Effects of a Restricted Ration on the Growth and Energetics of Juvenile Rainbow Trout Exposed to a Summer of Simulated Warming and Sublethal Ammonia

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Abstract.—Laboratory tests were conducted to determine the potential effects of a warmer and more polluted environment on the growth and energetics of juvenile rainbow trout *Oncorhynchus mykiss* fed a fixed restricted ration (1% wet body weight/d) during summer. The fish were exposed either to the naturally fluctuating ambient thermal regime (base, representative of inshore Lake Ontario) or to the ambient regime + 2°C (base + 2°C), both in the presence or absence of 70 μmol total ammonia(T_{amm})/L (0.013 mg NH_3-N/L at 15°C, pH = 7.6). The 90-d exposures lasted from June to September 1994 and were designed to mimic an earlier study in which juvenile rainbow trout were fed to satiation. Relative to the earlier study, the restricted ration markedly increased (4–9-fold) the metabolic costs of nitrogen retention, that is, oxygen consumption per unit protein growth. Rainbow trout from the present study exhibited O_2 consumption, and specific growth rates that were 50–75% and 13–20%, respectively, of the O_2 and growth rates of fish fed to satiation. In addition to the pervasive ration effects, juvenile rainbow trout exposed to +2°C in the present experiment managed to retain more nitrogen for growth, at a slightly decreased energetic cost. Fish exposed to +70 μmol T_{amm}/L also exhibited higher energetic costs, but this was accompanied by a comparatively large increase in nitrogen retention efficiency. Thus, their ''costs of growth'' were substantially reduced. We conclude that a restricted ration of 1%/d will not further impair the ability of juvenile rainbow trout to cope with a chronic small temperature increase. Moreover, sublethal ammonia even may be beneficial under these circumstances.

Global warming forecasts predict a mean rise in ambient air temperature from 1°C to 2°C during the next 30 years (Mohnen and Wang 1992), with a concurrent increase in water temperature (Meisner et al. 1987). The implications for fish production and distribution are profound (Christie and Regier 1988), because the body temperatures of fish, and hence their metabolic and feeding rates, depend on water temperature (Brett et al. 1969; Elliott 1976). Further, prey abundance and avail-

ability may be altered as a result of warming (Hill and Magnuson 1990), which could pose an additional problem. Normally, under conditions of unlimited food availability, the energy remaining for fish growth after maintenance (i.e., scope for growth) increases with increasing water temperature up to a maximum beyond which appetite is suppressed, but maintenance requirements continue to increase, leaving very little energy for growth (Brett and Groves 1979; Elliott 1982). Therefore, a small chronic temperature increase coupled with food deprivation may be expected to alter the scope for growth for many temperate fish species (Jobling 1997).

Climate warming is expected not only to increase water temperature but also to result in elevated concentrations of contaminants such as ammonia (Coutant 1981; Vitousek 1994). Ammonia, ubiquitous in surface waters, is highly toxic to fish (Russo 1985), and more molecules of this pollutant are manufactured each year than any other industrial chemical (Atkins 1987). Because ammonia is also a natural biological degradation product of nitrogenous organic matter, it is a particularly good candidate for examining sublethal environmental pollutant effects in conjunction with temperature. The lowest lethal concentration of un-ionized ammonia found for salmonids is 0.083 mg NH_3-N/L (Thurston et al. 1984), but several sublethal effects have been reported at concentrations as low as 0.010 mg NH_3-N/L (Meade 1985).

The present study examines the effects of a restricted ration on juvenile trout growing in a warmer (+2°C) and more polluted (+70 μmol total ammonia[T_{amm}]/L) environment. The un-ionized ammonia concentration in ammonia treatments ranged from approximately 0.008 to 0.015 mg NH_3-N/L. The experimental approach is similar to one we have adopted in earlier studies in which juvenile rainbow trout *Oncorhynchus mykiss* were fed to satiation (see Linton et al. 1997, 1998b). The satiation feeding provided a measure of voluntary appetite as well as a mechanism for dietary compensation. The limited ration chosen in the

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TABLE 1.—Mean (±SD) water total ammonia concentrations ($N = 18$) and pH ($N = 5$) in tanks during 90-d exposures (20 June to 18 September 1994) of juvenile rainbow trout to +2°C and 70 µmol/L total ammonia (Am) at a fixed ration equivalent to 1% wet body weight/d.

