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The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts

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ABSTRACT

The present paper describes the growth properties of Atlantic salmon (*Salmo salar*) post-smolts reared at 6, 10, 14 and 18 °C for 12 weeks following transfer to seawater. Growth rate, feed intake, feed conversion efficiency (FCE), and stomach evacuation rate were significantly influenced by temperature and fish size. Highest growth rate was seen in the 14 °C group (1.53% d^{-1}), no differences in growth were seen between the 10 and 18 °C groups (1.35% d^{-1}, 1.29% d^{-1}), and lowest growth observed at 6 °C (0.78% d^{-1}) group. Optimal temperature for growth ($T_{opt}G$) increased with fish size, whereas optimal temperature for feed conversion efficiency (T_{opt}FCE) decreased as fish size increased. The results suggest an optimum temperature for growth of 12.8 °C for 70–150 g to 14.0 °C for 150–300 g post-smolts. Optimum temperature for FCE dropped from 13.4 °C to 11.0 °C for the same size classes. A wide parabolic regression curve between growth, feed conversion efficiency and temperature indicates high temperature tolerance of Atlantic salmon in this size range studied. Highest stomach evacuation rate was seen in the 18 °C group, where the proportion of meal remaining in the stomach decreased from 100 to less than 5% after 24 h of starvation. No differences in stomach evacuation rate were recorded between the 10 and 14 °C groups, whereas a significant delay in stomach evacuation was seen in the 6 °C group. Overall, these findings may have important consequences for optimization of commercial production of Atlantic salmon post-smolts.

1. Introduction

Fish generally show temperature optima for growth and survival (Brett, 1979; Gadomski and Caddell, 1991). These may change with age and size, as juveniles of many species prefer warmer temperatures than adults do (McCauley and Huggins, 1979; Pedersen and Jobling, 1989). Early life stages may also have different optimal temperatures, which may reflect temporal and spatial field distributions (Gadomski and Caddell, 1991; Imsland et al., 1996). Further, the combined effects of size and temperature on growth have been described for several fish species (Brett, 1979; Elliott, 1975; Fonds et al., 1992; Imsland et al., 1996, 2006; Jonassen et al., 1999). A downshift in temperature optimum with increasing size, i.e. ontogenetic shift, has been demonstrated in Atlantic cod *Gadus morhua* L., (Pedersen and Jobling, 1989; Björnsson et al., 2001), plaice *Pleuronectes platessa* L. (Fonds et al., 1992), turbot *Scophthalmus maximus* L. (Imsland et al., 1996), halibut *Hippoglossus hippoglossus* L. (Jonassen et al., 1999), and spotted wolffish *Anahichas minor* (Imsland et al., 2006). In contrast, no shift in temperature optimum with increasing size was found in brown trout *Salmo trutta* L. (Elliott, 1975), nor in sockeye salmon *Oncorhynchus nerka* Walbaum (Brett et al., 1969). Recent experiments with Atlantic salmon parr have indicated temperature optima around 18–19 °C for 4–12 g fish (Forseth et al., 2001; Jonsson et al., 2001), whereas Handeland et al. (2003) reported 13 °C as temperature optima for 40–60 g Atlantic salmon smolts.

The optimal temperature for growth ($T_{opt}G$) is usually higher (Imsland et al., 1996; Jonassen et al., 1999) than the temperature the species meet in nature. This could indicate that the most 'favourable' trait for maximising individual fitness is not maximum growth, but maximum food utilization as fish must balance factors like growth, food utilization, resistance towards starvation, food availability and predation. Also, the optimal temperature for feed conversion efficiency (T_{opt}FCE) is generally lower than $T_{opt}G$ (Jobling, 1994; Björnsson and Tryggvadóttir, 1996; Imsland et al., 2006). This co-variation of food intake and food conversion with growth rate as temperature changes suggests that the effect of temperature on growth is at least in part mediated by the efficiency in which fish both feed and convert food to weight gain. At present no data have been published for Atlantic salmon on this topic.

Knowledge of fish stomach evacuation rates (SER) is a necessary component for both field and laboratory studies concerned with fish feeding rates, energy budgets, and the trophic dynamics of aquatic systems (Sweka et al., 2004; Kawaguchi et al., 2007). A combination of SERs with temperature and field estimates of stomach fullness is commonly used to estimate daily rations of fish in the wild (Forrester et al., 1994; Sweka et al., 2004; Kawaguchi et al., 2007). Temperature

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and the type and size of prey consumed influence SERs (Elliott, 1972; Sweka et al., 2004). SER has been estimated for Atlantic salmon, whereas these earlier studies have investigated SER in relation to particle size and protein concentration (Sveier et al., 1999) or protein type (Storebakken et al., 1999), but SER data for Atlantic salmon at reared at different temperatures is lacking in the literature.

The main objective of this study was to investigate the effects of temperature and fish size in Atlantic salmon, and their interaction on growth rate, feed intake, stomach evacuation rate and food conversion. Attempts were made to estimate optimal temperatures for growth for fish of different sizes in order to optimize culture conditions for Atlantic salmon post-smolts.

