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The Metabolic Costs and Physiological Consequences to Juvenile Rainbow Trout of a Simulated Winter Warming Scenario in the Presence or Absence of Sublethal Ammonia

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Abstract.—This experiment examined the metabolic costs and physiological consequences of growth and energetics of juvenile rainbow trout *Oncorhynchus mykiss* in a warmer, more polluted winter environment. Growth under the warm-winter conditions was approximately three times less than equivalent growth of experimental and control groups previously observed under warm-summer conditions. However, during winter exposure, wet weights and total lengths were roughly 30% higher in the ‘‘warmed’’ fish than in the base temperature group due to a combination of greater appetite and higher energy conversion efficiency. Oxygen consumption and nitrogenous (ammonia + urea) waste excretion rates were 30–40% higher for ‘‘warmed’’ fish but were less than one-third of levels recorded in the summer. A corresponding increase in food intake was associated with elevations in whole-body protein and lipid but not carbohydrate. Addition of 70 μmol ammonia/L elevated nitrogenous waste excretion much like in the previous summer exposure, but over this winter period it did not result in increased weight gain. Plasma total ammonia was not significantly higher in the ammonia-exposed fish, unlike the summer experiment. Although nitrogen retention efficiency was much lower for overwintering juvenile trout fed to satiation, the metabolic cost of nitrogen retention (growth) was similar to that of juvenile trout exposed during summer. We conclude that overwintering juvenile trout fed unlimited ration and subjected to simulated warming, both alone and in combination with elevated environmental ammonia, will exhibit increased growth with only a slight elevation in energetic cost.

Mean annual air temperature is predicted to rise in response to an increase in atmospheric greenhouse gases (Hansen et al. 1988), and rising with it will be mean annual water temperatures (Meisner et al. 1987). Such changes are expected to have profound effects on fish populations (Healey 1990), shifting species' geographic ranges (Meisner 1990; Shuter and Post 1990; Keheler and Rahel 1996) and altering population dynamics (DeAngelis and Cushman 1990; Magnuson et al. 1990). Yet despite attempts to predict the overall response of fish to climate change (Magnuson et al. 1990; Regier et al. 1990), considerable uncertainty still exists. In particular, those predictions at or near the extreme minimum and maximum survival temperatures remain ‘‘not fully satisfactory'' (Lin and Regier 1995).

We have designed a laboratory-based system that allows us to test the effects of a global warming scenario of +2°C to a reference coldwater fish species, rainbow trout *Oncorhynchus mykiss*, across a naturally occurring thermal regime (representative of nearshore Lake Ontario) that includes seasonal temperature extremes (Reid et al. 1997). In addition, we have incorporated chronic pollutant exposure (i.e., elevated ambient ammonia) in anticipation of the likely increase in the concentrations of aquatic pollutants which may accompany CO_2 enrichment of the atmosphere (Coutant 1981). Our goal has been to quantify the basic long-term bioenergetic, physiological, and toxicological responses of juvenile trout to a warmer and more polluted aquatic environment. Although this work is often considered in an ecological context, it is also particularly relevant to hatchery conditions. In our earlier study (Linton et al. 1997), we discovered that trout exposed to +2°C and fed unlimited ration during summer exhibited enhanced energy conversion efficiency and increased nitrogen retention at a metabolic cost equivalent to trout grown at the base thermal regime. Although the appetite of these ‘‘warmed'' fish was suppressed during maximum summer water temperatures, fuel use and particularly lipid appeared to have been optimized to meet the increased bioenergetic demands. Low-level ammonia exposure, on the other hand, enhanced nitrogen and energy conversion efficiency, resulting in increased nitrogen retention at a reduced metabolic cost. The beneficial ammonia effect was not exhibited in

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ammonia-exposed trout coping with the additional stress of +2°C.

Here we report a parallel study conducted in winter, posing the following questions: (1) will the additional +2°C induce greater physiological effects due to increased thermal sensitivity (Q_{10}s) of trout at lower temperatures? (2) will the beneficial effects of +70 μmol ammonia/L on nitrogen retention that were seen in juvenile trout during summer still occur at such low water temperatures at which ammonia is considerably more toxic (see Brown 1968; EIFAC 1973; Knoph 1992)? We adopted the same approach used in our earlier study, employing a number of physiological indices to assess the long-term consequences and metabolic costs for juvenile trout exposed to a small increase in temperature and an environmentally relevant concentration of priority pollutant, alone and in combination. These indices include food intake, growth, metabolic rate, nitrogen balance, and proximate composition.

