after Vinogradov and Erohina 1967)

The lowest common carp egg incubation temperatures are applied in Poland, and this is a response to the climate. Interestingly, the recommended temperatures applied in Germany (Albrecht 1986) were 22-24°C, which is high for such climatic conditions. A smaller range of temperatures was applied during grass carp incubation. The only mention of temperatures under 21°C was found in Fischer and Lyakhnovich (1973) in

a work that appeared quite a long time ago. Vinogradov and Erohina (1967), who are cited by these authors, reported a grass carp incubation temperature of 18-19°C. These same authors also concluded that lowering the temperature to 16-18°C resulted in higher mortality, while raising it to 28-30°C was not harmful.

In the present study, common carp embryonic development proceeded without disruption at a temperature range of 20-32°C, while that of grass carp did so at a range of 24-32°C. Only the temperature of 20°C was too low for the proper development of grass carp; although the embryos developed and hatched, swim bladder inflation happened in these larvae after a very long time (group IIG20) or not at all (group IIIG20) (Table 5).

The results of studies determining temperature tolerance as well as optimal temperature during the embryonic period can differ even within a single species. The ranges of tolerated temperatures and optimal temperatures for *T. tinca* embryonic development were determined by various authors to be as follows: Kokurewicz (1970) – 15-30°C and 19-24°C; Kouřil et al. (1988) – 18.3-28.6°C and 20-25.5°C; Peňáz et al. (1989) – 16.5-31°C and 20-25°C. Zhukinski (1986) explained that variations in the optimal temperatures for the embryonic development of *A. brama* and *C. carpio* resulted from different temperatures at spawning grounds, and thus was dependent on geographical location. Using data from Herzig and Winkler (1985) and Mills (1980), Kamler and Wolnicki (2006) calculated the theoretical temperatures of biological zero t_0 for *Leuciscus leuciscus* (L.) of various origins that were studied within a similar temperature range. They discovered that for individuals living in Austria t_0 was 5.1°C, while that of individuals living in Great Britain it was 4.1°C. A similar dependence is obtained when comparing t_0 calculated for the embryonic period of grass carp reproduced in Poland (12.84°C – Table 6) and in Russia (13.50°C – calculation based on data from Kokurewicz 1971). It must be kept in mind that in Russia grass carp spawns under natural conditions, while in Poland it was held at higher temperatures only immediately prior to reproduction, and that full egg maturity was attained with hormonal stimulation. Differences in the embryonic developmental rates of grass carp originating from various females but incubated under the same conditions is described by Goryunova (1971). She reports that these differences are usually linked to the conditions the spawners experienced prior to spawning. Korwin-Kossakowski and Jezierska

(1984) also confirmed the influence of the parental thermal history on the development of *T. tinca* larvae. Development was quicker in the progeny of spawners that had come from heated ponds, than in that of the larvae whose parents had been living under natural conditions. This dependency has also been noted in other poikilothermic animals. For example, Wang and Kang (2005) described variable thermal tolerance in the eggs of the migratory locust, *Locusta migratoria* (L.), that originated from the tropical and temperate zones.

The small differences in the theoretical temperature of biological zero of the two species examined in the current study (common carp – 13.86°C; grass carp – 12.84°C) can be linked to the fact that the spawners of both species had been living under the same conditions for many years. The grass carp appears to adapt quickly to changes in environmental temperature. Opuszyński (1967) reported that after a year of acclimatization in ponds (Żabieniec, Poland) the upper and lower lethal temperatures for this species had decreased and was then close to that of common carp. In the present paper, the similar temperature coefficients Q_{10} of 1.7-4.5 in common carp and 1.5-3.7 in grass carp might indicate the similarity of thermal preferenda of the two species examined. These values of temperature coefficients Q_{10} are placed on a similar level to those of the metabolic temperature coefficient Q_{10} typical for the Krogh normal curve Q_{10} – 2.3-2.2 (Kamler 1992) at a temperature level of 20-30°C. The temperature coefficient Q_{10} calculated for stages SB and FF was of a similar size and had an even smaller range (Tables 3 and 5). When the temperatures of the biological zero t_0 calculated for the current work are compared with the values calculated for other cyprinids (Fig. 4), it turns out that the data for the common carp and the grass carp are at levels typical of warm water species.

The temperature ranges applied in the experiments described in this paper are also possible to apply in hatcheries. The entire temperature range of 20-32°C fell within that which is tolerated by the common carp. For grass carp, the temperature of 20°C turned out to be inappropriate. Many authors (Stott and Cross 1973, Antalfi and Tölg 1975, Fedorenko and Fraser 1978, Shireman and Smith 1983, Chilton and Muoneke 1992) regard the temperature of 20°C as the lower threshold below which grass carp embryo mortality and the number of deformations increase significantly. It has happened, under natural conditions, that grass carp commenced their spawning even at 18.5°C (River Ili, Kazakhstan; Nezdoli and Mitrofanov 1975), and its peak was at a temperature of 19.5-19.9°C. Nevertheless, the fact that the eggs and freshly-hatched

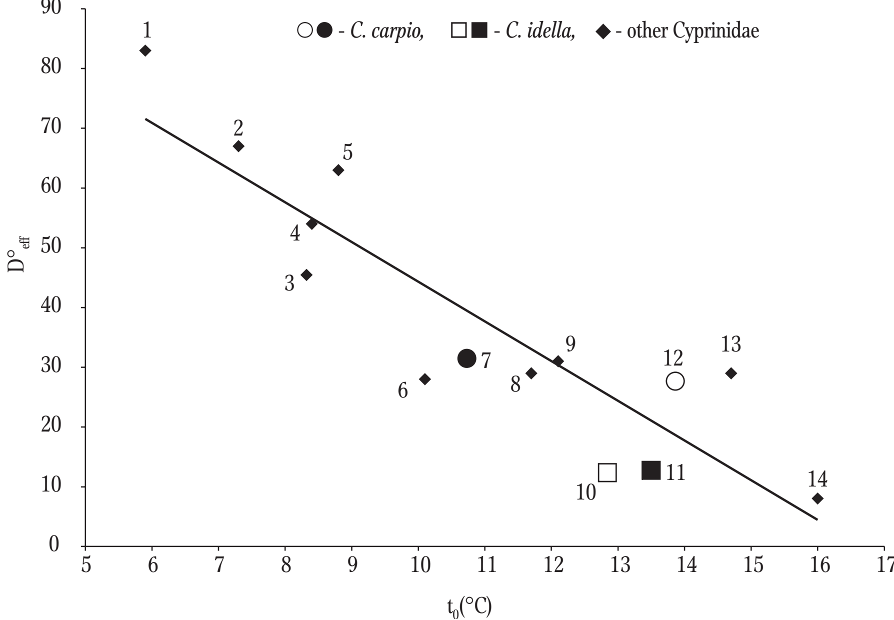


Fig. 4. Comparison of the dependence of $D°_{eff}$ on t_0 in different cyprinid species during the embryonic period (Fe-Ha).
Species: 1. *L. idus*, 2. *R. rutilus*, 3. and 5. *Ch. nasus*, 4. *E. percnurus*, 6. *V. vimba*, 7 and 12. *C. carpio*, 8. *T. tinca*, 9. *B. barbus*, 10 and 11 *C. idella*, 13. *C. carassius*, 14. *H. molitrix*.
Sources: 1-3, 5, 6, 8, 9, 13, 14 – Kamler (2002); 4 – Kamiński et al. (2006); 7 – calculated with data from Peňáz et al. (1983), 10 i 12 – the current study, 11 – calculated with data from Kokurewicz (1971).

larvae were noted in field studies does not provide information about further development and survival. In the current study, the survival of grass carp incubated at a temperature of 20°C was significantly lower than at the other temperatures, and after 14 days of rearing in experiment IIG it was under 40%, in comparison with over 60% at the other temperatures. In experiment IIIG at a temperature of 20°C hatching occured, but fish did not inflate their swim bladders (Table 13) and they all died.