2. Materials and methods

2.1. Fish stock and rearing conditions

The fish used in this study were 0+ smolts of the AquaGen strain reared at "Fitjar Laks" (Western Norway) from hatching (December 2002) to smoltification (October 2003). First feeding started in February 2003, at 700 degree days post-hatching, at constant light and in heated water (approximately 12 °C). In freshwater, the fish were fed a commercial dry diet (Biomar, 2 and 3 mm, Norway) according to temperature and size (Austreng et al., 1987). Between 1 March and 24 June the fish were maintained at constant light and average water temperature during this period was 10.1 ± 1.2 °C. A photoperiod regime known to stimulate the smoltification-related increase in gill Na^+,K^+-ATPase activity (Duston and Saunders, 1995; Handeland and Stefansson, 2001) was initiated on 25 June. This treatment included an abrupt decrease in daylength from LD24:0 to LD12:12 in which the fish was maintained on long day during the next 6 weeks, followed by another 6 weeks period on constant light (ending on 16 September). During this period, gill samples, length and weight were collected from 12 individuals on 29 July, 29 August and 16 September for further analysis of gill Na^+, K^+,-ATPase activity and growth during parr–smolt transformation.

2.2. Experimental design

The smolts (n = 891, length = 18.3 cm ± 1.1, weight = 77.0 g ± 14.6) were brought from "Fitjar laks" to the High Technology Centre in Bergen (HIB) on 18 September 2003, and immediately distributed randomly among eight rearing tanks, eighteen days prior to the start of the experiment. Each tank was supplied with running fresh water and the temperature was kept at approximately 9 °C (ambient). At the same time, a sub-group of 23 fish in each tank were individually tagged (Carlin tags, McAllister et al., 1992) for observations of individual growth rates. The tanks used in this study were circular (1 m, diameter) and with a rearing volume of approximately 500 L. Light was supplied by a fluorescent daylight tube mounted under the tank cover (200 lx at the bottom of the tanks). All tanks were covered with a lid to prevent light leakage. The fish were maintained on continuous light (LD24:0) before starting the experiment on 7 October. Five days after arrival at HIB, the freshwater temperature was gradually altered from ambient to temperature regimes (mean ± SE) referred to as: 6 (±0.2), 10 (±0.1), 14 (±0.3) and 18 (±0.1) °C over a period of 1 week. After this acclimation period, temperature was kept constant during the rest of the experiment. Two weeks later (7 October), the water in all tanks was changed from fresh water to seawater of identical temperature. Full salinity (33‰) was reached within 60 min. Water flow was kept between 15 and 20 L min^{-1} in the low temperature tanks (6 and 10 °C) and between 25 and 30 L min^{-1} in the high temperature tanks (14 and 18 °C). Oxygen saturation in the outlet water was measured regularly and was kept above 80% during the experiment. All tanks were checked twice daily during the experiment and dead fish were removed immediately. Following seawater transfer, the fish were exposed to a simulated natural light regime (60°25′N).

In seawater, all groups were fed a commercial dry diet (Ewos type, Micro boost 2 mm and 3 mm pellets) in excess from automatic feeders between 09.00–10.00 and 15.00–16.00 h. Uneaten pellets were flushed out within 15 min, and filtered from the outlet water using an automatic collection system. Uneaten pellets were removed from the filters and immediately put into a drying chamber for 24 h (70 °C). The amount of food consumed was calculated as the difference between dry weight of the feed given and dry weight of the uneaten pellets. When the experiment was terminated after three months in seawater (23 December), all smolts with except of 30 individuals from each temperature group were killed. The remaining fish sustained in their respective tanks, under the same conditions as described above, until 8 January 2004. On 9 January all groups were starved for a five days period, and thereafter fed in excess with EWOS, X-ray feed (see description below) between 09.00 and 15.00 h at day 6. After being fed to satiation, all groups were starved for another five days. During this period individual fish were X-rayed at the following occasions; when full fed (15.00, day 6), after 12, 24, 48 and 72 h of starvation for further analysis of the effect of temperature on individual stomach evacuation rate.

2.3. Sampling procedures

Gill samples collected during parr–smolt transformation were frozen in SEI buffer at −80 °C and subsequently analyzed for gill Na^+, K^+-ATPase activity using the method of McCormick (1993). Following transfer to seawater fork length (to nearest 0.1 cm) and weight (to nearest 0.1 g) of the individually tagged smolts were measured every second week. Total biomass in each group was determined every fourth week (all fish in the tank was collected and weighted in a bucket). Specific growth rate (SGR) was calculated as $(\ln W_2 - \ln W_1)/\Delta T$ where ΔT is the number of days between times T_1 and T_2. Food conversion efficiency (FCE) was calculated as: FCE = G/R, where R is the total food consumption between days T_1 and T_2, and G is the observed increase in biomass during the same period (Brett, 1979).