In this winter study, relatively large increases in food intake, oxygen consumption, and nitrogenous waste production occurred in the presence of +2°C. As a result, trout exposed to additional temperature, alone and in combination with 70 μmol ammonia/L, exhibited increased growth at only slightly higher energetic costs. Moreover, a metabolic depression similar to that of the warmed fish fed maximally during peak summer water temperatures was exhibited by maximally fed trout grown at the ''base'' thermal regime, indicating higher thermal sensitivity at these low winter water temperatures. Although nitrogen absorption efficiency was elevated in ammonia-exposed fish, they generally did not retain more nitrogen than fish grown in the absence of the additional ammonia.

Methods

Animal acclimation.—Juvenile rainbow trout (2–5 g) were obtained from Rainbow Springs Trout Farm, Thamesford, Ontario, in November 1993, approximately 6 weeks prior to testing and were held under similar conditions as in Linton et al. (1997). Hamilton tap water characteristics were $[Ca^{2+}]$ = 0.88 mmol/L, $[Na^{+}]$ = 0.50 mmol/L, $[Cl^{-}]$ = 0.73 mmol/L, pH = 7.5, and hardness = 140 mg/L as $CaCO_3$. Ambient water temperature ranged from 4°C to 6°C during this period in which fish were fed every other day a maintenance ration equivalent to 1% body weight (wet basis) of Zeigler's Trout Starter 3 (50% protein, 15% lipid, 12% moisture). All fish were kept under the natural photoperiod for Hamilton, Ontario, during acclimation and throughout the experiment.

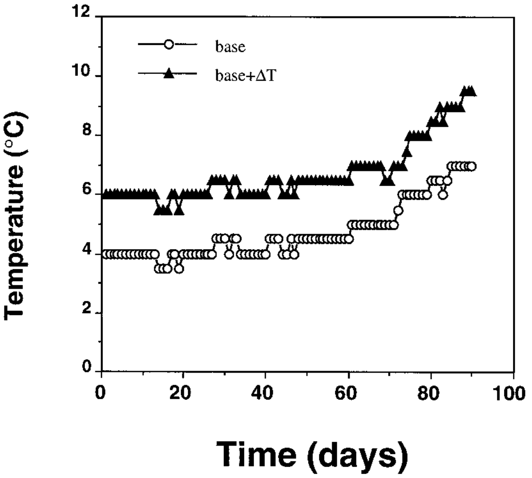

FIGURE 1.—Daily water temperature profile as measured each day during 90-d exposures from January to April 1994. Juvenile rainbow trout were exposed either to ambient laboratory water temperatures (base) or to ambient water +2°C (base+ΔT).

Experiments.—Groups of approximately 130 rainbow trout were randomly distributed among eight tanks representing four treatments (260 fish per treatment). The tanks (270 L) received 2.1–2.3 L/min flows of either ambient temperature water (dechlorinated City of Hamilton tap water drawn from the inshore region of Lake Ontario, which will be referred to as base water temperature) or this water plus 2°C (base+ΔT), each with or without the addition of 70 μmol total ammonia/L (T_{Amm} = NH_4^+ + NH_3; base+Am and base+ΔT+Am, respectively). The treatment conditions were achieved by using heat exchangers and mariotte bottles, respectively, as described in Linton et al. (1997). A mean difference of 2.01 ± 0.21°C existed between base and base+ΔT thermal profiles (Figure 1), which averaged approximately 5°C and 7°C for the entire 90-d period. Mean tank water T_{Amm} concentrations were 76.6 ± 1.9, 8.3 ± 0.3, 9.5 ± 0.3, and 88.8 ± 1.8 μmol/L for base+Am, base, base+ΔT, and base+ΔT+Am treatments, respectively. The partial pressure of oxygen in tank water was maintained at approximately 90% air saturation (44.7 ± 1.1 torr) throughout the study, and the pH averaged 7.50 ± 0.021.

Procedures, analyses, and calculations were as previously described in Linton et al. (1997). Specific growth rates (SGR, %/d) were determined for