The inability to inflate the swim bladder in temperatures that are too low (13°C) was observed in *E. percnurus* by Kamiński et al. (2006); this affected about 40% of the studied larvae. The larvae that did inflate their swim bladders already had resorbed yolk sacs. This differed in the grass carp studied in the current work. The larvae that had inflated swim bladders still had remnants of yolk sacs. At all of the viable temperature (this refers to both the grass carp as well as the common carp) the inflation of the

swim bladder and even the first exogenous feeding both took place before the yolk sac had been fully resorbed.

The inflation of the swim bladder can be used as a kind of indicator of the physicochemical conditions of water. Its retardation can be caused by inappropriate temperature (Trotter et al. 2003, Kamiński et al. 2006), but also by water that is too acidic (Korwin-Kossakowski 1988c, 1989b) or too alkaline (Ostaszewska et al. 1999), that has a high content of heavy metals (Sarnowski 2005, Sikorska and Wolnicki 2006a, b), and even by surface water pollution (Kindschi and Barrows 1994, Trotter et al. 2005), both bacterial and mechanical, which can be diminished, among others, by oxygenation and the flow of water (Ostaszewska 2002b). Other pathology of the developing swim bladder can be caused by excessive levels of nitrites, which Korwin-Kossakowski et al. (1995) confirmed in the larvae of *T. tinca*, Korwin-Kossakowski et al. (1996) in *C. idella* larvae, and Korwin-Kossakowski and Ostaszewska (2003) in *C. carpio* larvae.

It is worthwhile noting how increased temperature affects the length of subsequent developmental phases (Fig. 3). The first, and fairly predictable, dependency in both of the species was a shortened embryonic period (Fe-Ha) at higher temperatures. Shortened embryonic development in freshwater fish held at higher temperatures was observed by Kokurewicz (1970) and Peňáz et al. (1989) in *T. tinca*, by Kokurewicz (1970) and Kujawa et al. (2007) in *R. rutilus*, by Peňáz et al. (1983) in *C. carpio*, by Laurila et al. (1987) in *Carassius carassius* (L.), by Kamler et al. (1994) in *Clarias gariepinus* (Burchell), by Kucharczyk et al. (1997) in *A. brama*, by Kujawa et al. (1997) in *Aspius aspius* (L.), by Kamler et al. (1998) in *Ch. Nasus,* and Kamiński et al. (2006) in *E. percnurus*. Pepin (1991) wrote about a similar dependence in marine fish in a review work.

Developmental rate is characteristic in each species. In order to be able to compare the duration of embryonic period ($\tau_{Fe\text{-}Ha}$) at the experimental temperatures of 20, 24, 28, and 32°C with data from other temperatures, the following calculations were done. Using the duration of the embryonic period of carp at seven temperatures studied by Peňáz et al. (1983), linear regression was calculated for this species' rate of development. From these, t_0 and $D°_{eff}$ were calculated and then, using the transformed formula $D°_{eff} = \tau \cdot (t - t_0)$, the theoretical values of τ for the temperatures studied in this paper were determined. This same method was used to process data from six temperatures that were reported by Kokurewicz (1971) for grass carp. The length of the embryonic period in common carp and grass carp at the temperatures studied is very similar

to the values calculated from the data provided by these two authors (Table 17). The exception are common carp which exhibit a clear difference at 20°C, the temperature which slowed its development much more in the present work. This slow-down resulted in a higher value of the theoretical temperature of biological zero $t_{0(Fe\text{-}Ha)}$, a consequence of a steeper slope of the regression curve depicted in Fig. 4.

TABLE 17

Comparison of the duration of the embryonic period ($\tau_{Fe\text{-}Ha}$) in common carp and grass carp

	20°C	24°C	28°C	32°C
C. carpio – current work*	4.62	2.68	1.97	1.53
C. carpio – Peňáz et al. (1983)**	3.39	2.37	1.82	1.48
C. idella – current work*	1.75	1.11	0.81	0.65
C. idella – Kokurewicz (1971)**	1.77	1.14	0.84	0.66

** - mean values from two replicates*
*** - data recalculated to the temperatures studied in the current work*

The developmental rate and its dependence on temperature changes at the moment of hatching. This phenomena of slowed development following hatching is noted in both marine species (Pepin 1991) as well as freshwater species (Peňáz et al. 1983, Kamiński et al. 2006). To illustrate this, the regression curves of the developmental rates of carp studied in the present work (Fig. 5) were compared to those studied by Peňáz et al. (1983); the time intervals compared were from fertilization to hatching (Fe-Ha) and from fertilization to the first exogenous feeding (Fe-FF). The disparity in the curves from developmental intervals Fe-Ha and Fe-FF is significantly larger for grass carp (Fig. 6). Also noteworthy are the similar values of regression curve intercept and slope (Fe-Ha) of the grass carp studied in the present work and those calculated using data from Kokurewicz (1971). The data presented indicates that increased temperature was more advantageous for accelerating embryonic development in grass carp than in common carp (value b was nearly twofold greater; Tables 4 and 6). These tables present the comparison of regression equations calculated for development intervals Fe-Ha, Fe-SB, and Fe-FF, and these indicate that the longer the interval is that is investigated, the weaker the dependence of development is on temperature. The number of effective day-degrees necessary for achieving the hatching stage was nearly twofold higher in common carp (Table 4) than in grass carp (Table 6). Not much difference was noted between the two species in the number of effective day-degrees required to achieve the exogenous feeding stage.

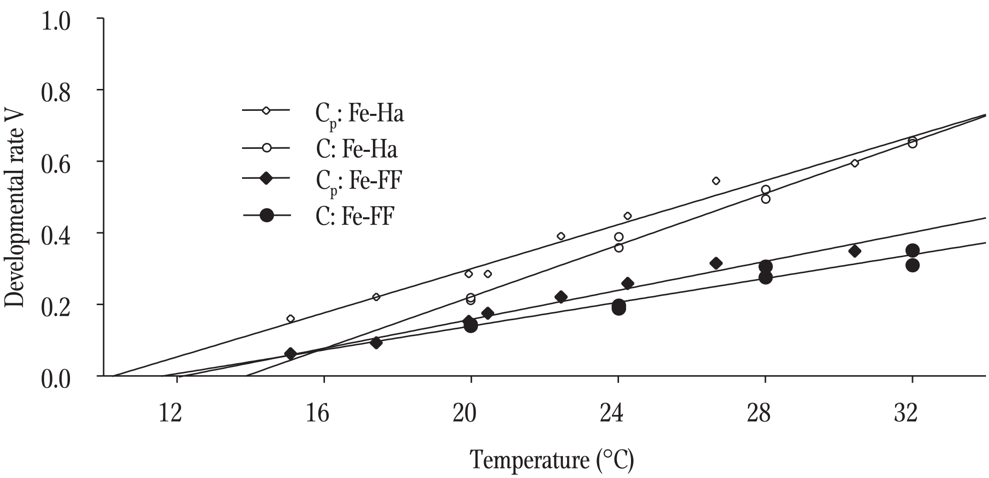


Fig. 5. Comparison of linear regression curves for the rate of development (V) of common carp from fertilization to hatching (Fe-Ha) and from fertilization to the first exogenous feeding (Fe-FF). C – common carp, the current study, CP – calculated with data from Peňáz et al. (1983).

