Aquatic Sciences

RESEARCH ARTICLE

Estimation of forest harvesting-induced stream temperature changes and bioenergetic consequences for cutthroat trout in a coastal stream in British Columbia, Canada

J. A. Leach · R. D. Moore · S. G. Hinch · T. Gomi

Abstract Data from a paired-catchment study in south coastal British Columbia, Canada, were analyzed to assess the thermal effects of clearcut harvesting with no riparian buffer on a fish-bearing headwater stream. The approach used time series of daily mean water temperatures for East Creek (control) and A Creek (treatment), both before and after harvest. Statistical models were developed to predict (a) what the temperatures would have been in the post-harvest period had harvesting not occurred, and (b) what temperatures would have been in the pre-harvest period had harvesting already occurred. The Wisconsin Bioenergetics Model was used to simulate growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) for the first year following fry emergence using the predicted and observed stream temperatures to generate scenarios representing with-harvest and no-harvest thermal regimes. A Monte Carlo approach was used to quantify the effects of uncertainty associated with the regression models on predicted stream temperature and trout growth. Summer daily mean temperatures in the with-harvest scenario were up to 5°C higher than those for the no-harvest scenario. Harvesting-induced warming reduced growth rates during summer, but increased growth rates during autumn and spring. In the with-harvest scenario, trout were 0.2–2.0 g (absolute weight) smaller throughout the winter period than in the no-harvest scenario. However, the bioenergetic simulations suggest that trout growth may be more sensitive to potential changes in food supply following harvesting than to direct impacts of stream temperature changes.

Keywords Stream temperature · Forest harvesting · Bioenergetics modelling · Paired-catchment study · Autocorrelation · Cutthroat trout

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Introduction

Forest harvesting along streams reduces canopy shade and typically increases summer stream temperature due to increased solar irradiance at the water surface (Beschta et al. 1987; Moore et al. 2005a). In some cases, temperatures may rise above known mortality thresholds for species of concern (typically cold-water species such as salmonids), with clear biological consequences. In other cases, temperature increases may not produce mortality, but could have behavioural or developmental consequences and influence disease resistance and/or species competition (McCullough et al. 2009). In addition, temperature changes could influence timing of emergence and/or developmental or growth rates. For example, at Carnation Creek, BC,

Canada, a small post-harvesting increase in winter stream temperature had a more profound effect on developmental stages of coho salmon (*Oncorhynchus kisutch*) than did the larger summer temperature increase (Holtby 1988).

Understanding the relative influences of direct and indirect impacts of increased stream temperature following harvesting on fish health, condition, growth, and survival poses a major challenge for two primary reasons. First, forest harvesting influences aquatic ecosystems in ways beyond just stream temperature effects; fish survival and growth response to forest harvesting are the result of complex interactions occurring in the aquatic environment (Hicks et al. 1991). Second, assessment of potentially sub-lethal effects on fish growth requires an estimate of what water temperatures would have been in the absence of harvesting. Such an estimate can be made using a paired-catchment approach, which involves the use of an untreated control stream and data collection both pre- and post-harvest. However, even where a paired-catchment approach is used to quantify stream temperature response to forest harvesting (e.g., Brown and Krygier 1970; Rishel et al. 1982; Johnson and Jones 2000), assessing the biological or ecological consequences can be difficult. The temperature metrics typically reported in paired-catchment studies, such as summer maximum temperature, may not be appropriate for estimating competitive interactions among species or seasonal bioenergetic effects (Moore et al. 2005a).

A potential approach for identifying sub-lethal seasonal impacts of stream temperature response to harvesting is through the use of fish bioenergetic modelling. Bioenergetics models simulate an energy budget for an individual fish (or cohort) given information on stream thermal conditions and fish diet (Hansen et al. 1993). Consumption and metabolic processes are simulated using biologically based equations parameterized using laboratory and field data to estimate fish growth rates (Hanson et al. 1997). Whereas bioenergetics models are recognized as being uncertain in their formulation and parameter values, they have been used and evaluated extensively in the last two decades and provide a heuristic tool to isolate the effects of temperature and diet on fish growth (Railsback and Rose 1999; Hartman and Kitchell 2008).

Most bioenergetics models require daily mean temperature time series, as the seasonal timing of temperature changes is important. Statistical approaches such as generalized least squares regression can account explicitly for the presence of autocorrelation in regression residuals, and have made it possible to develop reliable pre-harvest regression models for daily stream temperature using 1–2 years of data (Gomi et al. 2006; Groom et al. 2011). In this study, we analyzed daily stream temperature data from a paired-catchment study in order to understand seasonal effects of forest harvesting on stream temperature and its biological consequences. We build on the approach introduced by Gomi et al. (2006) and fit stream temperature regression models to develop paired scenarios for "with-harvest" and "no-harvest" stream temperatures, which are then used as input to a bioenergetics model to simulate cutthroat trout growth during the first year following emergence. Previous research suggests that post-harvest changes in fish food supply can strongly influence fish growth (Mellina and Hinch 2009). Therefore, sensitivity of the bioenergetics model to the value of the feeding parameter was evaluated to explore the potential effects of post-harvest changes in food supply. While this study focuses on the effects of forest harvesting, the approach provides a heuristic framework that may be more generally applicable for separating thermal influences of land-use and/or climatic change on aquatic organisms from other changes, such as increased food supply associated with changes in primary productivity.

Methods

Study site

The study was conducted at the University of British Columbia's Malcolm Knapp Research Forest, located approximately 60 km east of Vancouver, BC, Canada (Fig. 1), as part of a broader experiment on the effects of varying buffer width on stream-riparian ecology (Kiffney et al. 2000). The study area has a maritime climate with wet, mild winters and warm, dry summers. The forest cover is dominated by western hemlock (*Tsuga heterophylla*) with some western red cedar (*Thuja plicata*) and Douglas-fir (*Pseudotsuga menziesii*). Prior to experimental harvesting, the forest was dominantly mature second growth about 30–40 m tall, with crown closure from 75 to 95%.

This study focused on A Creek (treatment) and East Creek (control), which contain resident non-anadromous populations of coastal cutthroat trout (*Oncorhynchus clarki clarki*); no other fish species naturally occur in these streams. For A Creek, the monitoring site is located at the lower end of the cut block at an elevation of 125 m above sea level (masl). Drainage areas at the upstream and downstream ends of the cutblock are 46 and 59 ha, respectively. Channel morphology is dominated by step-pool structures formed by sediment accumulation upstream of woody debris and boulders, with scour downstream of the steps. The stream flows over bedrock at some locations. The mean pool spacing is about 8 m (Winfield 2002).

Between 19 October 1998, and 9 January 1999, clearcut harvesting with no buffer occurred along a 325 m section of the stream and comprised approximately 20% of the catchment area. Harvesting slash was left in the channels