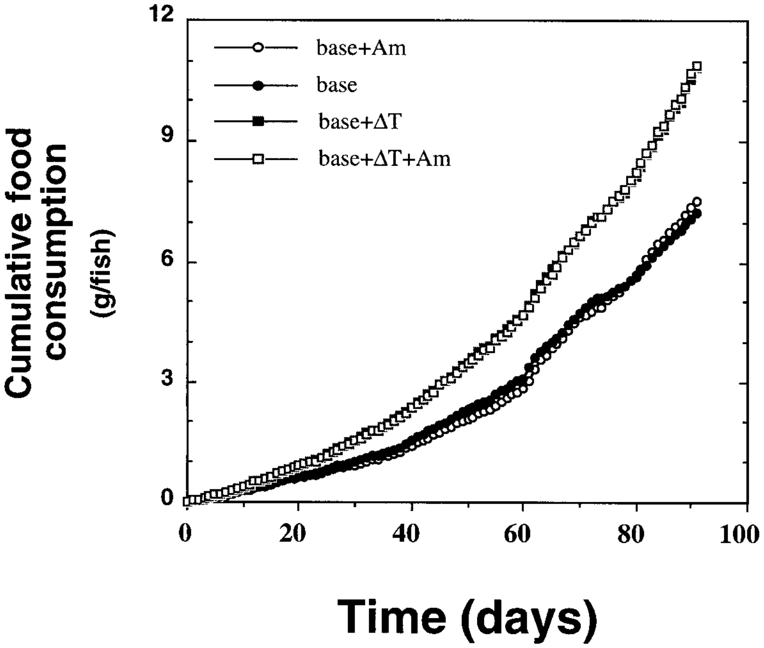

FIGURE 2.—Effects of +2°C (ΔT) and 70 μmol ammonia/L (Am) added to ambient laboratory water conditions (base) on appetite of juvenile rainbow trout fed to satiation twice daily. Appetite was measured as cumulative food intake during the 90-d exposures. The data are presented on a per-fish basis. Each value represents the mean of the two replicate tanks per treatment ($N = 2$). (Open and solid squares overlap throughout the time period.)

30 fish removed from each tank ($N = 60$ fish per treatment) calculated by the formula

$$\text{SGR} = 100(\log_e Y_2 - \log_e Y_1)/(t_2 - t_1),$$

where Y_1 and Y_2 are mean wet weights of fish at time t_1 and t_2. Condition factors were determined as the quotient of the wet weight (g) of the fish and its total length (cm) cubed, multiplied by 100. The values for the nitrogen and energy budget are reported on a per fish basis from the single experimental tank in each treatment where O_2 consumption and N-waste excretion were measured; that is, the O_2 consumption and N-waste excretion rates reported were from a whole tank of fish, as in the work of Brett and Zala (1975). All other data are expressed as means ± SD with the two replicate means as the basis for the estimation of error (df = 1). Two-way analysis of variance with leverage plots (SAS Jmp; SAS Institute, Inc., version 2.0.5) were employed to distinguish statistically significant levels of temperature (+2°C, marked by T in the tables), ammonia (+70 μmol ammonia/L, marked by A in the tables), and interactive (I) effects. The level of statistical significance for all analyses was $P \leq 0.05$.

Results

The thermal profile from the period of 20 January to 30 April 1994 was characterized by a relatively constant 4°C during the first 75 d, followed by a slow but gradual rise to 7°C during the last 15 d (Figure 1). Warming the water by +2°C during winter greatly stimulated the appetite of juvenile trout (Figure 2). The total amount of food consumed per fish at ambient water temperatures were 7.7 and 7.4 g for base+Am and base treatments, respectively, whereas their +2°C counterparts consumed 11.2 and 11.0 g. As a consequence, wet weight and total length were significantly greater in the +2°C groups throughout the exposure (Table 1). The SGRs for day 0 to day 90 were 0.77 ± 0.04, 0.72 ± 0.11, 1.08 ± 0.02, and 1.09±0.03%/d for the base+Am, base, base+ΔT, and base+ΔT+Am groups, respectively. The addition of 70 μmol/L T_{Amm}, therefore, had no significant effect on appetite or growth in either temperature regime.

Condition factors were elevated in the +2°C treatments after the first 75 d of exposure, but were not significantly different from those of fish grown at ambient temperature. The condition factors ex-

TABLE 1.—Growth and whole-body proximate chemical composition of juvenile rainbow trout fed to satiation and exposed to a +2°C warming scenario (ΔT) and 70 μmol ammonia/L (Am). Results are expressed as the mean ± SD of the two replicate tanks per treatment (5 individuals per tank for whole-body proximate chemical composition and 20 individuals per tank for growth). For each sampling day separately, statistically significant temperature (+2°C treatments = T), ammonia (+70 μmol/L T_{Amm} treatments = A), and interactive (I) effects are denoted underneath the respective columns (two-way ANOVA; $P \leq 0.05$); where there are no letters, there were no significant differences.