One day before registration of the individual growth data the ordinary diet was replaced with an identical diet containing X-ray dense Ballotini glass beads. This diet was prepared by EWOS Innovation, Dirdal, Norway, using the same methods and had identical nutrient composition, colour, particles size and texture as the normal commercial diet. Together with X-radiography (GeR XT-100 X-ray machine, AGFA Structurix DX7, Talbot and Higgins, 1983) this feed allowed individual rates of food intake and stomach evacuation in fish to be measured. Following the development of the X-ray plates, the number of marker particles present in the stomach was counted and the amount feed consumed calculated. This calculation was achieved using a standard curve prepared by X-raying known weights of the marked food and assessing the number of Ballotini glass beads. Using this information a linear regression of the relationship between the weight of the marked feed and number of Ballotini particles a standard curve was prepared, see below:

$$\text{Food intake}\left(\text{g*gfish}^{-1}\right) = 0.05 \times (\text{Ballotini glass beads}) + 0.05, (N = 12, r^2 = 0.97).$$

2.4. Data analysis and statistical methods

All statistical analyses were performed with Statistica™. Prior to statistical analysis, all data were tested for normality of distribution using the Kolmogornov–Smirnov test. The homogenity of variances among the different groups was tested using the Hartley F-max test (Sokal and Rolf, 1995). Data on gill Na^+,K^+-ATPase activity, length,

Table 1
Changes in length, weight, condition and gill Na+, K+-ATPase activity in Atlantic salmon smolts during smolting ($n = 12$, ±SE)

Parameter	29 July	29 August	16 September
Length	18.32 (1.11)[a]	19.25 (1.12)[a,b]	20.37 (0.75)[b]
Weight	77.00 (14.60)[a]	87.80 (12.27)[a,b]	93.80 (10.60)[b]
Condition	1.21 (0.04)[a]	1.22 (0.09)[a]	1.01 (0.08)[b]
Gill Na+, K+-ATPase	2.61 (1.14)[a]	5.87 (2.04)[b]	11.09 (2.37)[c]

Different letters ($p < 0.05$) indicates significant differences between each time points.

weight and condition during smolting were tested using a one-way ANOVA. A two-way nested MANOVA was applied to calculate the overall effect of temperature and time on weight, and the effect of temperature on stomach evacuation rate of PIT tagged fish. Stomach evacuation rate (SER) was calculated as: SER = [stomach content (g) at day T_2/initial stomach content (g) * 100], where T_2 refers to the day of sampling. Data on food intake were analyzed using a two-way nested ANOVA. Significant MANOVA/ANOVAs were followed by a Student–Newman–Keuls multiple comparison test within each time point to determine differences among experimental groups. The effect of fish size on the growth rates were tested in a two-way ANCOVA using geometric mean weight (GM) between T_1 and T_2 as co-variant. A linear regression was used to correlate individual growth rates with data on GM within each temperature group. The relationship between growth, food conversion efficiency, temperature and size was analysed with a parabolic regression (Zar, 1984), and optimal temperatures for growth ($T_{opt}G$) and food conversion efficiency (T_{opt}FCE) for two different size groups were calculated as the zero solution to the first derivative of the parabolic regression equations i.e. the solution of SGR or FCE = $aT^2 + bT + c$ where T is temperature, and a, b and c are constants determined by the regression. The asymptotic standard error of mean (SE) was calculated using individual growth data, and group data for $T_{opt}G$ and T_{opt}FCE respectively. The regression was made using the average growth rate of tagged fish (SGR) and group data (FCE) for two size groups; 70–150 and 150–300 g. A significance level (α) of 0.05 was used if not stated otherwise. All data in tables and text are given as means ± SE.

3. Results

3.1. Mortality

No mortality was observed during the first five days of seawater exposure in the 6, 10 and 14 °C groups, whereas 10 (9%) untagged fish died in the 18 °C group during the first 24 h. In the period between days 6 and 30, mortality increased in all groups reaching a total of 11, 9, 9 and 23% in the 6, 10, 14 and 18 °C groups, respectively. No moralities occurred for the remainder of the experiment.

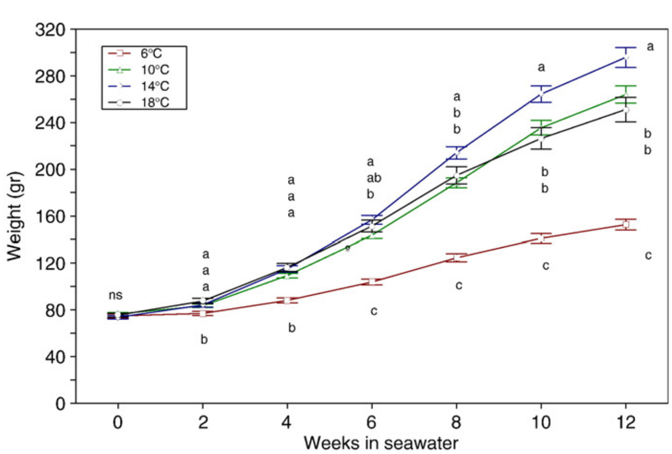

Fig. 1. Mean weight in Atlantic salmon smolts (±SE, $n = 23$) transferred to seawater at 6 (□), 10 (Δ), 14 (◇) and 18 (○) °C. The first point (week 0) refers to the freshwater group (control). Different letters indicates significant differences (Student–Newman–Keuls, $p < 0.05$) between temperature groups at same time of sampling, n.s., non significant.

