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Olin, Mikko

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The maternal effects on Pikeperch (*Sander lucioperca*) larvae depend on temperature

Mikko Olin[1] | Matti Kotakorpi[2] | Leena Nurminen[3] | Jukka Ruuhijärvi[1]

[1]Natural Resources Institute Finland, Helsinki, Finland

[2]Biological Research Stations, University of Helsinki, Helsinki, Finland

[3]The Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Correspondence

Mikko Olin, Natural Resources Institute Finland, PO-Box 2, 00791-FIN Helsinki, Finland.
Email: mikko.olin@luke.fi

Abstract

We studied the influences of female pikeperch (*Sander lucioperca*) length and growth (i.e., maternal effects) on the length of hatched and starved larvae as well as on larval starvation resistance in two different temperature conditions (mean temperatures 13.2 and 17.9°C). The data included fertilised eggs and reared larvae from 21 individuals caught during the spawning season from eutrophic Lake Pyhäjärvi in Finland. The length of the hatching larvae was dependent on female size but also on water temperature and on the potential energy the female had invested on reproduction. Maternal effects seemed to also influence the timing of larvae growth, and larvae that were large at hatching grew less on mere yolk sac reserves, and vice versa. Female length had a positive effect on the larval starvation resistance but only under cold conditions. The results suggest that higher temperature might reduce the advantage the larvae from large females get for starvation resistance.

KEYWORDS
climate change, female characteristics, larval growth, larval size, reproduction, starvation resistance

1 | INTRODUCTION

Maternal effects denote that the genotype or phenotype of a mother affects the phenotype of offspring (Wolf & Wade, 2009). In large-bodied piscivores, large/old females usually produce high-quality offspring in large numbers (Kamler, 2005). Quite recently, maternal effects have been proposed as being important drivers in fish population dynamics. For example, larval survival in walleye (*Sander vitreus*) has been found to increase with female age, and the maximum reproductive rate is much higher when old females are abundant in the population (Venturelli et al., 2010). Similarly, retention of large-sized individuals in Eurasian perch (*Perca fluviatilis*) populations can mitigate the adverse effects of fishing (Olin et al., 2017). Despite the increasing awareness of importance, maternal effects have often been neglected in fish stock assessment. One reason

may be that to date, species-specific maternal effects have not been identified for all exploited species. One of these species is pikeperch (*Sander lucioperca*) for which maternal effects on egg dry mass has only recently been documented (Olin et al., 2018). Earlier, maternal effects have been documented for several other percids (Johnston & Leggett, 2002; Johnston et al., 2012; Lauer et al., 2005; Olin et al., 2012), as well as for other piscivores (Berkeley et al., 2004; Kotakorpi et al., 2013).

Pikeperch is a greatly sought-after species in professional and recreational fisheries throughout its range in Europe (Kestemont et al., 2015). This is particularly true for Finland, where pikeperch is the third most abundant freshwater species in fisheries, with a total catch of 4,324 tons in 2018 (of which commercial 22%, recreational 78%, coastal 19%, inland 81%, Natural Resources Institute Finland, 2019). Owing to this popularity and the development of recirculation

aquaculture systems, pikeperch production with intensive aquaculture has also increased in Europe (Policar et al., 2019).

As a result of global warming, water temperature is forecasted to increase and water transparency to decrease in boreal aquatic ecosystems (Elo et al., 1998; Mooij et al., 2007), and both of these trends are beneficial for pikeperch as they enhance growth and condition (Lappalainen et al., 2003). In southern parts of the area of distribution however, the higher temperature might have adverse effects on pikeperch reproduction, for example, due to lower oxygen concentration in warmer water (Ruuhijärvi et al., 2010). In Finnish lakes, the simulated rise in epilimnetic water temperature during summer compared with the baseline period 1961–1990 is 2, 3–4 and 4–6°C in 2020, 2050 and 2090 respectively, and the maximum increase will occur in May (Elo et al., 1998) during the spawning time of pikeperch. Algal turbidity and dissolved organic carbon concentrations have increased in lakes, and the trend is prone to continue as the global warming proceeds (Mooij et al., 2007; Roulet & Moore, 2006). At present, pikeperch catches in commercial fishing are rapidly increasing further north the Finnish coastline (Natural Resources Institute Finland, 2019). Females reach sexual maturity at a total length of 40–46 cm and at the age of 4–7 years (Lappalainen et al., 2003; Olin et al., 2018). The variation in maturation size and age depends, for example, on growth rate and body condition (Olin et al., 2018). The egg dry mass increases with female size and age, body condition and the relative growth rate depending on environmental conditions (Olin et al., 2018). Therefore, consequences can be expected on the population parameters as well as on the maternal effects of pikeperch stocks in the northern parts of the distribution range.

Generally, larvae that hatch from heavy eggs of large females have a higher tolerance against starvation (Berkeley et al., 2004; Kotakorpi et al., 2013; Olin et al., 2012). To date, this maternal effect has not been documented for pikeperch. Furthermore, the role of temperature on maternal effects is largely unknown. Thus, in the present study, to mimic the consequences of the forecasted rise in water temperature, we explored the effect of female size on the starvation resistance of pikeperch larvae in two different temperature conditions. We hypothesised a positive effect of female size and a negative effect of temperature on starvation resistance. In addition, we studied the effects of maternal size and growth rate on hatched and starved larval length in two different incubation temperatures. We expected a positive effect of both maternal size and growth rate as well as temperature on larval length.

