

Stream temperature and the potential growth and survival of juvenile *Oncorhynchus mykiss* in a southern California creek

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SUMMARY

1. We asked whether an increase in food supply in the field would increase the ability of fish populations to withstand climate warming, as predicted by certain bioenergetic models and aquarium experiments.
2. We subsidised the *in situ* food supply of wild juvenile steelhead (*Oncorhynchus mykiss*) in a small stream near the species' southern limit. High-quality food (10% of fish biomass per day) was added to the drift in eight in-stream enclosures along a naturally-occurring thermal gradient.
3. The temperatures during the experiment were well below the upper thermal limit for the species (means of enclosures ranged from 15.1 to 16.5 °C). Food supplements had no discernible effect on survival, but raised mean (\pm SD) specific growth rate substantially, from 0.038 ± 0.135 in controls to 2.28 ± 0.51 in feeding treatments. Food supplements doubled the variation in growth among fish.
4. The mean and variance of water temperature were correlated across the enclosures, and were therefore transformed into principal component scores T_1 (which expressed the stream-wide correlation pattern) and T_2 (which expressed local departures from the pattern). Even though T_1 accounted for 96% of the variation in temperature mean and variance, it was not a significant predictor of fish growth. T_2 was a significant predictor of growth. The predicted time to double body mass in an enclosure with a large T_2 score (cool-variable) was half that in an enclosure with a low T_2 score (warm-stable).
5. Contrary to expectation, temperature effects were neutral, at least with respect to the main axis of variation among enclosures (cool-stable versus warm-variable). Along the orthogonal axis (cool-variable versus warm-stable), the effect was opposite from expectations, probably because of temperature variation. Subtle patterns of temperature heterogeneity in streams can be important to potential growth of *O. mykiss*.

Keywords: bioenergetics, climate change, *in situ* experiment, range limit, steelhead

Introduction

A thermal niche of a species is characterised as the range of temperature tolerable in the wild (Eaton *et al.*, 1995; Wehrly, Wiley & Seelbach, 2003). For fish, water temperature within these tolerance limits modulates an intricate set of energetic costs and

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benefits that are thought to have fitness consequences (Hughes, 1998). For example, experiments have revealed that a rise in temperature typically speeds up metabolism, with energy costs that must be balanced by higher food intake or else cause weight loss (Jobling, 1994). In aquarium experiments on *Oncorhynchus mykiss* (Walbaum), the food required to prevent weight loss was 2.2% of body weight per day at 6.9 °C, but about three times higher (7.5%) at 22.5 °C (Wurtsbaugh & Davis, 1977). Smith & Li (1983) observed juvenile *O. mykiss* in a Californian creek, and suggested that at higher water temperature the fish became concentrated in microhabitats where a high rate of food intake could be achieved, despite incurring other costs.

Aquarium experiments also show that, when food is abundant, a rise in temperature can confer a benefit that outweighs the extra metabolic costs incurred. Higher temperature enables more rapid growth under *ad libitum* feeding up to a species-specific 'global' optimum (Brett, 1971; Elliott, 1975a,b; Wurtsbaugh & Davis, 1977). Appetite and absorption efficiency may increase as the fish approaches its global optimum temperature, even though food conversion efficiency itself decreases (Elliott, 1982). The net effect is that a rise in temperature increases the range of possible growth trajectories, with a higher maximum potential but also a higher risk of weight loss if food is scarce. In this sense, temperature is a bioenergetic amplifier for the effects of food availability on growth and fitness, at least in experimental tanks.

These experiments sacrifice realism, however, as natural conditions might interfere with the expression of temperature-specific growth patterns observed in simpler aquarium environments. Natural systems exhibit spatial and temporal heterogeneity in both their physical traits and their biotic structure, and this strongly affects fish populations as illustrated by an extensive literature (e.g. Li & Brocksen, 1977; Werner & Hall, 1988; Harvey & Nakamoto, 1997; Hughes, 1998; Berejikian *et al.*, 2001; Keeley, 2001; Reese & Harvey, 2002; Connolly & Petersen, 2003; Keeley, 2003).

Climate warming is expected to heat up streams over the next century, perhaps by 2–5 °C in North America (Mohseni, Erickson & Stefan, 1999). Mohseni *et al.* (1999) assessed 764 sites in the U.S.A. and predicted that 36% of the coldwater fish sites will exceed those species' thermal tolerances by the end of the century (see also Eaton & Scheller, 1996), with

non-lethal rises in temperature for most of the remaining sites. The laboratory experiments described above suggest that the net cost of such warming for fish depends on food availability, but this inference is limited by a lack of experiments conducted under natural conditions.