Fig. 1 Map of study site
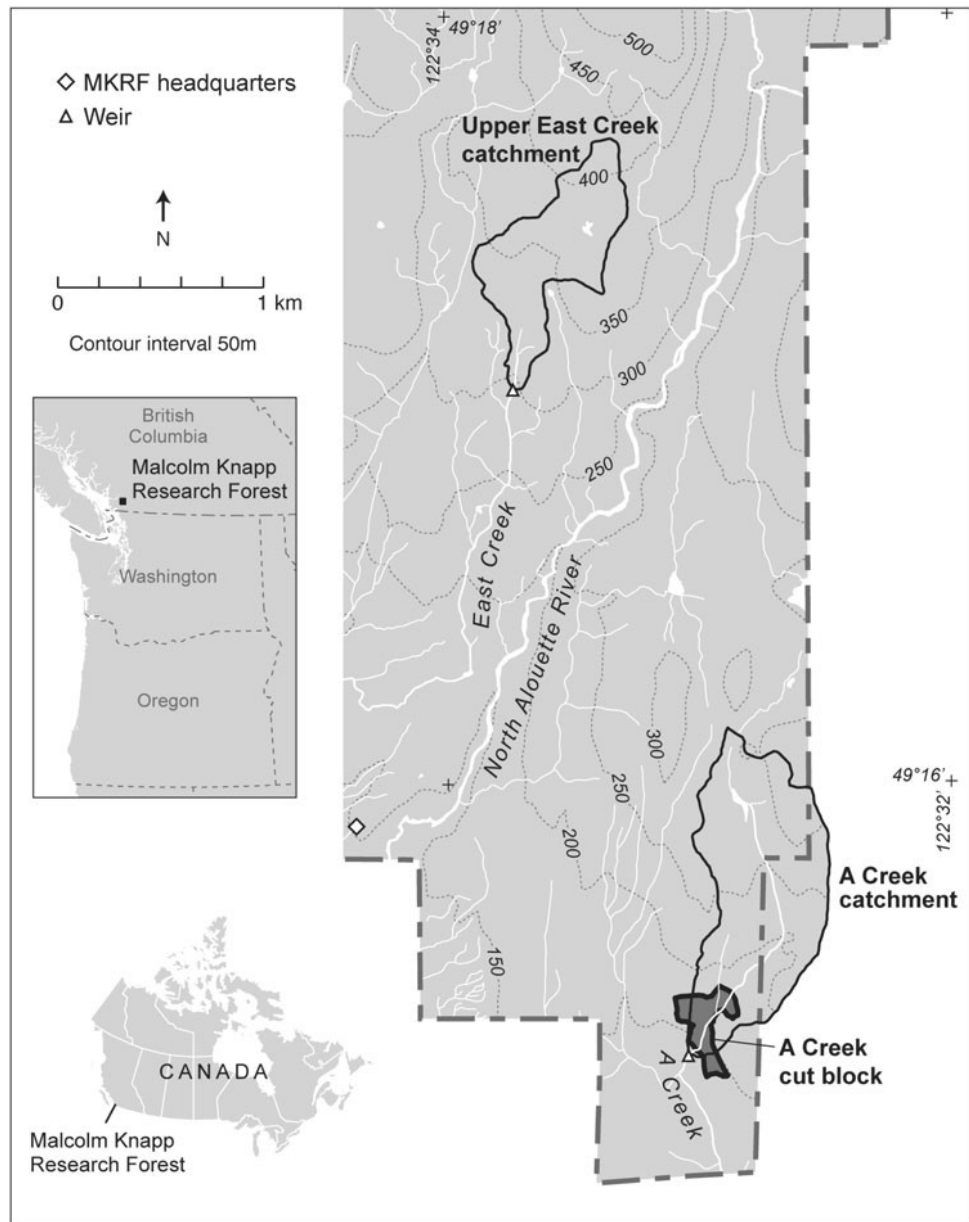
and riparian zone; however, excessive slash did not accumulate over the stream as has been observed, for example, in the Washington Coast Range (Jackson et al. 2001). Within the treatment unit, the stream has a mean gradient of 12% and a mean bankfull width of 4 m. The control stream, East Creek, is located about 3 km northwest of A Creek and has a mean gradient of 8% and a mean bankfull width of 3 m. At the monitoring site, East Creek has an elevation of 290 masl, a drainage area of 38 ha, and the riparian zone consists of mature forest vegetation. Further information about the study sites is provided by Moore et al. (2005b) and Gomi et al. (2006).

Field measurements

Stream temperature was recorded from 1997 to 2002 using submersible temperature loggers with ±0.2°C accuracy (Stowaway Tidbit and HOBO Loggers, Onset Computer Corporation). Loss of loggers during high-flow events resulted in some data gaps, mainly in winter. The loggers were housed in PVC pipe with multiple drill holes to promote water exchange and were placed at shaded locations (e.g., below undercut banks or large wood) in areas with deep, flowing water to ensure continuous submergence.

Daily mean stream temperatures were calculated from the stream temperature logger records. Recording intervals were initially 30 min in 1997, but were increased to 192 min later in the study. Whereas this increase in recording interval can result in under- and over-estimation of the daily maxima and minima, respectively, the diurnal temperature waves had sufficiently broad peaks and troughs that this error did not significantly influence the results, even after harvesting (Gomi et al. 2006). For example, using data with 10-min resolution collected at A Creek in 2001, the effect of sampling every 190 min on daily means was less than ±0.2°C, compared to means calculated from 10-min resolution data.

Daily weather observations were recorded at the Research Forest Headquarters station, located approximately 2 km from A Creek at an elevation of 145 masl. Measurements include daily maximum and minimum air temperature, as well as hourly and daily precipitation.

Stream temperature analysis

Statistical models were used to estimate what the stream temperatures would have been in the post-harvest period had harvesting not occurred, as well as what temperatures would have been during the pre-harvest period had harvesting occurred at that time (Table 1). Together, these models allowed us to generate time series of "no-harvest" and "with-harvest" daily mean stream temperatures for both the pre- and post-harvest periods. The statistical approach is similar to that of Moore et al. (2005b), but uses an autoregressive integrated moving average with external regressors (ARIMAX) model to account for autocorrelated residuals instead of generalized least squares regression. The following model was fitted to the pre-harvest data, in order to predict "no-harvest" stream temperature in the post-harvest period:

$$Tnh_t = \beta_0 + \beta_1 sin(2\pi j/T) + \beta_2 cos(2\pi j/T) + \beta_3 EC_t + \varepsilon_t \quad (1)$$

where Tnh_t is the mean daily water temperature (°C) at A Creek on day t, $\beta_0, \beta_1, \beta_2, \beta_3$ are coefficients to be estimated, j is the day of year ($j = 1$ on January 1), $T = 365.25$ is the number of days in a year, EC_t is the corresponding mean daily water temperature (°C) at the control stream (East Creek), and ε_t is an error term, which was modelled as an autoregressive process of order k:

$$\varepsilon_t = \rho_1\varepsilon_{t-1} + \rho_2\varepsilon_{t-2} + \cdots + \rho_k\varepsilon_{t-k} + u_t \quad (2)$$

where ρ_k is the autocorrelation between error terms at a lag of k days, ε_{t-k} is the error term k days before day t, and u_t is a random disturbance (white noise), assumed to be normally distributed with constant variance. The order k was

Table 1 Summary of the use of observed and predicted stream temperature time series at A Creek for generating with-harvest and no-harvest scenarios for the pre- and post-harvest periods

Scenario	Time period	
	Pre-harvest (May 1997 to October 1998)	Post-harvest (January 1999 to August 2002)
No-harvest	Observed	Predicted (Eqs. 1, 4)
With-harvest	Predicted (Eqs. 3, 5)	Observed

determined by examining partial autocorrelation functions and plots of the pre-harvest residuals and retaining only the terms with statistically significant partial autocorrelation coefficients (Venables and Ripley 1997). The sine and cosine terms in Eq. 1 account for seasonality in the residuals (Watson et al. 2001).

To estimate "with-harvest" stream temperatures for the pre-harvest period, the following model was fitted to the post-harvest data:

$$Twh_t = \beta_0 + \beta_1 sin(2\pi j/T) + \beta_1 cos(2\pi j/T) + \beta_3 EC_t + \beta_4 EC_t^2 + \beta_5 Ta_t + \varepsilon_t \quad (3)$$

where Twh_t is the mean daily water temperature (°C) at A Creek on day t, Ta_t is the mean daily air temperature (°C) at the Research Forest Headquarters, $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5$ are coefficients to be estimated, and the quadratic term for East Creek water temperature was included to remove nonlinearity as revealed in a plot of residuals against fitted values. The remaining terms are identical to those in Eq. 1. Table 1 summarizes the use of observed and predicted stream temperature time series for assessing the effect of harvesting.

