The rate of early development in perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.) at different temperatures

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The time (minutes from fertilization) when perch and ruffe embryos reached the 4 and 16 blastomere stage (τ_{II} and τ_{IV}, respectively) was recorded, and the duration of one synchronous cell cycle $\tau_0 = (\tau_{IV} - \tau_{II})/2$ and the rate of development $R = 1/\tau_0 \times 10^{-4}$ was calculated at different temperatures. R was higher for ruffe than for perch. The range of optimal temperatures for early development (determined from $\log \tau_0$-temperature plots according to Mazin and Dettlaff, 1985) was 8–18°C ($R_{opt} = 13$°C) for perch and 9–21°C ($R_{opt} = 15$°C) for ruffe. R and R_{opt} in perch and ruffe are higher than in salmonids and coregonids, and less than in warm-water cyprinids and cobitids.

1. Introduction

The effect of temperature on the duration of embryogenesis has been investigated in a variety of fish species (e.g. Mednikov 1982, Herzig & Winkler 1986, Blaxter 1988). However, the timing of development in these studies has been expressed in absolute time units or in fractions of the period from fertilization to hatching. Such data are hard to compare between species, due to dependence of developmental rate on temperature and other environmental factors (e.g. Carlson & Siefert 1974, Ignatieva 1976, 1979, Gudilov 1977, Mednikov 1982, Dettlaff *et al.* 1987), and wide inter- and intraspecific variation of the hatching stage (Dettlaff *et al.* 1987, Yamagami 1988).

The duration of one mitotic cycle during the period of synchronous cell divisions (τ_0) has proved to be an appropriate unit to compare the duration of development processes at different temperatures in all animal species undergoing synchronous cell divisions during their early development (Dettlaff & Dettlaff 1961, Dettlaff *et al.* 1987). The τ_0 value at different temperatures has been determined for several teleost species (Ignatieva & Kostomarova 1966, Ignatieva 1974, 1976, 1979, Gorodilov 1990, Saat 1991, Saat & Ignatieva 1991, Saat & Veersalu 1996). Percids have not been investigated in this respect.

The aim of the present study was to determine the τ_0 values at different temperatures for perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.), and to compare the rate of development with fish which reproduce at different temperatures.
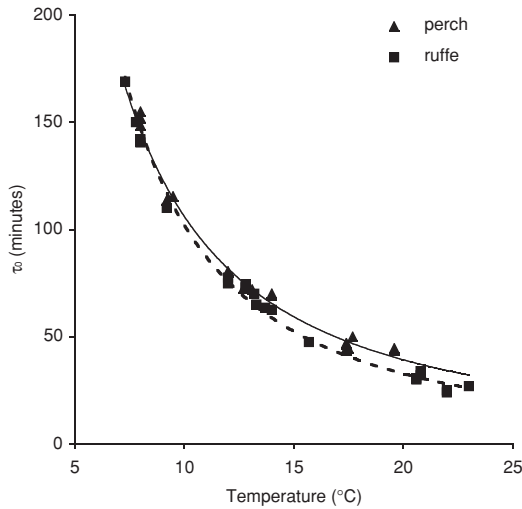
Fig. 1. The values of $\tau_0 = 0.5(\tau_{IV} - \tau_{II})$ (min) in perch and ruffe at different temperatures.

2. Materials and methods

Mature perch and ruffe were collected from spawning grounds (Pärnu Bay, Estonia) in May–June 1994 and 1995 using gill nets or commercial perch traps. Eggs and sperm were stripped from living specimens. Fertilization was usually performed at the temperature of the further experiment using the water taken from spawning grounds (salinity 3–5 ppt). However, in some of 1995 experiments, eggs fertilized at 13.4°C were transferred at various temperatures before the first cleavage. Experiments were carried out in 95×15 mm glass or plastic Petri dishes (each containing approximately 200–300 or 300–400 eggs of perch or ruffe, respectively) placed in the refrigerator or in a thermostated room at various temperatures between 6.0 ± 0.2 and $22.0 \pm 0.2°C$ (perch), or 6.0 ± 0.2 and $24.0 \pm 0.2°C$ (ruffe) (see Fig. 1). Every 3–5 min (depending on temperature and developmental stage), samples of eggs were preserved in Ringer's solution containing 5% acetic acid and observed under a dissecting microscope. Acid makes the cleavage furrows clearly visible within a few minutes. The time (minutes from fertilization) when approximately 10% of developing embryos reached the 4 and 16 blastomere stage (τ_{II} and τ_{IV}, respectively) was recorded (Ignatieva 1979). The τ_0 values in teleosts can be calculated as $\tau_0 = (\tau_{IV} - \tau_{II})/2$.