Test day, treatment, and statistic	Growth			Whole-body		
	Wet weight (g)	Total length (cm)	Condition factor	Lipid (mg/100 mg)	Protein (mg/100 mg)	Carbohydrate (mg/100 mg)
Initial	5.50 ± 1.54	8.47 ± 0.77	0.89 ± 0.13	4.98 ± 0.64	15.96 ± 0.82	0.174 ± 0.02
Day 75						
Base	9.18 ± 0.77	9.55 ± 0.09	1.03 ± 0.04	4.75 ± 0.01	16.07 ± 0.26	0.210 ± 0.157
Base+Am	7.75 ± 0.08	9.10 ± 0.06	1.01 ± 0.01	5.32 ± 0.29	16.85 ± 0.31	0.242 ± 0.033
Base+ΔT	11.37 ± 0.58	10.08 ± 0.12	1.07 ± 0.01	5.96 ± 0.35	17.11 ± 0.01	0.202 ± 0.003
Base+ΔT+Am	11.95 ± 0.86	10.32 ± 0.15	1.07 ± 0.03	5.66 ± 0.14	17.36 ± 0.66	0.210 ± 0.049
ANOVA	T	I		T	T	
Day 90						
Base	10.58 ± 1.06	9.87 ± 0.33	1.08 ± 0.01	6.27 ± 0.29	15.34 ± 0.03	0.256 ± 0.048
Base+Am	11.05 ± 0.38	9.94 ± 0.16	1.09 ± 0.01	6.02 ± 0.43	15.14 ± 0.06	0.331 ± 0.053
Base+ΔT	14.54 ± 0.28	11.00 ± 0.03	1.05 ± 0.00	5.78 ± 0.81	15.21 ± 0.15	0.170 ± 0.001
Base+ΔT+Am	14.66 ± 0.41	10.91 ± 0.02	1.08 ± 0.01	6.64 ± 1.02	15.69 ± 0.17	0.175 ± 0.052
ANOVA	T	T	A	I		T

hibited a trend similar to that of whole-body lipid content, which was significantly higher in the warmed fish at day 75 as was their protein content (Table 1). Following the temperature rise after day 75, protein content fell to near initial values in fish from all treatments, which corresponded to the general increase in white muscle ammonia concentration from 6.62 ± 0.63 to 8.20 ± 0.14 mmol/kg (data not shown). During this time, the base+ΔT+Am group contained the greatest amount of protein. There were no differences in carbohydrate until day 90 (Table 1), when fish exposed to +2°C contained significantly lower carbohydrate than fish at ambient temperature.

Despite the changes in whole-body proximate chemical composition of trout exposed to +2°C, there were no significant differences in whole-body water content, although mean water content decreased to 73% at the end from an initial 76.0 ± 0.5%. Likewise, the additional temperature exerted little effect on hematocrit and plasma composition, which varied from tank to tank and with the thermal regime. Overall, plasma T_{Amm} tended to be higher and hematocrit and Na^+ tended to be lower in fish exposed to ammonia, though these trends were not significant (data not shown).

Like food consumption, routine O_2 consumption and N-waste excretion rates were 30–40% higher in fish exposed to +2°C throughout the experiment (Figure 3A, B), and in general, ammonia-exposed fish oxidized more protein (as indicated by higher nitrogen quotients; see Figure 3C). Urea comprised only a small portion of the total N-waste produced, averaging 13%. The proportion of the oxygen consumed that was dedicated to protein catabolism averaged 84% and 69% for base+Am and base+ΔT+Am groups, respectively; whereas, the corresponding nonammonia-exposed groups averaged 43% and 47%. Yet despite the elevated protein catabolism, ammonia-exposed fish retained the same amount of N relative to the amount of N consumed due to a 14–21% higher N absorption efficiency (Table 2). An initial deficit in N retention in fish exposed to base+Am when compared with the base group between 0 and 75 d suggests at least some inhibition by ammonia at 4°C (Table 2).

Similar to the situation for N retention, fish at +2°C gained twice as much energy in body materials (ΔB), though there were no marked differences in conversion efficiency after 90 d of exposure (see 0–90; Table 3). This lack of difference in energy conversion efficiency appears to be related to trade-offs in fecal (F_E) and metabolic (R_E) energy loss. However, at the very low water temperatures to which the base groups were exposed between days 0 and 75 (4°C), energy conversion efficiency was noticeably reduced (Table 3) and more so in the base+Am group. As a result, this group's metabolic cost for N gain (N-cost index) was initially higher, but after base temperatures rose (from 4.5°C to 6.5°C; see days 75–90, Figure 1), it was markedly reduced (Table 3). The additional 2°C, in general, only slightly increased the metabolic costs of N gain (growth).