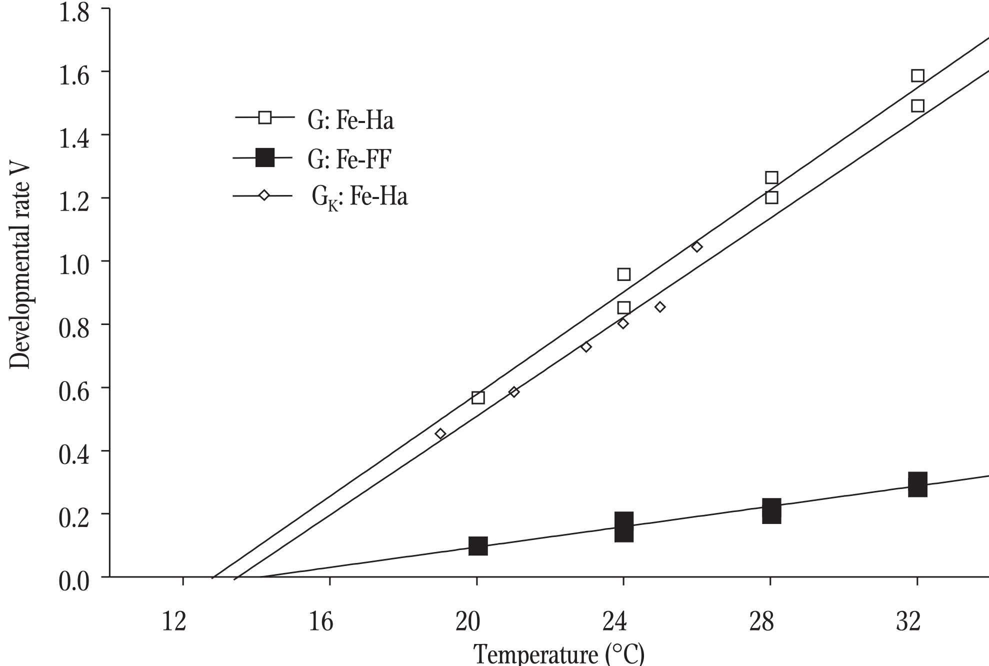


Fig. 6. Comparison of linear regression curves for the rate of development (V) of grass carp from fertilization to hatching (Fe-Ha) and from fertilization to the first exogenous feeding (Fe-FF). G – grass carp, the current study, GK – calculated with data from Kokurewicz (1971).

In the current experiments, the first exogenous feeding (FF) occurred at the common temperature of 23°C; however, this temperature was set when the first specimens could to feed exogenously. This means that stage FF occurred shortly after this and was dependent on the incubation temperature. The effect of incubation temperature persist after the temperature has been changed. Galloway et al. (1998) conducted incubation of *G. morhua* eggs at three temperatures, and after hatching all the larvae were held at a common temperature. The effect of incubation temperature on further development was confirmed as many as five days later. Georgakopoulou et al. (2007) also confirmed that variations in some meristic and biometric characters of the bodies of *Dicentrarchus labrax* (L.) that had developed during the embryonic and larval periods at two different temperatures were maintained for several weeks after the fish had been held at a common temperature. Thus, it can be assumed in the current study of common carp and grass carp that the temperature at which incubation and much of the compensatory development phase occurred had a greater impact on the timing of the first exogenous feeding than did the short time during which the larvae with inflated swim bladders were held at the common temperature of 23°C.

After the larvae hatch from the egg envelopes, the rate of yolk sac resorption increases rapidly because of the change of environment and increased activity (Kamler 2008). This is positively correlated to temperature, but only as long as it is within the range of those tolerated, and is the highest at the optimal temperature (Jaworski and Kamler 2002). These authors also reported that resorption begins to slow above the optimal temperature. In addition to survival, they consider the rate of yolk utilization as one of the indicators of the optimal temperature. Since most yolk sac resorption happens during the compensatory development phase, it is very likely that the shorter this phase is in a given species, the closer the temperature is to the optimal. The benefits of shortening the compensatory development phase stem from shortening the time during which the yolk is used less efficiently. Kamler et al. (1998) confirmed this in *Ch. nasus* larvae following hatching.

During development from fertilization to yolk sac resorption, oxygen consumption by *Oncorhynchus mykiss* (Walbaum) was greater at higher temperatures in individuals that were at the same age in days (Kamler and Kato 1983). However, these authors confirmed that the shorter development time at higher temperatures reduced the energy costs of achieving a certain stage. As reported by Ozernyuk (1985), the oxygen con-

sumption required to go through a certain developmental interval is lowest at the optimal temperature. The energy costs of development are lower within the optimal temperature range, and they begin to increase at higher temperatures (Kamler 1992); thus, at optimal temperatures development is not only rapid, but it happens at the lowest cost. This is advantageous from behavioral and energetic points of view alike.

The compensatory development phase (Ha-FF) in common carp was the shortest (and lasted far a similar time) in experiments IIC and IIIC at temperatures of 28 and 32°C (Fig. 3). This could indicate that these are in the range of optimum temperatures for development. Differences in the rate of development from fertilization to the first exogenous feeding (Fe-FF) between these two experiments stems from the difference in the lengths of the embryonic period (Fe-Ha). With grass carp, in both experiments subsequent stages (Ha, SB, FF) were attained more quickly as temperature increased at its full scope. To summarize, the optimum temperature for development in common carp is 28-32°C, while in grass carp it is 32°C.

4.5. INFLUENCE OF TEMPERATURE ON GROWTH

The influence of temperature on growth rate is a well-known phenomenon. As Jones (2002) stated, temperature, along with food, is the fundamental factor influencing growth. This has been confirmed by Peňáz et al. (1983) in *T. tinca*, Laurila et al. (1987) in *C. carassius*, Opuszyński et al. (1989) in *C. carpio* and *Hypophthalmichthys molitrix* (Val.), Wolnicki and Kossakowski (1991) in *Leuciscus idus* (L.), Wang and Eckmann (1994) in *Perca fluviatilis* L., Weltzien et al. (1999) in *Scophthalmus maximus* (L.), Myszkowski et al. (2002) in *B. barbus*, and Wolnicki (2005) in *Vimba vimba* (L.).

