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ABSTRACT

The objective of this study was to determine the effect of temperature on growth and survival of larval and juvenile burbot, *Lota lota maculosa*. Burbot aquaculture is developing primarily in response to declining wild stocks and a need to restore such populations. Beyond conservation efforts, there is also potential to culture this species commercially. However, many important aspects of burbot culture remain unaddressed. In this study larval and juvenile burbot were reared at three constant water temperatures (10, 15, and 20 °C) in an intensive culture setting. Two 30 day trials were conducted during the larval life stage and one 60 day trial during the juvenile life stage. In Trial 1, larval burbot (mean total length ± SD, 6.9 ± 1.0 mm, approximately 65 days post hatch) reared at 20 °C grew the fastest, while growth was lowest in the 10 °C treatment. Survival was inversely related to temperature, with the lowest average of 6.6% observed in larvae reared at 20 °C. The percentage cannibalized was quantified and found to be positively correlated with water temperature, and reached 58.0% in larvae reared at 20 °C. In Trial 2, as larvae approached metamorphosis (12.9 ± 1.9 mm, approximately 100 days post hatch), growth was also highest in fish at 20 °C and lowest in those at 10 °C. At this stage survival was higher in fish at lower temperatures, but the percentage cannibalized appeared independent of temperature, averaging over 50% in fish at all temperatures. In Trial 3, growth of juveniles (59.9 ± 12.4 mm, approximately 205 days post hatch) reared at 15 and 20 °C was not significantly different, yet both displayed significantly increased growth relative to juveniles reared at 10 °C. Juveniles were fully transitioned to a dry diet, and survival averaged >93% in all culture temperatures. The percentage cannibalized during this life stage averaged <5%, and was not affected by temperature. This study demonstrated the importance of water temperature, as it clearly affects culture performance of larval and juvenile burbot. Results from this study have implications for maximizing growth during larval and juvenile life stages of this species, and provide a comparative, empirical framework for establishing conservation, or commercial aquaculture programs for burbot.

1. Introduction

Following population declines in many parts of their geographic range (Argent et al., 2000; Arndt and Hutchinson, 2000; Keith and Allardi, 1996; Maitland and Lyle, 1990, 1996; Paragamian, 2000; Stapanian et al., 2011), along with prospective commercial aquaculture interests, development of burbot culture has recently begun for both North American *Lota lota maculosa* and Eurasian burbot *Lota lota lota* (Harzevili et al., 2003, 2004; Jensen et al., 2008; Trebelsi et al., 2011; Wocher et al., 2011; Wolnicki and Kaminski, 2001; Wolnicki et al., 2002; Żarski et al., 2009). Due to the delicate nature and specific biological requirements of burbot early life stages, high mortality remains common, and further refinement of culture methods is needed (Jensen et al., 2008; Wolnicki and Kaminski, 2001). Temperature directly affects metabolism and can influence growth, survival, and development of larval and juvenile fishes (Blaxter, 1992; Brett, 1979). Therefore, investigation of the effect of temperature on the culture performance of larval and juvenile burbot is critical to the continued development of culture techniques for this species.

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In the natural environment, the pelagic larvae of burbot reportedly inhabit water of approximately 10 °C from May through June (Wang and Appenzeller, 1998). Juvenile burbot have been reported to occupy littoral habitats in July where water temperatures average approximately 20 °C. However, this is not believed to be the optimal temperature for growth (Hofmann and Fischer, 2003). Culture temperatures ranging from 5 to 24 °C have been shown to influence growth and survival in larval and juvenile *L. lota lota*. Warmer temperatures (≤21 °C) typically increased growth, whereas colder temperatures, as low as 5 °C, increased survival (Donner and Eckmann, 2011; Harzevili et al., 2004; Wolnicki and Kaminski, 2001; Wolnicki et al., 2002). Despite this baseline work, a further understanding of the effect of temperature on growth, survival, and cannibalism, in critical early life history and grow-out stages, is needed, particularly for *L. lota maculosa*, to aid in the development of burbot aquaculture. The objective of this study was to identify the optimal culture temperatures to significantly increase burbot growth, relative condition factor, and survival, while significantly decreasing the percentage cannibalized during larval and juvenile stages.