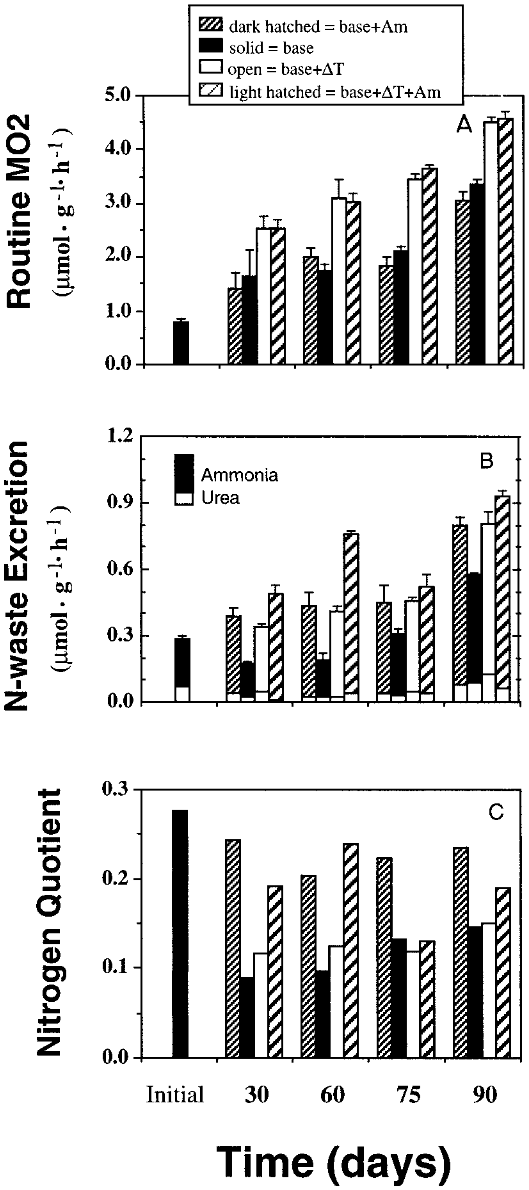

FIGURE 3.—Effects of +2°C (ΔT) and 70 μmol ammonia/L (Am) added to ambient laboratory water conditions (base) on **(A)** routine in-tank oxygen consumption (MO_2; $N = 5$ measurements on the same tank), **(B)** routine in-tank N-waste excretion (ammonia + urea N; $N = 6$ measurements on the same tank), and **(C)** the nitrogen quotients of juvenile rainbow trout fed to satiation twice daily. In panels A and B the data have been scaled for fish weight as detailed in Linton et al. (1997). Measurements were made on one tank of individuals per treatment. Error bars represent measurement SE (of the mean O_2 consumption and N-waste excretion rates calculated over the respective sample intervals) and cannot be used for statistical comparisons between treatments.

Discussion

Effects of an Additional 2°C

The impact of climate change on fish is a particular concern because of its potential influence on physiological and ecological rate processes, especially growth, which may contribute to large-scale events such as geographic shifts and local extinction (Lin and Regier 1995). It is predicted that if warming should actually occur, ice-free time on the Great Lakes will increase (Shuter et al. 1983) and, consequently, so too will the annual growth of yearling trout, providing that prey availability remains adequate (Hill and Magnuson 1990). The present study took full advantage of a natural temperature profile at the low winter extreme to investigate the likely impact of chronic small temperature elevation (+2°C) on trout in simulated pristine and polluted environments. Although the data are limited by design to conditions similar to those of southwest Lake Ontario, the contents provide the hard experimental evidence needed to predict the effects of chronic small temperature change on coldwater fish species living in many of today's environments. Furthermore, the data are complementary to those of the preceding study conducted over summer (Linton et al. 1997).

In the present experiment, trout exposed to the base thermal regime and fed to satiation twice daily achieved a SGR of only 0.7%/d, whereas their +2°C counterparts achieved a rate of 1.1%/d. By comparison, trout of equivalent age fed to satiation over summer (base thermal regime rising from 13°C to 21°C) grew at a rate of approximately 3.0%/d, as did the trout at +2°C in summer (Linton et al. 1997). In this summer study, we concluded that the most significant effect of the +2°C warming scenario was the 30% reduction in food intake experienced by the warmed fish in the last 30 d, when water temperatures were approaching their upper lethal maximum (Bidgood and Berst 1969). A significant temperature-dependent feeding effect was also experienced by the warmed fish of the present study; however, this time their food consumption increased by more than 30%.

It is evident from the present results that the increased appetite of fish at +2°C promoted the growth of juvenile rainbow trout on unlimited ration, which is in agreement with earlier findings; Elliott (1976) reported a five-fold increase in stored energy (ΔB) between maximally fed brown trout *Salmo trutta* weighing 50 g and exposed to constant temperatures of either 3.8°C or 5.6°C. In contrast, Wurtsbaugh and Davis (1977) examined

TABLE 2.—Nitrogen budgets for juvenile rainbow trout fed to satiation for 90 d (January–April 1994) and exposed to a +2°C warming scenario (ΔT) and 70 μmol/L ammonia (Am).