As an individual grows, the food it can consume is more and more diversified, thus its chances of growing more quickly are increased (Kamler and Kato 1983). Simultaneously, with size it is less likely to fall victim to predators (Fuiman 1994), and with size larvae becomes more resistant to hunger (Wolnicki and Opuszyński 1988, Fuiman 2002). Larvae that develop at higher temperatures are usually smaller at the moment of hatching. Although Pepin et al. (1997) reported an example of a positive correlation between temperature and the length of hatching *G. morhua* larvae, this did refer to the lower limit of temperature tolerance (at a range of –1°C to 7°C). Smaller larva size at hatching at higher temperatures has been confirmed by, among others, Kinne and

Kinne (1962) in *Cyprinodon macularius* Baird & Girard, Peňáz et al. (1983) in *C. carpio*, Wang and Eckmann (1994) in *P. fluviatilis*, Huuskonen et al. (2003) in *S. alpinus*, Ojanguren and Braña (2003) in *Salmo trutta* L., and Jordaan et al. (2006) in *G. morhua*. This length differentiation in larvae hatching after incubation at various temperatures becomes less evident during the compensatory development phase. As observed by Jordaan et al. (2006) *G. morhua* that had been incubated at higher temperatures hatched sooner, were less developed, and were smaller. However, by the time they had begun exogenous feeding, their sizes had equalized, which indicates that the smaller individuals grew faster. Length equalization in larvae that had been incubated at various temperatures was noted by the end of yolk sac resorption by Dostatni and Luczynski (1991) in *C. albula*, Kamler et al. (1998) in *Ch. nasus*, Geffen (2002) in *C. harengus*, Hutchinson and Hawkins (2004) in *P. flesus*, Van Eenennaam et al. (2005) in *A. medirostris*, Martell et al. (2005) in *M. aeglefinus*, and Kamiński et al. (2006) in *E. percnurus*. Although in the present study the larvae were not measured at the moment yolk sac resorption was complete, Tables 7 and 8 do indicate that the differences in length between larvae hatched at various temperatures are significantly smaller by the swim bladder inflation stage in both common carp and grass carp.

Growth rate generally decreases as the size of the fish increases (Brett 1979), and this is especially distinct in the first weeks of life (Machaček et al. 1986, Kamler et al. 1987, Wolnicki 2005). Thus, growth indicators like RGR or daily increments in total length (ITL) can only be compared in larvae of similar sizes. The results of two experiments conducted at similar temperatures and with natural food can serve to illustrate how relative growth rate can change as fish grow larger. The daily growth increment in total length (ITL) in *C. carpio*, calculated with data obtained by Szlamińska (1987) at a temperature of 24°C, was 0.51 mm d^{-1} on the seventh day, and 0.41 mm d^{-1} on the fourteenth. In turn, in *A. aspius* reared at a temperature of 25°C, the RGR was 26.75, 23.46, and 19.76% d^{-1} respectively on the tenth, fifteenth, and twentieth day (Wolnicki 2005).

The common carp larvae growth rate (RGR 34.9-42.1% d^{-1}, Table 9) is within the range Wolnicki (2005) reported for the larvae of this same species fed on natural food, while the reported results for grass carp larvae indicate that the results for RGR (25.9-36.3% d^{-1}, Table 10) obtained in the current work are relatively high.

Of all the experiments presented in this work of common carp reared at a temperature of 23°C, the greatest weight and length were attained by those that had been incu-

bated at temperatures of 24 and 28°C (temperature variants C24 and C28, Table 9). Also significant with regard to these variants is the slow growth of the larvae that had been incubated at a temperature of 32°C. A similar slowing down of growth at a temperature of 32°C (in comparison to 28°C) was confirmed by Wolnicki and Korwin-Kossakowski (1993) in *T. tinca* and Wolnicki et al. (2004) and Kamiński (2006) in *E. percnurus*. The largest sizes were attained by the grass carp larvae at 32°C, the highest temperature studied.

Differences in growth rate of larvae incubated at the same temperature in the current experiments could have resulted from the effect of diet and/or parental factors. Wolnicki (2005) maintains that when temperatures are close to the optimum, food (i.e., quality, quantity, and method of feeding) is the deciding factor determining carp larvae growth. Faster growth in both of the studied species in the experiments III in comparison to experiments II could be attributed to the feeding with Artemia nauplii, which has higher nutritional value than Artemia cysts. Even greater differences in weight between larvae fed Artemia nauplii and Artemia cysts than in the current work were reported by Vanhaecke et al. (1990) for common carp and by Wolnicki (1995) for grass carp. The fastest carp growth was noted in experiment IC, which leads to the conclusion that, in addition to possible quality differences among decapsulated Artemia cysts used in experiments I and II, the strong parental effect occurs. The comparison of the growth of the grass carp larvae from two different females from the same thermal and feeding conditions (groups IG24 and IG24$^{\#}$, Table 10) also suggests that parental factors have an influence, as was described earlier in section 4.1.1.

When comparing the growth of larvae originating from various temperature variants, it should be remembered that differences in the final weight and length of the larvae was influenced only by the different incubation temperatures since the rearing temperature was the same for all the larvae. Also noteworthy is the significant acceleration of the moment of first the exogenous feeding of the larvae at higher temperatures. The comparison of the growth results after 14 days of rearing indicated that while the differences between the temperature variants were not great, they were significant. It is worthwhile to compare the differences of larvae of the same age. Since at higher temperatures embryonic and larval development was faster, rearing larvae could begin sooner. The comparison of the sizes of grass carp larvae on the final day of rearing in the group in which rearing was finished last (IIG20) indicated that on this same day of the

study stocking material could be obtained that was nearly fourfold heavier (at temperatures of 20 and 32°C, Table 11), and that this was only due to the higher temperature during the embryonic period and compensatory development phase. After 20 days of rearing at a similar temperature range of 19-31°C throughout the experiment, Wolnicki (2005) obtained *V. vimba* larvae that differed in weight about threefold. Similarly, Machaček et al. (1986) produced *C. carpio* larvae that differed in weight about twofold after 20 days of rearing at the temperatures of 22.5°C and 32.5°C. In the current study, similar results were obtained as a result of applying a temperature difference of 8°C during the embryonic period and compensatory development phase (IIG24 – 63.45 mg, IIG32 – 105.99 mg, Table 11).

The comparison of the rearing results of groups IC20-24 and IC20 illustrates just how strongly temperature can modify growth. Increasing the temperature by only 4°C during the compensatory development phase increased the final larval body weight attained in later rearing by as much as 30% (Table 9). As noted in section 4.4, the utilization of the yolk increases at higher temperatures that do not exceed the optimal range (Kamler and Kato 1983, Kamler 1992). Since development is shorter, and its energetic costs are lower, this might, in effect, result in faster growth during the larval period.

The early development temperature range of 24-28°C, which is optimal for the further growth of common carp larvae, is at a level that is close to the optimal for the growth of many cyprinids, including *E. percnurus* (25°C – Kamiński 2006) and *A. aspius* and *B. barbus* (26°C – Wolnicki and Górny 2003). In his review of the literature, Wolnicki (2005) found that the temperature of 28°C ensures the highest growth rate for larvae of cyprinid fish, including *A. brama*, *Ch. nasus*, *T. tinca* and *V. vimba*. The temperature of 32°C during the early development of grass carp ensured the fastest growth during further rearing; however, since this was the highest temperature studied, the optimal temperature might be even higher.

