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Effect of daily oscillation in temperature and increased suspended sediment on growth and smolting in juvenile chinook salmon, Oncorhynchus tshawytscha

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Abstract

We examined the effect of temperature oscillation and increased suspended sediment concentration on growth and smolting in juvenile ocean-type chinook salmon (*Oncorhynchus tshawytscha*). Fish were ponded on February 26; each treatment group had three replicates of 250 fish. Mean temperatures for the entire experiment were 12.3 °C for all tanks with a total of 1348 and 1341 degree days for the constant temperature and oscillating temperature tanks, respectively. Daily fluctuation in temperature averaged 7.5 °C in the variable temperature groups and less than 1 °C for the constant temperature group. Starting on April 5, bentonite clay was added each day to tanks as a pulse event to achieve a suspended sediment concentration of 200 mg l⁻¹; clay cleared from the tanks within approximately 8 h. Fish were sampled at approximately two week intervals from ponding until mid-June. On the last sample date, June 12, a single gill arch was removed and fixed for histological examination of gill morphology. By early May, significant differences were seen in size between the groups; control>temperature=sediment>(temperature group had a mean weight significantly greater than the sediment group. Gill Na⁺,K⁺-ATPase activity was not affected by daily temperature oscillations, but groups subjected to increased suspended sediment had significantly lower enzyme activities compared to controls. Mean cell size for gill chloride cells did not differ between groups. Plasma cortisol increased significantly during the spring, but there were no significant differences between groups.

Keywords: Growth; Smolting; Temperature; Suspended sediment; Chinook salmon

1. Introduction

Smolting and the development of saltwater tolerance in juvenile salmon is dependent on growth as a minimum size must be attained before fish smolt (McCormick and Saunders, 1987; Hoar, 1988). Photoperiod and rearing temperature directly influence growth opportunity (Clarke et al., 1981) and for many species of salmon photoperiod stimulates the physiological transformation from parr to smolt (McCormick et al., 2000; 2002). For ocean-type chinook salmon, however, temperature and size are the principal factors that influence smolting as photoperiod manipulation does not affect development of saltwater tolerance (Clarke et al., 1981). In addition to temperature and photoperiod, there are other environmental factors that show seasonal changes that may influence smolting and seasonal movement downstream. It has been suggested

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that increased flow (Raymond, 1979; Youngson et al., 1986) and higher levels of suspended solids (Youngson et al., 1986; Specker et al., 2000) that naturally occur during the spring may also provide a stimulus for behavioral and physiological changes associated with the parr-smolt transformation. Changes in these environmental factors, however, have been shown to negatively affect fish. Flood events that cause an increase in flow and turbidity, decrease growth in juvenile Atlantic salmon (Salmo salar) (Arndt et al., 2002). Increased suspended sediment levels also stress fish and result in higher levels of cortisol (Redding et al., 1987). Additionally, fluctuations in daily temperature beyond a normal range elicit a stress response in juvenile coho salmon (O. kisutch) (Thomas et al., 1986). How these environmental stimuli serve to enhance smolting, yet may also stress fish is not clear.

It is anticipated that seasonal changes in temperature, flow and suspended sediment should enhance smolting; yet often these variables are altered by anthropogenic disturbance. Landscape disturbances associated with resource extraction have been shown to alter a number of aquatic variables. For example a reduction in canopy closure due to timber removal causes an increase in mean water temperature and greater daily fluctuations in temperature (Brown and Krygier, 1970); hydro-electric dam installation results in a hydrograph inversion (Raymond, 1979), and placer mining causes an increase in suspended sediment concentration (McLeay et al., 1984). Despite the relatively large environmental disturbances that have been observed, the impact of such changes on growth and smolting has not been assessed in combination.

In this study we examined the impact of daily oscillation in temperature and increased suspended sediment concentration on growth and smolting in juvenile chinook salmon. Magnitudes of fluctuating temperature and suspended sediment concentration used in this experiment were similar to what have been previously reported (Brown and Krygier, 1970; Thomas et al., 1986; Macdonald et al., 2003a; Mellina et al., 2005). Measurements of size were made over the spring to determine if treatments affected growth and size was limiting the ability of treated fish to smolt. Physiological status of smolts was assessed by measuring gill Na⁺,K⁺-ATPase activity, gill chloride cell numbers, and plasma cortisol levels.