Estimation of missing data

Computing total trout growth over the first year following emergence requires a complete time series of daily mean water temperatures. Unfortunately, there were some missing data for both A Creek (24 of 537 days during the pre-harvest period and 143 of 1,319 days during the post-harvest period) and East Creek (27 of 1,856 days). Missing mean daily stream temperatures for A Creek were interpolated using ordinary least squares (OLS) linear regression models. The predictor variables used were mean daily air temperature and the sine and cosine terms (Eq. 1). Separate models were developed for the pre- and post-harvest periods. Although the models exhibited autocorrelated residuals, the coefficient estimates from OLS regression are unbiased and can be used for interpolation (Kutner et al. 2005). The pre- and post-harvest models had R^2_{adj} values of 0.95 and standard errors of estimate of 0.80°C and 0.86°C, respectively.

Bioenergetics model

The Wisconsin Bioenergetics Model (Hanson et al. 1997) was used to explore the effects of stream temperature response to forest harvesting on fish growth. Unfortunately, no fish physiological parameter sets have been established for cutthroat trout for use in the Wisconsin Bioenergetics Model. Therefore, the physiological parameter set for rainbow (steelhead) trout (*Oncorhynchus mykiss*) established by Rand et al. (1993) was used. The validity of this substitution, which has been used in previous studies (Raggon 2010), is supported by the fact that hybridization of cutthroat and rainbow trout occurs naturally (Campton and Utter 1985).

Bioenergetic modelling requires both daily stream temperature data and information on fish diet. The regression models and observed data provided the temperature input data. Trout prey energy density was assumed to be 2,500 J/g wet mass, which represents both terrestrial and aquatic food sources (Hanson et al. 1997) and is a value that has been used elsewhere (Railsback and Rose 1999). No reasonable estimates of seasonal dynamics in prey energy densities were available; therefore, prey energy density was assumed constant throughout the study.

The Wisconsin Bioenergetics Model contains a parameter, P, which accounts for ecological constraints on the feeding rate. It is a ratio between the actual feeding rate of the fish and the ad libitum maximum feeding rate based on fish size at a specific water temperature (Hanson et al. 1997). Coastal cutthroat trout growth data collected at East Creek in 1997 and 1998 (Boss 2000; Boss and Richardson 2002) were used to calibrate P by finding the value that produced agreement between modelled and observed final trout weights given field measurements of initial trout weight, stream temperature and assumed trout prey energy densities. Fish weights were measured 8 August 1997 and 15 April 1998. The mean initial and final weights for a cohort of trout were 4.61 and 8.6 g, respectively. The calibrated value of P was 0.27. In addition to the calibrated P of 0.27, trout growth was simulated using values of P equal to 0.20 and 0.35. These values were chosen to reflect potential differences in feeding constraints (for both directions) between East and A creeks. Trout bioenergetics were simulated for the trout's first year following emergence, which was assumed to occur on May 1. The initial trout weight was set at 3 g. Bioenergetics modelling was restricted to the trout's first year because, in following years, trout begin to divert energy to reproduction and developing reproductive organs, which would add further uncertainty to the growth modelling, and first year overwinter survival is particularly sensitive to trout size compared to following winters (Trotter 1989).

Trout food supply can be altered following harvesting due to increases in primary production (Kiffney et al.

2003) or shifts in the amount and sources of food from aquatic and terrestrial sources (Wipfli 1997; Wipfli and Musslewhite 2004; Hoover et al. 2007). Therefore, a sensitivity analysis was conducted on the P parameter to explore the potential effects of post-harvest changes in trout food supply for the four post-harvest years. Bioenergetic simulations were run and the calibrated P of 0.27 was varied by ±10, 20, and 30%. This range in values was roughly based on results of a feeding experiment (Boss and Richardson 2002). Between 8 August 1997–16 September 1997, Boss and Richardson (2002) provided a steady supply of live mealworms to trout kept in an enclosure at East Creek. The daily rations were 16% of the biomass of all fish in the enclosure. The resulting calibrated P for the feeding experiment was 37% greater than the P of 0.27.

Uncertainty analysis

A Monte Carlo approach was used to quantify the effects of stream temperature uncertainty on fish growth, accounting for the inherent scatter about the statistical temperature models as well as uncertainty in the estimated coefficients in Eqs. 1 and 3. One thousand (1,000) stream temperature realizations were generated for each year of data. For each realization, parameter estimates were randomly generated from normal distributions with a mean given by the best-fit parameter estimate and a standard deviation equal to the standard error of each parameter estimate. The following model was applied to data for the post-harvest period to generate simulated "no-harvest" stream temperatures:

$$\widehat{Tnh}_t^i = (b_0 + e_{b0_i}) + (b_1 + e_{b1_i})sin(2\pi j/T) \\ + (b_2 + e_{b2_i})cos(2\pi j/T) \\ + (b_3 + e_{b3_i})EC_t + \varepsilon_t \tag{4}$$

where $\widehat{Tnh}_t^i$ is the predicted no-harvest stream temperature for day t in realization i, b_0 to b_3 are the best-fit estimates of the regression coefficients β_0 to β_3 (Eq. 1), e_{b_i} are normally distributed random errors associated with the estimated regression coefficients (mean of zero and a standard deviation equal to the standard error of the coefficient), and ε_t is the error term. Similarly, the following model was applied to data for the pre-harvest period to generate "with-harvest" stream temperatures:

$$\widehat{Twh}_t^i = (b_0 + e_{b0_i}) + (b_1 + e_{b1_i})sin(2\pi j/T) \\ + (b_2 + e_{b2_i})cos(2\pi j/T) + (b_3 + e_{b3_i})EC_t \\ + (b_4 + e_{b4_i})EC_t^2 + (b_5 + e_{b5_i})Ta_t + \varepsilon_t \tag{5}$$

where $\widehat{Twh}_t^i$ is the predicted with-harvest stream temperature for day t in realization i, b_0 to b_5 are the best-fit estimates of the regression coefficients β_0 to β_5 (Eq. 3).

For each realization, a separate time series of error terms was generated, incorporating the effects of autocorrelation:

$$\varepsilon_t = u_i + \hat{\rho}_1 \cdot \varepsilon_{t-1} + \hat{\rho}_2 \cdot \varepsilon_{t-2} + \cdots + \hat{\rho}_k \cdot \varepsilon_{t-k} \qquad (6)$$

where u_i is a randomly generated white noise disturbance with a mean of zero and a standard deviation of σ (the square root of the maximum likelihood estimate of the innovations variance from Eqs. 1 or 3), and $\hat{\rho}_k$ are the estimated autocorrelation coefficients. To compute the time series of error terms, the initial k values for each realization were generated as normally distributed uncorrelated random errors with mean of 0 and standard deviation of σ. The $k + 1$ and following terms were computed recursively using Eq. 6. The time series for each realization had an additional 150 time steps at the beginning, which were then discarded to minimize the effects of errors associated with specification of the first k random errors (i.e., to let the random errors evolve to the point that the memory of the initial values was negligible).

For each day, the statistical significance of the differences between the with-harvest and no-harvest stream temperature and trout growth was assessed. For example, for the post-harvest period, the observed stream temperature was compared to the distribution of the ensemble of 1,000 values generated using Eq. 4. If the observed stream temperature exceeded the 97.5th percentile or was below the 2.5th percentile of the realizations for a given date, the difference between with-harvest and no-harvest scenarios was considered to be significant at $\alpha = 0.05$. Similarly, for the pre-harvest period, the observed stream temperatures were compared to the distribution of the ensemble of values predicted using Eq. 5. Similar comparisons were made for the fish growth time series generated by the bioenergetic model. All statistical analyses and computations were performed using the software package R (R Development Core Team 2009).

Results

Stream temperature response to harvesting

The summer air temperatures during the pre-harvest period (30 April 1997 to 19 October 1998) tended to be higher than during the post-harvest period (Table 2). The maximum observed daily mean summer stream temperature over the study period was greatest during the first summer following harvesting (20.4°C in 1999). However, due to the cooler conditions in the post-harvest period, observed post-harvest mean daily stream temperatures at A Creek were not consistently higher than observed stream temperatures during the pre-harvest period (Fig. 2).