Here we asked whether an interaction of temperature and food supply affects the range of growth trajectories under natural conditions, and manipulated the food supply of juvenile *O. mykiss* in a set of stream reaches similar except for temperature. Specifically, our main questions were: (i) Does either growth or survival exhibit an interaction effect for temperature and food availability under the normal heterogeneity of in-stream conditions?; and (ii) If so, does growth exhibit the expected 'amplification' of possible trajectories under warmer conditions?

Methods

Study site

Oncorhynchus mykiss irideus (Gibbons) is distributed in coastal basins from western Alaska south to Baja California Norte (Behnke, 1992). Our study sites were in Lion Creek, just north of Los Angeles in the Santa Clara River basin (Fig. 1a), an arid montane region in which summer air temperature routinely reaches 32 °C. In this region the abundance of *O. mykiss* is negatively correlated with stream temperature, both within reaches (Matthews & Berg, 1997) and at catchment scales (Douglas, 1995).

Like many streams in the region (Spina, Allen & Clarke, 2005), Lion Creek is a mixture of intermittent and perennial reaches. The stream's confluence with the larger Sespe Creek was dry at the time of the study, but there was a perennial section from 150-m above the confluence to about 2.4-km above the confluence. Between 24 and 30 July 2006, four experimental feeding enclosures and four control enclosures were placed near each end of the perennial section (Fig. 1b; downstream site at 34°33.539'N, 119°9.737'W, alt. 911 m; upstream site at approximately 34°32.575'N, 119°9.802'W, alt. 985 m).

Experimental design

Enclosures were laid out in upstream/downstream pairs, consisting of adjacent sections of the channel

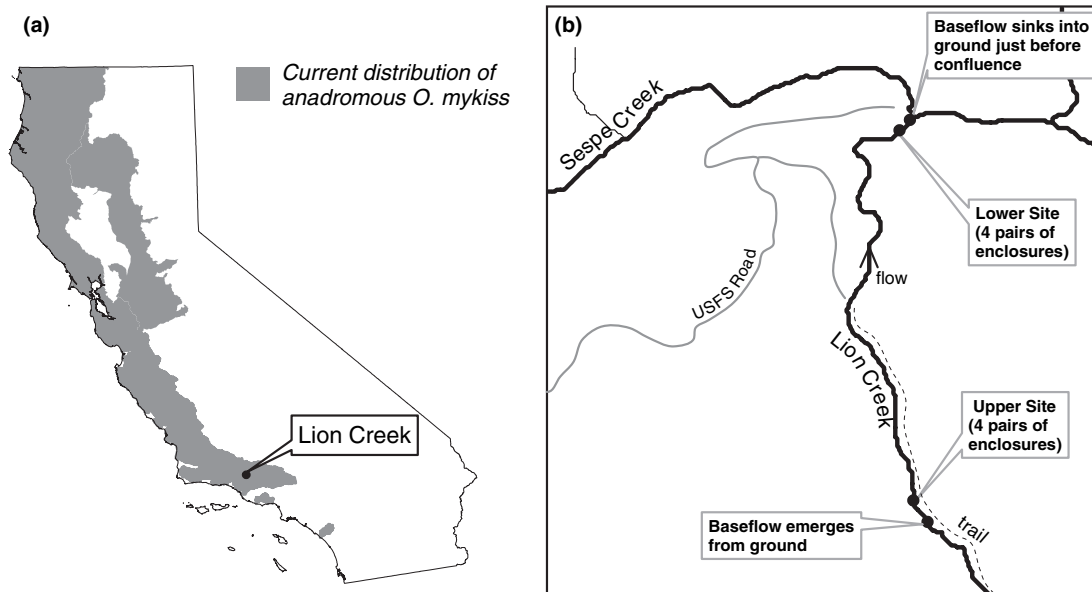


Fig. 1 (a) California and Lion Creek. (b) Locations of enclosures on Lion Creek.

enclosed by mesh fences at each end. One of each pair was randomly designated the control. Paired enclosures were matched in terms of depth, width, pool/riffle ratio and the size-composition of fish with which they were stocked. Among pairs, these same characteristics were allowed to vary randomly, thus incorporating natural heterogeneity. The density of fish in all enclosures was standardised as close to 0.5 m^{-2} as possible, a value determined by a preliminary survey of the natural fish density.

The paired enclosures shared a common fence when site conditions allowed (maximum gap was approximately 10 m). Fences made of 0.48-cm mesh polyethylene netting were stretched across the stream and attached to 0.64-cm rebar pounded into the streambed. The lower edge of the netting was buried in gravel. In each pair, we attached a temperature logger (HOBO Water Temp Pro logger, Onset Computer, Bourne, MA, U.S.A.) to the common fence or to one of the interior fences when there was a gap. The logger was positioned in the main current. To measure emigration attempts, we cut a small hole in the fence at each end of the enclosures, and attached minnow traps that would contain any fish trying to leave the enclosures.