2. Methods

2.1. Experimental design

Juvenile ocean-type chinook salmon originally from Robertson Creek and Big Qualicum stocks on Vancouver Island were used for this experiment. The fish were progeny of Yellow Island Aquaculture Ltd., Quadra Island, BC, domesticated for four generations. Twelve 140 l tanks were set up to hold the experimental fish. Six tanks were fitted with a manifold that introduced water that passed once through a heat exchange unit. Six tanks were fitted with two manifolds that were designed to alternately supply the tanks with water. One line introduced water into the tanks that was not heated; the second was passed through the heat exchanger three times. Temperatures for the oscillating tanks and control tanks are shown in Fig. 1a. The mean temperatures for the entire experiment were 12.3 °C for all tanks, and the total degree days (°C days) were 1348 and 1341 for the constant temperature and oscillating temperature tanks, respectively. The mean minimum and maximum daily temperatures for the constant temperature tanks were 11.8 and 12.8 °C, respectively; mean minimum and maximum daily temperatures for the oscillating temperature tanks were 8.8 and 16.1 °C, respectively. On February 26, 250 fish were ponded directly into each experimental tank from incubation Heath trays. Incandescent lights were used to simulate the ambient natural photoperiod (50° N). Fish were fed by hand up to six times per day at a ration of 2%



Fig. 1. A, Daily temperatures for experimental tanks. Solid line is temperature from constant temperature tanks and dashed line is temperature from fluctuating temperature tanks. Inset shows temperature fluctuations over the first week of the study. B, Suspended sediment concentrations after a pulse of bentonite clay was added to the tanks. Solid symbol represents mean from three tanks, open symbols from individual tanks.

body weight using EWOS #1 and #2 crumble (EWOS Canada Ltd. Surrey, BC).¹

The suspended sediment treatments began on April 5. Bentonite clay was used for its consistency in particle size and lack of organic matter allowing complete repeatability. Each day, 28 g of bentonite clay was suspended in approximately 1 l of water. The clay suspension was then added directly to a tank as a pulse event to achieve a suspended sediment concentration of 200 mg l⁻¹. Three of the constant temperature tanks were not exposed to bentonite clay (group C); the suspension was added to the other three constant temperature tanks (group S). Three of the oscillating temperature tanks were not exposed to bentonite clay (group T) and three were exposed daily to clay (group T × S). The pulse of suspended sediment made the water distinctly turbid, with visibility reduced to less than 10 cm. The suspended clay cleared from the tanks within approximately 8 h (Fig. 1b).

2.2. Sampling procedures

Fish were sampled at approximately two week intervals. Sampling dates were; February 26 (ponding), March27, April 15, May 2, May 16, May 30, and June 12. On each sample date, twelve fish from each tank were rapidly removed and transferred to a bucket containing 200 mg l^{-1} tricaine methane sulfonate (neutralized and buffered with sodium bicarbonate, pH 7.0). Once the fish were anesthetized, fork length (L) and body weight (W) were measured. The caudal peduncle was severed and blood collected in heparinized capillary tubes. Collection of blood from the first six fish was complete within 5 min of first disturbing the fish to ensure that a stress-associated rise in cortisol did not occur (Sumpter et al., 1986). Blood was stored on ice for less than 30 min, centrifuged at 3000 g for 5 min, plasma removed and frozen in liquid nitrogen. A gill biopsy was taken from every second fish sampled (approximately six to eight primary gill filaments) and placed in 100 µl of SEI (150 mM sucrose, 10 mM Na₂EDTA, 50 mM imidazole, pH 7.3) on ice for determining Na⁺,K⁺-ATPase activity. Samples were frozen in liquid nitrogen within 30 min. On the last sample date, June 12, a single gill arch was removed and fixed for histological examination of gill morphology from 4 fish per tank.

2.3. Analysis of gill Na⁺,K⁺-ATPase activity

Gill Na⁺,K⁺-ATPase activity was measured according to the microassay protocol of McCormick (1993) on six fish sampled per tank, 18 per treatment per sample date. Gill filaments were homogenized in SEI buffer containing 0.1% sodium deoxy-cholate. Following centrifugation (3000 g for 0.5 min) to remove large debris, Na⁺,K⁺-ATPase activity was determined by linking ATP hydrolysis to the oxidation of nicotinamide adenine dinucleotide (NADH), measured at 340 nm for 10 min

at 25 °C, in the presence and absence of 0.5 mM ouabain. Protein content in the gill homogenate was measured using a bicinchoninic acid (BCA) protein assay (Pierce, Rockford, IL, USA). Specific activities were expressed as μ mol ADP mg⁻¹ of protein h⁻¹.