2. Materials and methods

2.1. Experimental design, conditions, and apparatus

Three trials were conducted at the University of Idaho's College of Natural Resources Wet Lab (Moscow, ID, USA) to investigate the effect of temperature on total length (TL), weight, specific growth rate (SGR), relative condition factor (K_n), coefficient of variation of length (CV), survival, and percentage cannibalized during early larval (Trial 1), late larval (Trial 2) and juvenile (Trial 3) stages of burbot. In each trial, fish were subjected to constant temperature treatments of 10, 15, and 20 °C for 30 (Trials 1 and 2) and 60 days (Trial 3). For Trials 1 and 2, twelve 10 L flow through rectangular tanks (31.8 cm × 18.4 cm × 20.3 cm) receiving water at a rate of 0.8 L/min were the experimental units to which three treatments, with four replicates each, were assigned. For Trial 3, twelve 180 L flow through circular tanks (75 cm diameter, water depth 40 cm) receiving aeration and water at a rate of 3.0 L/min were the experimental units to which three treatments, with four replicates each, were assigned. The tanks used in Trials 1 and 2 were made from clear acrylic, however an outside lining of black polyethylene sheeting covered the ends, back and bottom of the tanks, whereas the tanks in Trial 3 were constructed of fiberglass with light blue paint.

Temperatures were maintained by blending heated, ambient, and chilled dechlorinated municipal water upon entry to a separate head box for each treatment. Water temperature was measured manually with a thermometer (model 21431, Taylor USA, Las Cruces, NM, USA) three times each day at each head box. Water source contributions were adjusted as needed to maintain constant temperature treatments. For the duration of Trial 1, temperature averaged 9.9 ± 0.3 °C, 15.3 ± 0.8 °C, and 20.0 ± 1.0 °C for treatments 10, 15 and 20 °C respectively. Throughout Trial 2, temperature averaged 10.1 ± 0.4 °C, 15.3 ± 0.6 °C, and 20.4 ± 0.7 °C for treatments 10, 15, and 20 °C respectively. During Trial 3, temperature averaged 10.0 ± 0.4 °C, 15.0 ± 0.8 °C, and 19.8 ± 1.0 °C for treatments 10, 15 and 20 °C respectively. The experimental room was lit continuously with overhead fluorescent lighting, as Harzevili et al. (2004) demonstrated that burbot larvae can be successfully cultured under continuous light. Ambient air temperature was maintained at 15 °C. Prior to each trial, fish were held at 15 °C. All fish were then acclimated gradually to treatment temperatures over a 24 h period immediately preceding each trial. During all trials, dead fish were removed from the tanks and quantified throughout the day. Sediments were siphoned from each tank daily.

2.2. Experimental animals

All experimental fish were produced at the University of Idaho-Aquaculture Research Institute (UI-ARI) as progeny of captive broodstock obtained from Moyie, Duncan, and Arrow reservoirs in southeastern British Columbia, Canada. Mixed stock progeny groups composed of 3000 larvae (250 per tank) for Trial 1, averaging (±SD) 6.9 ± 1.0 mm total length (TL, n = 30), 2400 larvae (200 per tank) for Trial 2, averaging 12.9 ± 1.9 mm TL (n = 30), and 600 juvenile burbot (50 per tank) for Trial 3, averaging 59.9 ± 12.4 mm TL (n = 30). Trials 1, 2 and 3 began when larvae and juveniles were approximately 65, 100 and 205 days post hatch, respectively.

2.3. Feeding regimes

All fish were fully transitioned to their respective diets prior to initiation of each trial. During Trial 1, larvae in each tank were fed newly hatched nauplii of *Artemia franciscana* three times a day at a target quantity of 1000 organisms L^{-1} (10,000 total) at each feeding. On day 15 of Trial 1, the target *Artemia* density in each tank was increased to 2000 organisms L^{-1} at each feeding (20,000 total), to avoid underfeeding. During Trial 2, 20,000 enriched *Artemia* were fed per tank three times per day. Nauplii were enriched for 24 h post hatch with *Nannochloropsis* sp. algae paste (Reed Mariculture, Campbell, CA, USA) and Roti-Rich (Florida Aqua Farms Inc., Dade City, FL, USA). During Trial 3, the commercial diet Otohime C2 (Reed Mariculture, Campbell, CA, USA) was fed twice per day at approximately 5% of their body weight per day, a quantity empirically determined to be an excessive amount. Feed amounts were determined from burbot biomass estimates for each tank and were adjusted every 15 days.

2.4. Sampling

For Trials 1 and 2, random samples of 30 fish were collected from each tank on days 5, 10, 20, and 25, then transferred to a flat-bottomed container filled to a depth of 1 cm with culture tank water along with a scale for measuring. Digital photographs were taken with a Kodak EasyShare C330 Digital Camera (Eastman Kodak Company, Rochester, NY, USA). Upon completion of sampling, fish were returned to their respective tanks. Total length was calculated for each fish to the nearest 0.1 mm from digital photographs using image analysis software (ImageJ 1.40, Wayne Rasband, Open Source).