Based on the results, it can be concluded that the temperature during embryonic development and endogenous feeding leaves a particular imprint on the metabolism of the developing fish. Stroganov (1956) confirmed a phenomenon that had been observed many times previously in poikilothermic animals; at common temperature, fish acclimated to lower temperatures had greater oxygen demands, as compared to those acclimated to higher temperatures. This indicates that the acclimation tempera-

ture can influence further metabolism. Thus, the thermal history can influence not only subsequent development, which Galloway et al. (1998) described in *G. morhua,* Georgakopoulou et al. (2007) in *D. labrax*, and Martell et al. (2006) in *M. aeglefinus*, but also on growth. Martell et al. (2005) confirmed that incubation temperature had a significant and long-term influence on later growth of of *M. aeglefinus* larvae and juveniles reared at a common temperature. Martell et al. (2006) also suggested that the development rates of cells, tissues, and organs is dependent on the temperature at which embryogenesis occurred. They confirmed, among other effects, that the intestine of *M. aeglefinus* developed faster in larvae that has been incubated at higher temperatures, even later at a common rearing temperature. The number and cross-sectional areas of white muscle fibers might also depend on incubation temperature, as was demonstrated in a few marine fish species (Johnston et al. 1998 – *C. harengus*, Galloway et al. 1998 – *G. morhua*). This might be different in freshwater fish. As confirmed by Alami-Durante et al. (1997, 2000) based on comparisons of *C. carpio* larvae in the compensatory development phase, incubation temperatures in the range of 15-28°C did not significantly influence the number of fibers or the size (cross-sectional area) of the white muscles. The authors link this to the significant thermal adaptation ability of carp embryos, and recognize that this species has exceptionally well-developed eurythermal characters. This concurs with the statement by Johnston and Maitland (1980) that species living under conditions with strongly fluctuating daily and seasonal temperatures exhibit significant compensation in metabolic rate that occurs following the thermal adaptation period. Considering that the grass carp is also highly flexible in its adaptive ability, it is reasonable to expect that elevated temperature can be used safely with both species to shorten early development.

Thus, the comparisons conducted indicate that the optimal temperature range for embryonic and early larval development in common carp and that which has a beneficial influence on further larval growth is 24-28°C. With grass carp, the optimal temperature for early development is 32°C, which also has a beneficial effect on subsequent growth. However, determining the optimal temperature will require further study. Although the present data indicate that the growth of common carp and grass carp larvae could be accelerated as a result of high temperature during early development, the detailed study will be required to elucidate mechanism of this acceleration.

4.6. INFLUENCE OF TEMPERATURE ON SURVIVAL

The survival of fish embryos under natural conditions is generally very low. According to Zhukinski (1986), for six species of Cyprinidae (including *C. carpio*), mortality ranges from 27.8 to 99%. Significant numbers also die during the larval period, and only about 5.3% of freshwater fish survive until metamorphosis (Houde 1994). Jones (2002) concluded that only about 1% of freshwater fish survive to sexual maturity. Mortality in marine fish is significantly higher. Houde (1994) reports that only about 0.12% survive to metamorphosis, although this author points out that hatched marine fish larvae are usually smaller than freshwater larvae and their development lasts longer, which prolongs pressure of predators. Causes of mortality other than predation include such factors as the lack of food or poor quality food, diseases, and unsuitable environmental conditions (Houde 2002). The survival of embryos under experimental conditions is, in turn, usually high, especially if conditions are close to optimal. The differences between natural and hatchery conditions are not limited to the obvious ones such as water physicochemical conditions or predation. Although not documented in the literature, one condition that can affect common carp survival is, for example, egg swelling that is weaker under natural conditions than under hatchery ones, which, as noted in section 4.3, might have a significant influence on proper embryonic development.

The results presented in the current work indicate that the survival of carp larvae was very high (80.47-89.33%, cumulated from fertilization to the end of the 14-day rearing period; Table 12), and was similar at all the temperatures studied. Development also proceeded correctly and was without deviation within the studied temperature range (20-32°C). The only sudden drop in survival (of about 9%) was noted at swim bladder inflation in group IIC32. It is possible that larvae might have difficulty inflating the swim bladder at temperatures that are too high, as they do at those that are too low. Non-inflated swim bladders at temperatures that are too low, which was observed in the current study with grass carp, was also described by Kamiński et al. (2006) in *E. percnurus* larvae, and by Trotter et al. (2003) in *Latris lineata* (Forster) larvae at temperatures below and above the optimal.

In a comparison of the results of carp egg incubation at various temperatures, Peňáz et al. (1983) confirmed that the largest percentage of hatched larvae occurred within the temperature range of 15-22.5°C (45.8-79.1%), while at temperatures exceeding 22.5°C

the percentage of deformed individuals increased. In the range of 25-30°C, only 25.6-28% of the hatched individuals were properly developed. It appears that the number of deformed individuals was generally very high in these experiments. Tatarko (1977a) also confirmed increased numbers of deformations in carp that had undergone embryonic development at temperatures of 27 and 30°C. Lowered survival and a greater number of deformations can also occur at temperatures that are too low. The incubation of *C. carassius* eggs (Wiegand et al. 1989) at a temperature of 13°C resulted in lowered survival following hatching (80-90%) and in a significantly higher number of deformities (14-91%) in comparison with that at 22°C (90.6-95.9% and 1.2-2.3%, respectively). In the current study, there were only trace numbers of deformed individuals at all the temperatures. It is plausible that the number of deformities is related more to the origin of the eggs than to the thermal conditions of incubation, especially if these are close to optimal. This is confirmed by the results attained by Hansen and Falk-Petersen (2001). In the case of *A. minor*, mortality and the number of deformed embryos were independent of temperature and similarly high in the progeny of the same females. Kjørsvik et al. (1990) suggested that in marine species the simplest egg quality indicator might be the symmetry of the blastomeres formed at early cell division. Avery and Brown (2005) maintain, however, that about 40% of larvae produced from unsymmetrically divided eggs continued to develop normally. Perhaps, in temperatures that are divergent from optimal, the mortality of larvae developing from such eggs increases at both the upper (Tatarko 1977a, Peňáz et al. 1983) and lower temperature ranges (Wiegand et al. 1989).

Carp eggs reacted to sudden temperature changes at differences of just 6°C (from 22°C to 28°C, group IVC28). This change had an adverse impact on the survival of embryos, and lowered it by 12-15% in relation to groups IVC20 and IVC24, when temperature changes were of just 2°C. Rapid temperature changes at this state of development of 10°C (group IVC32) resulted in the death of practically all of the embryos. For the sake of comparison, temperature changes of 9°C at a rate of 3°C h^{-1} did not have an impact on the survival of *C. carassius* embryos (Wiegand et al. 1989). Tanck et al. (2000) studied the reaction of juvenile *C. carpio* to rapid changes in temperature of 7, 9, and 11°C occurring in one hour and concluded that fishes could revert to the state prior to the changes; however smaller and younger individuals reacted stronger. Similarly stronger reactions were observed in marine fish species, as they rarely encounter great

temperature fluctuations. Bunn et al. (2000) have concluded that the eggs of most saltwater fish can tolerate temperature differences of about 6°C; they do, however, indicate that the embryos of these fish are more sensitive when they are in the cleavage phase.