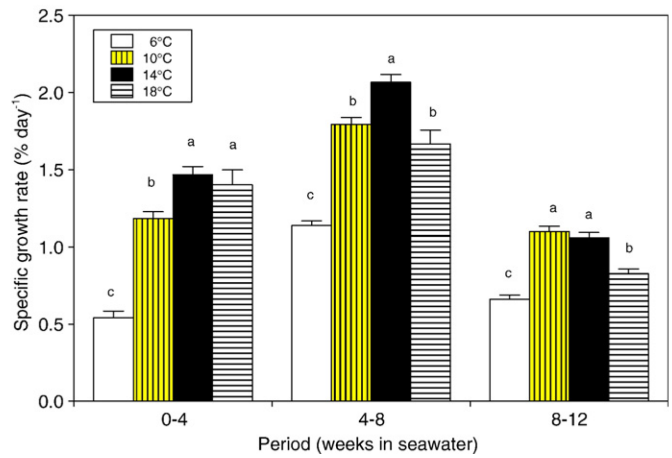

Fig. 2. Mean specific growth rates (SGR) of individually tagged Atlantic salmon smolts reared at four temperature regimes during the experimental period. Vertical whiskers SE. Different letters denote significant differences (Student–Newman–Keuls test, $p < 0.05$) between temperature treatments within each time period.

3.2. Development of gill Na+, K+-ATPase activity, growth and condition during smolting

Between 29 July and 26September, gill Na^+,K^+-ATPase activity increased four fold from 2.61 to 11.09 µmol ADP mg protein^{-1} h^{-1} ($p < 0.001$, Table 1). During the same period, an increase in length and weight were recorded whereas condition decreased significantly ($p < 0.01$).

3.3. Growth in seawater: effect of temperature and size

There were significant differences in mean weight between treatments with the 14 °C group having the highest mean weight from week 8 onwards ($p < 0.001$, Fig. 1). In contrasts no differences in mean weight were recorded between the 10 and 18 °C groups, whereas the 6 °C group showed a mean weight significant below theses groups from week 2 onwards ($p < 0.05$). A temporary increase in growth rate was observed in all groups between weeks 0–4 and 4–8 in seawater ($p < 0.05$, Fig. 2). Furthermore, between the second and last period a significant decline in growth rates were recorded in all groups ($p < 0.001$). Overall, highest growth rate was seen in the 14 °C group (1.53% d^{-1}, $p < 0.001$), whereas no differences in SGR were seen between the 10 and 18 °C groups (1.35% d^{-1}, 1.29% d^{-1}). Lowest growth was seen at 6 °C (0.78% d^{-1}, $p < 0.001$) group. Furthermore, a positive relationship between individual SGR and geometric mean weight was seen in all groups (Fig. 3 A–D, $p < 0.001$ in all groups). The regression lines for the four temperature groups were non-parallel (ANCOVA, $p < 0.001$), and SGR was highly correlated with size (ANCOVA, $p < 0.01$). The same trend of increasing growth rates at high temperatures was seen when growth rates were plotted against temperature for two size classes of fish (70–150 g, and 170–300 g, Fig. 4). The resulting parabolic regressions (Fig. 4) indicated that the temperature optimum for maximum growth ($T_{opt.}$ SGR ± SE) increases with size and were estimated to be 12.8 ± 0.2 °C for 70–150 g, and 14.0 ± 0.4 °C for 170–300 g fish (Fig. 4A and B, respectively).

3.4. Feed conversion efficiency: effect of temperature and size

Overall, highest feed conversion efficiency (FCE) was seen in the 10 °C group. Furthermore, in the 6, 10, 14 °C groups an overall increase in FCE