In Trials 1 and 2, all fish were counted on days 15 and 30 to determine the number of survivors. In Trial 3 all fish were counted at each sampling point (days 15, 30, 45 and 60). Fish not recovered as survivors at each sampling point, and not previously accounted for as mortalities, were assumed to be cannibalism mortalities. At these time points 30 fish were randomly sampled from each tank to manually quantify weight and TL. In Trial 1, the 30 fish samples were euthanized with MS-222 (Argent, Redmond, WA, USA) and subsequently transferred to a 10% neutral buffered formalin solution for preservation, as these fish were too small to measure and weigh individually without inducing handling mortality. Total length and weight were subsequently measured. Fish removed for lethal sampling in Trial 1 were not counted as mortalities; rather, they were deducted from the initial population size when calculating survival and percentage cannibalized at day 30. In Trials 2 and 3, live fish were measured and weighed wet. Upon completion of sampling, all non-lethally sampled fish were returned to their respective tanks.

2.5. Calculations and statistical methods

Calculated fish weight, relative condition factor, coefficient of variation, specific growth rate, survival, and cannibalism metrics were calculated using the following equations:

1. Calculated fish weight (W_c, mg) = $a \times TL\ (mm)^b$, where a and b are constants derived from the ordinary least squares regression of Log weight (mg) by Log TL (mm) of each fish weighed and measured

during the respective trials (Le Cren, 1951). The constants *a* and *b* were estimated in this manner for each individual trial, and the resulting equations are as follows:

$$Trial\,1.\,W_c = 0.0215 \times TL^{2.7188}$$

$$Trial\,2.\,W_c = 0.0259 \times TL^{2.6438}$$

$$Trial\,3.\,W_c = 0.0237 \times TL^{2.7307}.$$

2. Relative condition factor (K_n) = [observed weight (W)/W_c], (Le Cren, 1951)
3. Coefficient of variation of length (CV) = 100 × (standard deviation total length/mean total length) (Gomes et al., 2000)
4. Specific growth rate (SGR, %/day) = 100 × [ln(final weight) − ln(initial weight)]/days (Ricker, 1975)
5. Survival (%) = 100 × (final fish number)/(initial fish number)
6. Cannibalism (%) = 100 × (final fish number cannibalized)/(initial fish number).

The values for SGR, survival, and cannibalism were calculated in a cumulative manner at each sampling point (i.e., the SGR values calculated on day 30 of Trial 1 are based upon the changes in weight over the entire 30 day trial). All data were expressed as mean values ± the standard error (SE), except for temperature, which was expressed as the mean ± standard deviation (SD) for the duration of each trial. Data analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC). One way analysis of variance (ANOVA) was used to compare tank averages of: TL, W, SGR, K_n, CV, transformed (arc sine square root) proportion surviving, and transformed (arc sine square root) proportion cannibalized among the treatments. Tukey's post hoc comparisons were used to test for differences between treatments. Statistical significance was defined at $P<0.05$ for all comparisons.

3. Results

3.1. Larval life stage trial

Growth differences emerged by day 5, with larvae in the 20 °C treatment significantly greater in TL than fish at 10 °C (Table 1). By day 10, and continuing to the end of the trial, TL differed significantly among all treatments, with larvae reared at 20 °C being longest and those at 10 °C being shortest. Weight differed significantly between all treatments at day 15 and day 30, with 20 °C being the heaviest and 10 °C the lightest. Specific growth rates (%/day) at days 15 and 30 differed significantly between all treatments, with the highest growth rates resulting from the 20 °C treatment and the lowest occurring at 10 °C (Table 1). No significant effect of temperature on K_n, or CV was observed during Trial 1 (Table 1).

Survival declined significantly by day 15 in fish reared at increasingly warmer temperatures (Table 2). By day 30, survival was significantly higher in fish at 10 °C than for those reared at 15 and 20 °C (Table 2), and no significant difference was detected between 15 and 20 °C. The percentage cannibalized on day 15 differed significantly between all treatments, with the highest occurrence in fish at 20 °C followed by 15 °C and the lowest occurrence in larvae at 10 °C (Table 2). By day 30, the percentage cannibalized in fish reared at 10 °C was significantly lower than in fish at both 15 and 20 °C, with no significant difference occurring between 15 and 20 °C (Table 2).