2.4. Determination of plasma cortisol levels

Plasma cortisol levels were quantified using a competitive solid-phase microtitre enzyme immunoassay (EIA) following the protocol outlined by Carey and McCormick (1998) on the first four fish sampled from each tank, 12 fish per treatment per date. Briefly, microtitre plates (Costar high binding polystyrene EIA plates, Corning, NY) were coated with rabbit anticortisol antibody (Clinical Endocrinology, Department of Population Health & Reproduction, University of California, Davis, CA) and incubated overnight at 4 °C and then washed with a 0.15 M NaCl and 0.05% Tween 20 solution. A blocking solution of EIA buffer 0.1 M phosphate, 0.15 M NaCl, pH 7.0, with 0.1% BSA was added before the addition of 2.5 µl of standard or sample along with 100 µl of cortisol-horseradish peroxidase conjugate (University of California, Davis, CA). Plates were incubated overnight at 25 °C, washed and 200 µl of 3,3',5,5''-tetramethylbenzidine containing 0.01% hydrogen peroxide TMB (Kirkegaard and Perry, Gaithersburg, MD) was added to each well. Each plate was incubated at 25 °C with shaking in a reader for approximately 5 min. Then 0.5 M HCl, 50 µl per well, was added to stop color development and an endpoint reading was taken at 450 nm. Analysis of standards and samples was done on a 4 parameter logistic curve fit. A stock solution of cortisol was made in ethyl alcohol and standards were diluted in Ringers. Sensitivity, as defined by the dose–response curve, was measurable from 1 ng ml^{-1} to 200 ng ml^{-1} .

2.5. Gill histology

To measure chloride cell size and numbers, gill arches were removed and placed into freshly mixed Champy–Maillet's fixative (0.2% osmium tetraoxide, 25 mg ml⁻¹ iodine, and saturated metallic zinc) for 16 h (Avella et al., 1987). The tissue was rinsed with deionized water and dehydrated to 70% ethanol for storage. The gill tissue was examined using a compound microscope at 40× magnification. Number and size of chloride cells from the first gill arch were measured from a digital image and applying a computerized image analysis system (Image-J, National Institutes of Heath, Bethesda, MD). A stage micrometer was used for calibration.

3. Statistical analysis

For seasonal changes in length, weight, and condition factor (CF; $100 \times WL^{-3}$), a three-way analysis of variance (ANOVA) was used to determine whether time of sampling, temperature regime or suspended sediment treatment had a significant effect on these variables. For

¹ Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

seasonal changes in gill Na⁺,K⁺-ATPase activity and plasma cortisol concentration, a three-way analysis of covariance (ANCOVA) was used to determine whether time of sampling, temperature regime or suspended sediment treatment had a significant effect on these variables; length was used as a covariate. A two-way ANCOVA was used for chloride cells sampled on June 12. When factors were found to be statistically significant, Tukey's test was used to determine differences between the treatments and time interval. Statistical significance was accepted at a level of p < 0.05. All values are expressed as means ± 1 SE.

4. Results

Weight and length increased steadily from February to June in all groups (Fig. 2a and b). Three-way ANOVA indicated that there was a significant effect of date ($F_{5,867}$ =1220, p<0.001), temperature regime ($F_{1,867}$ =21.8, p<0.001), and suspended sediment treatment ($F_{1,867}$ =76.6, p<0.001) on weight. Similarly, there was a significant effect of date ($F_{5,867}$ =2000, p<0.001),



Fig. 2. A, Mean weight (g), B, length (cm), and C, condition factor (CF, 100 g cm⁻³) for juvenile chinook salmon sampled from February 26 to June 12. The four groups were control (C), daily fluctuation in temperature averaging 7.5 °C (T), pulsed increase in suspended sediment concentration of 200 mg Γ^{-1} (S), or a combination of both treatments (T×S). Each group was composed of three replicate tanks. * indicates values significantly different from control fish. Values are mean±1 SEM.