In the experimental enclosures, we placed 24-h clockwork belt feeders on rebar frames (Dynamic Aqua Supply Ltd, Surrey, BC, Canada), positioned to drop

food into the main current at the head of the enclosure (Boss & Richardson, 2002). Fine mesh was lashed to the downstream fence to prevent food from drifting to the rest of the stream. After completion all enclosures were allowed to 'rest' for half a day or more, and then electrofished until two consecutive passes yielded no fish.

For the experiment we used *O. mykiss* electrofished from the enclosures and the surrounding stream reaches. Each fish was anaesthetised with sodium bicarbonate, weighed to the nearest 0.1 g, and uniquely marked with elastomer tags (Northwest Marine Technologies, Shaw Island, WA, U.S.A.). We measured fork length (FL) to the nearest 1 mm, assigned fish to 10-mm size classes and, within each class, randomly assigned fish to controls versus experimental enclosures. Fish were allowed to recover in buckets with aerators, and then gently introduced to their designated enclosure by laying the bucket on its side in the water. Fish smaller than 60-mm FL were too small to tag and were not used. A few adults larger than 150-mm FL were not used because they were too rare to arrange as size-matched pairs for the enclosure-pairs.

Supplementary feeding lasted 23 days (31 July–22 August 2004). We stocked the belt feeders daily with small live mealworms at 10% of the total fish biomass in the enclosure, and checked migration traps every 2 days. Fish occurring in the traps were identified and

returned to their enclosure, the latter to minimise variation in density among enclosures over the course of the experiment. On 24 and 25 August 2006, all fish were recaptured, identified and measured. We electrofished each enclosure repeatedly until two consecutive passes yielded no fish.

Data analysis

Initial fish size was bimodally distributed, with a minimum at 90 mm. We labelled fish smaller than 90 mm as YOY and all others 1++ (a possible alternative interpretation is bimodal growth within a single age class, as documented for *Salmo salar* L. by Thorpe, 1977). Enclosures varied in wetted area, the per cent of the wetted area consisting of riffles, and the ratio of number of 1++ fish to YOY fish, and these were treated as random covariates in the analysis.

The mean and variance of water temperature were found to be correlated ($r = 0.92$; $P < 0.001$), apparently because of the groundwater from the spring tending to approach equilibrium with air temperature as it flowed downstream. The temperature data were therefore transformed into principal component scores, with the first principal component (designated T_1) being a measure of how warm and variable the water temperature was for a pair of enclosures, and the second principal component (T_2) being a measure of a pair's departure from this stream-wide pattern. Thus, pairs with high scores for T_2 had a combination of high variance and low mean temperature; pairs with low scores had a combination of low variance and high mean temperature. To aid in interpretation of the results, we also conducted a parallel analysis using the untransformed mean and variance of water temperature (designated M and V).

Response variables for fish i of enclosure-pair r were:

1 Migration $m_{i,r}$ = the number of times fish i was found in a migration trap.

2 Survival $s_{i,r}$ = 1 if fish i was recovered at the end of the experiment; 0 otherwise.

3 Specific growth $G_{i,r} = [(\ln W_{2,i,r} - \ln W_{1,i,r}) / (\text{duration})] \times 100$, where $W_{1,i,r}$ and $W_{2,i,r}$ are initial and final weight of fish i , and duration is days of feeding (Jobling, 1994).

We analysed the data with hierarchical Bayesian models (Gelman *et al.*, 1995; Carlin & Louis, 2000). Hierarchical models allow random and fixed effects to

be deployed flexibly within a statistical model, so that one can construct models with probabilistic and deterministic elements tailored to mimic the system being studied (Clark *et al.*, 2003). We compared models in which variation among enclosure-pairs was a random effect, and models in which variation was attributed to covariates, to determine which model best explained the data. Imagine that each covariate has a small additive effect. Under the central limit theorem, their net effect would be normally distributed across the pairs, suitably modelled as a single random effect. Only if one (or a few) covariates stands out against this 'random noise' would the covariate be explanatory. We could thus ask some key questions directly:

1 Did temperature covariates explain growth or survival better than a random effect?

2 Did temperature covariates better explain growth or survival relative to other covariates? (i.e. wetted area, 1++/YOY ratio, and per cent riffles).