3.2. Late larval life stage trial

Growth differences emerged by day 15, with significantly higher TL values observed in larvae reared at 20 °C than in 10 °C. This trend persisted through day 30 (Table 3). Total length of larvae reared at 20 °C was also significantly greater than 15 °C on day 20 and day 25. Total length of fish reared at 10 and 15 °C did not differ significantly during the trial (Table 3). No significant effect of temperature on weight was observed during Trial 2 (Table 3). No significant effect of temperature on SGR at day 15 was observed. However, on day 30 mean SGR was significantly higher in larvae reared at 20 °C than in 10 °C (Table 3). Intermediate SGR values were observed in larvae reared at 15 °C,

Table 1
Growth and condition of early larval stage burbot reared at temperatures of 10, 15 and 20 °C over 30 days during Trial 1.

Temperature (°C)	Days							
	n*	0	0–5	0–10	0–15	0–20	0–25	0–30
Total length (mm)								
10	4	6.9 ± 1.0	7.2 ± 0.1^{b}	8.0 ± 0.2^{c}	9.8 ± 0.3^{c}	10.4 ± 0.2^{c}	11.6 ± 0.3^{c}	12.6 ± 0.3^{c}
15	4	6.9 ± 1.0	7.6 ± 0.2^{ab}	9.4 ± 0.3^{b}	11.9 ± 0.1^{b}	13.3 ± 0.3^{b}	17.6 ± 0.7^{b}	22.2 ± 0.9^{b}
20	4	6.9 ± 1.0	7.9 ± 0.1^{a}	10.9 ± 0.2^{a}	15.9 ± 0.4^{a}	23.3 ± 0.8^{a}	27.7 ± 0.8^{a}	30.7 ± 0.9^{a}
Weight (mg)								
10	4	4.8 ± 2.5	–	–	11.4 ± 0.9^{c}	–	–	22.8 ± 1.7^{c}
15	4	4.8 ± 2.5	–	–	20.8 ± 0.8^{b}	–	–	112.2 ± 9.5^{b}
20	4	4.8 ± 2.5	–	–	42.9 ± 2.3^{a}	–	–	230.6 ± 27.4^{a}
Specific growth rate (% weight gain/day)								
10	4	–	–	–	10.1 ± 0.5^{c}	–	–	7.4 ± 0.2^{c}
15	4	–	–	–	14.1 ± 0.2^{b}	–	–	12.7 ± 0.3^{b}
20	4	–	–	–	18.9 ± 0.4^{a}	–	–	15.0 ± 0.4^{a}
K_n								
10	4	1.15 ± 0.27	–	–	1.00 ± 0.02^{a}	–	–	0.99 ± 0.02^{a}
15	4	1.15 ± 0.27	–	–	1.08 ± 0.04^{a}	–	–	1.06 ± 0.05^{a}
20	4	1.15 ± 0.27	–	–	1.00 ± 0.02^{a}	–	–	0.92 ± 0.04^{a}
Coefficient of variation of length (%)								
10	4	14.8	18.5 ± 1.4^{a}	18.6 ± 1.0^{a}	16.7 ± 2.2^{a}	19.1 ± 2.2^{a}	17.5 ± 0.8^{a}	14.8 ± 1.0^{a}
15	4	14.8	18.4 ± 0.8^{a}	16.1 ± 1.1^{a}	17.1 ± 0.9^{a}	18.2 ± 1.9^{a}	17.6 ± 0.7^{a}	17.0 ± 1.4^{a}
20	4	14.8	17.0 ± 0.5^{a}	17.5 ± 1.1^{a}	15.7 ± 0.6^{a}	16.4 ± 0.5^{a}	15.6 ± 1.5^{a}	13.0 ± 1.0^{a}

Values presented are means ± S.E. except for day 0 values which are means ± SD. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

Table 2
Survival and cannibalism of early larval stage burbot reared at temperatures 10, 15 and 20 °C over 30 days during Trial 1.

Temperature (°C)	Days		
	n*	0–15	0–30
Survival (%)			
10	4	82.5 ± 2.4[a]	55.1 ± 4.1[a]
15	4	62.7 ± 4.6[b]	13.5 ± 1.6[b]
20	4	23.1 ± 2.5[c]	6.6 ± 1.2[b]
Cannibalism (%)			
10	4	3.2 ± 1.2[c]	7.8 ± 3.9[b]
15	4	23.6 ± 2.7[b]	56.5 ± 3.4[a]
20	4	47.0 ± 1.7[a]	58.0 ± 2.6[a]

Values presented are mean ± S.E. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

Table 4
Survival and cannibalism of late larval stage burbot during metamorphosis cultured at temperatures 10, 15 and 20 °C for 30 days during Trial 2.