Interval and treatment	Nitrogen (mmol/fish)[a]					Retention efficiency[b] (%)	Absorption efficiency[c] (%)
	I	E	R_{N}	F_{N}	A		
Days 0–75							
Base	29.1	5.3	7.0	16.9	12.3	23.9	42.1
Base+Am	27.7	10.6	4.9	12.2	15.5	17.5	55.9
Base+ΔT	40.9	11.6	12.2	17.0	23.9	29.9	58.4
Base+ΔT+Am	40.7	19.4	13.5	7.8	32.9	33.1	80.9
Days 75–90							
Base	13.2	3.0	1.6	8.6	4.6	11.9	34.6
Base+Am	16.2	4.7	4.4	7.1	9.1	27.2	56.2
Base+ΔT	22.2	6.1	3.5	12.6	9.6	15.6	43.3
Base+ΔT+Am	23.2	7.8	3.7	12.9	10.3	16.0	44.2
Days 0–90							
Base	42.3	8.3	8.5	25.5	16.8	20.2	39.7
Base+Am	44.0	15.4	9.3	19.3	24.6	21.1	56.0
Base+ΔT	63.1	17.8	15.7	29.6	33.5	24.9	53.1
Base+ΔT+Am	63.9	27.2	16.0	20.7	43.2	25.0	67.6

[a] I = total N consumed; E = N lost via branchial and urinary excretion; R_{N} = N retained in body materials; F_{N} = N lost in fecal material and all unaccounted N; A = N absorbed from food.

[b] Retention efficiency = 100 × R/I.

[c] Absorption efficiency = 100 × A/I.

the effect of temperature and ration level on growth and conversion efficiency in rainbow trout during 25-d seasonal experiments. Simulated warming of 3°C and 6°C were superimposed on the natural fluctuating thermal regime of a small trout stream. The authors reported very little change in the winter (January–February 1972) growth rates of warmed trout (2 g) consuming rations equivalent to those used in the present study (4–5%/d, dry basis). However, the water temperatures in their study were higher and much more variable (e.g., range of 3.9°C to 10.1°C around the mean base temperature of 6.9°C) and the exposure period much shorter (by 65 d) than in the present study.

The accelerated growth of trout exposed to the +2°C winter warming scenario was manifest in their greater lipid and protein content, but only up to day 75 when water temperatures were a relatively constant 4°C and 6°C, respectively. During

TABLE 3.—Energy budgets and metabolic costs of growth (N-cost index) for juvenile rainbow trout fed to satiation for 90 d (January–April 1994) and exposed to a +2°C warming scenario (ΔT) and 70 μmol/L ammonia (Am).

Interval and treatment	Energy (kJ/fish)[a]					Conversion efficiency[b] (%)	N-cost index
	C	U	ΔB	R_{E}	F_{E}		
Days 0–75							
Base	90.4	1.8	21.1	21.1	46.3	23.4	7.0
Base+Am	86.0	3.7	15.6	21.2	45.4	18.1	10.0
Base+ΔT	126.8	4.1	41.4	40.3	41.0	32.7	7.6
Base+ΔT+Am	126.2	6.8	43.8	41.3	34.3	34.7	7.0
Days 75–90							
Base	41.2	1.1	12.2	9.4	18.5	29.7	13.8
Base+Am	50.4	1.6	20.7	10.0	18.0	41.1	5.2
Base+ΔT	69.1	2.1	14.3	19.2	33.5	20.7	12.7
Base+ΔT+Am	71.9	2.7	16.6	20.3	32.5	23.1	18.8
Days 0–90							
Base	131.3	2.9	33.4	30.5	64.6	25.4	8.2
Base+Am	136.4	5.4	36.3	31.3	63.4	26.6	7.6
Base+ΔT	195.7	6.2	55.7	59.4	74.4	28.5	8.7
Base+ΔT+Am	198.0	9.5	60.4	61.5	67.7	30.5	8.8

[a] C = total energy (E) consumed from food; U = energy lost via branchial and urinary excretion; ΔB = energy stored in body materials; R_{E} = total metabolic energy lost as heat; F_{E} = energy lost in feces and unaccounted energy.

[b] Conversion efficiency = 100 × $\Delta B/C$.

this time, whole-body proximate composition was considerably altered compared with juvenile trout exposed during summer (Linton et al. 1997); in particular, lipid content was less than about half the values previously reported, and protein content was as much as 15% greater. Overall, the whole-body proximate composition of these trout was not unlike fingerling sockeye salmon *Oncorhynchus nerka* fed equivalent rations and acclimated to 5°C (Brett et al. 1969), although the SGR of the latter study was only 0.6%/d.

Elevated rates of O_2 consumption and N-waste excretion were associated with the increased feeding and growth of the warmed fish. Soofiani and Hawkins (1982) showed that the metabolic rate of Atlantic cod *Gadus morhua* increased linearly with ration size. Jobling (1983) suggested that the magnitude of the increase in O_2 consumption observed after feeding (specific dynamic action, SDA) is reflective of the cost of growth. This hypothesis was later confirmed through an ingenious experiment designed by Brown and Cameron (1991) with channel catfish *Ictalurus punctatus*: blockade of growth-associated protein synthesis eliminated the SDA effect.