2 | METHODS

Pikeperch were captured with fyke nets during 9–20 May 2012 at spawning grounds in the southern part of Lake Pyhäjärvi (N 6812111, E 3314751), Lempäälä, Finland. Lake Pyhäjärvi is 121.6 km^2, eutrophic (mean total phosphorus was 32 µg L^{-1} during growing season), shallow (mean depth 5.5 m) and has high humic content (water colour ca. 60 mg Pt L^{-1}, syke.fi/avoindata). The fish were sexed, measured for total length (TL, to the nearest 5 mm) and

weighed (to the nearest 10 g). For females (total $n = 21$, Table 1), age and back-calculated growth were determined from scales by 1–2 expert readers using a modified version of the Fraser–Lee method (Ruuhijärvi et al., 1996). In pikeperch, scale determination is found to be a robust method to estimate both age and back-calculated growth (Lappalainen et al., 2009; Ruuhijärvi et al., 1996). We used a relative latest TL increment (L_{ri}), based on back-calculated growth data, as a proxy for the potential energy to be invested on reproduction, as in many fish species, the reproductive investment depends on the amount of energy stored during the preceding summer (McBride et al., 2015). We calculated L_{ri} as standardised residuals of the TL increment (L_i) during the growing season preceding the sampling year in relation to female TL ($L_i = 13.682 - 0.143123613 \times L$, $r^2 = 0.646$, $p < .001$).

We used pikeperch farming methods described in Ruuhijärvi and Hyvärinen (1996) to produce spawned fertilised eggs: one female pikeperch (mean of females = 66 cm TL, minimum–maximum = 47–84 cm TL) was kept together with one to five males (mean of males = 45 cm TL; minimum–maximum = 30–65 cm TL) in a net cage (2 × 2 m) in the spawning area. No hormonal stimulation was used as it may have an effect on the results. Each cage contained an artificial spawning nest (coconut fibre tufts, 50 × 50 × 20 cm) with an extra, loose tuft in the middle of the nest. The spawning took place during 16th to 20th of May in 2012, with an average water temperature of 11.7°C (minimum–maximum = 11–13°C) in the net cages. The cages were inspected every evening at 21:00–23:00 to see if the females had spawned. After the spawning, the fish were released, and the nests were removed. The extra tuft in the artificial spawning nest was used as the sample of fertilised egg. The egg samples were transported under moist and cool (<15°C) conditions to the laboratory within 5 h from emptying the cage. To obtain the mean egg fresh and dry weight, a subsample of 24–130 eggs was taken and weighed immediately, dried at 60°C for 24 h and re-weighed (to nearest 0.1 mg). The egg results were used in Olin et al. (2018) as a part of the larger data set of pikeperch reproductive characteristics.

For incubation, each egg sample (tuft) was partitioned to 4–6 weighed (0.1 mg) subsamples, and 1–3 subsamples were subjected to cold and warm water temperature treatments (mean ± SD water temperature 13.2 ± 0.5 and 17.9 ± 0.4°C respectively). The two temperatures represented the assumed present (ca. 13°C) temperature and the predicted higher (ca. 18°C, in 2090) mean water temperature during pikeperch spawning period. The egg subsamples were incubated in a divided water circulation system (one division for each temperature) in 5-L sieve pails (63 cm^2 sieve with 0.2 mm mesh size). The sieve pails were held in flow-through tubs (1–7 pails/tub), and the order of the pails was randomised twice a day to balance the conditions. Water temperature was maintained with thermostat-controlled electrical heating elements kept in separate containers. Water temperature (0.5°C accuracy) was measured every hour with automatic temperature loggers (iBCod - Alpha Mach). Illumination of the incubation room was continuous during the incubation to prevent the possible light rhythm-caused differences between the subsamples. The developmental status of eggs was visually checked

TABLE 1 Characteristics of 21 female pikeperch (from smallest to largest) and the properties of their larvae under two temperature regimes (T = 13.2 or 17.9°C)

Length (cm)	Weight (g)	Age (y)	L_i (cm)	L_{ri}	Egg w (mg)	T (°C)	First hatch (T sum)	Last hatch (T sum)	Hatched length (mm)	Starved length (mm)	Survival (T sum)
46.5	1070	5	7.7	0.5	0.224	13.2	97.4	191.5	4.13	5.58	66.4
						17.9	75.0	168.5			
52.0	1450	7	8.4	1.8	0.140	13.2	83.9	208.3	4.50	5.26	274.3
						17.9	57.5	165.2	3.92	4.63	260.6
53.5	1680	7	4.6	−1.1	0.142	13.2	75.0	208.7	4.47	5.17	288.3
						17.9	60.5	187.0	4.04	4.87	202.3
54.0	1670	7	5.5	−0.4	0.110	13.2	83.9	112.6	4.44		
						17.9	59.9	150.1	4.10	4.80	246.8
54.5	1580	7	6.0	0.1	0.138	13.2	83.4	6.8	4.53	5.62	265.6
						17.9	74.0	169.0	4.34	4.82	231.7
56.0	1850	7	5.0	−0.5	0.131	13.2	85.9	128.0	4.30	5.09	219.9
						17.9	75.2	168.7	4.34	4.81	231.5
57.0	1960	8	6.3	0.7	0.150	13.2	84.1	192.1	4.52	4.94	200.4
						17.9	59.4	169.3	4.12	4.58	254.8
57.5	1800	9	2.5	−2.4	0.117	13.2	83.4	6.6	4.15		
						17.9	75.3	168.8	4.26	4.57	268.1
61.0	2190	7	7.1	1.8	0.141	13.2	86.6	153.5	4.50	5.03	240.6
						17.9	58.1	167.2	4.01	4.82	247.7
62.0	2560	9	3.8	−0.8	0.171	13.2	115.5	130.4	4.58		
						17.9	80.2	166.6	4.27		
63.5	2610	8	5.4	0.7	0.158	13.2	86.5	180.4	4.28	4.89	292.5
						17.9	62.5	167.1	4.30	4.45	245.6
65.5	3000	9	4.9	0.5	0.178	13.2	84.1	192.4	4.53	5.00	260.2
						17.9	59.6	167.2	4.10	4.77	232.8
70.0	3890	13	2.4	−1.0	0.114	13.2	84.0	207.8	4.27	4.73	224.0
						17.9	57.5	166.6	4.17	4.54	265.6
72.0	3940	10	3.0	−0.3	0.137	13.2	97.3	181.5	4.40	5.15	306.5
						17.9	63.1	153.6	4.16	4.89	257.5
75.0	4390	11	3.9	0.7	0.208	13.2	96.5	8.4	4.54		
						17.9	92.3	126.2	4.66		
77.0	4850	12	1.5	−0.9	0.167	13.2	72.5	180.6	4.20	5.01	294.7
						17.9	77.3	166.0	4.44	4.83	241.6
77.5		14	1.5	−0.9	0.181	13.2	44.3	209.3	4.10	5.16	298.1
						17.9	57.4	165.7	4.04		213.1
80.0	5100	13	2.9	0.5	0.147	13.2	83.3	6.8	4.33	4.91	266.5
						17.9	74.3	168.5	4.05	5.05	302.0
81.0	6240	15	2.9	0.7	0.163	13.2	97.3	165.6	4.61	5.08	293.6
						17.9	74.9	169.1	3.94		56.8
82.0	6480	14	2.6	0.5	0.199	13.2	82.7	180.2	4.51	5.16	311.4
						17.9	60.6	183.9	4.32	4.77	246.5
84.0	7100	15	1.6	0.0	0.192	13.2	95.3	177.5	4.47	4.99	294.1
						17.9	72.5	184.8	4.23	4.61	227.6