Grass carp survival after hatching is usually about 70% (after incubation in Weiss jars; Antalfi and Tölg 1975). These authors noted temperatures from 18-20°C and higher than 28°C to have an adverse effect on egg survival. Vovk (1974) confirmed survival below 70% at temperatures lower than 22.5°C and above 25.5°C with lethal levels below 17°C and above 30°C. The cumulative survival achieved in the current experiments after incubation and the 14-day rearing period exceeded 60% (Table 13), this can be viewed as high enough to declare the 24-32°C temperature range as appropriate for incubating grass carp eggs.

In hatcheries where eggs are incubated on a large scale, any factor that reduces mortality is critically important. At higher temperatures, development is more synchronized, which is significant for technical reasons, especially at hatching. For example, the number of days that passed between the hatching of 5% and 95% of *Ch. nasus* individuals at temperatures of 10, 13, 16, and 19°C was 10.6, 5.6, 3.1, and 2.8, respectively (Kamler et al. 1998). Rechulicz (2001) noted that in *L. idus* embryos incubated at optimal temperature the hatching gland cells (HGCs) are the largest. Presumably, this is linked to a greater amount of hatching hormone being released that either makes egg envelopes digestion easier or quicker, which can shorten hatching time. Under hatchery conditions, the high density of as yet non-swimming larvae, including dead ones, crowded on the bottom provide good conditions for the growth of mold. Saprolegnia will not develop at temperatures above 30°C (Olah and Farkas 1978), which undoubtedly lowers mortality of the larvae that are in the compensatory development phase. Seeking optimal temperatures for development in a range that is higher than the one applied to date is, thus, justified, especially since Wolnicki (2005) confirmed that also a significant portion of the Cyprinidae early growth studies have been conducted at temperatures lower than the optimum for growth.

The results of common carp survival indicate that all of the temperatures studied with in the 20-32°C range are appropriate for early development. The appropriate temperature range (among those studied) for embryonic grass carp development was between 24°C and 32°C.

4.7. CHOOSING THE OPTIMAL TEMPERATURE

The primary goal of producing stocking material is to obtain larger individuals in a shorter period of time (Kamler et al. 1998). As Fuiman (1994) stated, larval size has a significant influence on losses to predators, and it is indeed predators that in addition to oxygen availability, have the greatest impact during early ontogenesis on the survival of embryos and larvae (Kryzhanovski 1949). Since high temperatures in the viable range shorten development time and accelerate growth, thus limiting losses caused by predation and periods of starvation (Kamler et al. 1998, Jones 2002), the usefulness of applying high temperatures is obvious. While it is true Fuiman et al. (1998) noted that higher temperatures increase the developmental rate more than they do the growth rate, they still hasten the moment when the larvae begin exogenous feeding. In effect, this provides them with the opportunity of attaining larger sizes in a shorter time. This is why shortening the compensatory development phase and accelerating growth is actually a method for lowering fish mortality.

As was mentioned earlier, the most difficult phase in the life history of fish may well be the compensatory development phase, which begins after hatching and lasts until the first exogenous feeding. Shortening this phase, speeding growth, and greater larval survival are considered to be the fundamental criteria for choosing the correct hatchery incubation temperature. Figure 7 presents the overall impact temperature during early development had on the length of the compensatory phase and on the survival and body weight achieved during the 14-day rearing period.

The optimal thermal range is different for each of the parameters. The most appropriate range for common carp survival is 20-28°C; however only in one experiment (IIC) did the temperature of 32°C lower it in a significant way. For grass carp, the range was shifted toward the higher temperature (24-32°C), while that of 20°C was decidedly inappropriate. In terms of growth, the optimal range for common carp was 24-28°C, and for developmental rate it was 28-32°C. In grass carp the optimal temperature for both growth and development was 32°C. While all three parameters indicate that the optimal temperature for grass carp is 32°C, the situation is not as clear with common carp. The range of optimal temperatures for growth and development overlap (24-28°C and 28-32°C, respectively). Growth in experiment IIC was faster at a temperature of 28°C, and in experiment IIIC at 24°C. The length of the compensatory developmental

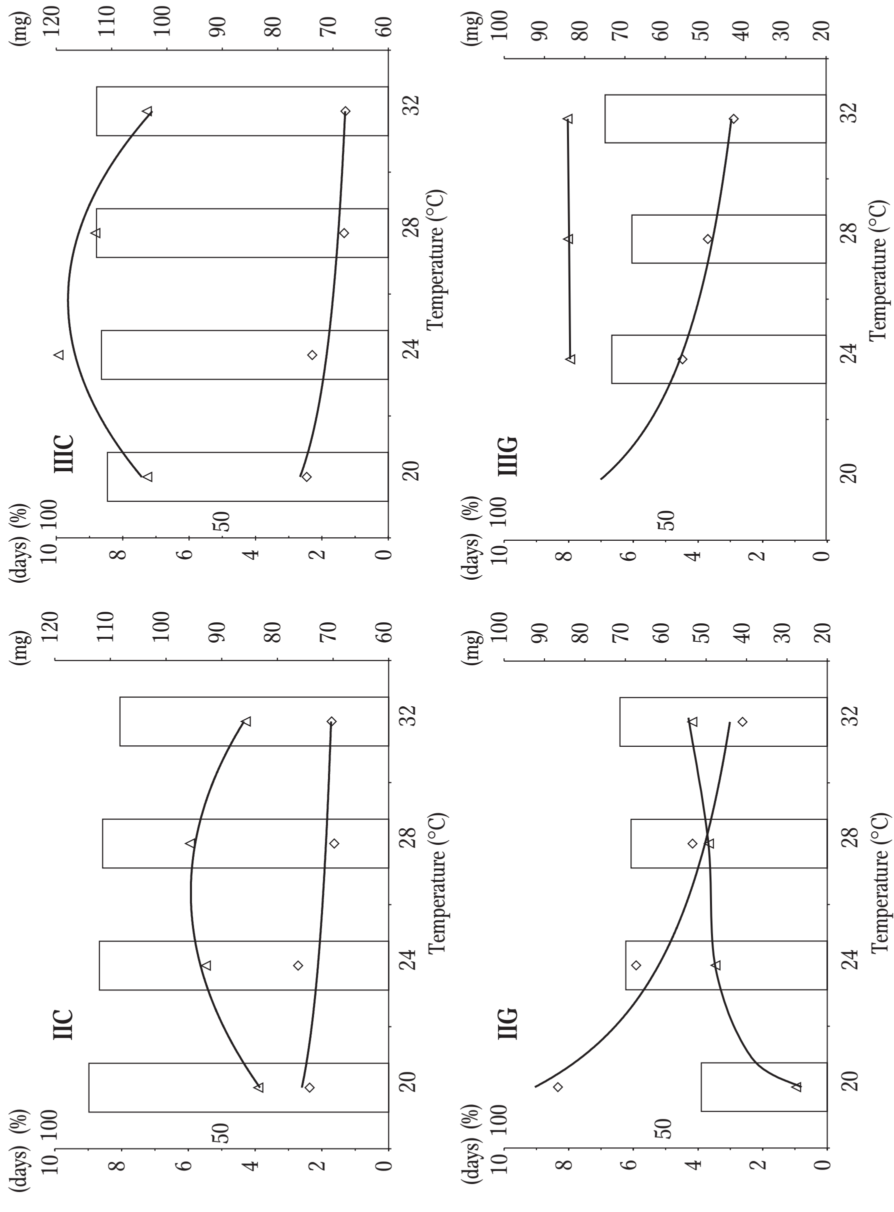


Fig. 7. Comparison of the influence of temperature on length of the compensatory development phase (◇ – days) and survival (columns – %), and weight (△ – mg) of common carp larvae (IIC and IIIC) and grass carp larvae (IIG and IIIG) after the 14-day rearing period.