3 Did temperature covariates exhibit the predicted interactions with feeding?

To answer these questions we formally compared models using the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002). In comparisons, lower DIC scores correspond to higher explanatory power. Each candidate model had the form:

$$\mu_{i,r} = \alpha + \beta_K K_{i,r} + \beta_Q Q_{i,r} + \beta_{QK} Q_{i,r} K_{i,r} + \theta_r,$$

where $\mu_{i,r}$ is the expected response for fish i in enclosure-pair r , and the α and β s are the usual regression coefficients for a general linear model. The predictors were initial size $K_{i,r}$ (log-transformed weight); the experiment/control indicator $Q_{i,r}$ (binary); their interaction, and a set of enclosure-level predictors signified by θ_r . Candidate models varied only in the structure of θ_r and the inclusion of the QK term. Two candidates treated θ_r as a normal random effect with mean 0 and variance estimated (i.e. a hyper-parameter). The other candidates treated θ_r as various combinations of five covariates and their interactions (see Results for a complete list of candidates).

Survival and growth required different link functions. Survival was binary, modelled as a logistic link with Bernoulli error. Growth was modelled as a linear link with normal error. However, the experimental enclosures had greater variation than controls, so we defined two separate error terms:

$$\phi_{i,r} \sim N(\mu_{i,r}, I_{i,r}\sigma_{\text{fed}})$$

$$G_{i,r} \sim N(\phi_{i,r}, \sigma_{\text{fish}})$$

where 'N' represents the normal PDF, and $I_{i,r}$ is an indicator function equal to 1 for experimental fish versus 0 for controls. The parameter σ_{fish} is within-enclosure variation present in all fish; the parameter σ_{fed} is additional variation present only in the fed fish.

We used the OpenBUGS software package to estimate parameters of the candidate models (see <http://mathstat.helsinki.fi/openbugs/>). Regression parameters were assumed to be normally distributed with non-informative priors (prior mean = 0; variance = 10^6). Following Gelman *et al.* (1995), we standardised and centred the covariates. Estimation used two Markov chains, iterated 1000 times for burn-in, 50 000 times more for estimation, and sampled every 10 iterations. Inspection of the traces showed these settings to be sufficient.

Standard summary statistics of parameter estimates (posterior densities) (Carlin & Louis, 2000) were augmented with a 'Bayesian P-value' denoted by S (Ge & Epstein, 2004). For insight on contrasts between Bayesian and frequentist statistics, see Wolpert (2004) and Bayarri & Berger (2004).

Results

Temperature

Mean temperature in pairs of enclosures ranged from 15.13 to 16.5 °C. For reference the optimum growth

temperature reported in the literature for unlimited rations is about 17 °C (Jobling, 1981). Temperature variance ranged between 1.01 and 2.14. If this is partitioned into within-day variance and between-day variance, most of the heterogeneity among sites was between-day variance. The maximum temperature recorded in any of the eight pairs of enclosures was 19.7 °C (the lowest was 13.0 °C).

Emigration

Of 270 fish marked for the experiment, 21 were found in an emigration trap at some point (<8% of fish). The vast majority of these fish (90%) emigrated during the first 5 days of the study. Consequently, we assumed that emigration attempts were because of recent handling of the fish rather than a response to conditions inside the enclosures. We did not analyse these data any further.

Survival

The sample size and mean survival for each enclosure are given in Table 1. Mean survival (\pm SD) across all pairs of enclosures was 0.785 ± 0.076 in the controls ($n = 8$) and 0.805 ± 0.072 in the feeding-treatments ($n = 8$). The candidate model with the lowest DIC score was the random-effects model (Table 2), implying that none of the covariates had much explanatory power. The 95% credible interval for the treatment effect was $(-0.2455, 0.3553)$ (Table 3), which spans zero and thus indicates no

Table 1 Summary of sample sizes and response variables by enclosure

	Enclosure pairs							
	1	2	3	4	5	6	7	8
Controls								
Number of fish	11	24	16	15	17	20	21	20
Fraction YOYs	0.727	0.750	0.875	0.733	0.706	0.600	0.810	0.850
Survival (mean)	0.818	0.750	0.750	0.667	0.882	0.850	0.714	0.850
Survival (SD)	0.116	0.088	0.108	0.122	0.078	0.080	0.099	0.080
Growth (mean)	0.014	-0.232	0.027	-0.212	-0.097	0.016	-0.003	0.150
Growth (SD)	0.394	0.348	0.430	0.364	0.569	0.409	0.376	0.507
Feeding treatments								
Number of fish	14	17	16	15	20	17	15	12
Fraction YOYs	0.786	0.765	0.875	0.733	0.650	0.647	0.800	0.750
Survival (mean)	0.786	0.824	0.813	0.867	0.700	0.765	0.933	0.750
Survival (SD)	0.110	0.092	0.098	0.088	0.102	0.103	0.064	0.125
Growth (mean)	1.497	2.335	1.946	2.647	2.042	1.933	2.533	2.463
Growth (SD)	0.719	0.804	1.123	0.712	0.966	0.463	1.002	0.449