Abbreviations: Egg w, average egg dry weight; first/last hatch, temperature sum (degree days) when first/last larvae hatched; hatched length, mean TL of the first hatched free embryos; L_i, latest total length (TL) increment during the growing season preceding the sampling; L_{ri}, standardised residuals of the linear regression between L_i and female TL; starved length, mean TL of the starved larvae; Survival, survival time of the last larvae with yolk sac reserves.

twice a day until the hatching. To calculate the temperature sum (degree days) of incubation, the onset of hatching (first hatched larvae) and the end of hatching (no eye-spotted eggs observed) were detected. In an ecological perspective, hatching is a crucially important event, and thus, hatching was used as a boundary between the embryonic and larval periods, even though from an ontogenetic point of view, newly hatched pikeperch are free embryos until they start exogenous feeding (Urho, 2002), which was prevented in this study.

After the onset of hatching, larvae from each incubation subsample were randomly sampled to measure individual TL (0.01 mm). The water in the pail was gently mixed, and the larvae were collected by a pipette to a white plastic spoon and counted. Apparently damaged larvae were not measured. In total, 62 subsamples from 21 females produced an adequate number of larvae for TL measurements (n = 5–35 per female). The samples for starvation resistance experiments were then taken with a similar procedure. Subsamples of each female in each temperature treatment had to be pooled, and larvae from two females were excluded, to ensure an acceptable number of larvae (n > 5) per experiment. Thus, there were 6–161 larvae per female from 19 females in the starvation experiments.

The newly hatched pikeperch larvae were exposed to a no-food condition to determine whether female TL and age influenced the survival time of larvae in possession of sole yolk sac reserves (starvation resistance). This was done in two different temperatures (13.4 ± 0.6 and 17.9 ± 0.5°C) to mimic the effects of the forecasted higher water temperature on incubation conditions of pikeperch eggs in lakes. The larvae in the starvation resistance experiments were kept in 0.7-L plastic containers with a 25-μm sieve cover under similar light and temperature conditions as during the incubation period. The water in the containers was sieved (mesh size = 25 μm) and boiled (10 min.) to exclude any external food items in the containers. Dead larvae (based on immobility when disturbed) were counted and removed, and the container locations were randomly mixed once a day during the experiment. Dead larvae were conserved in 60% alcohol for later TL measurements (0.01 mm, n = 5–87 per experiment). The experiment was terminated when the last larva was starved. The oxygen concentration (7.5–10.0 mg L^{-1}) was measured at the end of the experiment to exclude the possibility of oxygen depletion.

We analysed the maternal effects on the onset of hatching, and on the length of newly hatched and starved larvae with separate mixed linear models (SAS 9.4) including temperature treatment (warm = 18°C *vs* cold = 13°C), incubation time (temperature sum at the onset of hatching), female length and L_{ri} (and all interactions) as dependent variables, and female individual as a random factor. We used a stepwise reducing procedure starting from the 3-level interaction model, and the best model was chosen according to corrected Akaike's information criteria (AICC). Type 3 *F*-tests and t-tests were used as significance tests for fixed effects and t-tests as significance tests for random factor. When there were newly hatched or starved larval length results of more than one subsample per female, these results were pooled before analyses. The incubation time and length of starved larvae were not normally distributed

and were ln-transformed. We used survival analysis (Cox regression, SPSS 15.0) to analyse the maternal effects on larval starvation resistance. In the analysis, temperature sum was used as the time variable, death of each larvae as status variable and female length as continuous covariate. As the effect of time variable was different depending on the temperature treatment, assumption of the constant hazard ratio was not fulfilled, and a time-dependent covariate (temperature sum × temperature treatment) was included in the model (Cox, 1972).