Treatment and replicate	Total ammonia (µmol/L)	pH
Base		
1	7.8 ± 3.3	7.40 ± 0.22
2	8.4 ± 3.7	7.30 ± 0.37
Base + Am		
1	66.3 ± 9.6	7.60 ± 0.10
2	66.3 ± 8.7	7.60 ± 0.07
Base + 2°C		
1	8.1 ± 3.5	7.20 ± 0.49
2	8.6 ± 3.7	7.40 ± 0.24
Base + 2°C + Am		
1	66.1 ± 15.1	7.40 ± 0.30
2	63.1 ± 13.4	7.40 ± 0.22

present study eliminated this option. These data provide hard experimental evidence that chronically elevated temperature in environments with moderately elevated ammonia levels will not further impair the growth of fish contending with poor food availability. Moreover, such sublethal ammonia levels may have beneficial effects on protein retention.

Methods

Experimental animals and procedures.—Juvenile rainbow trout (approximately 4.5 g) were acquired from Rainbow Springs Trout Farm, Thamesford, Ontario, in the spring of 1994. The trout were held in a 600-L aerated polyethylene tank receiving approximately 2.5 L/min dechlorinated Hamilton tap water as described in Linton et al. (1997). The temperature regime of Hamilton tap water represents that of nearshore Lake Ontario from which it is derived (Ca^{2+} = 0.94 µmol/L, Na^+ = 0.60 µmol/L, Cl^- = 0.76 µmol/L, pH = 7.5, hardness = 140 mg/L as $CaCO_3$). During this period, water temperatures ranged from 11°C to 13°C. On 20 June, groups of 150 fish were randomly distributed to eight tanks representing four treatments with two replicates per treatment. The tanks (270-L, approximately two-thirds full) received 2.0 L/min of water either at ambient temperature (base treatment) or at ambient temperature plus 2°C (base + 2°C) or with an additional 70 µmol T_{amm}/L (base + Am) or with both (base + 2°C + Am). Exposure conditions were as in Table 1. Un-ionized ammonia concentrations ranged from 0.010 to 0.015 mg NH_3-N/L at base temperatures, and from 0.008 to 0.012 mg NH_3-

N/L at base + 2°C. Treatments that did not receive additional ammonia did not exceed 0.002 mg NH_3-N/L. The dissolved oxygen content of the water was maintained above 95% saturation throughout the experiment.

The experimental procedures, analyses, and calculations of Linton et al. (1997) were followed with the exception of fish biomass monitoring, which was conducted weekly via bulk weighing to determine the ''fixed restricted'' ration that would be provided. Briefly, fish were netted from their tanks into a bucket containing 10 L water and a removable plastic sieve. The bucket and contents were weighed on a tared scale (GSE 450 Scale Systems, Michigan, USA), and the fish were then removed and placed back into their tank. The bucket and contents were reweighed, and fish biomass was calculated by difference. Each group was subsequently fed a restricted ration equivalent to 1% wet body weight/d of the base group, the experimental control. Half of the daily ration was provided at 0830 hours and half at 1630 hours.

Statistical analysis.—As noted in the earlier studies (Linton et al. 1997, 1998b), the values for the energy budget and nitrogen retention efficiencies are reported on a per fish basis from the single experimental tank in each treatment for which O_2 consumption was measured; that is, the O_2 consumption rates reported were from a whole tank of fish, as in the work of Brett and Zala (1975), and statistical analyses were not performed. All other data are expressed as means ± SD with the two replicate means as the basis for the estimation of error (df = 1). Multiple analysis of variance (ANOVA) with leverage plots (SAS Jmp; SAS Institute, Inc., version 2.0.5) was employed to distinguish statistically significant temperature, ammonia, and interactive effects, factored by time (0, 30, 60, and 90 d, respectively). The level of statistical significance for all analyses was $P \leq 0.05$.