Fig. 3. A, Gill Na⁺,K⁺-ATPase activity (μ mol ADP mg⁻¹ of protein h⁻¹) and B, plasma cortisol concentration (ng ml⁻¹) for juvenile chinook salmon. Groups as described in Fig. 2. * indicates values significantly different from control fish. Values are mean±1 SEM.

temperature regime ($F_{1,867}$ =13.9, p<0.001), and suspended sediment treatment ($F_{1,867}$ =59.5, p<0.001) on length. In the first month of the study, there was little difference between any of the treatment groups. By late April, however, group T×S was significantly smaller than group C (Fig. 2a). On May 30 and June 12 sample dates, groups S and T×S fish were significantly smaller than control fish. Although, temperature treatment alone did not result in a significant difference in size from the control fish, T fish did not differ significantly from the S or T×S fish until the last sample time.

Condition Factor increased over the spring (Fig. 2c). Threeway ANOVA indicated that there was a significant effect of date ($F_{5,867}$ =74.0, p<0.001), temperature regime ($F_{1,867}$ =8.54, p<0.005), and suspended sediment treatment ($F_{1,867}$ =13.6, p<0.001) on CF. Generally control fish had the highest values of CF, followed by T, then S, and the T × S fish had the lowest levels of CF. Tukey's test, however, did not indicate significant differences between the group means sampled on a common date.

Gill Na⁺,K⁺-ATPase activity increased over the spring, but the increases were markedly greater in May for the C and T fish, than the S and T×S fish (Fig. 3a). ANCOVA using length as a covariate indicated that there was a significant effect of date $(F_{5,393}=8.25, p<0.001)$ and suspended sediment treatment $(F_{1,393}=21.7, p<0.001)$, but not temperature regime $(F_{1,393}=$ 0.12, p=0.73) on Na⁺,K⁺-ATPase activity. Statistics for the length covariate were also not significant $(F_{1,393}=0.231, p=0.63)$. Gill Na⁺,K⁺-ATPase activities did not show a significant increase over the spring for S and T×S fish. For C and T fish, gill Na⁺,K⁺-ATPase activities peaked at the end of

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Table 1 Length, weight, gill Na⁺,K⁺-ATPase activity, and gill chloride cell size and density for juvenile chinook salmon sampled on June 12

Group	Length ¹	Weight ²	Na ⁺ ,K ⁺ - ATPase	Chloride cell	
			Activity ³	Size ⁴	Density ⁵
С	8.1 ± 0.1	5.79 ± 0.27	$3.29 {\pm} 0.26$	$130.9 {\pm} 9.6$	1.61 ± 0.05
Т	$8.2\!\pm\!0.1$	$6.16{\pm}0.34$	$3.61\!\pm\!0.37$	113.1 ± 15	1.63 ± 0.07
S	$8.0\!\pm\!0.1$	$5.29\!\pm\!0.21$	2.64 ± 0.33	83.1 ± 4.6	1.43 ± 0.07
$T \times S$	$7.8\!\pm\!0.1$	$5.12 {\pm} 0.18$	$2.35 \!\pm\! 0.29$	87.6 ± 8.1	1.48 ± 0.06

The four groups were control (C), daily fluctuation in temperature averaging 7.5 °C (T), pulsed increase in suspended sediment concentration of 200 mg l^{-1} (S), or a combination of both treatments (T × S). Each group was composed of three replicate tanks and four fish were sampled per tank.

¹ cm, ² g, ³µmol ADP mg⁻¹ of protein h⁻¹, ⁴average surface area of chloride cells on the primary lamellae, μ m², and ⁵average number of gill chloride cells on the primary lamellae between two secondary lamellae.

May and then declined significantly by the last sample date on June 12. Peak activities for the C and T fish were significantly greater than the S and $T \times S$ fish.

There was a significant effect of date ($F_{4,227}$ =4.01, p<0.005), but not suspended sediment treatment ($F_{1,227}$ =0.38, p=0.54) and not temperature regime ($F_{1,227}$ =0.88, p=0.35) on plasma cortisol concentrations (Fig. 3b). Statistics for the length covariate were also not significant ($F_{1,227}$ =1.04, p=0.31). Plasma cortisol levels increased during the spring and had the highest values in mid-and late-May. Tukey's test indicated that the oscillating temperature group and suspended sediment group showed significant increases in plasma cortisol concentration during the month of May. Significant differences between sample dates were not seen for the control or combined treatment groups.