3 | RESULTS

First larvae hatched on average in 68 degree days (minimum–maximum: 57–92) and in 4.8 calendar days (3–6) under warm conditions, and on average in 86 (44–116) degree days and 7.3 calendar days (4–9) under cold conditions (Table 1). The female characteristics did not have a statistically significant effect on the onset of hatching (Type 3 *F*-tests: p > .1). On average, the larvae hatched at a larger size under cold conditions (4.40 mm, 4.10–4.61 mm) than under warm water (4.19 mm, 3.92–4.66 mm; Type 3 *F*-test for temperature treatment: p < .001 in Table 2). The average effect of incubation time on the TL of hatching larvae was positive, especially under warm conditions (Type 3 *F*-test for temperature treatment × incubation time interactions: p < .001 in Table 2). Depending on the relative latest length increment (L_{ri}), temperature conditions and incubation time during the experiment, female TL had either a positive or negative effect on the TL of hatching larvae (Figure 1a–c, Table 2). At the average L_{ri} and incubation time, the TL of hatching larvae decreased with female TL under warm conditions but slightly increased with female TL under cold conditions (Type 3 *F*-test for female TL × L_{ri} × temperature treatment interaction: p = .001 in Table 2). In females with high L_{ri}, the aforementioned effects were similar but stronger. At low L_{ri} however, the effects were opposite, and the TL of larvae decreased with female size under cold and increased under warm conditions. The incubation time mainly affected the magnitude of the previous effects (Appendix 1). However, when the incubation time was low, the negative effect of female TL on larval TL under warm conditions changed to slightly positive (at average L_{ri}) or disappeared (at high L_{ri}).

Female TL, L_{ri}, temperature conditions and incubation time all affected the TL of starved larvae but not in the same way as on the TL of the hatching larvae (Figure 1d–f, Table 3). In cold water, the TL of starved larvae was higher (mean = 5.11 mm; min–max = 4.73–5.62 mm) than that in warm water (4.74 mm, 4.45–5.05 mm; Type 3 *F*-test for temperature treatment: p < .001 in Table 3) in the end of the experiments. At the average L_{ri} and incubation time, the effect of female TL on the TL of starved larvae was negative under cold conditions but positive under warm conditions (Type 3 *F*-test for female TL × L_{ri} × temperature treatment interactions: p < 0.001 in Table 3). High L_{ri} strengthened and low L_{ri} weakened the aforementioned effects on the TL of starved larvae. Similarly, the incubation time mainly affected the magnitude of the previous effects (Appendix 1).

TABLE 2 Mixed lineal model results of the effects of female total length (TL), latest TL increment (L_{ri}), temperature conditions (cold 13.2°C or warm 17.9°C) and incubation time (inc. time, degree days) on hatched larval TL

Effect	Estimate	SE	df	t Value	p > |t|	F value	p > F
Intercept	−18.5650	3.2780	197.0	−5.66	<.001		
Female TL	0.2942	0.0478	215.0	6.15	<.001	11.28	<.0001
T = cold	21.9965	4.6964	508.0	4.68	<.001	21.94	<.0001
T = warm	0.0000						
L_{ri}	−5.3980	3.1318	77.7	−1.72	.089	3.11	.0817
Incubation time	5.3662	0.7810	202.0	6.87	<.001	14.45	.0002
Female TL × T = cold	−0.2847	0.0657	530.0	−4.33	<.001	18.79	<.001
Female TL × T = warm	0.0000						
Female TL × L_{ri}	0.0981	0.0480	92.0	2.05	.044	4.42	.0382
L_{ri} × T = cold	−0.6112	0.2336	98.9	−2.62	.010	6.85	.0103
L_{ri} × T = warm	0.0000						
Female TL × incubation time	−0.0692	0.0114	219.0	−6.09	<.001	11.76	.0008
T = cold × incubation time	−5.1691	1.0755	526.0	−4.81	<.001	23.1	<.0001
T = warm × incubation time	0.0000						
L_{ri} × incubation time	1.3158	0.7483	79.3	1.76	.083	3.09	.0825
Female TL × L_{ri} × T = cold	0.0115	0.0035	133.0	3.33	.001	11.08	.0011
Female TL × L_{ri} × T = warm	0.0000						
Female TL × L_{ri} × incubation time	−0.0239	0.0114	93.5	−2.09	.039	4.37	.0394
Female TL × T = cold × inc. time	0.0675	0.0150	548.0	4.49	<.001	20.12	<.0001
Female TL × T = warm × inc. time	0.0000						

However, when the incubation time was high, the negative effect of female TL on the TL of starved larvae under cold conditions changed to slightly positive at average and high L_{ri}.

In the starvation resistance experiment, the first deaths occurred in 71 degree days (minimum–maximum: 15–224) and in 68 degree days (minimum–maximum: 54–90) under cold and warm experiments respectively. The survival time of pikeperch larvae was longer in the cold experiment than that in the warm experiment (Figure 2, Wald test for temperature effect: $p < 0.001$ in Table 4). The model-estimated maximum survival time for larvae from median-sized females was 322 degree days under cold conditions, whereas it was 302 degree days under warm conditions. The maternal effects deviated under cold and warm conditions: Under cold conditions, larvae from large females had the longest survival time, whereas under warm conditions, the effect of female length on larvae survival time was very small but negative (Wald test for female TL effect: $p < 0.001$ in Table 4).

4 | DISCUSSION

Our study showed for the first time that maternal properties affect the TL and starvation resistance of pikeperch larvae, but the effects are adjusted by water temperature and incubation time. Generally, the maternal effects were stronger, both on larval TL and survival, under cold compared with warm conditions. This suggests, also as a novel result, that higher temperature might change the magnitude of maternal effects on juvenile traits in fish. The effects of maternal traits (length and growth rate) and temperature on larval properties (starvation resistance and length) were not only positive as hypothesised, but the effect of female TL on larval traits was significantly dependent on temperature and maternal growth rate.