phase was similar at temperatures of 28 and 32°C, thus, it is safe to assume that raising the temperature to 32°C did not produce the desired effect, and, additionally, this temperature reduced survival in one of the experiments (group IIC32). Thus, the optimal temperature for common carp is somewhere between 24 and 28°C.

Quality indicator q, which was determined by Kolman (1975) and used in previous studies (Kamler et al. 1982, Żuromska and Markowska 1984), was applied to determine the optimal temperature for the early larval development of common carp and grass carp. It was calculated as the mean of the quality indicators calculated for three parameters: growth rate during the compensatory development phase and survival and body weight after the 14-day rearing period (Fig. 8). The results of the comparisons for the grass carp indicate that the temperature of 32°C is the best of those studied, while that for common carp is 26°C for experiment IIC and 28°C for experiment IIIC. Bearing in mind that the shape, and thus, the apex, of the dome curve, is dependent on both the temperature range and number of temperature levels (Kamler 2008), and that four temperature variants of 4°C each were performed within the framework of the experi-

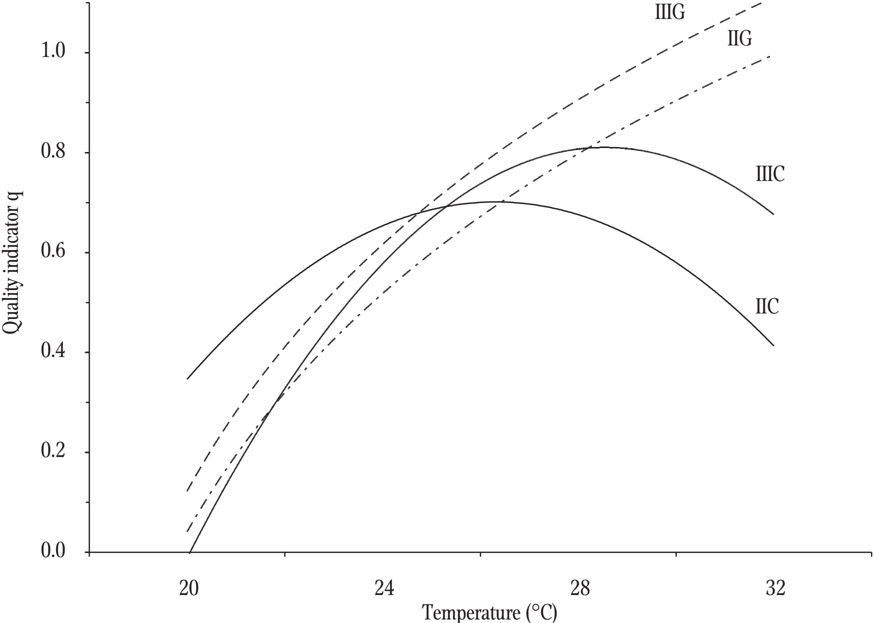


Fig. 8. Comparison of the effects of different incubation temperatures on common carp and grass carp using the quality indicator. A higher value indicates a higher evaluation.

ments, it is possible that the optimal temperature lies somewhere between those presented in Fig. 8. Without this certainty, the experiments conducted provide the basis for designating the temperature range of 26-28°C as the optimal for common carp.

The results of the comparisons indicate that it is indeed possible to accelerate common carp and grass carp larval development and to increase their subsequent growth rates by increasing the temperature of early development (i.e., from fertilization to the first exogenous feeding). The application of higher egg incubation temperatures might produce measurable biological and economic advantages by reducing mortality and accelerating larval growth, and by shortening the production cycle of stocking material. With lower energy costs and a shorter stocking material production time, the economic advantages might be the most significant. This, however, requires conducting detailed comparisons.

5. CONCLUSIONS

5.1. ISSUES IN EARLY DEVELOPMENT

1. Numerous developmental stages, described precisely and unambiguously, were determined to be the easiest to compare and objective developmental elements.
2. The new name proposed for the developmental phase between hatching and the first exogenous feeding, which is most frequently referred to as either the “free embryo phase” or the “yolk-sac larva phase”, is the “compensatory development phase”. This name does not require declaring if the hatched individual is considered as an embryo or a larva.
3. In addition to ensuring survival and growth, shortening the compensatory development phase should be one of the criteria employed when choosing the optimal temperature for development.
4. It is suggested to unify the divisions of early development by modifying the currently used classifications of embryonic (E1-E9) and larval (L1-L6) steps. The modified designation of the final embryonic steps during the compensatory development phase can be referred to from now on as E9/L0, or E8/L0 and E9/L01. Thanks to the dual designation of “embryonic/larval”, this division will be able to be applied by a greater number of researchers, which, in turn, will facilitate the flow of information and the comparison of development studies.

5.2. POSSIBILITIES OF INFLUENCING GROWTH RATE THROUGH INCUBATION TEMPERATURE

1. The thermal history of the early development (from fertilization to the first exogenous feeding) of common carp and grass carp has a significant influence on the further development and growth of larvae. Raising the temperature during early development (Fe-FF) resulted in faster development and growth in the subsequent larval period that took place at a common lower temperature.
2. Water temperatures within the range of 26-28°C during the early development of common carp embryos ensures optimum results during further rearing; while for grass carp the optimal temperature for early development is 32°C.
3. Increased temperature following hatching and during the compensatory development phase accelerates further growth of carp larvae, but to a lesser extend than did a higher temperature applied from the beginning of embryonic period.