Results and Discussion

Food availability is a powerful temperature-dependent selective force affecting growth of aquatic ectotherms—as temperature rises, so does their maintenance metabolism and appetite. Therefore, food limitation precludes growth in favor of meeting maintenance energy requirements. The present study was designed to assess whether a restricted ration caused juvenile rainbow trout to respond differently to small chronic elevations in water temperature and sublethal environmental ammonia (approximately 0.013 mg NH_3-N/L) when compared with fish fed to satiation (see Linton et al.
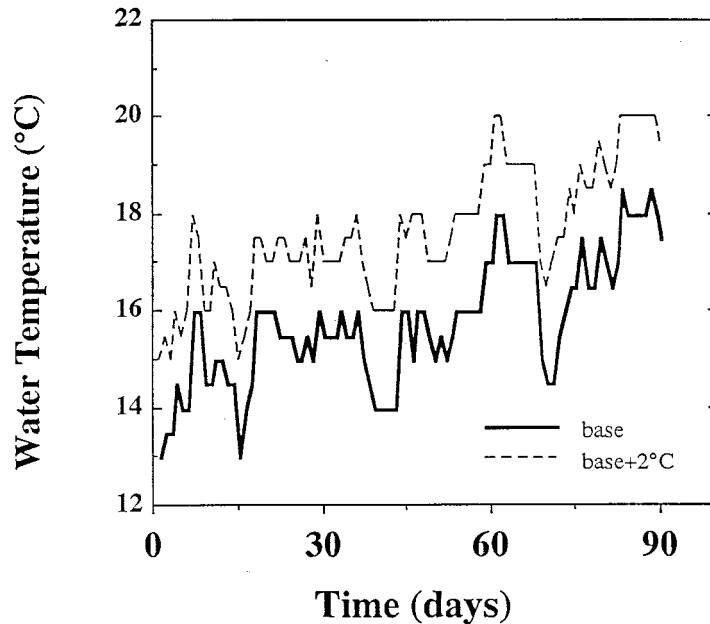
FIGURE 1.—Water temperature profile as measured daily for 90 d from June to September 1994. Juvenile rainbow trout were exposed either to ambient laboratory water temperatures (base, representative of nearshore Lake Ontario) or to ambient water + 2°C (base + 2°C).

1997). In the satiation feeding experiment conducted during the summer of 1993, appetite, oxygen consumption, and protein metabolism were critically impaired in the base + 2°C groups during maximum summer (August–September) water temperatures (Reid et al. 1995; Linton et al. 1997). Based on these results, we predicted that food limitation might impose further restriction on the ability of juvenile trout to compensate for a small chronic temperature change. Furthermore, with food restriction, growth may not be stimulated by sublethal ammonia as seen in juvenile trout fed to satiation during summer (Linton et al. 1997).

The thermal profiles between the present (Figure 1) and previous summer exposures (Linton et al. 1997: Figure 1) were slightly different, but the degree-days of exposure were similar. The thermal profile for nearshore Lake Ontario from 20 June to 18 September 1994 was characterized by a slow but gradual rise in ''base'' water temperature from 13°C to 18°C, which amounted to 1,419 degree-days of exposure, just slightly lower than the 1,445 degree-days the base fish were exposed to during the summer of 1993 (Linton et al. 1997). In the present study, fish exposed to an additional 2°C experienced water temperatures ranging from 15°C to 20°C or a total of 1,585 degree-days of exposure

(Figure 1), compared with 1,584 degree-days in the +2°C treatment of the previous experiment.

Contrary to prediction, the +2°C did not further impair the ability of rainbow trout to cope with chronic temperature change. On a ration of only 1% body weight/d based on the growth of the base treatment group, these trout consumed an average 0.06 g food/d resulting in a mean specific growth rate of only 0.42%/d. There were no statistical differences in wet weights (range: 4.73 ± 0.27 g initial to 7.42 ± 0.44 g final) or total lengths (range: 7.89 ± 0.14 mm initial to 8.98 ± 0.19 mm final) between treatment groups, and condition factors did not change appreciably from an initial value of 0.94 ± 0.01. Likewise, only very subtle differences existed in the partitioning of food energy into body materials of fish between groups (Table 2). Time alone had the greatest effect on the partitioning of body materials (Table 2). For instance, all trout exhibited a small increase in whole-body water content and a large reduction (>30%) in lipid after the first 30 d of exposure, and by day 60 total carbohydrate (glucose, glycogen, and lactate) content had approximately doubled (Table 2).

Compared with the satiation experiment (Linton et al. 1997), however, the restricted ration dramatically altered the metabolic costs of N retention

TABLE 2.—Effects of +2°C and 70 μmol total ammonia/L (Am) on whole-body carbohydrate (glucose, glycogen, and lactate), lipid, protein, and water content of juvenile rainbow trout fed a restricted ration equivalent to 1% wet body weight/d for 90 d (June to September 1994). Results are expressed as the mean ± SD of the two replicate tanks per treatment (5 individuals/tank per time period). All values are reported as percentage composition (g/100 g) of wet tissue. Statistically significant effects were time (t) and total ammonia (Am) but not temperature or temperature + ammonia interaction (multiple analysis of variance; $P \leq 0.05$).