The results indicated that larvae from large females had the highest potential to grow large at hatching. The high growth potential of the larvae could be due to greater female energy resource allocation to eggs (Olin et al., 2018) and/or to a fast-growing genotype (Kuparinen & Hutchings, 2019; Machiels & Wijsman, 1996). However, this growth potential was more efficiently used in low temperatures as larvae were much larger at hatching under the cold conditions than in warm water. This can be an adaptation to a low food situation in cold weather when energy saving and slower development are beneficial, and the larvae use all the yolk reserves to grow as large as possible before hatching (Laurel et al., 2008). Environmental conditions might change to be more favourable during slow larval development but also large larvae have a wider prey spectrum (Fulford et al., 2006). On the other hand, egg incubation at near to optimal temperatures can lead to increased larval size at hatching in percids, and cold conditions in the present study were closer to the optimum incubation temperature of pikeperch, 12–16°C (Kokurewicz, 1969; Wang & Eckmann, 1994). A prolonged egg stage can also increase the risk of egg predation, and warmer conditions may reduce that risk owing to earlier hatching (Huff et al., 2004; Ivan et al., 2010; Lappalainen et al., 2003; Roseman et al., 1996).
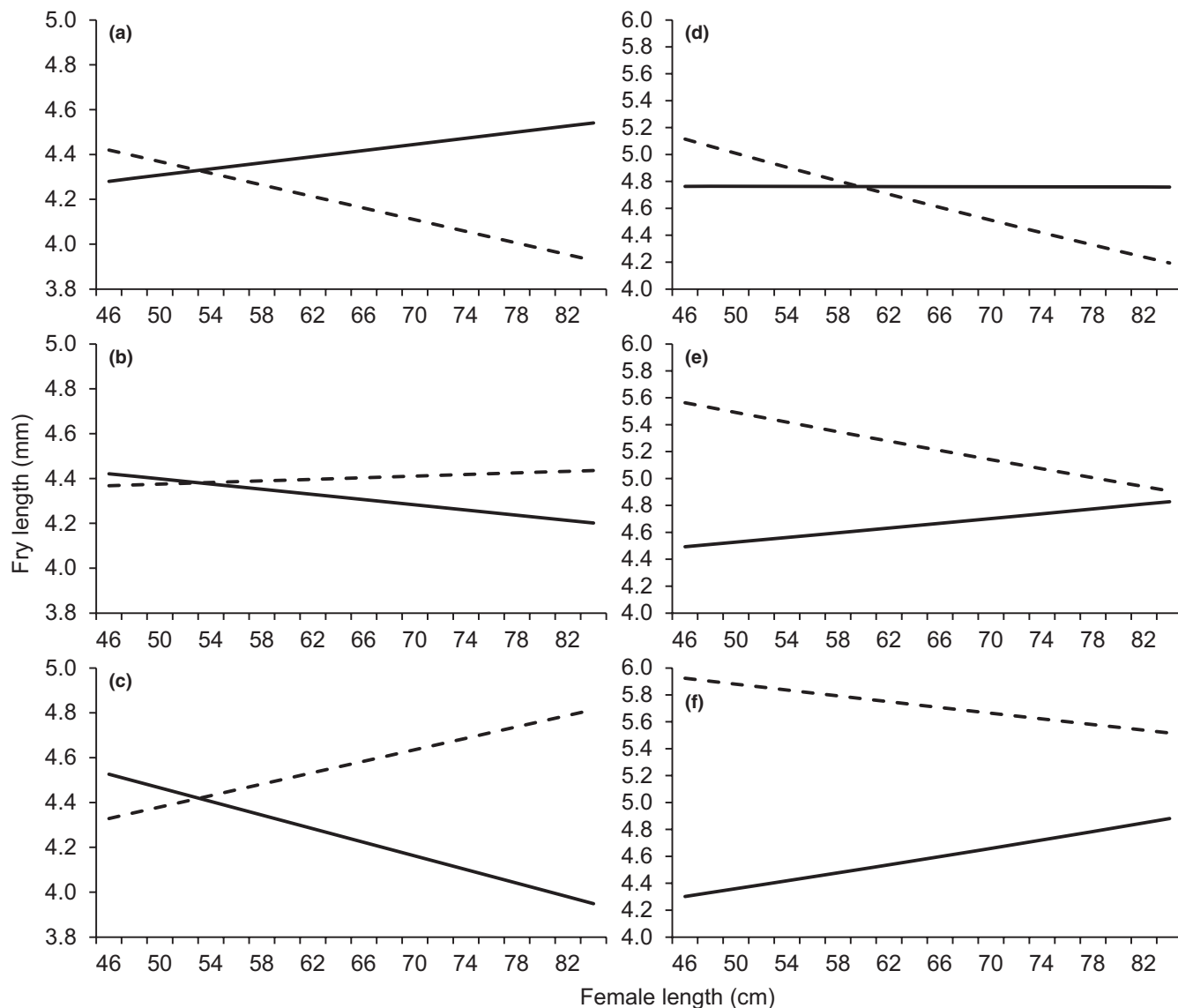
FIGURE 1 Estimated effect of female total length (TL) and the relative latest TL increment (L_{ri}) on first-hatched (a–c) and starved (d–f) larval TL in the two temperatures 13 (dashed line) and 18°C (solid line) and in average incubation time (geometric average of all samples in the two temperature treatments = 76 degree days). The effects are based on the mixed linear models described in Table 2 (a–c) and Table 3 (d–f). L_{ri} is low (lowest observed = −2.378) in panels a and d, average ($L_{ri} = 0$) in panels b and e, and high (highest observed = 1.771) in c and f

Under warm conditions, the TL of hatched larvae was generally smaller. In a warm environment, metabolism is usually high and larvae hatch early, and therefore, relatively little of the yolk sac reserves is consumed before hatching (Konstantinov, 1957; Post, 1990; Quist et al., 2004). For the sake of comparison, larvae of the wild pikeperch population in Tunisia (Ben Khemis et al., 2014) with similar temperature conditions and TL range of females, the larvae hatched at a much smaller size than in the present study (Table 1).

There was substantial variation in the incubation time within the temperature treatments, which was not due to the maternal traits studied. The incubation time had a strong effect on the magnitude of the observed maternal and temperature-related effects, but it did not have a strong directional effect on the observed results. The source of variation in the incubation time remained unclear but may

originate from genetic or paternal influence or other maternal characteristics that were not investigated in this study.