Temperature (°C)	Days		
	n*	0–15	0–30
Survival (%)			
10	4	41.8 ± 2.8[a]	23.0 ± 3.5[a]
15	4	39.6 ± 4.5[a]	13.0 ± 4.1[ab]
20	4	21.1 ± 1.5[b]	4.3 ± 1.7[b]
Cannibalism (%)			
10	4	38.4 ± 3.2[a]	52.1 ± 4.2[a]
15	4	32.2 ± 5.5[a]	58.1 ± 5.3[a]
20	4	43.9 ± 1.8[a]	58.9 ± 2.7[a]

Values presented are mean ± S.E. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

however, they were not significantly different from fish reared at either of the other two temperatures (Table 3).

Mean K_n for late stage burbot larvae in the 10 °C treatment at day 15 was significantly higher than values in both 15 and 20 °C (Table 3). At day 30 K_n was no longer significantly different between treatments. Coefficient of variation of TL did not differ significantly between the treatments with the exception of day 30, where fish reared at 15 °C were less homogeneous than those at 10 °C (Table 3).

Survival at day 15 was significantly greater for fish reared at 10 and 15 °C than at 20 °C (Table 4). By day 30, survival of fish at 10 °C was significantly higher than at 20 °C (Table 4). Mean survival of fish in the 15 °C treatment at day 30 was not significantly different from 10 or 20 °C (Table 4). The percentage cannibalized was not observed to differ significantly between treatments during Trial 2.

3.3. Juvenile life stage trial

Growth differences emerged by day 15, with mean TL and weight values of juveniles reared at 15 and 20 °C being significantly greater than analogous values in 10 °C treatment (Table 5). This trend persisted throughout the trial. Mean TL and weight values for juveniles reared at 20 and 15 °C did not differ significantly.

Specific growth rates at day 15 and day 30 were significantly higher in juveniles at 15 and 20 °C than at 10 °C, a trend that persisted throughout the trial (Table 5). No significant differences in SGR were observed for juveniles reared at 15 and 20 °C during the trial (Table 5). Mean K_n on day 45 was significantly higher for fish reared at 15 °C than at 10 or 20 °C (Table 5). No differences were observed at the other sampling times. Temperature was not observed to significantly affect CV in this trial (Table 5).

Survival was high in all treatments, with juveniles at 10 °C sustaining no mortalities (Table 6). No significant effect of temperature was observed in juvenile burbot in this trial (Table 6). The percentage cannibalized was minimal in this trial, occurring only during the first 15 days in fish reared at 20 °C, and was not significantly different among treatments (Table 6).

Table 3
Growth and condition of late larval stage burbot reared at temperatures of 10, 15 and 20 °C over 30 days during Trial 2.

Temperature (°C)	Days							
	n*	0	0–5	0–10	0–15	0–20	0–25	0–30
Total length (mm)								
10	4	12.9 ± 1.9	16.5 ± 0.4[a]	18.5 ± 0.5[a]	20.7 ± 0.7[b]	22.5 ± 0.8[b]	24.7 ± 0.7[b]	27.1 ± 0.9[b]
15	4	12.9 ± 1.9	16.8 ± 0.9[a]	19.5 ± 0.8[a]	22.5 ± 1.3[ab]	24.1 ± 1.5[b]	28.0 ± 1.8[b]	32.7 ± 2.6[ab]
20	4	12.9 ± 1.9	17.6 ± 1.1[a]	20.8 ± 0.6[a]	25.1 ± 0.5[a]	28.8 ± 0.8[a]	35.7 ± 1.6[a]	43.8 ± 4.8[a]
Weight (mg)								
10	4	24.9 ± 14.3	–	–	114.0 ± 12.0[a]	–	–	186.0 ± 17.7[a]
15	4	24.9 ± 14.3	–	–	102.2 ± 11.2[a]	–	–	345.2 ± 76.3[a]
20	4	24.9 ± 14.3	–	–	140.0 ± 7.4[a]	–	–	687.7 ± 215.4[a]
Specific growth rate (% weight gain/day)								
10	4	–	–	–	10.0 ± 0.8[a]	–	–	6.7 ± 0.3[b]
15	4	–	–	–	9.3 ± 0.7[a]	–	–	8.5 ± 0.8[ab]
20	4	–	–	–	11.5 ± 0.4[a]	–	–	10.6 ± 1.0[a]
K_n								
10	4	1.02 ± 0.23	–	–	1.32 ± 0.09[a]	–	–	1.07 ± 0.03[a]
15	4	1.02 ± 0.23	–	–	0.93 ± 0.01[b]	–	–	1.01 ± 0.04[a]
20	4	1.02 ± 0.23	–	–	0.87 ± 0.01[b]	–	–	0.98 ± 0.03[a]
Coefficient of variation of length (%)								
10	4	14.9	15.0 ± 0.9[a]	14.7 ± 0.9[a]	17.8 ± 1.8[a]	14.2 ± 2.5[a]	18.1 ± 2.5[a]	18.2 ± 1.3[b]
15	4	14.9	15.0 ± 1.3[a]	13.0 ± 1.1[a]	15.1 ± 1.5[a]	16.5 ± 2.5[a]	22.0 ± 1.3[a]	26.1 ± 1.1[a]
20	4	14.9	14.8 ± 1.4[a]	14.1 ± 1.1[a]	20.8 ± 1.8[a]	24.4 ± 4.0[a]	26.0 ± 2.4[a]	23.8 ± 2.3[ab]