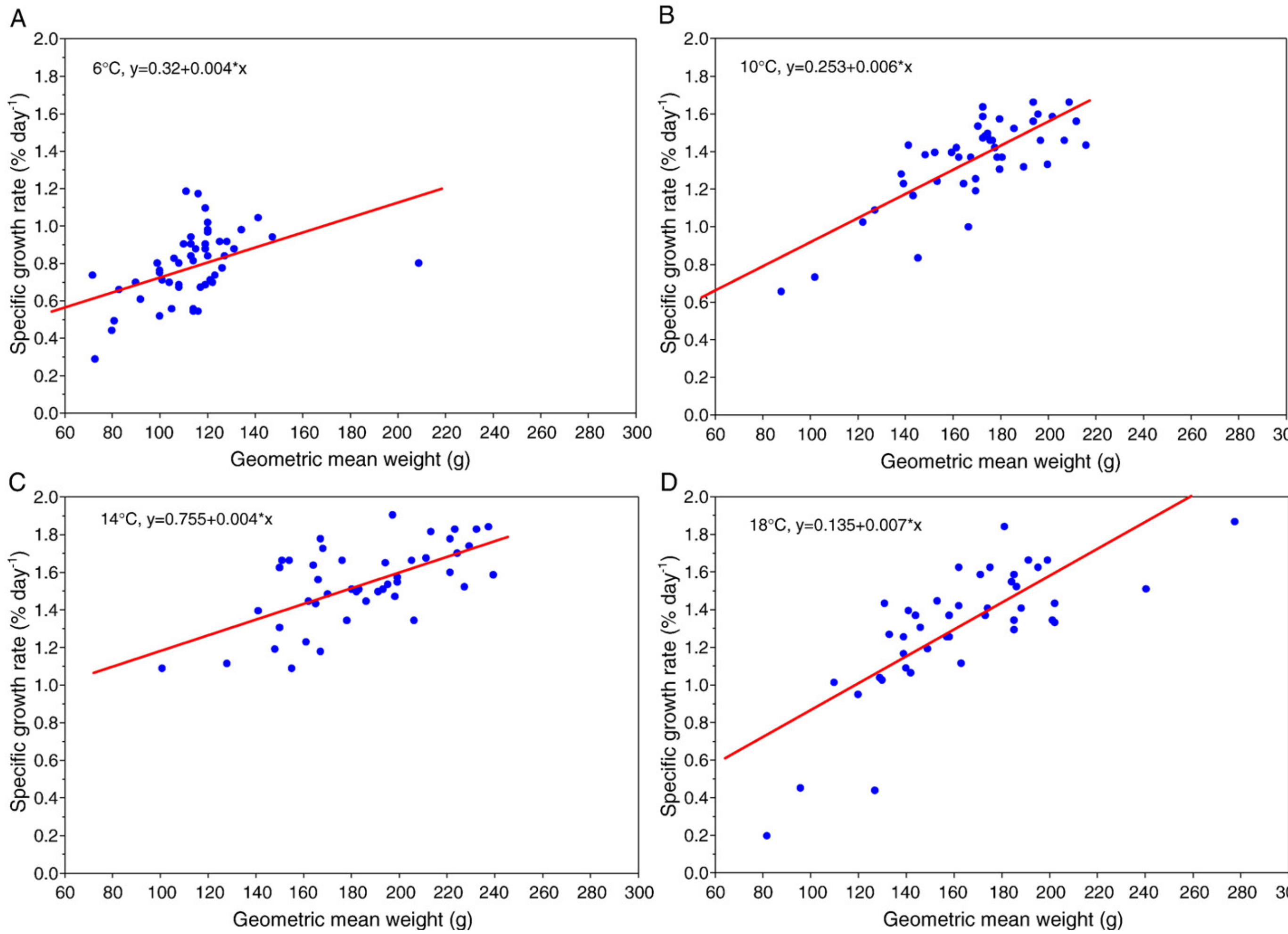

Fig. 3. Growth rate (SGR)–geometric mean (GM) regression in of Atlantic salmon smolts transferred to seawater at 6, 10, 14 and 18 °C. A: SGR = 0.32 + 0.004GM, r^2 = 0.21, p < 0.001. B: SGR = 0.253 + 0.006GM, r^2 = 0.60, p < 0.001. C: SGR = 0.755 + 0.004GM, r^2 = 0.40, p < 0.001. D: SGR = 0.135 + 0.007GM, r^2 = 0.57, p < 0.001.

was observed as the experiment progressed (Fig. 5). In contrasts no difference in FCE was recorded in the 18 °C group during the experimental period. Mean FCE for all three periods was 0.24, 0.77, 0.63 and 0.36for the 6, 10, 14 and 18 °C groups receptively. The optimal temperature for FCE (T_{opt}FCE) (±SE) varied among size classes (Fig. 6) and was estimated to be 13.4 ± 0.4 and 11.0 ± 0.6for the size classes of 70–150 and 150–300 g, respectively.

3.5. Food intake

Food intake was significant influenced by temperature and time (Fig. 7, p < 0.001). Highest overall food intake was observed in the 14 °C group (1.46 g*g fish^{-1}, p < 0.001), while the 6 °C showed the lowest food intake (0.84 g*g fish^{-1}, p < 0.001), significantly below the 10 and 18 °C groups (10 °C 1.30 g*g fish^{-1}, 18 °C: 1.98 g*g fish^{-1}). No differences in food intake were seen between the 10 and 18 °C groups. Following transfer to seawater, a significant increase in food intake was seen in all groups (p < 0.001). In the 10 and 14 °C groups, peak levels in food intake were reached after 6 weeks in seawater. However, no changes in food intake were observed in the 6 °C group during the first 2 weeks in seawater, whereas a significant increase and a further stabilization in food intake was recorded between weeks 2 and 6 (p < 0.05). Furthermore, in the 18 °C group highest food intake was observed after three weeks in seawater. Thereafter a fall in food intake was observed reaching levels comparable to those at 6 °C after 6 weeks in seawater. No further changes in food intake were seen throughout this study.

3.6. Stomach evacuation rate

Stomach evacuation rate was significantly influenced by temperature (p < 0.001, Fig. 8). Highest evacuation rate was seen in the 18 °C group, in which the proportion of meal remaining in the stomach decreased from 100 to less than 5% after 24 h of starvation. No differences in stomach evacuation rate were recorded between the 10 and 14 °C groups, showing a stomach fullness of less than 5% after 48 h of starvation. Compared to the 10 and 14 °C groups, a delay in stomach evacuation was seen in the 6 °C group. In this group, stomach fullness was significantly higher than the other groups after 24 and 48 h of starvation (p < 0.05), and was below 5% after 72 h of starvation.