When the experiment was continued in containers without any external food (starvation resistance experiment), the responses in larvae TL were nearly a mirror image of the results of the newly hatched larvae, for example, the larvae that hatched at a small size grew more in the starvation resistance experiment than did larvae that were larger at hatching. It seemed that under warm conditions, larvae from large females with low reproduction investment potential used all their energy reserves to be large at hatching and had no further reserves to grow in the starvation resistance experiment. Whereas larvae from small females with low reproduction investment potential, which hatched at a relatively small size, still had energy reserves to grow larger after hatching in the starvation resistance experiment. These differences in the timing of larval growth

TABLE 3 Mixed lineal model results of the effects of female total length (TL), latest TL increment (L_{ri}), temperature conditions (cold 13.4°C or warm 17.9°C) and incubation time (degree days) on starved larval TL

| Effect	Estimate	SE	df	t Value	p > |t|	F value	p > F
Intercept	4.9276	1.1919	545.0	4.13	<.0001		
Female TL	−0.0472	0.0168	637.0	−2.80	.0052	26.17	<0.0001
T = cold	6.2139	1.7142	1790.0	3.62	.0003	13.14	0.0003
T = warm	0.0000	.	.	.	.		
L_{ri}	0.1121	0.1804	178.0	0.62	.5349	0.94	0.3327
Incubation time	−0.8105	0.2848	547.0	−2.85	.0046	26.79	<0.0001
Female TL × T = cold	−0.0753	0.0233	1511.0	−3.24	.0012	10.48	0.0012
Female TL × T = warm	0.0000	.	.	.	.		
Female TL × L_{ri}	0.0008	0.0009	28.2	0.86	.3955	0.05	0.8257
L_{ri} × T = cold	0.1529	0.0426	544.0	3.59	.0004	12.87	0.0004
L_{ri} × T = warm	0.0000	.	.	.	.		
Female TL × incubation time	0.0113	0.0040	640.0	2.83	.0049	25.81	<0.0001
T = cold × incubation time	−1.3296	0.3930	1775.0	−3.38	.0007	11.45	0.0007
T = warm × incubation time	0.0000	.	.	.	.		
L_{ri} × incubation time	−0.0401	0.0431	249.0	−0.93	.3533	0.86	0.3533
Female TL × L_{ri} × T = cold	−0.0020	0.0006	1151.0	−3.53	.0004	9.19	0.0025
Female TL × L_{ri} × T = warm	0.0000	.	.	.	.		
Female TL × T = cold × inc. time	0.0162	0.0053	1511.0	3.03	.0025	12.46	0.0004
Female TL × T = warm × inc. time	0.0000	.	.	.	.		
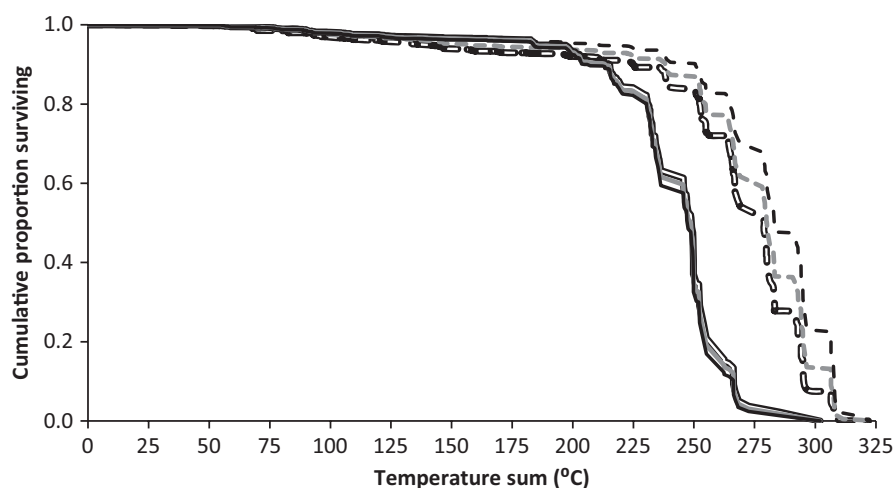
FIGURE 2 Cumulative survival of pikeperch larvae with plain yolk sac reserves according to Cox regression model in the two temperatures 13.2 (dashed lines) and 17.9°C (solid lines). White, grey and black lines represent modelled survival curves of larvae from 52-, 66- and 84-cm females (total length, TL) respectively. The sizes of the females represent the minimum, median and maximum TL of females that produced larvae for starvation resistance experiments

TABLE 4 Cox regression survival analysis of newly hatched pikeperch larvae with female total length (TL) as a covariate in the two temperature conditions (T = 13.2 or 17.9°C)

Variable	β	SE	Wald score	df	p	Exp(β) (CI 95%)
Female TL	−0.007	0.002	14.883	1	<.000	0.993 (0.990–0.997)
Female TL × time-dep. covariate	0.014	0.001	601.483	1	<.000	1.014 (1.013–1.015)
T	1.395	0.110	159.902	1	<.000	4.033 (3.249–5.007)

Note: β = regression parameter, SE of the regression parameter and Exp(β) = odds ratio, that is, change in the estimated survival probability for a unit increase in the predictor (female TL). As the covariate effect of female TL varied with time, a time-dependent covariate was included in the model.

probably reflect acclimation to changes in environmental conditions in relation to growth potential and existing larval energy reserves. In this study, the timing of growth, in addition to the reached length of larvae, differed between the larvae from small and large females. Notably, larvae of greater length can have low mass and shorter larvae can be heavy—a phenomenon observed in Eurasian perch (Heyer et al., 2001; Olin et al., 2012).