Table 2 Survival and growth models compared via DIC

Treatment of block effects	Covariates*		Survival model		Growth model	
	Main	Interactions	Parameters	DIC	Parameters	DIC
Covariates	<i>K, T₁, T₂, C, H, A</i>	<i>KQ, QT₁, QT₂, QKT₁, QKT₂, CK</i>	14	294.5	16	313.1
	<i>K, T₁, T₂</i>	<i>KQ, QT₁, QT₂, QKT₁, QKT₂</i>	10	291.2	12	312.9
	<i>K, T₁, T₂, C, H, A</i>	<i>KQ, QT₁, QT₂</i>	11	293.4	13	309.5
	<i>K, T₁, T₂</i>	<i>KQ, QT₁, QT₂</i>	8	287.1	10	308.3
	<i>K, T₁, T₂, C, H, A</i>	<i>KQ</i>	9	293.0	11	312.5
	<i>K, T₁, T₂</i>	<i>KQ</i>	6	286.9	8	311.0
	<i>K, T₁, T₂, C, H, A</i>	<i>QT₁, QT₂</i>	10	291.4	12	308.2
	<i>K, T₁, T₂</i>	<i>QT₁, QT₂</i>	7	285.1	9	307.2 [†]
	<i>K, T₁, T₂, C, H, A</i>	–	8	290.7	10	311.6
	<i>K, T₁, T₂</i>	–	5	284.8	7	310.1
	<i>K, C, H, A</i>	<i>KQ</i>	7	288.9	9	308.1
	<i>K, C, H, A</i>		6	286.8	8	308.0
Random effect	<i>K</i>	<i>KQ</i>	5	284.2	7	309.7
	<i>K</i>	–	4	282.2 [†]	6	308.8

*Terms: *Q*, treatment; *K*, initial size; *T₁*, first principal component of water temperature; *T₂*, second principal component of water temperature; *C*, ratio 1++/YOY; *H*, proportion of habitat composed of riffles; *A*, area of enclosure.

[†]Most favourable deviance information criterion (DIC) score.

Table 3 Parameter estimates of the selected survival model

Parameter	Mean	SD	95% CI	Effect direction
Core model				
<i>K</i> (initial size)	–0.1024	0.1463	(–0.3809, 0.1887)	Neutral
<i>Q</i> (treatment)	0.05229	0.1533	(–0.2455, 0.3553)	Neutral
Other parameters				
Intercept	1.374	0.1635	(1.067, 1.704)	n/a
σ_r (enclosure-pair var.)	0.1207	0.09593	(0.02465, 0.3731)	n/a

n/a, not applicable.

discernible consistent effect of the feeding treatment on survival.

Growth

The mean specific growth for each enclosure is in Table 1. Mean growth (\pm SD) across all pairs of enclosures was 0.038 ± 0.135 per day ($n = 8$) in controls, and 2.280 ± 0.506 per day ($n = 8$) in feeding treatments. The candidate model with the lowest DIC score retained terms for the two temperature covari-

ates and for their interactions with treatment (i.e. T_1 , T_2 , QT_1 and QT_2); the other covariates were not retained (Table 2).

In the selected model, many of the predictors had credible intervals that excluded zero effect (Table 4). Supplementary feeding had a large positive effect on growth (term Q ; $S < 0.0001$), increasing the mean specific growth rate 60-fold and also doubling the SD of growth rate for fish sharing an enclosure [$\sigma_{\text{fish}} = 0.4106$; $(\sigma_{\text{fish}}^2 + \sigma_{\text{fed}}^2)^{1/2} = 0.8188$]. Growth was negatively related to initial size of the fish (term K ; $S < 0.0001$). The interaction term for growth and initial size was not retained in the selected model, despite the possibility that larger fish may be more food limited because of scaling issues (negative interaction) or conversely, better able to compete for the resource because of their large body size (positive interaction).

The inflated variation in growth suggests that the fish divided the supplementary food unevenly, but if this was because of size-based competitive effects (e.g. Harvey & Nakamoto, 1997), one would expect the QK interaction to have had explanatory power and thus be retained in the best model. It was not (Table 2).