Summaries of the ARIMAX model fits for pre-harvest and post-harvest data are shown in Table 3. The pre-harvest model required $k = 2$ orders of autocorrelation and the post-harvest model required $k = 3$ orders of autocorrelation. As indicated by the residual standard error (s_e), the post-harvest fit ($s_e = 0.30$°C) was weaker than the pre-harvest fit ($s_e = 0.16$°C).

Figure 2 presents observed and predicted stream temperatures for 1 May to April 30 for two pre-harvest years and four post-harvest years. For pre-harvest years the predicted temperature for the with-harvest scenario is significantly higher (up to 5°C) than observed (no-harvest) stream temperature during the summer period for both 1997 and 1998. Throughout the winter of 1997–1998, observed and predicted stream temperatures mostly show no significant difference. During the spring and summer of the post-harvest period, observed (with-harvest) stream temperature was often significantly higher (up to 1 to 5°C) than the predicted no-harvest temperature scenario. Higher observed with-harvest stream temperatures persisted into September for all post-harvest years (1999–2001), and into late October for the first post-harvest year (1999). During winter 1999–2000, observed with-harvest

Table 2 Summer (July and August) hydroclimatic conditions during the study period

Variable	Year					
	1997	1998	1999	2000	2001	2002
P (mm)	258	89	201	136	224	57
Air T_{max} (°C)	31.0	34.0	28.0	29.0	30.5	32.0
Air T_{mean} (°C)	18.2	18.9	17.3	16.4	17.3	17.8
Air T_{min} (°C)	9.5	9.5	8.0	6.5	8.0	7.0
East Ck Q_{mean} (m^{3}s^{-1})	0.017	0.004	0.010	0.003	0.007	0.003
East Ck T_{max} (°C)	14.7	16.1	14.0	13.8	14.0	14.3
A Creek T_{max} (°C)	16.5	19.4	20.4	19.2	19.2	18.6

Shown are climate data (air temperature, precipitation) measured at the Research Forest Headquarters Station; streamflow and water temperature measured at the control stream, East Creek; and water temperature measured at A Creek. Maximum, mean, and minimum air and water temperatures are determined from daily mean temperatures

Fig. 2 Observed stream temperature at A Creek (*black line*) and predicted stream temperature (*grey bands* represent the suite of Monte Carlo realizations) for both pre-harvest (1997–1998) and post-harvest periods (1999–2002). During the pre-harvest (post-harvest) period, observed stream temperature is for the no-harvest (with-harvest) scenario and the with-harvest (no-harvest) scenario is based on predicted values. The 1998–1999 year ends in October because that was when harvesting began. The *horizontal line* segments at the *bottom* of each plot indicate days on which the value represented by the *black line* is significantly different from the values represented by the *grey lines* ($\alpha = 0.05$)
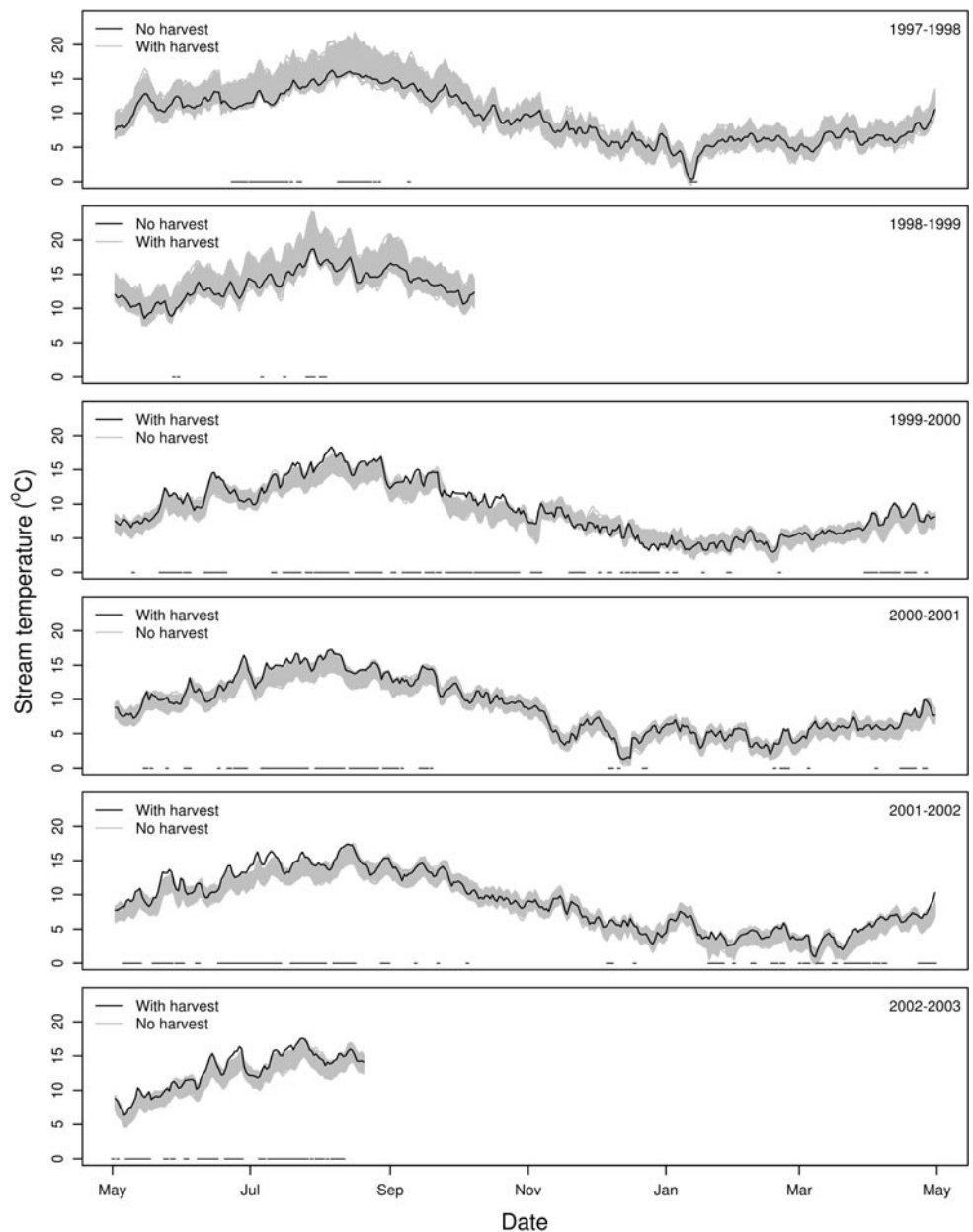
Table 3 Results of ARIMAX analysis for the pre-harvest and post-harvest model fits

Model	s_e	k	$\hat{\rho}_1$ (s.e.)	$\hat{\rho}_2$ (s.e.)	$\hat{\rho}_3$ (s.e.)	b estimates					
						intercept (s.e.)	cosine (s.e.)	sine (s.e.)	EC (s.e.)	EC^2 (s.e.)	Ta (s.e.)
Pre-harvest fit (Eq. 1)	0.16	2	1.064 (0.044)	−0.234 (0.044)	–	0.739 (0.160)	−0.369 (0.091)	0.047 (0.078)	1.075 (0.019)	–	–
Post-harvest fit (Eq. 3)	0.30	3	0.825 (0.029)	−0.080 (0.037)	0.085 (0.028)	2.982 (0.163)	−0.783 (0.093)	−0.174 (0.088)	0.427 (0.039)	0.028 (0.003)	0.134 (0.005)

The coefficients b are estimates of the parameters β, with standard errors (s.e) shown in brackets, k is the order of the residual autocorrelation, s_e is the residual standard error, $\hat{\rho}$ is the estimated autocorrelation of the error terms

stream temperature tended to be lower (up to 4°C) than predicted no-harvest temperatures. This pattern of lower observed with-harvest temperatures relative to predicted no-harvest temperatures did not persist as strongly in the winters of 2000–2001 and 2001–2002. For all post-harvest years, observed (with-harvest) stream temperatures began increasing earlier (starting in March and April) than predicted no-harvest temperatures. As a result of cooler climatic conditions from 1999 to 2002, predicted maximum mean daily temperatures under the with-harvest scenario

were higher during the pre-harvest period than observed with-harvest temperatures in the post-harvest period.