As the period from the fertilization to the first cleavage (τ_I) in teleosts usually lasts approximately $2\tau_0$, a less laborious method ($\tau_0 = \tau_{IV}/5$) can also be used (Ignatieva 1979). The range of optimal temperatures for early development was determined according to Mazin and Dettlaff (1985), and the rate of development was expressed as $R = 1/\tau_0 \times 10^{-4}$ (min^{-1}) (Neyfakh 1988).

All the data are expressed as mean $\pm$ *S.D.* Descriptive statistics and the coefficients of regression lines were calculated using the EXCEL 5.0 program package.
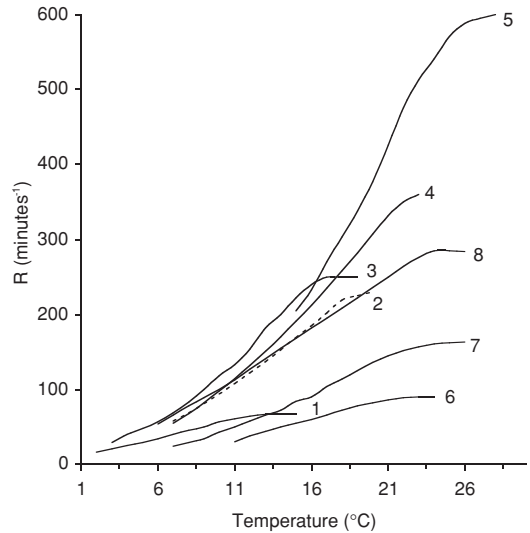

Fig. 2. The rate of development (R, min^{-1}) at different temperatures in some lower vertebrates: 1) rainbow trout *Oncorhynchus mykiss* (Walb.), 2) perch, 3) pike *Esox lucius* L., 4) ruffe, 5) gibel carp *Carassius auratus gibelio*, 6) river lamprey *Lampetra fluviatilis* (L.), 7) newt *Triturus vulgaris* L. (Dettlaff 1975), 8) sturgeon *Acipenser gyldenstaedti* Brandt (Dettlaff 1975). Other sources: see Table 2.

3. Results

3.1. The duration of one cleavage cycle (τ_0) and the rate of development (R) in perch and ruffe

The τ_0 values were calculated as $\tau_0 = (\tau_{IV} - \tau_{II})/2$ and $\tau_0 = \tau_{IV}/5$. A comparison of the two methods showed that the second method usually results in significantly higher τ_0 value, due to longer τ_I (over $2\tau_0$) in perch and ruffe (Table 1).

Table 1. Comparison of two methods of τ_0-value calculation in perch and ruffe (mean $\pm$ *S.D.*). *n*, number of experiments.

Species	Temp. °C	*n*	τ_0 calculated as		*t*-test *P*
			$(\tau_{IV} - \tau_{II})/2$	$\tau_{IV}/5$	
Perch	8.0	3	152 ± 3	163 ± 5	< 0.05
	9.2	3	114 ± 1	122 ± 1	< 0.01
	17.4	4	45 ± 2	54 ± 1	< 0.001
Ruffe	8.0	2	141 ± 2	142 ± 1	> 0.05
	12.0	4	75 ± 2	81 ± 3	< 0.05
	22.0	2	25 ± 1	27	> 0.05

The $\tau_0 = (\tau_{IV} - \tau_{II})/2$ exhibit an exponential curve when plotted against temperature (Fig. 1) which gives $\tau_0 = 2903T - 1.4367$ ($r^2 = 0.985$) for perch and $\tau_0 = 4464.7T - 1.6407$ ($r^2 = 0.989$) for ruffe (T, temperature in °C).

The rate of development (R) in ruffe is higher than in perch (Table 2). The middle parts of R curves show linear temperature dependence (Fig. 2); this zone approximately corresponds to the zone of optimal temperatures for early development (cf. 3.2. and Table 2). Within this linear zone, R can be calculated from equation $R = aT + b$ (Table 2).

3.2. Threshold and optimal temperatures for early development

Eggs of both species showed normal cleavage in a rather wide temperature range, between approximately 6–8 and 20°C in perch, and 8 and 21–22°C in ruffe. No cleavage of perch eggs was observed at 22°C, and eggs from some females showed significantly reduced cleavage rate at 6–8°C. Eggs of ruffe did not divide at 6.0 and 24.0°C, and showed reduced cleavage rate at 7.3 and 23.0°C (Table 3).