The first principal component of temperature pattern had no discernible co-variation with growth:

the credible intervals for the regression coefficients spanned zero for both the direct effect and the interaction effect with feeding treatment (terms T_1 and QT_1 in Table 4). In contrast, the second principal component had positive co-variation with growth overall (term T_2 in Table 4) and also a positive interaction with the effect of feeding (term QT_2 in Table 4). That is to say, the feeding treatment had a larger effect on growth in the enclosures that were unusually cool and variable versus warm and stable. Inspection of the actual model predictions indicates that this pattern is most biologically significant in the feeding treatments (Fig. 2). For the range of T_2 scores observed in the experiment (-1.88 to 1.08), the predicted increase in specific growth rate would be about 0.87 in the feeding treatments, but only 0.06 in the controls (top and bottom of Fig. 2, respectively).

In the parallel analysis, in which the untransformed mean and variance of water temperature were used as predictors (rather than T_1 and T_2), we obtained the following results: mean water temperature had negative covariance with growth, and a negative interaction with the feeding treatment (term $M = -0.4025 \pm 0.1302$; 95% CI = $-0.655, -0.149$; $S = 0.0011$. Term $QM = -0.3542 \pm 0.1281$; 95% CI = $-0.599, -0.098$; $S = 0.0038$). Variance of water temperature had positive covariance with growth, and a positive interaction with the feeding treatment (term $V = 0.3635 \pm 0.1285$; 95% CI = $0.111, 0.614$; $S = 0.0024$. Term $QV = 0.3970 \pm 0.1260$; 95% CI = $0.149, 0.640$; $S = 0.0008$).

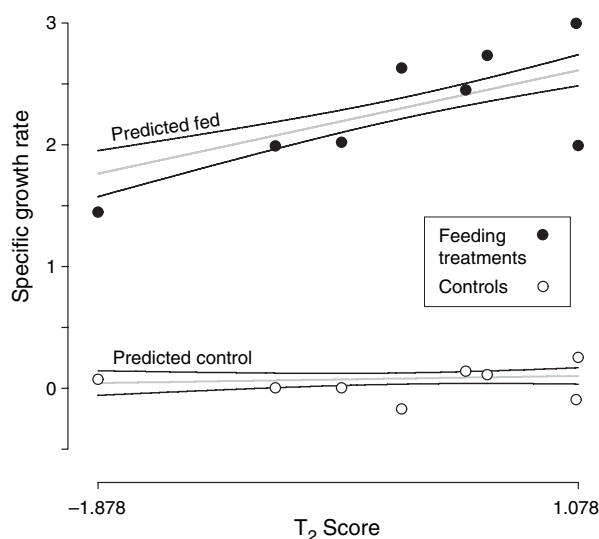


Fig. 2 Predicted growth response of YOY fish as a function of T_2 , the second principal component score for water temperature. High scores for T_2 indicate low but variable water temperatures; low scores indicate high, stable temperatures. T_2 measures the degree of departure from the main pattern in the temperature data (T_1), which was for stream temperature to rise and be more variable at sites further from groundwater sources. Datapoints indicate mean growth in each of eight pairs of enclosures; lines indicate predicted mean growth with standard deviation of the prediction.

Discussion

The experiment supports three conclusions. First, feeding treatments had a large effect on growth, suggesting that Lion Creek *O. mykiss* are generally food-limited during the summer. Indeed, specific

Table 4 Parameter estimates of the selected growth model

Parameter	Mean	SD	95% CI	Effect direction	S
Core model					
K (initial size)	-0.1837	0.03557	(-0.2535, -0.1145)	Negative	<0.0001
Q (treatment)	1.111	0.04539	(1.022, 1.198)	Positive	<0.0001
Random covariates					
T_1 (temperature PC1)	-0.03962	0.04787	(-0.134, 0.05466)	Neutral	0.20
T_2 (temperature PC2)	0.1535	0.05071	(0.0537, 0.2524)	Positive	0.0012
QT_1	0.03782	0.04767	(-0.05518, 0.03779)	Neutral	0.22
QT_2	0.1336	0.05001	(0.1336, 0.2317)	Positive	0.0045
Other parameters					
Intercept	1.063	0.04567	(0.9705, 1.153)	n/a	
σ_{fish} ('error')	0.4106	0.02816	(0.3606, 0.4713)	n/a	
σ_{fed} (extra treatment var.)	0.7084	0.07105	(0.5752, 0.8548)	n/a	

n/a, not applicable.

growth rate in the controls was close to zero. Secondly, the feeding treatment induced extra variation in growth among fish, doubling the SD of growth relative to controls (Table 1). Finally, the second principal component of the temperature data exhibited a pattern of co-variation with growth, suggesting that reaches with unusual components of coolness and variability were the ones in which the fish growth responded most strongly to supplements.