Bioenergetics modelling

Figure 3 shows simulated trout growth (g) following emergence on 1 May until 30 April of the following year using observed and predicted stream temperature and a P of 0.27. During the warmer pre-harvest period, predicted with-harvest stream temperatures resulted in trout growth

Fig. 3 Simulated fish growth for 1 year following emergence (May 1st) at an initial weight of 3 g. For 1997–1998 and 1998–1999, *grey bands* represent the suite of Monte Carlo realizations for the with-harvest scenario, whereas for the remaining years (1999–2002) the grey bands represent the predicted no-harvest scenario. The 1998–1999 year ends in October due to the beginning of harvesting. The *horizontal line* segments at the *bottom* of each plot indicate days on which the value represented by the *black line* is significantly different from the values represented by the *grey lines* ($\alpha = 0.05$). Note that the y-axis is in *logarithmic scale*
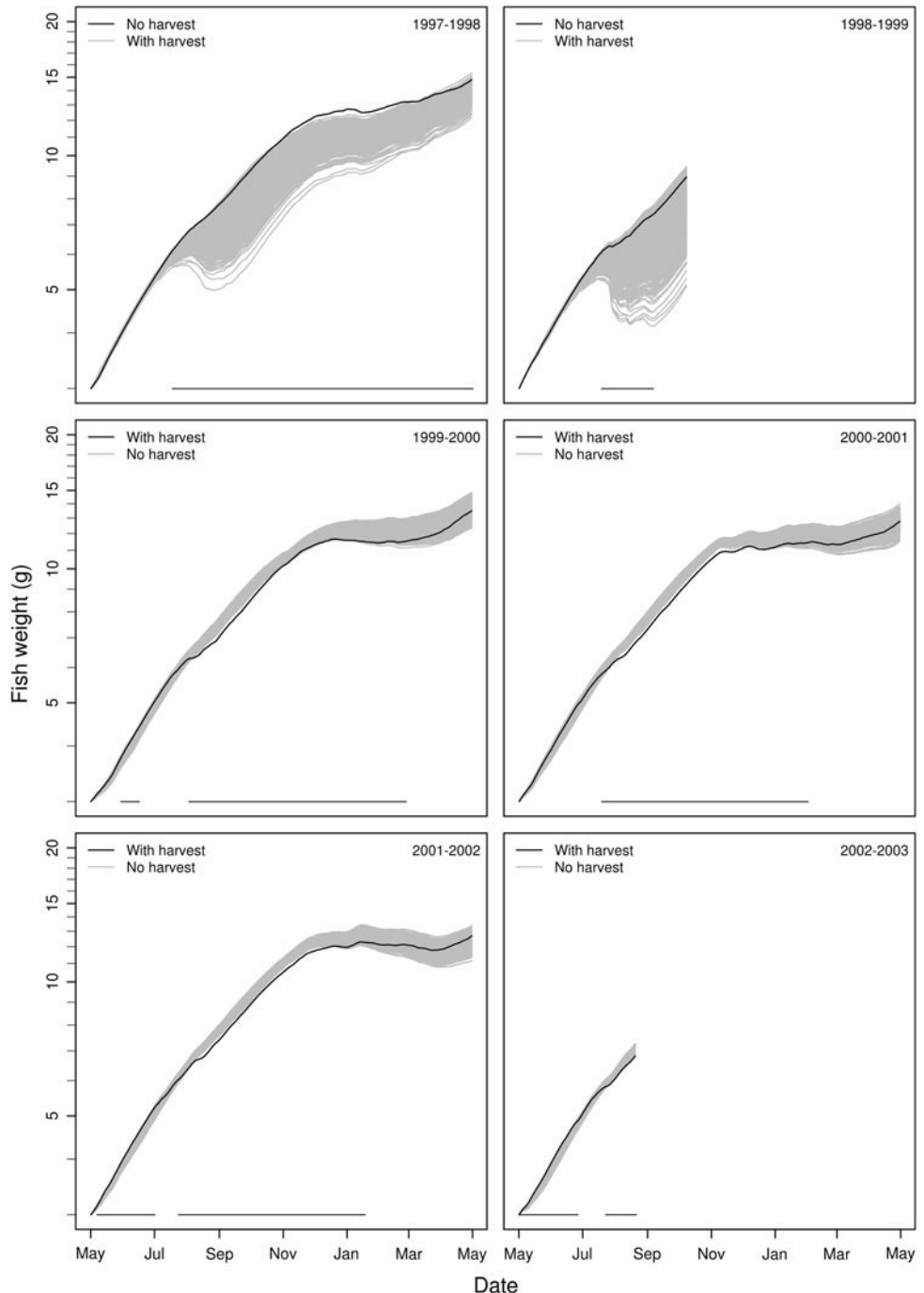
Table 4 Final trout weights (g) after one year (May to April) following emergence using observed daily mean stream temperature (T_w), predicted daily mean stream temperature and different values of the (P) parameter

Year	Final fish weight (g)					P−30%	P−20%	P−10%	P+10%	P+20%	P+30%
	$P = 0.27$										
	Observed T_w	Predicted T_w									
		Min	Mean	Max							
Pre-harvest period											
1997	14.82	12.20	13.86	15.34		–	–	–	–	–	–
1998*	8.96	5.08	7.77	9.44		–	–	–	–	–	–
Post-harvest period											
1999	13.49	12.34	13.62	14.84		3.64	5.96	9.19	19.06	26.06	34.70
2000	12.77	11.50	12.75	13.98		3.49	5.68	8.72	18.00	24.56	32.64
2001	12.70	11.16	12.31	13.37		3.44	5.62	8.65	17.92	24.50	32.60
2002*	6.81	6.79	7.06	7.27		3.36	4.33	5.47	8.36	10.14	12.15

The no-harvest (with-harvest) scenario is the observed values in the pre-harvest (post-harvest) period and the predicted values in the post-harvest (pre-harvest) period. 1998* and 2002* were partial years consisting of May to October and May to August due to harvesting and end of data collection, respectively

being significantly less than predicted for the no-harvest scenario. For the relatively cooler post-harvest years, the total trout growth over the year was about equal for both with-harvest and no-harvest scenarios. However, the timing of trout growth differed between scenarios. The with-harvest scenario resulted in faster trout growth during the spring, but significantly slower growth during the summer. The with-harvest scenario trout remained smaller (by 0.2–2.0 g absolute weight) throughout the fall and winter. In the spring, trout growth in the with-harvest scenario was more rapid, resulting in similar final trout weights of approximately 12–13 g (Table 4).

Uncertainty in applying the calibrated P from East Creek trout growth field data to A Creek was assessed by comparing simulated trout growth using different values of P. Figure 4 shows simulated trout growth (g) following emergence on 1 May until 30 April of the following year for the 1999–2000 post-harvest year using the East Creek calibrated P of 0.27 and two additional values (0.20 and 0.35). Adjusting P to reflect potential differences in constraints on feeding rates between East Creek and A Creek influences the magnitude of trout growth. However, the relative pattern of growth under different values of P is similar. With a smaller value of P, simulated trout growth is more sensitive to the altered thermal regime. A larger value of P results in simulated trout growth that is less sensitive to the altered thermal regime. These findings were similar for all years, but only the 1999–2000 year is presented here.

Figure 5 shows simulated specific trout growth rates ($g\,g^{-1}\,day^{-1}$) for the two pre-harvest years and four post-harvest years. The warmer pre-harvest summers resulted in negative specific growth rates not only for the predicted with-harvest scenario, but also for a short period in summer

1998 for the no-harvest scenario (observed pre-harvest stream temperature). During the cooler post-harvest years, observed stream temperatures only briefly resulted in negative specific growth rates during summer. Specific growth rates were greater for the no-harvest scenario than for the with-harvest scenario during the summer, but this pattern reversed during the spring and fall periods.