Gill chloride cell size did not differ significantly due to temperature ($F_{1,45}$ =0.20, p=0.66) or suspended sediment ($F_{1,45}$ = 2.67, p=0.11) treatments (Table 1). The number of chloride cells on the primary lamellae between each secondary lamellae also did not differ significantly due to temperature ($F_{1,45}$ =1.97, p=0.17) or suspended sediment ($F_{1,45}$ =4.00, p=0.051) treatments.

Mortality was low for each treatment group. Temperature manipulations and suspended sediment treatments did not appear to influence survival. Cumulative mortality as a percentage for each group over the duration of the study was also similar for the different treatments; control, 1.7 ± 1.1 ; temperature, 2.4 ± 1.2 ; suspended sediment, 3.1 ± 1.5 ; and combined, 0.7 ± 0.7 .

5. Discussion

Rearing environment has previously been shown to affect growth and smolting in juvenile salmonids (Shrimpton et al., 1994a). In enhancement facilities, water quality guidelines have been established to minimize deleterious effects on fish. Sufficient flows are used to maintain oxygen levels, limit particulates, and maintain temperatures. In natural systems, however, these parameters vary and often exceed criteria established for enhancement. Yet, indices of smolting have been found to be much greater in wild than hatchery-reared coho (Shrimpton et al., 1994b) and Atlantic salmon (McCormick and Björnsson, 1994). The magnitude and/or the duration of such perturbations in water quality must, therefore affect the response of the fish to the stimulus.

5.1. Growth

Our results demonstrate that daily oscillation in temperature and pulsed treatment with suspended sediment negatively affected growth. For our experimental regimes, suspended sediment had a greater effect on fish growth than oscillating temperature (Fig. 2a,b). The impact of suspended sediment on fish is dependent on the sediment concentration and duration of exposure and the response of fish to suspended sediment varies with these two variables (Newcombe and Jensen, 1996). In juvenile coho salmon, a sudden increase in suspended sediment (60 nephelometric turbidity units; NTU) produced an alarm reaction and fish were observed to swim sporadically (Berg and Northcote, 1985). Increased flaring was observed following a sediment pulse that may have been due to gill irritation. McLeay et al. (1984) observed avoidance and downstream movement of Arctic grayling (Thymallus arcticus) in response to a sediment pulse. In association with behavioral changes, physiological and stress responses have been documented in fish exposed to increased suspended sediments. Plasma cortisol levels increased within 3 h in yearling steelhead (O. mykiss) exposed to clay, ash or topsoil suspended at concentration of approximately 400 mg 1^{-1} (Redding et al., 1987). Although, our concentration of suspended sediment was approximately half of that used by Redding et al. (1987), the daily pulses likely elicited a stress response in the juvenile chinook in the present study.

Rate of growth in salmonids is dependent on mean temperature (Brett et al., 1982). Mean temperatures of all tanks in the present experiment were similar and the total degree days over the duration of the study were also similar; yet oscillating temperature had a significant effect on growth. Lyytikäinen and Jobling (1998) found that rates of oxygen consumption under fluctuating temperature conditions (2 °C) were higher than at constant temperatures in Arctic charr. These authors suggested that the additional metabolic cost was the result of the increased activity that fish exhibit when temperature changes. Greater daily oscillations in temperature cycles from 6.5 to 20 °C resulted in significant increases in plasma cortisol

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concentrations; plasma cortisol concentrations for fish held in water that oscillated from 9 to 15 °C did not differ from the constant 11 °C group (Thomas et al., 1986). We did not assess whether the daily oscillations in temperature were stressful for the fish, but the temperature treatment in combination with the suspended sediment treatments lead to the greatest reduction in growth and is suggestive of a stress (Fig. 2a and b). Barton et al. (1986) demonstrated that multiple acute disturbances were cumulative in juvenile chinook salmon. A similar effect may have occurred in the present experiment, where temperature oscillation was stressful and cumulative to the suspended sediment treatment.

Daily stresses have previously been demonstrated to reduce growth rate in Atlantic salmon, and the more severe stress lead to a greater reduction in growth (McCormick et al., 1998). The magnitude of temperature oscillations (Thomas et al., 1986) and the duration and dose of suspended sediment treatments (Newcombe and Jensen, 1996) is associated with the severity of effect. Larger oscillations in temperature and higher concentrations of suspended sediment would have been more stressful and likely lead to a greater reduction in growth rate in the present experiments. The levels chosen for our study were similar to values measured by researchers examining water quality following landscape disturbances from forest harvesting (Brown and Krygier, 1970; Macdonald et al., 2003a,b; Mellina et al., 2005; Shrimpton, unpublished data). We did not, however, find any synergism between suspended sediment concentration and oscillating temperature on growth.