Along with the elevated O_2 consumption and N-waste production over the first 75 d, fish exposed to the additional +2°C also exhibited substantial increases in both N absorption and energy conversion efficiencies (Tables 2, 3). As a consequence, the temperature coefficients (Q_{10}s) for appetite and other related physiological processes (growth, oxygen consumption, and N-waste excretion) were extraordinarily high; the mean was equal to 19.6. The differences in response may be related to temperature-dependent metabolic depression (Hazel 1993) of fish at these extreme low temperatures, which is parallel to the metabolic suppression observed in warmed fish at peak summer temperatures (Reid et al. 1995; Linton et al. 1997). During the last 15 d of the present experiment, the water temperatures rose 2°C from approximately 4.5°C and 6.5°C to 6.5°C and 8.5°C in the base and base+ΔT thermal regimes, respectively (see Figure 1). Net energy conversion efficiency in warmed fish was actually lower than in base fish during this period, and the mean temperature coefficient (Q_{10}) for all the physiological parameters measured dropped to 6.6. We suspect that the changes were due to physiological adjustments to rising water temperature that allowed the fish acclimated to colder water (base) to compensate for the imposed metabolic depression, possibly even promoting a compensatory growth response after relief from a long period of depressed feeding (Kim and Lovell 1995).

Effects of Elevated Ammonia

Overwintering juvenile trout exposed to additional ammonia, although exhibiting a similar elevation in N-waste excretion and NQ (protein turnover) as in summer (see Linton et al. 1997), did not show greater growth, and their appetite, again, was unaffected. In the summer exposure, with the exception of fish exposed to the combination of +2°C and ammonia at peak water temperatures, the stimulated N retention (as protein) was associated with higher rates of protein synthesis (Reid et al., in press). At the very low winter temperatures of the present study, ammonia-exposed fish exhibited greater N absorption than control fish (base and base+ΔT), but protein synthesis was not elevated (Morgan et al., in press). This difference suggests a possible low-temperature threshold below which the stimulating effect of sublethal ammonia on protein growth is not observed. It may be that the lack of growth stimulation by sublethal ammonia at extremely low winter temperature (e.g. 4–7°C) is a reflection of inadequate energy availability. Alternatively, Houlihan et al. (1995) observed that trout with higher nitrogen retention efficiencies also had reduced rates of protein degradation and, consequently, a lower cost of growth per mole of N gain. This observation deserves further clarification however, because Tomas et al. (1991) suggested that protein degradation rates are genetically determined whereas protein synthesis rates are more responsive to ration and environmental factors such as temperature.

Ecological Perspective

The focus of the present study was to provide hard experimental data on the metabolic and physiological effects of chronic small increases (+2°C) in water temperature with or without sublethal pollutant exposure (70 μM ammonia) on overwintering rainbow trout compared with a similar summer exposure (see Linton et al. 1997). The results clearly show a simulated warming of +2°C superimposed on the base temperature regime during winter stimulates the appetite of juvenile rainbow trout, eventually leading to greater growth. Although some additional metabolic cost was incurred as temperature rose, the extra energetic cost during the 90 d period was negligible. The overall cost of growth for juvenile trout fed to satiation in winter was similar to the costs incurred by maximally feeding trout in summer owing to stoichiometrically equivalent reductions in the amounts of oxygen consumed and N retained. The low winter temperatures of the present experiment also acted to moderate the ammonia effects experienced by trout during summer, resulting in a lack of growth stimulation at base temperatures and no elevation of metabolic costs at +2°C. We conclude that an increase in ambient water temperature of only +2°C over the winter thermal profile of southern Lake Ontario, both in the presence or absence of sublethal ammonia, will promote the growth of juvenile trout at no additional metabolic cost, placing these fish at an ecological advantage leading into the summer growth period.

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References

Bidgood, B. F., and A. H. Berst. 1969. Lethal temperatures for Great Lakes rainbow trout. Journal of the Fisheries Research Board of Canada 26:456–459.

Brett, J. R., and C. A. Zala. 1975. Daily pattern of nitrogen excretion and oxygen consumption of Sockeye salmon (*Oncorhynchus mykiss*) under controlled conditions. Journal of the Fisheries Research Board of Canada 32:2479–2486.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka,* in relation to temperature and ration size. Journal of the Fisheries Research Board of Canada 26:2363–2394.

Brown, C. R., and J. N. Cameron. 1991. The induction of specific dynamic action in channel catfish by infusion of essential amino acids. Physiological Zoology 64:276–297.

Brown, V. M. 1968. The calculation of the acute toxicity of mixtures of poisons to rainbow trout. Water Research 2:723–733.

Coutant, C. C. 1981. Foreseeable effects of CO_2-induced climatic change: freshwater concerns. Environmental Conservation 8:285–297.

DeAngelis, D. L., and R. M. Cushman. 1990. Potential application of models in forecasting the effects of climate change on fisheries. Transactions of the American Fisheries Society 119:224–239.