Interval and treatment	Carbohydrate	Lipid	Protein	Water
Day 0	0.078 ± 0.004	8.04 ± 1.64	8.33 ± 1.34	77.4 ± 1.69
Day 30				
Base	0.077 ± 0.000	5.35 ± 0.62	6.75 ± 0.45	78.8 ± 1.00
Base + Am	0.076 ± 0.008	4.94 ± 0.45	7.70 ± 0.40	80.0 ± 0.60
Base + 2°C	0.106 ± 0.001	5.97 ± 0.28	7.60 ± 0.10	78.7 ± 0.40
Base + 2°C + Am	0.075 ± 0.002	4.90 ± 0.17	7.05 ± 0.25	80.9 ± 0.25
Day 60				
Base	0.157 ± 0.011	4.48 ± 0.48	6.15 ± 0.05	79.5 ± 0.60
Base + Am	0.179 ± 0.021	4.09 ± 0.85	7.40 ± 0.30	79.8 ± 0.90
Base + 2°C	0.181 ± 0.033	4.36 ± 0.47	6.35 ± 0.25	79.4 ± 0.75
Base + 2°C + Am	0.153 ± 0.021	4.30 ± 1.65	7.70 ± 0.70	79.5 ± 1.05
Day 90				
Base	0.114 ± 0.001	4.16 ± 0.15	7.80 ± 0.20	75.7 ± 0.75
Base + Am	0.140 ± 0.001	4.44 ± 0.26	8.95 ± 0.55	78.3 ± 0.40
Base + 2°C	0.156 ± 0.005	4.89 ± 0.60	7.95 ± 0.75	78.3 ± 0.70
Base + 2°C + Am	0.160 ± 0.003	5.49 ± 0.62	9.90 ± 1.00	77.1 ± 0.45
Significant effect	t	t	t, Am	t, Am

(protein growth). The total O_2 consumed by fish in the present exposure was 24–28% of the O_2 consumed by maximally feeding rainbow trout during the previous summer, but their body N gain was only 3–6% (Table 3). Moreover, the 90-d metabolic expenditures of fish in the present study constituted 62–80% of the total energy consumed (quotient of R and C in Table 4), as opposed to only 36–47% for juvenile trout fed to satiation (Linton et al. 1997). Such relations between

TABLE 3.—Comparison of total oxygen consumption, total nitrogen (N) retention, and the metabolic cost of growth (quotient of moles of oxygen consumed and moles of nitrogen retained, or N-cost index) of juvenile trout fed a restricted ration equivalent to 1% wet body weight/d for 90 d during the summer of 1994 (present study) or fed to satiation for 90 d during the summer of 1993 (summer satiation, from Linton et al. 1997).

Exposure and treatment	Total O_2 consumed (mol)	Total N retained (mol)	N-cost index
Summer restricted			
Base	0.136	0.0017	80.0
Base + Am	0.152	0.0026	58.5
Base + 2°C	0.140	0.0018	77.8
Base + 2°C + Am	0.179	0.0039	45.9
Summer satiation			
Base	0.570	0.0590	9.7
Base + Am	0.537	0.0816	6.6
Base + 2°C	0.570	0.0573	9.9
Base + 2°C + Am	0.676	0.0611	11.1

growth, O_2 consumption, and feeding level have been shown before (Wurtsbaugh and Davis 1977; Soofiani and Hawkins 1982; Hogendorn 1983). With food restriction, however, trout exposed to +2°C exhibited higher energy conversion efficiencies (Table 4), and thus a slightly lower metabolic cost of N retention compared with the base temperature group (Table 3). This latter effect was not observed in the previous summer satiation feeding experiment in which trout appeared to optimize fuel use (lipid) to meet the increased energetic demands of the additional 2°C (Linton et al. 1997). In the present case, we suspect that the slightly reduced ''cost of growth'' experienced by the ''warmed'' fish may reflect their not having to contend with the added energy required for the uptake, digestion, and transformation of excessive food into body materials. By comparison, trout exposed to the combination of temperature and ammonia (base + 2°C + Am), despite greater energy demands (Table 4), had a much reduced cost of N retention (Table 3).