It is possible that the increased turbidity of the suspended sediment treatments may have negatively affected feeding. Gregory and Northcote (1993) found that reaction distance to surface, planktonic and benthic prey decreased with higher turbidity. Foraging rates, however, for surface and benthic prey increased at intermediate turbidity levels (35-150 NTU). The authors speculated that increased feeding rate in turbid conditions may reflect a reduced potential risk to predation. Although, fish were fed throughout the day in the present experiment, there is also the possibility that increased activity may have occurred after the sediment pulse when food was not available. This behavior would have had a negative effect on growth in the sediment treatment groups due to an increase in activity. In our study, the pulse of sediment cleared from each tank in less than 8 h and all tanks were visibly clearer in approximately 3 h. Although CF was significantly affected by temperature and suspended sediment treatments, fish were also fed in the morning before sediment treatment and at the end of the day and would have had an opportunity to feed in clear water.

5.2. Smolting

Suspended sediment treatment, but not daily oscillating temperature had a significant effect on gill Na⁺, K^+ -ATPase activity (Fig. 3a), and a similar trend was found for the number of chloride cells on the primary lamellae (Table 1). The natural run of Robertson Creek and Big Qualicum chinook is from mid-May to early-June and enhanced fish released past mid-June show poor return rates (R. Volk, Robertson Creek Salmonid Enhancement Facility, Port Alberni, BC, personal *communication*). Gill Na⁺,K⁺-ATPase activity in control and oscillating temperature fish peaked within the natural smolt window for this stock; suspended sediment treatment, therefore, appears to have inhibited smolting. Fish in the suspended sediment treatments were smaller than control fish or the oscillating temperature groups. The significant size difference may have contributed to differences in gill enzyme activity and smolting. Size has been shown to be an important factor in development of saltwater tolerance for a number of species of salmonids (Hoar, 1988). A minimum size also appears necessary before smolting can occur; this appears to be approximately 5 g in juvenile chinook (Clarke, 1982). Mean weight of fish at the final sample date was greater than 5 g for all groups, except for the combined temperature and suspended sediment group. The maximum gill Na⁺, K⁺-ATPase activities, however, were not measured for the last sample date, but 2 weeks earlier. At this time, all fish were approximately 4 g in size. The oscillating temperature fish and the suspended sediment treated fish did not differ significantly in size, yet Na⁺,K⁺-ATPase activities differed significantly between these two groups. Size, therefore, does not appear to account for the effect of suspended sediment on smolting.

The increases in water flow during the spring, not only increase migration rate in juvenile salmonids (Raymond, 1979), but also increase the level of suspended sediments (Youngson et al., 1986). A pulsed increase in suspended sediment concentration has been found to be associated with a change from upstream to downstream swimming that increases during the smolt window (Specker et al., 2000). The change in orientation may be associated with avoidance of the turbidity (Berg and Northcote, 1985), but Specker et al. (2000) found that increased turbidity elevated thyroxine levels and changed direction of movement in Atlantic salmon. Their results suggest that suspended sediment during spring may also provide an environmental cue for migration during the parr-smolt transformation. Chronic elevation in suspended sediment content, however, is stressful for fish (e.g. Redding et al., 1987). Shrimpton et al. (1994a) found that hatcheryreared coho salmon subjected to water with higher suspended sediment content showed impaired smolt performance; lower gill Na⁺,K⁺-ATPase activities and poorer saltwater survival. The daily pulses of suspended sediment treatment were started in early April in the present study and were found to inhibit smolting.

The thermal regime that the fish experience is of importance and will affect the timing and duration of smolting (McCormick et al., 1997; Clarke et al., 1981). In our experiment, indices of smolting did not differ between the fluctuating temperature groups and the constant temperature groups: degree days were similar for all experimental tanks. The number of degree days has been shown to be linked to physiological and behavioral changes associated with smolting. In an experiment where Atlantic salmon were reared under different temperature regimes, the initiation and termination of downstream movement occurred at the same number of degree days (Zydlewski et al., 2005).