In semilogarithmic coordinates ($\log\tau_0$ versus temperature) the τ_0 curves are divided into three parts. The intermediate exponent corresponds to the zone of optimal temperatures for early development (Mazin & Dettlaff 1985). The range of optimal temperatures for early development was approximately 8–18°C for perch and 9–21°C for ruffe (Fig. 3), and the midpoint of this zone (T_{opt}) was at 13 and 15°C, respectively.

The rate of development at T_{opt} (R_{opt}) in perch and ruffe was 141 and 196 min^{-1}, and the maximum rate of development (R_{max}) was 230 and 417 min^{-1}, respectively (Table 2).

4. Discussion

4.1. Rate of development

The temperature dependence of τ_0 in perch and ruffe (Fig. 1) is similar to that in other lower vertebrates (cyclostomes, chondrostean and teleost fish, amphibians; Dettlaff 1975, Ignatieva 1979, Dettlaff *et al.* 1987, Saat & Tambets 1990).

R_{opt} and R_{max} in perch and ruffe are distinctively higher than in cold-water teleosts (*Salmo*,

Table 2. The optimal temperature (T_{opt}) for early development and the rate of development (R) in some teleost species. R_{opt}, R at T_{opt}; R_{max}, the maximum R.

Species	Optimal temp. range	T_{opt}	Regression $R = aT + b$ T (range)	a	b	R_{opt}	R_{max}	Source
Salmo salar		5[2]	3–8	3.2	5.2	21		Gorodilov 1990
Salmo trutta fario[1]	3–10	6.5	3–14	3.9	2.7	28	59	Ignatieva 1979
Oncorhynchus mykiss[1]	3–9	6	2–12	5.1	5.2	36	67	Ignatieva 1975
Coregonus peled[1]	3–8	5.5	2–12	4.8	8.6	42	67	Ignatieva 1979
C. nasus[1]	1–8	4.5	1–10	4.3	11.5	35	53	Ignatieva 1979
C. lavaretus baeri[1]	4–8	6	3–9	6.1	9.5	46	71	Ignatieva 1979
Esox lucius[1]	4–14	9	7–16	20.1	− 79.5	101	246	Ignatieva 1979
Clupea harengus membras	1–12.5	7	1–12	16.4	7.5	111	246	Saat & Veersalu 1996
Misgurnus fossilis[1]	10–20	15	12–22	23.1	− 162.4	184	345	Kostomarova 1975
Perca fluviatilis	8–18	13	8–18	15.4	− 59.6	141	230	Present study
Gymnocephalus cernus	9–21	15	9–20	20.9	− 116.2	196	417	Present study
Cyprinus carpio	16–26	21	16–26	37.3	− 406.5	378	571	Ignatieva (pers.comm.)
Carassius auratus gibelio	15–26	20.5	14–24	37.82	− 370.02	405	606	Saat & Ignatieva 1991
Cobitis (triploid biotype)	16–24	20	16–24	32.46	− 380.99	268	513	Saat 1991

[1] The τ_0 values were obtained from τ_0-temperature curves; otherwise empirical data
[2] Zhukinskii 1986
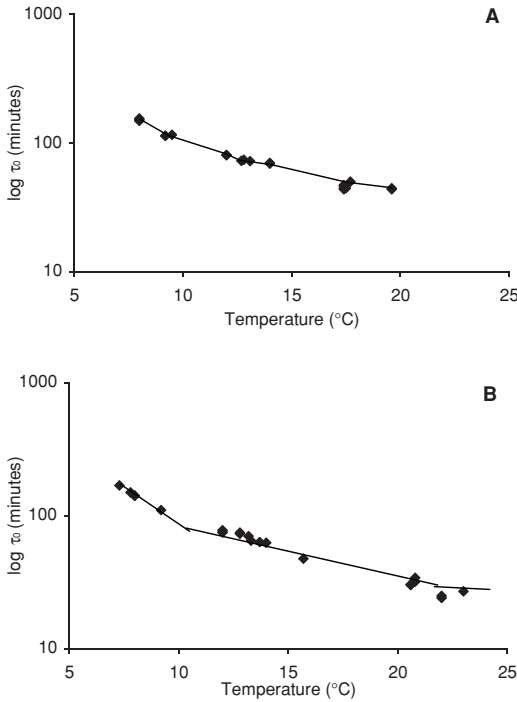
Fig. 3. The $\log\tau_0$-temperature plots for perch (A) and ruffe (B).