Although the absence of replication prevents statistical validation of these results, the apparent stimulatory effect of 70 μmol T_{amm}/L on protein–N retention of fish fed restricted rations certainly warrants further investigation. Linton et al. (1997) proposed a mechanism whereby protein was retained in fish exposed to +70 μmol T_{amm}/L due to an increase in liver protein synthesis induced as an

TABLE 4.—Energy budgets and N retention efficiencies for juvenile rainbow trout fed a restricted ration equivalent to 1% wet body weight/d for 90 d (June to September 1994) and exposed to a + 2°C warming scenario and 70 μmol/L total ammonia (Am).

Interval and treatment	Energy (kg/fish)[a]				Net energy conversion efficiency[b]	N retention efficiency[c]
	C	ΔB	R_E	(F_E+U)		
Day 0–30						
Base	25.9	−3.0	17.6	11.3	−11.6	−1.4
Base + Am	26.4	−2.5	17.7	11.2	−9.3	6.7
Base + 2°C	27.4	−0.7	18.3	9.8	−2.4	5.0
Base + 2°C + Am	27.6	−4.3	19.3	12.6	−15.5	−0.4
Days 30–60						
Base	30.6	0.4	20.6	9.6	1.4	3.3
Base + Am	30.5	0.9	21.7	7.9	2.9	6.5
Base + 2°C	32.5	−1.3	22.6	11.3	−4.1	0.4
Base + 2°C + Am	32.9	3.3	27.7	1.8	10.1	12.8
Days 60–90						
Base	38.8	4.9	21.2	12.7	12.7	16.6
Base + Am	38.9	7.9	25.0	6.0	20.2	18.4
Base + 2°C	42.3	8.8	20.1	9.5	20.7	17.3
Base + 2°C + Am	42.7	12.5	34.7	−4.5	29.2	22.9
Days 0–90						
Base	95.3	2.4	59.3	33.6	2.5	7.5
Base + Am	95.7	6.3	64.3	25.1	6.6	11.4
Base + 2°C	102.2	6.8	64.9	30.5	6.6	8.6
Base + 2°C + Am	100.9	11.5	81.7	7.7	11.4	13.4

[a] C = total energy consumed from food; ΔB = energy stored in body materials; R_E = total metabolic energy lost as heat; F_E = energy lost in feces and unaccounted energy; U = energy lost via branchial and urinary excretion. Both F_E and U were determined by back-calculation.
[b] Conversion efficiency = 100ΔB/C.
[c] Nitrogen retention efficiency = 100 × N retained/N consumed (as determined from whole-body and food protein measurements, assuming an N content of 16%).

ammonia-detoxifying process. In the present study, there was neither a significant increase in the liver protein synthesis rates of ammonia-exposed fish (Morgan et al. 1999) nor any significant differences in either liver and white muscle ammonia or urea levels (data not shown). The whole-body protein content of ammonia-exposed fish, on the other hand, was significantly elevated (Table 2). As a result of this latter effect, the ammonia-exposed fish exhibited nitrogen retention efficiencies (expressed as a percentage of the total N consumed) that were approximately 1.5 times greater than those fish growing in the absence of ammonia (Table 4).

The present study indicates that changes in metabolic fuel use play a significant role in the growth and energetics of juvenile rainbow trout fed a restricted (1% wet body weight/d) ration during summer. Moreover, restricting the ration during a naturally fluctuating summer temperature regime will invoke changes in energy reserves, such as lipid and carbohydrate, similar to those seen in fasting fish at constant temperatures (Morata et al. 1982; Black and Love 1986). Despite the gross changes in energy partitioning associated with this restricted ration, the addition of +2°C did not cause juvenile trout to respond unfavorably to the warmer environment. However, food limitation probably did inhibit the ability of juvenile trout to acclimate to this small chronic temperature increase (see Linton et al. 1998a), due to less energy being available for any necessary physiological adjustments (i.e., enzymatic stability, membrane fluidity, heat shock proteins, etc.). Trout exposed to +70 μmol T_{amm}/L managed to incorporate comparatively more N into body materials, thereby reducing their overall metabolic costs of nitrogen retention. The cost of growth for trout exposed to +2°C and ammonia was similarly reduced. However, absolute growth was not stimulated, as it was in juvenile trout fed to satiation. Thus, we conclude that restricted ration will not further impair the ability of juvenile rainbow trout to grow and cope with a warmer and polluted environment.

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