Bioenergetics simulations for the with-harvest scenario, using different values for the P parameter, are presented for three post-harvest years (Fig. 6). Trout growth for simulations using an increase in P resulted in considerably greater trout weights throughout the entire first year following trout emergence, indicating that even a modest increase in food supply could more than compensate for the effects of increased stream temperature (Table 4). Decreases in P resulted in significantly lower trout weights throughout the year.

Discussion

Stream temperature

Daily mean stream temperature response to harvesting at A Creek was estimated to be up to a 5°C increase, which is within the range of previous studies examining stream temperature response to forest harvesting (Moore et al. 2005a). During the post-harvest winter 1999–2000, observed stream temperature tended to be lower (up to 4°C) than predicted no-harvest temperatures, but this pattern did not persist as strongly in the winters of 2000–2001 and 2001–2002. This recovery pattern is likely due to observed riparian vegetation regrowth following harvesting (Gomi et al. 2006) and

Fig. 4 Simulated fish growth for the first post-harvest year ▶ (1999–2000) following emergence (May 1st) at an initial weight of 3 g using the calibrated value of parameter *P* (0.27) and two other values of *P* (0.20 and 0.35). The *grey bands* represent the suite of Monte Carlo realizations for the predicted no-harvest scenario. The *horizontal line* segments at the *bottom* of each plot indicate days on which the value represented by the *black line* is significantly different from the values represented by the *grey lines* ($\alpha = 0.05$). Note that the *y*-axis is in *logarithmic scale*

subsequent increase in longwave radiation reaching the stream surface associated with a reduction in the sky view. For a detailed discussion on the stream temperature response to forest harvesting at A Creek and stream energy balance estimates see Moore et al. (2005b).

A novel aspect of this analysis is the use of a statistical model fitted to the post-harvest data to generate a scenario of with-harvest temperatures for the pre-harvest period (i.e., to estimate what temperatures would have been had harvesting occurred earlier). One complication is that growth of riparian vegetation resulted in some level of thermal recovery during the post-harvest period (Gomi et al. 2006). Therefore, the predicted with-harvest temperatures for the pre-harvest period will represent an averaged effect of reduced riparian vegetation cover, and will not be as extreme as would be the case for canopy conditions in the first year immediately following harvest.

Fish are known to seek out thermal refugia when water temperature falls below or exceeds optimum levels (Torgersen et al. 1999; Ebersole et al. 2001). Spatial variability of stream temperature was not considered in this study, although Moore et al. (2005b) observed differences in instantaneous stream temperature within the cutblock of up to 2°C over distances as short as 5 m. At night and during cooler weather, this variability was <0.5°C. However, daily mean stream temperatures would be less variable than instantaneous observations. In addition, trout at A Creek have been observed to travel <6 m over periods as long as 5 months (De Groot et al. 2007). Therefore, it is likely that the stream temperatures reported here are representative of thermal conditions experienced by trout resident near the monitoring site.

Trout bioenergetic response to harvesting

The response of fish abundance and growth to forest harvesting is the result of complex interactions between streamflow, water quality, food supply, habitat availability, disease, and competition (Hicks et al. 1991; Mellina and Hinch 2009). Much of the concern about post-harvest stream temperature increases is related to the potential for increased mortality for cold and cool-water species such as salmonids. For coastal cutthroat trout, the lethal limit is 23°C (50% mortality after 1,000 min; fish acclimated at 20°C; Bjornn
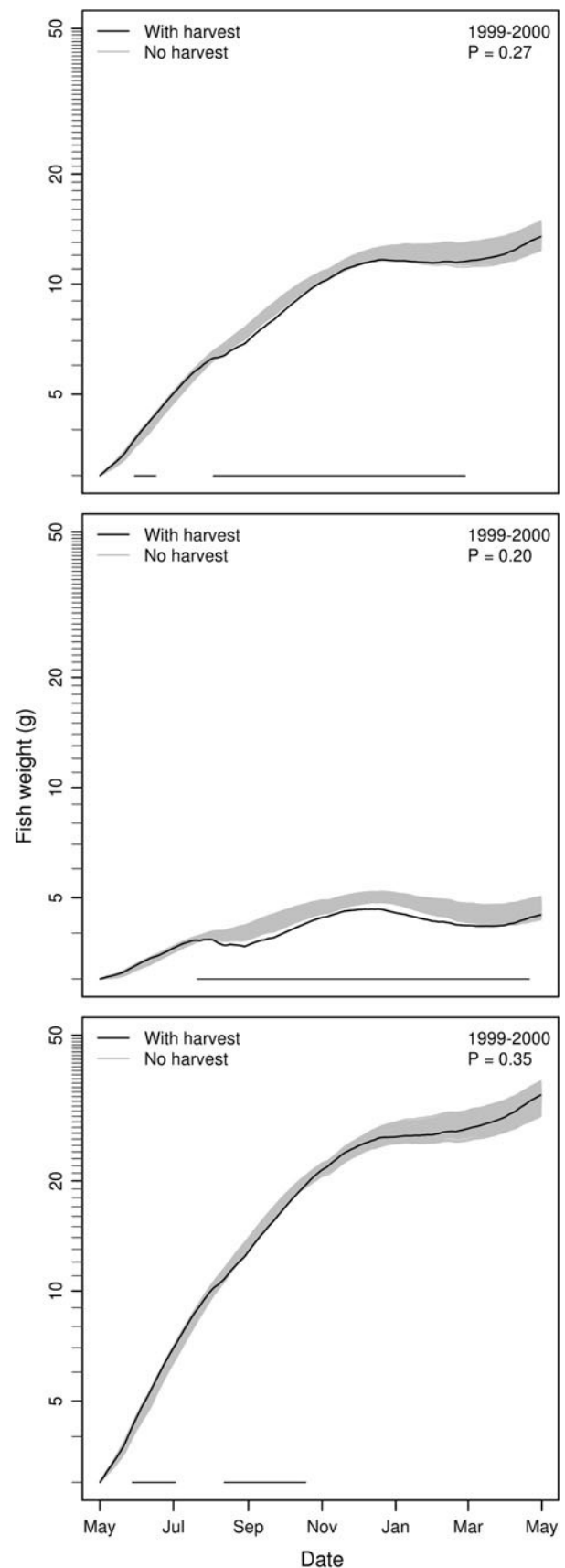
Fig. 5 Simulated specific fish growth rates using observed stream temperature (*black line*) and predicted stream temperature (*grey bands* represent the suite of Monte Carlo realizations) for both pre-harvest (1997–1998) and post-harvest periods (1999–2002). The 1998–1999 year ends in October due to the beginning of harvesting. The *horizontal line* segments at the *bottom* of each plot indicate days on which the value represented by the *black line* is significantly different from the values represented by the *grey lines* ($\alpha = 0.05$)
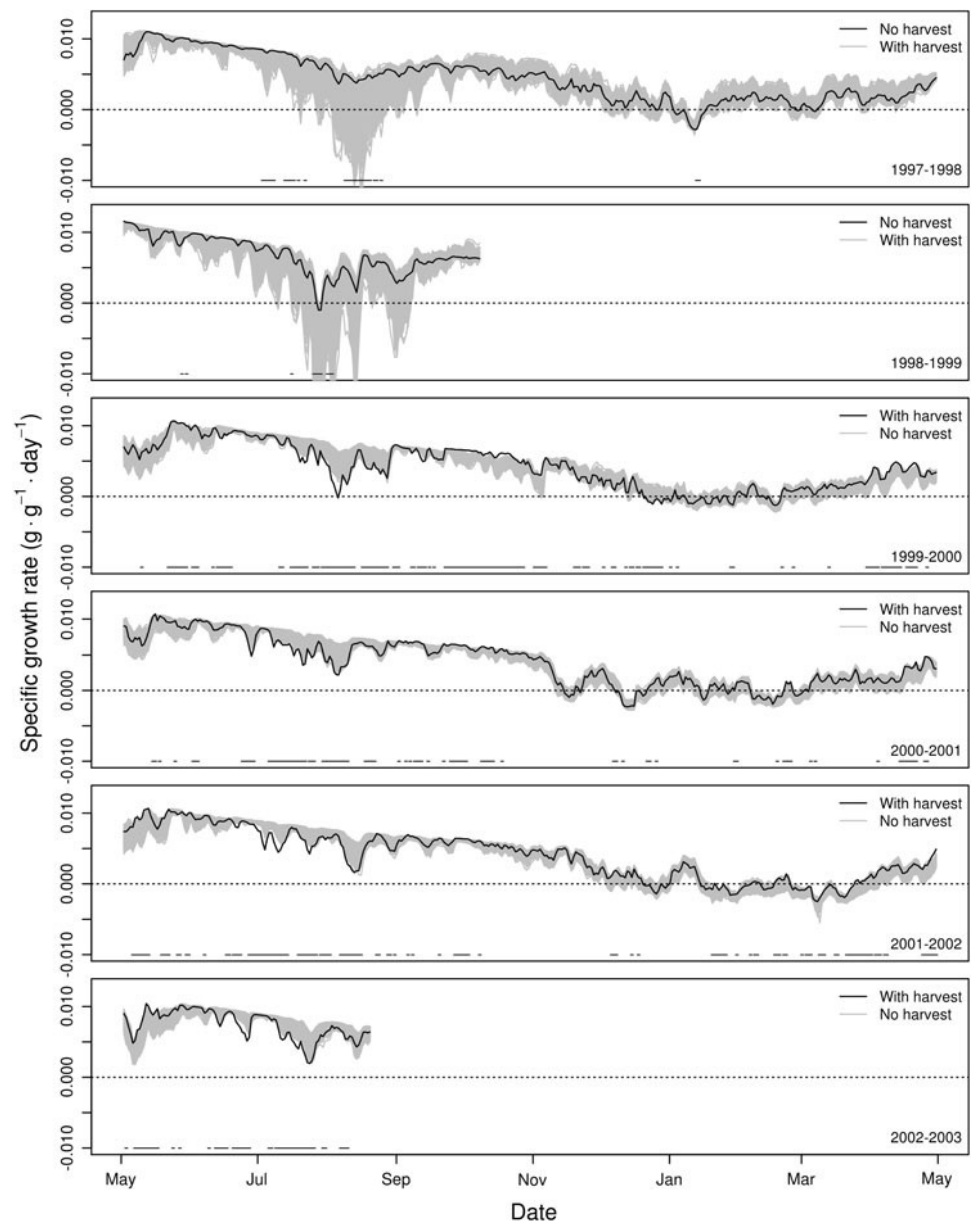