A seasonal increase in plasma cortisol was seen among the groups, but there was no effect of oscillating temperature or suspended sediment treatment on cortisol. Circulating cortisol levels, therefore, did not contribute to the significant differences in gill Na⁺,K⁺-ATPase activities among treatments. We did not measure daily changes in plasma cortisol in response to temperature change or suspended sediment, but both of these treatments have previously been shown to stress fish. Stress-associated with rearing conditions has also been linked to impaired smolting in coho salmon (Shrimpton et al., 1994b). A potential mechanism for impaired smolting is that stress decreases gill responsiveness to cortisol through a downregulation of gill cortisol receptors (Shrimpton and Randall, 1994; Shrimpton and McCormick, 1999). Decreased gill responsiveness, but not interrenal responsiveness, therefore, may account for the differences in smolting observed among the groups.

6. Consequence

The recovery of aquatic systems following landscape disturbance may take many years. For example, temperatures during the summer remained 4 to 6° warmer, and diurnal temperature variation remained higher than in control streams following forest harvesting (Macdonald et al., 2003b). Additionally, hydrologic recovery did not occur during five years of monitoring. Suspended sediment levels, however, did show a return to pre-treatment levels within five years (Macdonald et al., 2003a). The effect of decreased water quality on fish has been less well documented, but results are equivocal. Some researchers have found little or no difference in fish size (Mellina

et al., 2005), while others have found a negative effect due to landscape disturbance (Arndt et al., 2002; Shrimpton, unpublished data). Given the findings of Macdonald et al. (2003a, b), environmental disturbance may impact multiple year classes of salmon.

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References

- Arndt, S.K.A., Cunjak, R.A., Benfey, T.J., 2002. Effect of summer floods and spatial-temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams. Trans. Am. Fish. Soc. 131, 607–622.
- Avella, A., Masoni, A., Bornancin, M., Mayer-Gostan, N., 1987. Gill morphology and sodium influx in the rainbow trout (*Salmo gairdneri*) acclimated to artificial freshwater environments. J. Exp. Zool. 241, 159–169.
- Barton, B.A., Schreck, C.B., Sigismondi, L.A., 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. Trans. Am. Fish. Soc. 115, 245–251.
- Berg, L., Northcote, T.G., 1985. Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. Can. J. Fish. Aquat. Sci. 42, 1410–1417.
- Brett, J.R., Clarke, W.C., Shelbourn, J.E., 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon *Oncorhynchus tshawytscha*. Can. Tech. Rep. Fish. Aquat. Sci. 1127, 29.
- Brown, G.W., Krygier, J.T., 1970. Effects of clear-cutting on stream temperature. Water Resour. Res. 6, 1133–1139.
- Carey, J.B., McCormick, S.D., 1998. Atlantic salmon smolts are more responsive to handling and confinement stress than parr. Aquaculture 168, 237–253.
- Clarke, W.C., 1982. Evaluation of the seawater challenge test as an index of marine survival. Aquaculture 28, 177–183.
- Clarke, W.C., Shelbourn, J.E., Brett, J.R., 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. Aquaculture 22, 105–116.
- Gregory, R.S., Northcote, T.G., 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can. J. Fish. Aquat. Sci. 50, 233–240.
- Hoar, W.S., 1988. The physiology of smolting salmonids. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, vol. 11B. Academic Press, New York, pp. 275–344.
- Lyytikäinen, T., Jobling, M., 1998. The effect of temperature fluctuations on oxygen consumption and ammonia excretion of underyearling Lake Inari Arctic charr. J. Fish Biol. 52, 1186–1198.