Values presented are means ± S.E. except for day 0 values which are means ± SD. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

Table 5
Growth and condition of juvenile burbot reared at temperatures of 10, 15 and 20 °C over 60 days during Trial 3.

Temperature (°C)	Days					
	n*	0	0–15	0–30	0–45	0–60
Total length (mm)						
10	4	59.9 ± 12.4	79.1 ± 1.0^{b}	89.3 ± 0.9^{b}	98.2 ± 1.2^{b}	105.6 ± 1.1^{b}
15	4	59.9 ± 12.4	85.8 ± 0.6^{a}	100.2 ± 0.8^{a}	110.9 ± 1.9^{a}	122.4 ± 1.9^{a}
20	4	59.9 ± 12.4	88.1 ± 1.2^{a}	104.5 ± 1.6^{a}	115.5 ± 2.1^{a}	125.6 ± 2.0^{a}
Weight (g)						
10	4	1.7 ± 1.0	3.9 ± 0.2^{b}	5.3 ± 0.1^{b}	6.6 ± 0.3^{b}	8.5 ± 0.3^{b}
15	4	1.7 ± 1.1	4.6 ± 0.2^{a}	7.2 ± 0.1^{a}	9.9 ± 0.3^{a}	13.1 ± 0.3^{a}
20	4	1.7 ± 1.2	5.2 ± 0.2^{a}	7.9 ± 0.3^{a}	10.4 ± 0.6^{a}	13.4 ± 0.7^{a}
Specific growth rate (% weight gain/day)						
10	4	–	5.3 ± 0.3^{b}	3.7 ± 0.1^{b}	2.9 ± 0.1^{b}	2.6 ± 0.1^{b}
15	4	–	6.5 ± 0.2^{a}	4.7 ± 0.1^{a}	3.9 ± 0.1^{a}	3.4 ± 0.0^{a}
20	4	–	7.3 ± 0.2^{a}	5.0 ± 0.1^{a}	4.0 ± 0.1^{a}	3.4 ± 0.1^{a}
K_n						
10	4	0.94 ± 0.09	1.03 ± 0.02^{a}	1.00 ± 0.02^{a}	0.97 ± 0.01^{b}	1.01 ± 0.01^{a}
15	4	0.94 ± 0.09	0.98 ± 0.02^{a}	0.99 ± 0.00^{a}	1.04 ± 0.01^{a}	1.05 ± 0.01^{a}
20	4	0.94 ± 0.09	1.04 ± 0.02^{a}	0.98 ± 0.01^{a}	0.99 ± 0.01^{b}	1.01 ± 0.01^{a}
Coefficient of variation of length (%)						
10	4	20.6	13.7 ± 1.2^{a}	13.7 ± 0.9^{a}	14.1 ± 1.0^{a}	13.3 ± 0.7^{a}
15	4	20.6	15.8 ± 0.7^{a}	12.6 ± 0.4^{a}	13.75 ± 0.7^{a}	13.5 ± 1.0^{a}
20	4	20.6	12.7 ± 0.4^{a}	12.0 ± 0.7^{a}	11.2 ± 0.4^{a}	11.9 ± 0.2^{a}

Values presented are mean ± S.E. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