4. Discussion

Growth rate, food intake and feed efficiency ratio of juvenile Atlantic salmon smolts was significantly influenced by temperature and fish size. Overall growth rate was highest at 14 °C (1.53% d^{-1}). However, at 10 °C and the 18 °C growth rates were equal or only slightly lower during the later stages of the experiment, while the fish at 6 °C showed significantly lower overall growth rate (0.78% d^{-1}, Fig. 2). Increased growth at elevated temperatures agrees with previous studies on Atlantic salmon (Solbakken et al., 1994; Handeland et al., 2000, 2003). Handeland et al. (2000) found a significant decrease in growth rate between 14.4 and 18.9 °C and indicated that this was the upper temperature limit for growth and development in

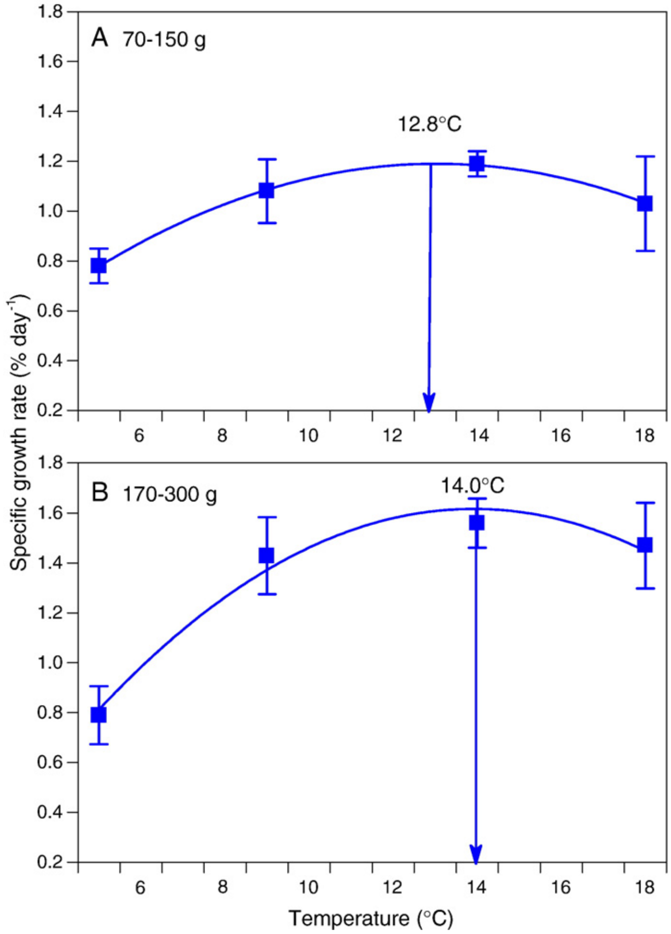

Fig. 4. Changes in specific growth rate with temperature for two different size classes of Atlantic salmon smolts. The lines represent the least-squares second order polynomial fit to the data: $G=aT^2+bT+c$ where G = Specific growth rate, T = temperature, and a, b and c are constants determined by the regression. Vertical lines indicate standard error of mean, n=43–50 for each data point. A. SGR=−0.007 T^2+0.166 T−0.104. B. SGR=−0.010 T^2+0.282 T+0.345 For the two size classes optimum temperature for growth ($T_{opt}G$) indicated by the broken lines were calculated from the first order derivative of the parabolic regressions (i.e. when dSGR/dT=0).

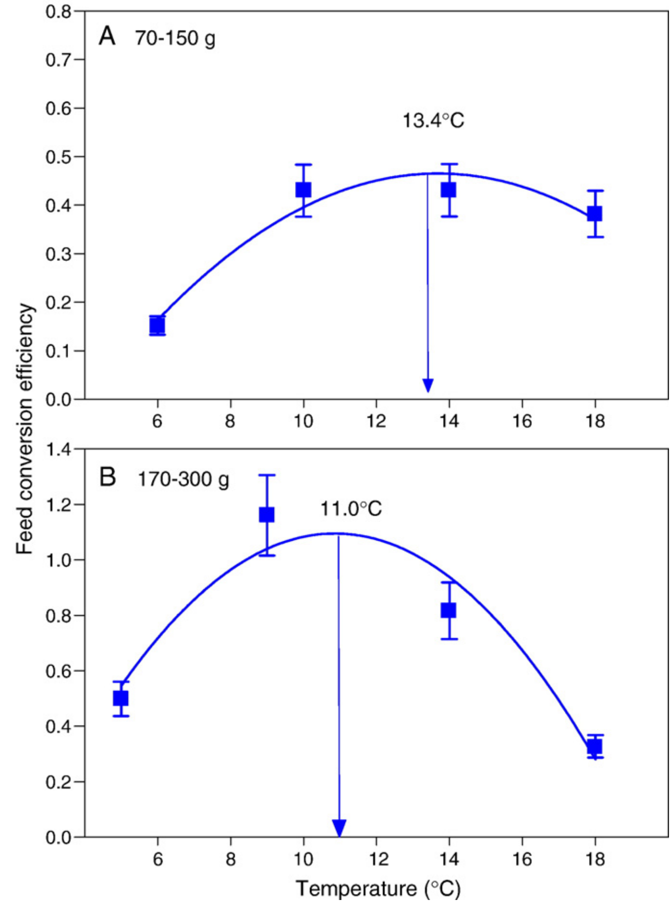

Fig. 6. Changes in feed conversion efficiency with temperature for two different size classes of Atlantic salmon smolts. The lines represent the least-squares second order polynomial fit to the data: FCE=aT^2+bT+c where FCE = Feed conversion efficiency, T=temperature, and a, b and c are constants determined by the regression. Vertical lines indicate standard error of mean, n=2 for each data point. A. FCE=−0.005 T^2+0.119 T+0.319 B. FCE=−0.0159 T^2+0.347 T+0.792 For the two size classes optimum temperature for growth (T_{opt}FCE) indicated by the broken lines were calculated from the first order derivative of the parabolic regressions (i.e. when dG/dT=0).