- Macdonald, J.S., Beaudry, P.G., MacIsaac, E.A., Herunter, H.E., 2003a. The effects of forest harvesting and best management practices on streamflow and suspended sediment concentrations during snowmelt in headwater streams in sub-boreal forests of British Columbia, Canada. Can. J. For. Res. 33, 1397–1407.
- Macdonald, J.S., MacIsaac, E.A., Herunter, H.E., 2003b. The effects of variable-retention riparian buffer zones on water temperatures in small headwater streams in sub-boreal forest ecosystems of British Columbia. Can. J. For. Res. 33, 1371–1382.
- McCormick, S.D., 1993. Methods for the nonlethal gill biopsy and measurements of Na⁺,K⁺-ATPase activity. Can. J. Fish. Aquat. Sci. 50, 656–658.
- McCormick, S.D., Saunders, R.L., 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. Am. Fish. Soc. Symp. 1, 211–229.
- McCormick, S.D., Björnsson, B.Th., 1994. Physiological and hormonal differences among Atlantic salmon parr and smolts reared in the wild and hatchery smolts. Aquaculture 121, 235–244.
- McCormick, S.D., Shrimpton, J.M., Zydlewski, J.D., 1997. Temperature effects on osmoregulatory physiology of anadromous fish. In: Wood, C.M., McDonald, D.G. (Eds.), Society for Experimental Biology Seminar Series 61: *Global Warming: Implications for freshwater and marine fish.* Cambridge University Press, pp. 279–301.
- McCormick, S.D., Shrimpton, J.M., Sloan, K.E., O'Dea, M.F., Carey, J.B., Moriyama, S., Björnsson, B.Th., 1998. Repeated acute stress reduces growth rate of Atlantic salmon parr and alters plasma growth hormone, insulin-like growth factor 1 and cortisol. Aquaculture 168, 221–235.
- McCormick, S.D., Moriyama, S., Björnsson, B.Th., 2000. Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. Am. J. Physiol. 278, R1352–R1361.
- McCormick, S.D., Shrimpton, J.M., Moriyama, S., Björnsson, B.Th., 2002. Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. J. Exp. Biol. 205, 3553–3560.
- McLeay, D.J., Ennis, G.L., Birtwell, I.K., Hartman, G.F., 1984. Effects on Arctic grayling (*Thymallus arcticus*) of prolonged exposure to Yukon placer mining sediment: a laboratory study. Can. Tech. Rep. Fish. Aquat. Sci. 1241, 96.
- Mellina, E., Hinch, S.G., Donaldson, E.M., Pearson, G., 2005. Stream habitat and rainbow trout (*Oncorhynchus mykiss*) physiological stress responses to streamside clear-cut logging in British Columbia. Can. J. For. Res. 35, 541–556.

- Newcombe, C.P., Jensen, J.O.T., 1996. Channel suspended sediment and fisheries: a synthesis for quantitative assessment of risk and impact. N. Am. J. Fish. Manag. 16, 693–727.
- Raymond, H.L., 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108, 505–529.
- Redding, J.M., Schreck, C.B., Everest, F.H., 1987. Physiological effects on coho salmon and steelhead of exposure to suspended solids. Trans. Am. Fish. Soc. 116, 737–744.
- Shrimpton, J.M., Randall, D.J., 1994. Downregulation of corticosteroid receptors in the gills of coho salmon due to stress and cortisol treatment. Am. J. Physiol. 267, R432–R438.
- Shrimpton, J.M., McCormick, S.D., 1999. Responsiveness of gill Na⁺K⁺ATPase to cortisol is related to gill corticosteroid receptor concentration in juvenile rainbow trout. J. Exp. Biol. 202, 987–995.
- Shrimpton, J.M., Bernier, N.J., Iwama, G.K., Randall, D.J., 1994a. Differences in measurements of smolt development between wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) before and after saltwater exposure. Can. J. Fish. Aquat. Sci. 51, 2170–2178.
- Shrimpton, J.M., Bernier, N.J., Randall, D.J., 1994b. Changes in cortisol dynamics in wild and hatchery reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. Can. J. Fish. Aquat. Sci. 51, 2179–2187.
- Specker, J.L., Eales, J.G., Tagawa, M., Tyler III, W.A., 2000. Parrsmolt transformation in Atlantic salmon: thyroid hormone deiodination in liver and brain and endocrine correlates of change in rheotactic behavior. Can. J. Zool. 78, 696–705.
- Sumpter, J.P., Dye, H.M., Benfey, T.J., 1986. The effect of stress on plasma ACTH, -MSH, and cortisol in salmonid fishes. Gen. Comp. Endocrinol. 62, 377–385.
- Thomas, R.E., Gharrett, J.A., Carls, M.G., Rice, S.D., Moles, A., Korn, S., 1986. Effects of fluctuating temperature on mortality, stress, and energy reserves of juvenile coho salmon. Trans. Am. Fish. Soc. 115, 52–59.
- Youngson, A.F., McLay, H.A., Olsen, T.C., 1986. The responsiveness of the thyroid system of Atlantic salmon (*Salmo salar L.*) smolts to increased water velocity. Aquaculture 56, 243–255.
- Zydlewski, G.B., Haro, A., McCormick, S.D., 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. 62, 68–78.