4. Discussion

During the larval stage through metamorphosis, which reportedly occurs between 20 and 30 mm TL in burbot (Eloranta, 1985; Fischer, 1999; McPhail and Paragamian, 2000; Ryder and Pesendorfer, 1992), growth was consistently greatest in fish reared at 20 °C. This increase was similar to the findings of Wolnicki et al. (2002) and Donner and Eckmann (2011) where growth of early larval stage *L. lota lota* was greatest at 21 °C and 19 °C respectively. Wolnicki and Kaminski (2001) suggested that in *L. lota lota* entering metamorphosis, 15 °C provided the greatest growth. This finding differed from our findings in Trial 2, in which 20 °C produced greater growth, however no cannibalism was reported by Wolnicki and Kaminski (2001) under *ad libitum* feedings of live *Artemia*. This discrepancy may have been due to dietary differences, where the cannibal's diet may provide sufficient nutrients to maintain heightened metabolism at 20 °C whereas feeding on *Artemia* may not, particularly at an advanced stage if feeding on small live prey becomes inefficient. Additionally, the presence of cannibalism in our trials may have inflated growth rates through size selective mortality. If the smaller individuals are removed by cannibalism, our estimates of specific growth rate, which are based on the mean of the population in a given tank, would be inflated. The findings of Donner and Eckmann (2011) involving *L. lota lota* entering metamorphosis supported our growth results, as they also found that fastest growth occurred in fish reared in their highest temperature treatment (19.2 °C) while feeding burbot to satiation with *Artemia*, with no cannibalism reported. Collectively this suggests that fish reared at temperatures at or near 20 °C may grow optimally only if the feeding regime provides adequate energy input to keep pace with heightened metabolism. During the juvenile stage, the largest fish were produced at 20 °C. However, 15 °C produced similar results. These findings suggest that the optimal growing temperature may fall between 15 and 20 °C during the juvenile life stage. Hofmann and Fischer (2003) reported an optimal growing temperature of 16 °C for juvenile *L. lota lota*, similar in size to those in Trial 3. Collectively, these findings provide a framework for temperature mediated growth manipulations. Accelerated growth may be particularly useful to shorten early, labor-intensive phases of culture such as larval rearing during which live feeds are required. Additionally, increased growth during early life stages could provide larger fish at release for conservation programs, which are often more robust, exhibit greater survival, and present more tagging options than smaller fish.

Table 6
Survival and cannibalism of juvenile burbot cultured at temperatures 10, 15 and 20 °C for 60 days during Trial 3.

Temperature (°C)	Days				
	n*	0–15	0–30	0–45	0–60
Survival (%)					
10	4	100.0 ± 0.0^{a}	100.0 ± 0.0^{a}	100.0 ± 0.0^{a}	100.0 ± 0.0^{a}
15	4	99.5 ± 0.5^{a}	99.0 ± 0.6^{a}	99.0 ± 0.6^{a}	97.0 ± 1.3^{a}
20	4	94.0 ± 2.9^{a}	93.5 ± 3.2^{a}	93.0 ± 3.5^{a}	93.0 ± 3.5^{a}
Cannibalism (%)					
10	4	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}
15	4	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}
20	4	5.0 ± 3.0^{a}	5.0 ± 3.0^{a}	5.0 ± 3.0^{a}	5.0 ± 3.0^{a}

Values presented are mean ± S.E. Within a column, means denoted by different superscripts are significantly different ($P<0.05$) as determined by ANOVA and Tukey's comparison of mean values.
* Number of replicates per treatment.

However, increased growth was associated with reduced survival, resulting primarily from heightened cannibalism. Observed decreases in survival with increased temperatures were consistent with the findings of Wolnicki et al. (2002), Harzevili et al. (2004) and Donner and Eckmann (2011) for larval *L. lota lota*. In burbot of a similar size to those used in Trial 2, Wolnicki and Kaminski (2001) found only a slight decrease in survival at warmer temperatures up to 21 °C, with survival no less than 92% over 20 days, which may have been due to the absence of cannibalism. Donner and Eckmann (2011) noted findings similar to ours with the lowest survival (approximately 40% over 25 days) of *L. lota lota* comparable in size to Trial 2 in their highest temperature treatment (19.2 °C). At a temperature of 13.0 °C, Donner and Eckmann (2011) reported survival to be 87.3 % over 25 days, much higher than the values

seen at 10 or 15 °C in Trial 2. This discrepancy can be attributed to the high losses attributed to cannibalism in our study.