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7. SUMMARY

The first aim of the thesis was to attempt to systematize terminology referring to early fish ontogenesis based on an analysis of the literature and observations of the embryonic and larval development of common carp and grass carp (Table 2). Hatching fish are viewed by some researchers as embryos and by others as larvae. The use of these terms, which stems from varied approaches to early developmental biology, hampers communication and understanding among those writing on this topic. Depending on the convictions of the researcher describing it, the developmental phase following hatching is referred to variably as the “free embryo phase” or the “yolk-sac larva phase”. The current work proposes two changes that will enable the proponents of these two theories to apply one common system for describing ontogenesis. The disputed phase from hatching to the first exogenous feeding is referred to as the “compensatory phase of development” (Figs. 1, 2). During this phase, the hatched individual, whose state of development varies depending on the influence of environmental conditions, must achieve locomotor independence by the inflation of the swim bladder with gas. Next, it must achieve a developmental state that permits it to attain energy independence, which means consuming and digesting exogenous food. Thus, regardless of its initial state, the individual must reach the subsequent crucial point after hatching through its own development. The term “compensatory phase of development” does not describe whether the individual is an embryo or a larva, which means that it is acceptable to proponents of either theory. The second important modification regards the division of the embryonic (E1-E9) and larval (L1-L6) steps, which have long been in use and are still used currently (Peňáz 2001). The present work proposes to supplement the names of the steps after hatching, considered in this division to be embryonal (E), with symbols referring to larval development (L). This means that if hatching occurred at step E8 (as in common carp), the subsequent step would be referred to as E9/L0. If, however, hatching occurred at step E7 (as in grass carp), then the subsequent step would be referred to as E8/L0, and the next as E9/L01. The names of later steps, which refer to larvae, would remain unchanged (Table 15). This modification would allow disseminating this clear and convenient division that has been in use for many years, while also making easier the comparison of results described by proponents of various approaches to the concepts of “embryo” and “larva”.

The second aim of the thesis was to attempt to verify if the temperature during early ontogenesis (from fertilization to the first exogenous feeding) influences subsequent growth and development. The development of common carp and grass carp was studied at four temperatures (20, 24, 28, and 32°C), and then further development, growth, and survival were studied at the common temperature of 23°C. It was confirmed that the duration of development (τ) was shortened at higher temperatures (Tables 3, 5 and Fig. 3). It was also observed that increased temperature hastened embryonic development more in grass carp (Table 4 and Fig. 5) than it did in common carp (Table 6 and Fig. 6). As reported in the literature, the equalization of differences in hatched larva length during the compensatory phase of development was confirmed in both species (Tables 7, 8). Temperature during early ontogeny was confirmed to have an influence on subsequent growth and development during rearing at a common temperature of 23°C (Tables 9, 10). It was also confirmed that by applying various temperatures during the early ontogenesis of grass carp (from 20°C to 32°C), it is possible, at the same moment following fertilization, to obtain larvae that are nearly fourfold larger, at weights of 27.72 and 105.99 mg, respectively (Table 11). Using the duration of the compensatory phase of development and survival and growth (Fig. 7), the temperatures during early ontogenesis which are the optimal for subsequent rearing of the larvae of both species were determined. The optimal temperature for later common carp growth was 26-28°C during early ontogenesis, while the most appropriate of the studied temperatures for grass carp was 32°C (Fig. 8).

8. STRESZCZENIE

Pierwszym celem pracy była próba usystematyzowania nomenklatury wczesnego rozwoju dokonana na podstawie analizy literatury i przeprowadzonych obserwacji przebiegu rozwoju zarodkowego i larwalnego karpia i amura białego (tab. 2). Wykluwający się organizm uważany jest przez niektórych za zarodek, przez innych za larwę. Używanie takich określeń, wynikające ze zróżnicowanego podejścia do biologii wczesnego rozwoju, utrudnia komunikację i porozumiewanie się osób o tym piszących. Faza rozwoju następująca po wykluciu, zależnie od przekonania piszącego, nazywana jest „free embryo phase" lub „yolk-sac larva phase". W pracy zaproponowano dwie zmiany pozwalające na stosowanie przez zwolenników obu teorii wspólnego systemu opisującego rozwój. Sporną fazę od wyklucia do pobrania pierwszego pokarmu nazwano „fazą wyrównawczą rozwoju" (rys. 1 i 2). W czasie trwania tej fazy wykluty osobnik, rozwinięty w różnym stopniu zależnie od wpływających na rozwój czynników środowiska, musi osiągnąć samodzielność lokomotoryczną przez napełnienie powietrzem pęcherza pławnego. Następnie osiągnąć on musi stan rozwoju pozwalający na uzyskanie samodzielności energetycznej, czyli na pobranie i trawienie pokarmu zewnętrznego. Tak więc, bez względu na stan początkowy, dojść on musi w swoim rozwoju do kolejnego po wykluciu punktu przełomowego. Nazwa „faza wyrównawcza rozwoju" nie określa, czy chodzi o zarodek czy larwę, jest więc do przyjęcia przez przedstawicieli obu teorii. Druga ważna modyfikacja dotyczy znanego od dawna i wciąż aktualnego (Peňáz 2001) podziału na etapy rozwoju zarodkowego (E1-E9) i larwalnego (L1-L6). Nazwy etapów po wykluciu, uważanych w tym podziale za zarodkowe (E), proponuje się uzupełnić dodając do nich symbole etapów rozwoju larwalnego (L). Oznacza to, że jeśli wyklucie ma miejsce w etapie E8 (jak u karpia), to kolejny etap nosiłby nazwę E9/L0. Jeśli zaś wyklucie następuje w etapie E7 (jak u amura białego) to kolejny etap nazywałby się E8/L0 a następny E9/L01. Dalsze etapy, funkcjonujące w tym podziale jako larwalne, miałyby nazwy niezmienione (tab. 15). Modyfikacja taka pozwoliłaby upowszechnić istniejący od dawna, wygodny i klarowny podział, ułatwiłaby też porównywanie wyników opisywanych przez zwolenników różnego podejścia do pojęć „zarodek" i „larwa".

Drugim celem pracy była próba sprawdzenia, czy temperatura wczesnego rozwoju (od zapłodnienia do pobrania pierwszego pokarmu) wpływa na wzrost i rozwój w późniejszym czasie. Rozwój karpia i amura białego badano w czterech temperaturach (20, 24, 28 i 32°C) a następnie dalszy rozwój, wzrost i przeżywalność we wspólnej temperaturze 23°C. Stwierdzono skrócenie czasu trwania rozwoju (τ) ze wzrostem temperatury (tab. 3 i 5 i rys. 3). Zaobserwowano, że wzrost temperatury bardziej przyspiesza rozwój zarodkowy amura białego (tab. 4 i rys. 5) niż karpia (tab. 6 i rys. 6). Potwierdzono dla badanych gatunków znaną z literatury zależność zmniejszania się zróżnicowania długości wyklutych larw w czasie trwania fazy wyrównawczej rozwoju (tab. 7 i 8). U larw obu gatunków stwierdzono wpływ temperatury wczesnego rozwoju na tempo dalszego wzrostu i rozwoju podczas podchowu w jednej wspólnej temperaturze 23°C (tab. 9 i 10). Stwierdzono, że przy zastosowaniu różnych temperatur wczesnego rozwoju amura białego (od 20°C do 32°C), w tym samym czasie od zapłodnienia uzyskać można w podchowie niemal czterokrotnie większe larwy, o masie odpowiednio 27.72 i 105.99 mg (tab. 11). Posiłkując się czasem trwania fazy wyrównawczej rozwoju oraz przeżywalnością i wzrostem (rys. 7) ustalono temperatury wczesnego rozwoju optymalne dla późniejszego podchowu larw obu gatunków. Dla karpia jako optymalny dla późniejszego wzrostu uznano zakres temperatur wczesnego rozwoju 26-28°C, natomiast dla amura białego najodpowiedniejszą z badanych okazała się temperatura 32°C (rys. 8).