The positive maternal effect on starvation resistance was only observed under cold conditions. Larvae from large females grew relatively little but survived longer than larvae from small individuals. Under warm conditions, female size did not affect the survival in the starvation resistance experiment probably because larvae used most of the energy reserves on fast growth. The present results indicate that the forecasted higher temperature can decrease the starvation resistance of pikeperch larvae because the larvae survived a shorter time under warm conditions. Also, the fitness lead of the large individuals can be reduced. Low food conditions might become more frequent if global warming increases the probability of a mismatch between zooplankton community succession and pikeperch larval development (Thackeray et al., 2010).

Pikeperch reproduction is flexible, and populations can acclimate to the warming of the environment and shortening of winters by spawning earlier in the spring. Temperature during the pikeperch spawning time usually varies between 8 and 16°C (Lappalainen et al., 2003). The onset of spawning can vary more than 2 weeks depending on the prevailing temperature, occurring earlier in warm springs (Salminen et al., 1993). However, if the rise in water temperature is specifically high in spring as predicted (Elo et al., 1998), then pikeperch eventually will spawn, and larvae will develop in warmer water than at present. Based on an earlier finding of Schlumberger and Proteau (1996), the temperature at the onset of the spawning was warmer in France (14–16°C) than that in Finland (10–12°C). Specific monitoring of pikeperch spawning times is needed to show whether the spawning takes place earlier than documented in Salminen et al. (1993). Temperatures >20°C, or striking perturbations in water temperature during incubation, can disturb the normal development of percid eggs (Muntyan, 1977; Schneider et al., 2002). Such conditions might be possible in the future spawning times in shallow areas and may decrease survival of pikeperch eggs and larvae.

From the fisheries management perspective, the present study supports existing evidence that retention of large individuals to sustain genetic and phenotypic diversity, which is profitable for the persistence of pikeperch populations. Similar results on the positive effects of female size or age on offspring quality, and the importance of large females have been previously documented in perch (Olin et al., 2012), yellow perch (Heyer et al., 2001), pike (Kotakorpi et al., 2013) and walleye (Venturelli et al., 2010). As several trade-offs in pikeperch reproduction have been reported in this and earlier studies (Olin et al., 2018), a diverse spawning stock most likely increases the population's ability to thrive in more unpredictable conditions. It can be assumed that climate variability is increasing and, in addition to potentially higher summer temperatures, very cold springs are also likely to occur in the future (Elo et al., 1998).

These mechanisms might also explain the suggested variation in the strength of maternal effects over time and populations (Venturelli et al., 2010). As the relative fitness of large individuals was observed to be reduced under warm conditions, it is even more important that fisheries management, when fishery targets large individuals, aims to retain genetic and phenotypic diversity in pikeperch populations.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Mikko Olin https://orcid.org/0000-0003-4240-6669

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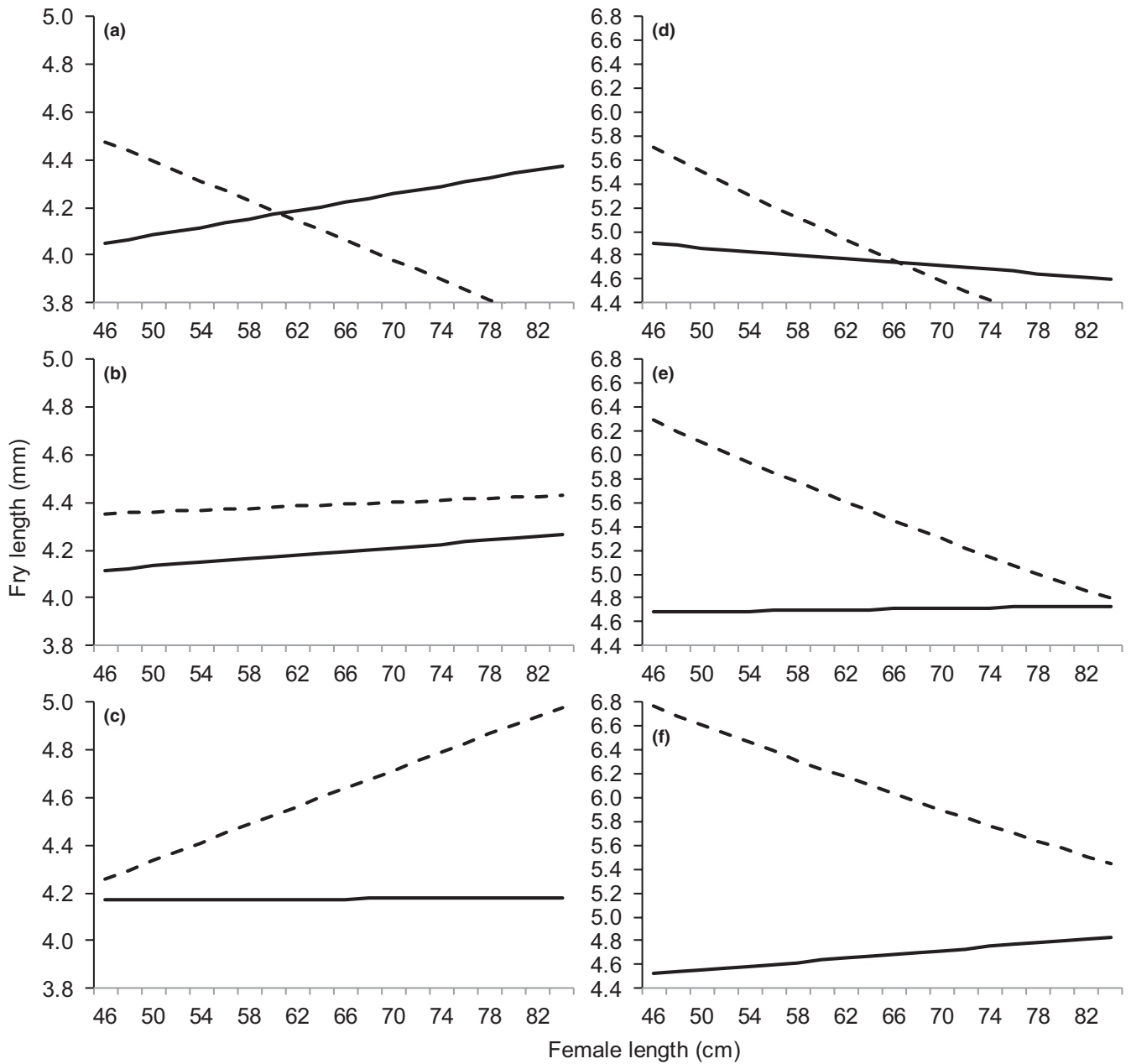