and Reiser 1991). Of the 1,000 with-harvest realizations for the pre-harvest period, 19 predicted mean daily stream temperature above 23°C for one to three days during the period of 28–30 July 1998, with a maximum mean daily temperature of 24.2°C. Since these are mean daily values, maximum daily temperature would have been higher. Therefore, had harvesting occurred prior to July 1998, the simulations suggest a small but finite probability of trout mortality caused directly by elevated stream temperature.

Empirical research on sub-lethal cutthroat trout response to riparian forest harvesting has been varied. Some studies have found an increase in trout biomass and/or abundance following harvesting (Murphy and Hall 1981; Bisson and Sedell 1984), whereas other studies have found no significant response (Murphy et al. 1986; Bilby and Bisson

1992; De Groot et al. 2007) or a decrease (Moring and Lantz 1975). A meta-analysis of salmonid response to riparian forest harvesting found that salmonid density and biomass generally increase following harvesting, although individual study results varied and long-term response is unknown (Mellina and Hinch 2009). Studies that have observed an increase in trout biomass and/or abundance have generally attributed the increase to greater food supply (Hicks et al. 1991). However, studies of post-harvest changes in fish food supply have yielded varying results and few have directly linked changes in food supply with fish growth (Wipfli 1997; Hoover et al. 2007).

In our study, although stream temperatures were generally well below lethal limits, stream temperature increases had a significant influence on simulated trout growth rates at

Fig. 6 Simulated fish growth for 1 year following emergence (May 1st) at an initial weight of 3 g for three post-harvest years. Seven with-harvest scenario fish growth estimates are provided using different values of P (0.27 ± 10, 20, and 30%). The no-harvest predicted growth assumes a P of 0.27. Note that the y-axis is in *logarithmic scale*
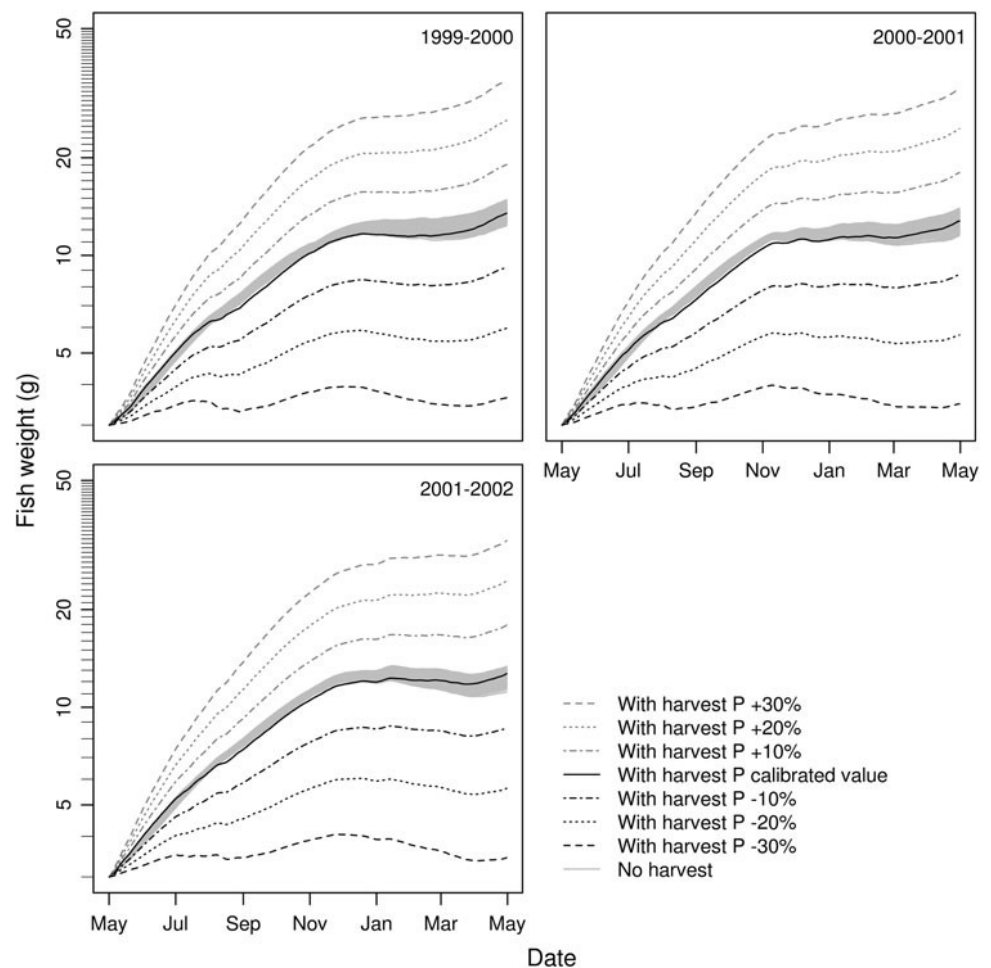
seasonal time scales. Trout growth for the with-harvest scenario was greater during spring and fall but lower during summer compared to the no-harvest scenario. However, potential changes in food supply and subsequent trout feeding rates appear to have a potentially more profound impact on trout growth than direct impacts of the altered thermal regime. Because cutthroat trout in the study area are food limited during summer (Boss and Richardson 2002), an increase in food supply may result in increased trout growth rates despite the influence of sub-optimal post-harvest stream temperature. However, decreased feeding rate following harvesting has the potential to compound the metabolic costs of increased stream temperature, resulting in significantly smaller trout.