4.2. Threshold and optimal temperature for early development

The lower lethal temperature for perch embryos is 6°C, and the upper lethal temperature approximately 22–24°C (Swift 1965, Kokurewicz 1969, Guma'a 1978, Hoestlandt & Devienne 1980). These are in accordance with the present study. These limits are obviously determined by the so-called critical (or more sensitive) developmental periods. Nikiforov (1939) suggests that the critical periods in perch (as well as other spring-spawning species) include cleavage, beginning of gastrulation and organogenesis. Between these critical periods, perch embryos can develop even at 28–32°C (Nikiforov 1939).

T_{opt} for early development in teleosts in temperate zone is from 4.5–6.5°C in salmonids and coregonids, and 20–21°C in warm-water cyprinids (Table 2). Perch and ruffe share an intermediate position and can be classified as temperate-water fish, together with for example pike *Esox lucius* L., Baltic herring *Clupea harengus membras* L., mud loach *Misgurnus fossilis* (L.) (Table 2). The range of optimal temperatures for early development in cold-water fish (from 4°C in *Coregonus lavaretus baeri* to 7°C in *C. nasus* and *Salmo trutta fario*, see Table 2; mean ± *S.D.* 5.8 ± 1.3, *n* = 5) is less than for temperate-water fish (10–12°mean 10.7 ± 1.0°C, *n* = 5) or warm-water fish (carp

Coregonus) normally reproducing at temperature below 10°C, and lower than in warm-water fish (*Cyprinus, Carassius, Cobitis*) (Table 2). R_{opt} and R_{max} as well as the slope *a* of the regression line $R = aT + b$ in teleost species listed in Table 2 show very strong linear correlation with T_{opt}. The corresponding regressions can be given by:

$T_{opt} = 19.9R_{opt} - 76.7$ ($r = 0.960$, $P < 0.001$, $n = 14$),
$T_{op} = 31.8R_{max} - 95.4$ ($r = 0.965$, $P < 0.001$, $n = 13$),
and $T_{op} = 1.94a - 4.87$ ($r = 0.954$, $P < 0.001$, $n = 14$).

However, the temperature dependence of *R* in teleosts differs from that of other lower vertebrates. Generally, the rate of development in teleosts (having meroblastic eggs and partial cleavage) is higher than in animals with holoblastic eggs and total cleavage (chondrosteans, lampreys, and amphibians) reproducing at similar temperature (Saat, unpublished, and Fig. 2). T_{opt} for embryos of river lamprey *Lampetra fluviatilis* (L.) is 16°C (Saat & Tambets 1990), or slightly higher than for ruffe, but R_{opt} and R_{max} for lamprey embryos are several times lower (Fig. 2).

Table 3. Percentage of normal cleavage in perch and ruffe at different temperatures

Species	Temp. °C	Cleavage No.	%	% of control[1]
Perch	6.0	12/197	6	7
	8.0	121/204	59	70
	8.0	84/196	43	48
	9.5	208/227	92	101
	17.4	164/188	87	98
	19.6	201/237	85	102
	22.0	0/187	0	0
Ruffe	6.0	0/340	0	0
	7.3	85/325	26	30
	20.6	318/342	93	101
	23.0	144/308	47	51
	24.0	0/304	0	0

[1]Controls were reared at 13.4°C (close to T_{opt}); 86.6 ± 3.6 and 83.4 ± 1.6% normal cleavage in perch and ruffe, respectively

Cyprinus carpio L., gibel carp *Carassius auratus gibelio* (Bloch), spined loach *Cobitis* sp. in Table 2; 8–11°C, mean 9.6 ± 1.5°C, *n* = 3).

Optimal temperatures for perch embryogenesis have been estimated at 14°C (Privolnev 1935 cited in Nikiforov 1939, Kokurewicz 1969, Guma'a 1978), 9–16°C (T_{opt} = 12.5°C) (Meshkov & Zavyalova 1976), or between 8 and 18–20°C (T_{opt} = 13–14°C (Hoestlandt & Devienne 1980). These data are in good accordance with our estimate (8–18°C T_{opt} = 13°C) and correspond to the ordinary spawning temperatures of perch (7–15°C; Zhukinskii 1986).

Ruffe is an intermittent spawner with prolonged spawning season during spring and summer (Koshelev 1984). Accordingly, T_{opt} for ruffe embryos (15°C) is higher than that of perch. The normal range of spawning temperatures for ruffe is 11.6–18°C (Hokanson 1977); the middle of this range (T_{opt}) is 15°C which corresponds to our estimate.

The temperature ranges specified above are applicable for early development. Optimal and lethal temperatures for further development in temperate-zone fish are usually shifted to higher temperature, and the range of temperatures supporting the normal development is broader. Data for perch larvae and fry (Craig 1987) confirm this conclusion.

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