seawater. In brown trout reared in freshwater, a decrease in appetite has been observed when temperature exceeds 18 °C (Brett, 1979), whereas increased osmotic stress has been suggested to temporarily reduce growth in salmonids during seawater transfer (Clarke et al., 1981). In the present study growth was slightly reduced between 14–18 °C, whereas a peak in appetite is reached after 3 weeks in

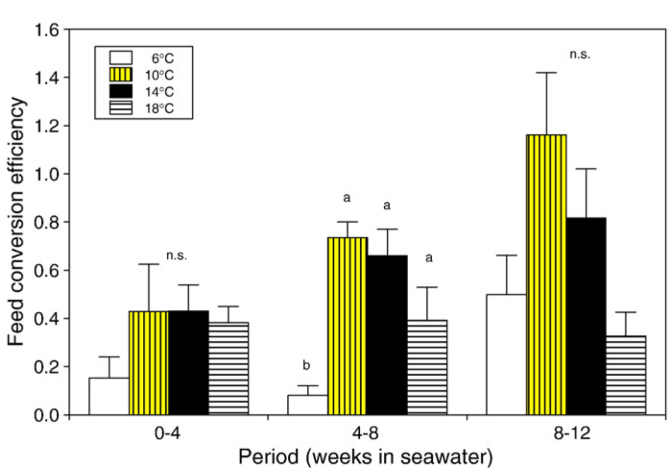

Fig. 5. Feed conversion efficiency (FCE) of Atlantic salmon smolts during the first 90 days in seawater at different temperatures (6, 10, 14 and 18 °C). Vertical whiskers SE. Different letters denote significant differences (Student–Newman–Keuls test, $p<0.05$) between temperature treatments within each time period. n.s., non significant.

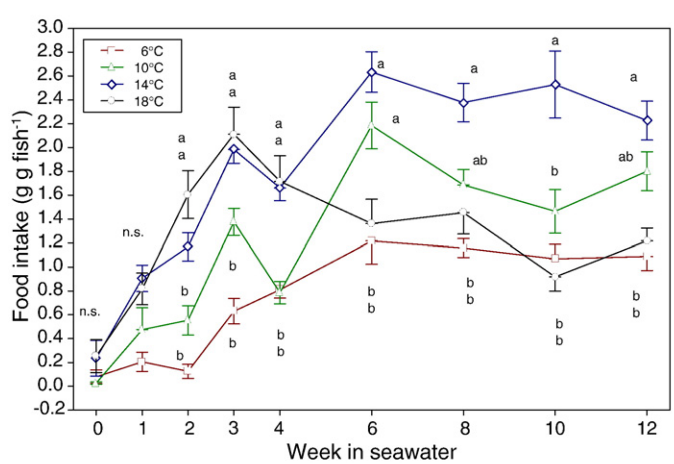

Fig. 7. Mean food intake in Atlantic salmon smolts (±SE, n=23) transferred to seawater at 6 (□), 10 (Δ), 14 (◇) and 18 (○) °C. The first point (week 0) refers to the freshwater group (control). Different letters indicates significant differences ($p<0.05$) between temperature groups at same time of sampling, n.s., non significant.

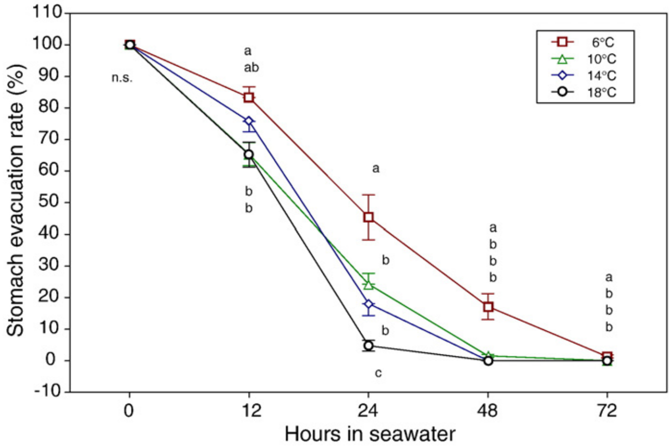

Fig. 8. Stomach evacuation rate in Atlantic salmon smolts at four temperatures, 6 (□), 10 (Δ), 14 (◇) and 18 (○) °C. Different letters indicates significant differences ($p<0.05$) between temperature groups at same time of sampling, n.s., non significant.

seawater at 18 °C with a significant drop after that to same appetite levels as seen at 6 °C. According to Elliott (1981), energy losses in faeces and excretory products increase markedly with temperature, and the same is seen for food evacuation rate in our study (Fig. 8). This indicates that the upper threshold for growth and development is around 18 °C for 50–300 g Atlantic salmon in line with the suggestions of Handeland et al. (2000).