No cannibalism was reported by Wolnicki and Kaminski (2001), Wolnicki et al. (2002) or Donner and Eckmann (2011) who studied burbot up to 24.6, 14.4, and 29.3 mm in length at the end of their trials respectively. Initial coefficients of variation of TL reported by Wolnicki and Kaminski (2001) and Wolnicki et al. (2002) were 8.3 and 7.5% respectively, supporting the theory that low CV reduces opportunity for cannibalism. These published CV values were lower than values observed in our three trials, and suggest that fish size (TL) was more homogenous in their populations, which may have prevented the occurrence of cannibalism. Trebelsi et al. (2011) reported cannibalism mortality during rearing to the juvenile life stage of up to 45% over 36 days, which corresponded with a final CV of 23%. However, initial CV values for the larval burbot used in two trials by Donner and Eckmann (2011), which corresponded with the size of fish used in Trials 1 and 2, were comparable (14.6% in 7.5 mm larvae, 14.0% in 12.1 mm larvae) to initial CV values observed here. Despite the similarity in CV, higher feeding rates employed by Donner and Eckmann (2011) may have prevented cannibalism. Alternatively, cannibalism may not have been quantified by Donner and Eckmann (2011) despite its potential contribution to the substantial mortality that occurred. Cannibalism can easily go un-noticed in a typical intensive culture setting, where high fish densities combined with opaque culture tanks that limit the culturist to an overhead view, may obscure cannibalistic events. Unless the initial population size is known and mortalities are removed judiciously and quantified, the percentage cannibalized cannot be estimated, and the culturist may not be aware that cannibalism occurred. Piscivory, including cannibalism, has been reported in the natural environment for burbot as small as 21.1 mm TL (Kahilainen and Lehtonen, 2003), but may occur earlier if the opportunity arises. For example, cannibalism observed early in Trial 1 indicated that piscivory and cannibalism can occur earlier, with nearly half the population cannibalized in a population averaging 15.9 mm TL. Cannibalism was also observed in this study in a population of burbot averaging just 9.8 mm TL.

Cannibalism in a related species, Atlantic cod *Gadus morhua*, began at a length of 12 mm, with reports of mortal wounds inflicted on prey too large for ingestion (Øiestad et al., 1985). Mortal wounding during failed cannibalistic attempts was observed during Trials 1 and 2, resulting in mortalities that could not be attributed to cannibalism as they were not ingested. These observations suggested that previous estimates of the percentage cannibalized were likely conservative if these mortalities were not consumed before they were removed. As with burbot in this study, cannibalism in Atlantic cod was positively correlated with water temperature (Øiestad et al., 1985). This increase in cannibalism may have been due to increased metabolism and feeding at higher temperatures, and increased growth may have allowed fish to reach a stage of development more prone to cannibalism earlier. A relatively large mouth during metamorphosis in Atlantic cod predisposes them to higher losses to cannibalism than during larval and juvenile stages, with only a 25% difference in body length between predator and prey needed for successful ingestion (Folkvord, 1997). This function, if similar in burbot, may explain in part why cannibalism was prevalent in Trials 1 and 2, when burbot began to pass through metamorphosis, and was reduced in juvenile burbot during Trial 3. Additionally, the feeding regimen used in Trial 3 may have aided in reducing cannibalism as the fish were offered an excessive quantity of a food item they could efficiently consume regardless of fish size. Relative condition factor did not appear to be greatly affected by temperature, which is perhaps an indication that the larval and juvenile burbot were finding adequate food. The only biologically significant change in K_n was noted at the midpoint of Trial 2 in fish reared in 10 °C. These fish may have had a much higher relative condition factor due to the combined effect of a high rate of cannibalism (mean 38.4%) that allowed for increased nutrient uptake paired with a lower metabolic rate in cooler water.

In conclusion, burbot growth from larval rearing through metamorphosis was maximized at 20 °C relative to 10 and 15 °C. However, maximized growth was associated with high mortality due primarily to cannibalism. Strategies to prevent or eliminate cannibalism in burbot, along with an understanding of the conditions under which cannibalism occurs require further study. Once burbot reached the juvenile stage and were fully transitioned to dry diets, they grew faster at higher temperatures, with both 15 and 20 °C providing acceptable growth. Juvenile burbot survival was high even in warmer temperatures, and cannibalism was observed to be minimal to nonexistent at this stage. This study provides valuable information for further development of burbot aquaculture, and provides a baseline for understanding the effects of water temperature on burbot growth and survival in an intensive culture setting.

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