APPENDIX 1

FIGURE A1 The estimated effect of female total length (TL) and the relative latest TL increment (L_{ri}) on first-hatched (a-c) and starved (d-f) larval TL in the two temperatures 13 (dashed line) and 18°C (solid line) and in short incubation time (geometric average of minimum incubation times in the samples in the two temperature treatments = 66 degree days). The effects are based on the mixed linear models described in Table 2 (a–c) and Table 3 (d–f). L_{ri} is low (lowest observed = −2.378) in panels a and d, average (L_{ri} = 0) in panels b and e, and high (highest observed = 1.771) in c and f
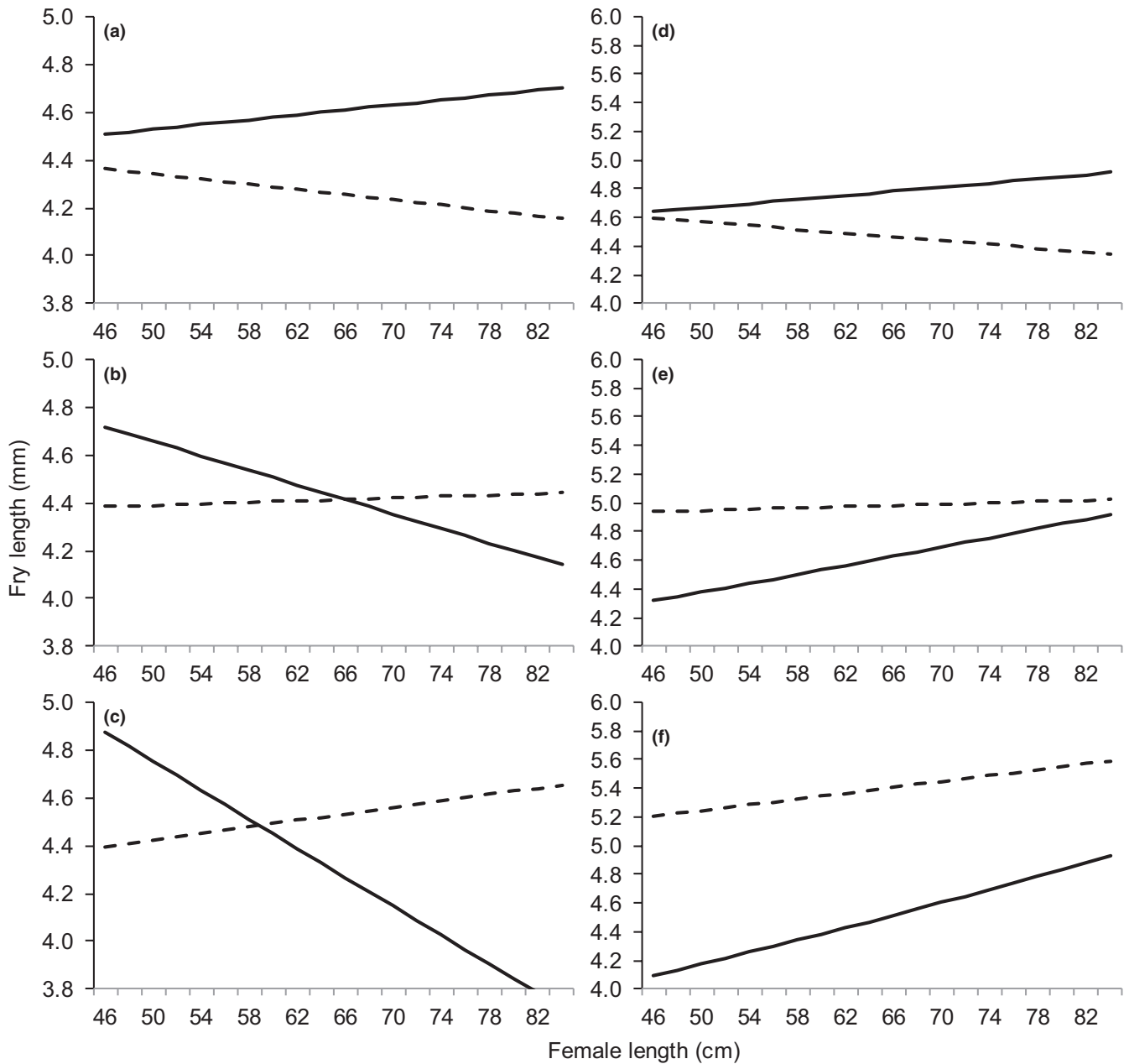
FIGURE A2 The estimated effect of female total length (TL) and the relative latest TL increment (L_{ri}) on first-hatched (a–c) and starved (d–f) larval TL in the two temperatures 13 (dashed line) and 18°C (solid line) and in long incubation time (geometric average of maximum incubation times in the samples in the two temperature treatments = 87 degree days). The effects are based on the mixed linear models described in Table 2 (a–c) and Table 3 (d–f). L_{ri} is low (lowest observed = −2.378) in panels a and d, average (L_{ri} = 0) in panels b and e, and high (highest observed = 1.771) in c and f