EIFAC (European Inland Fisheries Advisory Committee). 1973. Water quality criteria for European freshwater fish. Report on ammonia and inland fisheries. Water Research 7:1011–1022.

Elliott, J. M. 1976. The energetics of feeding, metabolism, and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45:923–948.

Hansen, J., and six coauthors. 1988. Global climate changes as forecast by Goddard Institute for space studies three-dimensional model. Journal of Geophysical Research 93:9341–9364.

Hazel, J. R. 1993. Thermal biology. Pages 427–467 *in* D. H. Evans, editor. The physiology of fishes. CRC Press, Boca Raton, Florida.

Healey, M. C. 1990. Implications of climate change for fisheries management policy. Transactions of the American Fisheries Society 119:366–373.

Hill, D. K., and J. J. Magnuson. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fishes. Transactions of the American Fisheries Society 119:265–275.

Houlihan, D. F., C. G. Carter, and I. D. McCarthy. 1995. Protein synthesis in fish. Pages 191–220 *in* P. W. Hochachka, and T. Mommsen, editors. Biochemistry and molecular biology of fishes. Elsevier Science, New York.

Jobling, M. 1983. Towards an explanation of specific dynamic action (SDA). Journal of Fish Biology 23: 549–555.

Keheler, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society 125:1–13.

Kim, M. K., and R. T. Lovell. 1995. Effect of restricted feeding regimes on compensatory weight gain and body tissue changes in channel catfish *Ictalurus punctatus* in ponds. Aquaculture 135:285–293.

Knoph, M. B. 1992. Acute toxicity of ammonia to Atlantic salmon (*Salmo salar*) parr. Comparative Biochemistry and Physiology 101 C:275–282.

Lin, P., and H. A. Regier. 1995. Use of Arrhenius models to describe temperature dependence of organismal rates in fish. Canadian Special Publication of Fisheries and Aquatic Sciences 121:211–225.

Linton, T. K., S. D. Reid, and C. M. Wood. 1997. The metabolic costs and physiological consequences to juvenile rainbow trout of a simulated summer warming scenario in the presence and absence of sublethal ammonia. Transactions of the American Fisheries Society 126:259–272.

Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Transactions of the American Fisheries Society 119:254–264.

Meisner, J. D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis.* Canadian Journal of Fisheries and Aquatic Sciences 47:1065–1070.

Meisner, J. D., J. L. Goodier, H. A. Regier, B. J. Shuter, and W. J. Christie. 1987. An assessment of the effects of climate warming on Great Lakes basin fishes. Journal of Great Lakes Research 13:340–352.

Morgan, I. J., and five coauthors. In press. The effects of elevated winter temperature and sub-lethal pollutants (low pH, elevated ammonia) on protein turnover in the gill and liver of rainbow trout (*Oncorhynchus mykiss*). Fish Physiology and Biochemistry.

Regier, H. A., J. A. Holmes, and D. Pauly. 1990. Influence of temperature changes on aquatic ecosystems: an interpretation of empirical data. Transactions of the American Fisheries Society 119:374–389.

Reid, S. D., J. J. Dockray, T. K. Linton, D. G. McDonald, and C. M. Wood. 1995. Effects of a summer temperature regime representative of a global warming scenario on growth and protein synthesis in hardwater- and softwater-acclimated juvenile rainbow trout (*Oncorhynchus mykiss*). Journal of Thermal Biology 20:231–244.

Reid, S. D., J. J. Dockray, T. K. Linton, D. G. McDonald, and C. M. Wood. In press. Protein synthesis in juvenile rainbow trout: the impact of a simulated summer global warming regime in the presence and absence of sublethal ammonia. Canadian Journal of Fisheries and Aquatic Sciences 55.

Reid, S. D., D. G. McDonald, and C. M. Wood. 1997. Interactive effects of temperature and pollutant stress. Pages 325–349 *in* C. M. Wood and D. G. McDonald, editors. Global warming: implications for freshwater and marine fish. Cambridge University Press, London.

Shuter, B. J., and J. R. Post. 1990. Climate, population variability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314–336.

Shuter, B. J., D. A. Schlesinger, and A. P. Zimmerman. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. Canadian Journal of Fisheries and Aquatic Sciences 40:1838–1845.

Soofiani, N. M., and A. D. Hawkins. 1982. Energetic cost at different levels of feeding in juvenile cod, *Gadus morhua* L. Journal of Fish Biology 21:577–592.

Tomas, F. M., R. A. Pym, and R. J. Johnson. 1991. Muscle protein turnover in chickens selected for increased growth rates, food consumption or efficiency of food utilization: effects of genotype and relationship to plasma IGF-I and growth hormone. British Journal of Poultry Science 32:363–376.

Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri,* Richardson. Journal of Fish Biology 11:87–98.

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