Temperature effects

Our original hypothesis was that higher temperature should increase growth rate (and survival) where food is not limiting, but do the opposite where food is insufficient. The data do not support the hypothesis, however. Higher temperature was also more variable, and the joint effect on growth (estimated as covariance with the first principal component score of the temperature data) was apparently neutral. This first principal component explained 96% of the variation among enclosures in mean and variance of water temperature, yet it was the second component T_2 (which explained the remaining 4%) that had a large interaction effect with the feeding treatment. It should be recalled too that this model performed better, in terms of DIC, than a random-effects model or a model retaining other habitat covariates (Table 2).

Variable temperature has been shown to have a positive effect on growth in aquarium experiments on various fish species, although negative effects have also been observed (Spigarelli, Thomemes & Prepejchal, 1982; Diana, 1984; Flodmark, Vollestad & Forseth, 2004; Meeuwig *et al.*, 2004). Most tellingly, Hokanson, Kleiner & Thorslund (1977) conducted *ad lib* feeding experiments on *O. mykiss* held in aquaria at a variety of mean temperatures, some treatments holding the temperature constant and others imposing a large diel cycle (amplitude 3.8 °C). Their data suggested that under constant temperature, growth rate peaks at a mean temperature of about 17 °C, but under strongly fluctuating temperature it peaks at a mean of about 15 °C (Fig. 3). That is to say, in water with a mean temperature >16 °C, an increase in variability caused a decrease in the growth rate, but <16 °C it led to an increase, suggesting a 'zone of complexity' between 15 and 17 °C (Fig. 3). This zone probably lies between the temperature for maximum

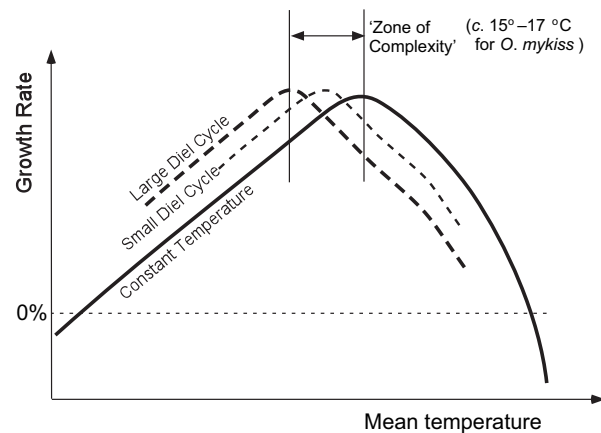


Fig. 3 Interpretation of results obtained by Hokanson *et al.* (1977), from an aquarium study of *ad lib* feeding in *Oncorhynchus mykiss* under constant and varying temperatures. Their results suggest a zone of complexity in which maximum growth depends on the relationship between mean temperature and the magnitude of temperature variation.

achievable growth (17 °C) and the temperature for optimum food conversion efficiency, which generally occurs at a slightly lower temperature (Elliott & Hurley, 2000).

In our experiment, ambient water temperature tended to fall into this zone of complexity (mean ranged 15.1–16.5 °C), thus suggesting an explanation for our results. In this zone, variable temperatures may allow gains in growth through some combination of the higher maximum growth rates achievable near 17 °C, and the higher conversion efficiencies achievable near 15 °C. Apparently the overall pattern of the correlated mean and variance tended to cancel out these countervailing effects, and it was only the departures from this pattern (measured by T_2) that showed an effect of temperature on growth. That effect was not trivial. For the average YOY fish with high food availability, the model of Fig. 2 predicts a mass-doubling time of 118 days in reaches with a low T_2 score, versus 53 days in those with a high T_2 score.

Variation among fish

The 'Hokanson interpretation' above, however, is an incomplete explanation because it does not predict our other principal result, the inflated growth variance in the feeding treatments (σ_{fed}). The co-efficient of variation for σ_{fed} was about 30%, meaning that high food availability dramatically widened the difference

between slow and fast growers. One potential explanation is that the fish varied in their potential growth rate; a second is that the food induced different energetic costs in different fish; and a third is that the fish had unequal access to food. The latter may be likely, as unequal access to food (due to shadow competition) has been directly observed in juvenile *Salmo trutta* L. inhabiting small streams (Elliott, 2002). However, the hypothesis of unequal energetic costs may also contribute, as this has been observed in *O. mykiss* inhabiting laboratory streams (Li & Brocksen, 1977). Li & Brocksen (1977) attributed the unequal energy loss to three factors mediated by dominance hierarchies and territoriality: starvation by submissive individuals, higher energy expenditures by trout forced into areas with high water velocity, and generally higher 'planes of excitation' among the trout. Another possible factor is a trade-off between foraging and other costs such as predation risk (e.g. Metcalfe, Fraser & Burns, 1998), which might induce higher energetic costs of predator evasion for individuals inhabiting unsafe parts of the stream.