There is some evidence that food supply could have increased following harvest at A Creek. Kiffney et al. (2003) found that periphyton biomass and Chironomidae abundance were two to three times higher in A Creek following harvesting due to an increase in solar radiation reaching the stream surface. However, firm conclusions regarding post-harvest food supply cannot be drawn from these results because terrestrial invertebrates can comprise more than half of energy ingested by fish (Wipfli 1997;

Allan et al. 2003; Baxter et al. 2005). If food supply decreases, as was observed at the Torpy River, central British Columbia (Hoover et al. 2007), trout growth may suffer from the combined effects of increased stream temperature and a lack of food (Fig. 6).

Pre- and post-harvest field measurements of cutthroat trout condition at A Creek revealed no differences in fish condition (mass for given length) that could be attributable to harvesting (De Groot et al. 2007). Comparisons between these field data and the bioenergetic modelling are limited since the field study focused on fish older than one year, whereas the bioenergetic modelling focused on trout in their first year. De Groot et al. (2007) speculated that fish condition did not appear to benefit from higher food supply because the metabolic costs were higher in A Creek as a result of increases in stream temperature. The bioenergetic results suggest that this could be the case, but even a small increase in parameter P results in significantly greater growth rates, which were not observed in the field. However, given the available field data there are limits to establishing a direct relationship between food supply and the P parameter of the bioenergetic model. Also, De Groot et al. (2007) suggested that their analytical approach may

not have had sufficient power to detect modest changes to trout condition. Results from the current study generally did not predict a significant difference in fish growth until mid-July (Fig. 3). Therefore, field measurements made in June and July may miss a potentially significant response that occurs later in the season.

Evaluation of the modelling approach

Bioenergetics modelling has been used and evaluated extensively in the last two decades (Hartman and Kitchell 2008). In particular, Railsback and Rose (1999) explored the relative sensitivity of stream temperature and food consumption on trout growth using bioenergetics modelling. However, to the authors' knowledge, no studies have coupled bioenergetics modelling to daily stream temperature dynamics in a forest harvesting context, particularly through the use of a paired-catchment analysis to generate realistic estimates of the magnitude and seasonal expression of post-harvest temperature changes.

Bioenergetics modelling is recognized as being uncertain in model formulation and parameterization (Railsback and Rose 1999; Chipps and Wahl 2008). In this study, constant values of P and food energy densities were used across years and also among seasons. In reality, feeding, food supply and type of food can vary seasonally (Hawkins and Sedell 1981), particularly as streams recover from forest harvesting (Zhang et al. 2009). There is also a feedback effect between stream temperature and food consumption rate that is not represented in the Wisconsin Bioenergetics Model (Railsback and Rose 1999). Applying a value of P calibrated for an unharvested reach of East Creek to both the no-harvest and with-harvest scenarios at A Creek may not be appropriate due to the sensitivity of calibrating P to local ecological feeding constraints (Hanson et al. 1997). However, our analysis suggests that if the East Creek calibrated P over- or under- estimates feeding constraints at A Creek, the magnitude of trout growth is altered but the relative pattern of trout growth remains similar (Fig. 4). Although P was calibrated for a specific thermal regime, Railsback and Rose (1999) found that when predicting fish growth under altered thermal regimes P can be treated as independent of stream temperature particularly when stream temperature changes are modest, as was found at A Creek.

In this study the physiological parameter set for rainbow (steelhead) trout was used because no parameter set exists for cutthroat trout. This substitution has been used in other studies (Raggon 2010), but it introduces further uncertainty into modelled trout growth. Interactions between fish species or individuals competing for food resources or habitat are not accounted for. The assumption of no inter-species competition is valid at A Creek because cutthroat trout are the only fish species present. Habitat changes other than stream temperature (such as streamflow, channel morphology and sedimentation) were not considered in this study. However, De Groot et al. (2007) observed no detectable changes to channel morphology and habitat units following harvesting. Further, changes in streamflow associated with harvesting are likely to have been minor: as part of the experimental design, harvesting was limited to 20% of the total catchment area, and the effects of harvesting on streamflow are generally statistically detectable only for higher levels of harvesting (Moore and Wondzell 2005).

In this study, the emergence date was held constant at 1 May. However, stream temperature is also known to influence the timing of fry emergence. At Carnation Creek, BC, Canada, coho salmon fry emerged up to six weeks earlier following harvesting due to modest increases in winter and spring stream temperatures (Holtby 1988). The earlier emergence was believed to be the reason that fish growth was greater following harvesting because it would produce a longer feeding period. At A Creek, the post-harvest warming resulted in higher growth rates in April, which would further support increased growth associated with earlier emergence. However, temporal dynamics in food availability, which are not accounted for in our study, could have complex effects on seasonal fish growth.

The bioenergetics model uses daily mean temperatures to define the thermal environment of fish. However, particularly following harvesting, diurnal stream temperature variation can be up to several degrees Celsius (e.g., Johnson 2004). In a study focused on spring and summer stream temperatures, Gomi et al. (2006) found that harvesting significantly increased A Creek daily maximum stream temperatures (up to 4.9°C). This diurnal variation, which is not represented in the bioenergetics model, could have an influence on fish respiration, feeding behaviour, and survival. This constitutes another source of uncertainty.

The bioenergetic modelling approach can assess the effects of changes in stream temperature and diet on fish growth, but these are not the only impacts on fish that are associated with harvesting. Changes in streamflow, addition of harvesting slash to the stream, erosion of streambanks and increased sedimentation can also influence fish survival, growth rates, food supply, predation, habitat, and spawning success (Hicks et al. 1991; Mellina and Hinch 2009). All these impacts interact in complex ways that control fish abundance, growth and health. Further research should focus on clarifying the nature of these interactions to provide the basis for a more comprehensive modelling assessment of fish response to forest harvesting and other land-use changes. In addition, trout bioenergetics beyond the first year are complicated by additional physiological and competitive processes not considered in the

current analysis due to lack of information. These processes need to be considered to allow an assessment of longer-term impacts of forest harvesting beyond the first year of a cohort.

Conclusion

During spring, summer and fall, with-harvest daily mean stream temperatures were generally greater (up to 5°C) than no-harvest stream temperatures. For the first post-harvest winter, with-harvest temperatures were up to 4°C lower than no-harvest temperatures. In the second and third winters following harvesting, differences between with-harvest and no-harvest temperatures were not significant or showed slightly warmer with-harvest stream temperatures. Observed and predicted with-harvest stream temperatures indicate a small but finite probability that upper lethal limits for cutthroat trout would be exceeded.

Over the first year following emergence the simulated with-harvest trout growth was greater than simulated no-harvest trout growth during spring and fall, but lower during summer. Both scenarios resulted in similar fish weights at the end of the first year following emergence. Adjusting the feeding parameter in the model to represent potential changes in macroinvertebrate prey abundance following harvesting resulted in greater changes to trout growth than direct effects of the altered stream temperature regime when considering the entire spring to winter growth period.

The use of a paired-catchment analysis, involving both pre- and post-disturbance monitoring and an undisturbed control, ensured that the temperature differences between with-harvest and no-harvest scenarios were realistic, particularly in terms of their seasonal expression. However, a significant source of uncertainty for the bioenergetics model was the lack of information on the seasonal and interannual variability of food supply and feeding. Future research should focus on determining temporal dynamics in trout food supply following harvesting. Timing of trout emergence following harvesting and the subsequent implications for trout feeding and growth should also be explored. It is also uncertain how trout health is affected by sub-lethal stream temperature changes associated with harvesting beyond the trout's first year. Determining a physiological parameter set for coastal cutthroat trout bioenergetics would further reduce uncertainty in modelling.

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