Only a few published temperature growth studies using similar sized Atlantic salmon smolts as in the present study exist. A similar temperature effect on growth was found by Handeland et al. (2000), who reported a linear relationship between specific growth rate and temperature in Atlantic salmon smolts in seawater between 4.6 and 14.4 °C, while a rapid decrease in growth rate was observed when temperature reached 18.9 °C. To our knowledge, optimum temperature for growth of Atlantic salmon post-smolts in seawater has only been calculated in the study of Handeland et al. (2003). They used combination of the temperature-dependent growth rates derived in the that study, with the results of Handeland et al. (1998) and Handeland et al. (2000) and Arnesen et al. (1998), and suggested that the optimal temperature for growth in Atlantic salmon smolts in seawater is approximately 13.0 °C for smolts between 40–60. This figure is very close to our calculated optimal temperatures for the smaller size class (i.e. 70–150 g), whereas our data indicate that this value increases for Atlantic salmon smolts during the first weeks in seawater. The increasing growth with size seen in present study is in contrast with studies on most investigated fish species (Brett, 1979; Pedersen and Jobling, 1989; Fonds et al., 1992; Imsland et al., 1996, 2006; Jonassen et al., 1999). Cuenco et al. (1985) indicated that, in general, the temperature optimum for growth in fish declines 1–2 °C with increasing weight in the range of 10–500 g, whereas we find that $T_{\mathrm{opt}}G$ increases with approximately 1.2±0.3 °C in the size range 70–300 g. Our study also shows that Atlantic salmon smolts are rather eurythermal, which is expressed by high growth rates over a relatively wide temperature range (here 10–18 °C), and flat parabolic regressions between growth rate and temperature. This also conforms to the pelagic thermal range in the distribution area for Atlantic post-smolts in the North Atlantic (Friedland et al., 1998, 2005).

Maximum FCE was seen at 10 °C and a parabolic regression suggested the optimum temperature for FCE decreasing with size from 13.4 to 11.0 °C. The present findings are in line with those reported in Handeland et al. (2003), where feed conversion efficiency (9.4 °C) peaked approximately 3 °C below optimum temperature (13.0 °C) for growth in seawater. This agrees with the general pattern for salmonids in freshwater (Brett, 1979; Fleming et al., 2000; Forseth et al., 2001; Jonsson et al., 2001) and is in line with findings on Atlantic halibut (Björnsson and Tryggvadóttir, 1996; Jonassen et al., 1999), Atlantic cod (Björnsson et al., 2001) and turbot (Imsland et al., 2001). The suggested explanation for this finding is the at unrestricted ration growth rate reaches a maximum at a temperature lower than the temperature giving maximum ingestion rate (Jobling, 1994). Thus, as the temperature is lowered slightly below $T_{\mathrm{opt}}G$ the growth rate decreases less than the ingestion rate, resulting in increased feed efficiency ratio.

Stomach evacuation rate (SER) was highly temperature dependent in our study. Most studies with salmonids show that SER increase exponentially as temperature increases (Elliott, 1972; He and Wurtsbaugh, 1993; Sweka et al., 2004; Kawaguchi et al., 2007), and that SER depends primarily on water temperature, with their consumed food being a secondary factor (Kawaguchi et al., 2007). In our study the rate of increase was slowing as temperature increased. Changes in SER were most evident between the lowest (6 °C) and the other three temperatures which all had similar SER trajectories. This observation is consistent with some studies in which evacuation rates stabilize nearer the upper thermal tolerance limit of a species (Sweka et al., 2004). Further, the t_{50} stomach evacuation time in our study was estimated to be between 14 (at 18 °C) and 22 h (at 6 °C). This is in within the range reported by He and Wurtsbaugh (1993) using brown trout, Olsson et al. (1999) with large rainbow trout, and Storebakken et al. (1999) and Sveier et al. (1999) using Atlantic salmon.

A decrease in condition and increased gill Na+,K+-ATPase activity are generally accepted indicators of good smolt quality, and are correlated with seaward migration, hypoosmoregulatory ability and high seawater survival rates in salmonids (McCormick and Saunders, 1987; Handeland et al., 2003), Consequently the Atlantic smolts used in the present trial can be considered to be fully smoltified as Na+,K+-ATPase activity increased significantly in the period prior to the study, i.e. 29 July–26 September, concurrent with a decrease in condition.

In conclusion, the present study shows ontogenetic variation in optimum temperature for growth in juvenile Atlantic salmon smolts, with increased temperature optimum for growth and decreased temperature for feed conversion efficiency as the fish grow bigger. Temperature tolerance increases with size, but Atlantic salmon smolts are eurythermal in the size range investigated. Feed intake and stomach evacuation rates are tightly linked to temperature. Maximum feed intake was seen at 14 °C and minimum intake at 18 and 6 °C, whereas stomach evacuation rate was similar from 10–18 °C, but significantly slower at 6 °C. Overall, these findings may have important consequences for optimization of commercial production of Atlantic salmon post-smolts.

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