Another partial explanation may be that high constant temperature increases the metabolic cost of feeding and assimilation (Morgan, McDonald & Wood, 2001). However, this does not explain why the fish failed to compensate by feeding at higher rates. Such failure (a form of endogenous appetite suppression) is observed at temperatures in the range of 18–22 °C (Morgan *et al.*, 2001), and even the lower part of this range was experienced only during the hottest parts of some days in our study. At lower temperature it seems more likely that, if appetite was suppressed, it was suppressed externally by competitors or predators. Perhaps constantly high temperature, by maintaining high fish metabolism, raises the general level of aggression or excitation in the population, with negative consequences for growth rate all around (Li & Brocksen, 1977; Metcalfe, Taylor & Thorpe, 1995; Sakakura & Tsukamoto, 1997; Vollestad & Quinn, 2003).

As our experiment treated temperature as an unmanipulated covariate, it could always be argued that temperature is confounded with some other habitat trait that is the true cause of the growth patterns we observed. But the most compelling possibilities can be ruled out: the growth effects were probably not caused by differences between the two sites, because site was confounded with T_1 but not with T_2 . It could

be argued that the pool versus riffle component of an enclosure might be confounded with T_2 , but we included a direct measure of this trait in seven of our candidate models (term H in Table 2), none of which were retained by the DIC selection method. The pairs of enclosures had similar riparian vegetation and geographical aspect, and, by design, identical fish species composition (*O. mykiss* only) with similar size distributions. To us, the most parsimonious explanation is to attribute the growth effects to T_2 .

General implications

In fish, large size and high fitness tend to be associated (Fleming, 1996; Sogard, 1997), and for *O. mykiss* in particular, fast growth in juveniles is thought to improve survival and shorten time to maturation. In an example from a small steelhead population south of San Francisco, scale analysis revealed that fish with rapid first-year growth survived disproportionately well to spawning age (Hayes *et al.*, 2004; Bond, 2006); a similar result was found for steelhead in British Columbia by Ward *et al.* (1989). Despite this benefit of being a fast-grower, *O. mykiss* can exhibit highly seasonal patterns of growth. For example, Johnsson, Clarke & Withler (1993) observed that *O. mykiss* growth slowed during the winter on Vancouver Island, even when the fish were kept warm and provided with abundant food. In the Central Valley of California in contrast, Merz (2002) observed that feeding activity is greatest in winter, suggesting that summer is a time of growth limitation. S. Sogard (personal communication) has collected data indicating a similar seasonal pattern for *O. mykiss* in a coastal redwood catchment in central California. Similarly, Harvey, White & Nakamoto (2005) observed generally low summer growth rates for *O. mykiss* inhabiting a tributary of Humboldt Bay in northern California. In their large sample of habitat units ($n = 59$), however, fully 15% of the units supported a mean specific growth rate in the range of 0.3–0.55, higher than the mean observed in any of our food-supplemented enclosures (Table 1). The controls for our experiment suggest that summer is, in general, a time of food limitation and slow growth for *O. mykiss* in southern California, but our replication was too small to rule out a pattern such as that described by Harvey *et al.* (2005). So far, the only habitats south of San Francisco documented to support high summer growth in

O. mykiss appear to be coastal estuary-lagoons (Bond, 2006).

Even under conditions of extremely high food availability, the experiment suggests that the potential for *O. mykiss* to realise rapid growth is constrained by water temperature and, interestingly, implies that the constraints are closely linked to stream-wide patterns of temperature and local-scale deviations from that pattern. The results also suggest that some component of the constraints involves a population-level mechanism of competition.

In general, mean temperature of streams in summer is expected to increase from headwater to confluence, as groundwater discharged to the channel gradually reaches equilibrium with air temperature (which tends to be warmer than the ground in summer, although cooler in winter; Bogan, Mohseni & Stefan, 2003). The diel variability of stream temperature is similarly expected to increase from headwater to confluence, since air temperature is more variable than ground temperature. However, the amount of water, and thus the thermal mass of the stream, also tends to increase from headwater to confluence, and this should reduce diel variation in temperature. This may cause temperature variability to plateau and perhaps even decline in a downstream direction. However, one would expect many local or regional departures from these expected patterns of mean and variance, because of influences such as groundwater flux and heterogeneity in hyporheic exchange, mesoclimate, channel shape or riparian vegetation (Matthews & Berg, 1997; Constantz, 1998; Bogan *et al.*, 2003). Our study suggests that such heterogeneity is important for fish populations near the edge of their range, particularly at sites in which the fish occupy a 'zone of complexity' where realised growth depends on complex interactions between mean temperature, temperature variability and food availability.

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