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Energy partitioning during fish development: additive or compensatory allocation of energy to support growth?

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Summary

1. The goal of this study was to estimate the impact of the metabolic cost of growth (COG) on the energy budget of chinook salmon (*Oncorhynchus tshawytscha*) during embryonic and larval development.

2. In attempting to estimate COG, it was assumed that, as with juvenile and adult fish, energy is allocated in an additive fashion with respect to routine metabolism and mass-specific COG remains constant during early life. According to this model, there should be a direct relationship between metabolic intensity and specific growth rate.

3. In chinook salmon, however, there was no significant relationship between the two variables during embryonic development, during larval development, or during the combined embryonic–larval period at any of the four test temperatures (5·0, 7·5, 10·0 and 12·5 °C).

4. The lack of correlation between metabolic intensity and specific growth rate suggests that the assumptions underpinning the additive model of energy partitioning may not hold during early life. An alternative model in which (a) energy is allocated in a compensatory manner and/or (b) mass-specific COG varies is presented.

Key-words: Cost of growth, embryo, larva, metabolism, *Oncorhynchus tshawytscha*

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Introduction

Energy is viewed by most biologists as being the closest thing there is to a common currency of life (Kleiber 1961; Calow 1985). As energy (or some correlate of energy) is normally limiting, there is great interest in understanding how organisms partition energy among a multitude of competing life processes. The simplest model of energy partitioning, represented algebraically as $C=R+P+E$, assumes that available energy (C) is used either to support life (R), to elaborate new tissue (P) or is lost from the system (E). The energy used to support life (R), usually referred to as total metabolism, can be subdivided into a number of components, each representing the cost of carrying out a particular life process.

In very young fish, one such component, the cost of growth (COG), is of particular interest. The elaboration of new tissue requires the expenditure of metabolic energy (it is important to distinguish COG from the cost of production, P, in the balanced energy equation presented above). For example, in juvenile and adult fish COG represents a cost equivalent to about 35–45% of the energy content of the tissue formed (Jobling 1985; Jørgensen 1988). Juvenile and adult fish, however, grow comparatively slowly so the total cost is relatively small. This is not the case during early life. It is not unusual for fish embryos and larvae to grow at rates of 20–30% day^{-1} and rates as high as 50% day^{-1} have been reported (Bryant & Matty 1981). Such high rates of growth clearly represent a significant drain on energy reserves. What is not clear is how much of a drain. At present, there is no consensus as to how much energy is required to support the formation of a unit mass of new tissue (mass-specific COG) during embryonic and larval development. Published estimates range from 9% (Kiørboe & Møhlenberg 1987) to 49% (Wieser & Medgyesy 1990a,b) of the energy content of the tissue formed. Obviously, the net impact growth has on total metabolism will depend to a large extent on which value applies. Which value applies also has implications on the way energy is partitioned. If mass-specific COG is in the order of 9% of tissue energy content, embryos and larvae may be able to accommodate growth costs within their aerobic scope for routine physiological performance (SRPP; SRPP = maximum routine metabolic rate – standard metabolic rate). On the other hand if mass-specific COG is in the order of 49%, total COG would likely exceed SRPP during much of early life. This would necessitate a

major reallocation of energy resources which, in turn, could have significant ecological and evolutionary implications (Wieser 1991). Thus, it would seem that if we are to understand how very young fish (and other small, rapidly growing organisms) partition energy we must first have a better idea of actual growth costs.

The proximate goal of this study was to estimate growth costs during the embryonic and larval development of chinook salmon *Oncorhynchus tshawytscha* (Walbaum) at each of four temperatures (5·0, 7·5, 10·0 and 12·5 °C). An approach similar to that used by Smith (1957) to estimate growth costs during rainbow trout (*O. mykiss*) development was adopted. Smith (1957) argued that the major factors influencing metabolic rate ($M\mathrm{O}_2$) during teleost development are tissue mass (m) and absolute growth rate ($\delta m/\delta t$):

$$M\mathrm{O}_2 = am + b(\delta m/\delta t) \qquad \text{eqn 1}$$

where a and b are constants. If this model is correct, a plot of metabolic intensity ($M\mathrm{O}_2/m$) against specific growth rate ($\delta m/m\delta t$)

$$M\mathrm{O}_2/m = a' + b'(\delta m/m\delta t) \qquad \text{eqn 2}$$

should yield a straight line with a slope (b') equal to the mass-specific cost of growth (the x-intercept, a', represents the mass-specific cost of other routine activities).

Materials and methods

Gametes were obtained from chinook salmon returning to spawn in the Big Qualicum River, Vancouver Island, British Columbia. Eggs were taken from a single female and fertilized by the dry method with milt pooled from two to three males in each of 2 successive years. Eggs collected in the first year had a mean (±SD) water-hardened wet mass of 340±9 mg (n=30) while those collected the next year had a mean (±SD) water-hardened wet mass of 341±36 mg (n=30). The average diameter of both groups of eggs was 8·44 mm.

Eggs and alevins were incubated at various constant temperatures in vertically stacked incubation trays (Heath Techna Corp., Tacoma, Washington, USA). Initial loading densities were approximately 2000 eggs per tray. Water temperatures were monitored daily. Mean (±SD) temperatures were 5·0±0·4 °C, and 10·0±0·3 °C the first year and 7·3±0·3 °C, 10·2±0·4 °C, and 12·5±0·9 °C the second year. Water flow in the Heath trays was held at 12 litres min^{-1} using dechlorinated water from the Nanaimo, British Columbia city water supply (total hardness 12 mg l^{-1} as CaCO_3, pH 7·2). Dissolved oxygen levels in the outflow water were monitored periodically and always exceeded 90% of the air-saturated value.

Routine metabolic rates ($M\mathrm{O}_2$) were determined for unfed chinook incubated at each of the various temperatures at 18–22 intervals (shorter intervals at higher temperatures) between fertilization and complete yolk absorption. Measurements were made using a four-channel, closed-system respirometer. One channel was run as a simultaneous control providing three independent measurements of $M\mathrm{O}_2$ for each test interval. Respirometer volumes ranged from 70·25 to 71·88 ml. Between five and 80 individuals, the precise number depending on the stage of development (more at earlier stages of development), were placed in each test chamber. Tests were conducted at nominal temperatures of 5·0 °C and 10·0 °C in year 1 and at 7·5 °C, 10·0 °C and 12·5 °C in year 2. Temperatures were monitored periodically during tests and were always within 0·1 °C of the nominal temperature. Oxygen levels in the respirometers were monitored continuously using polarographic electrodes (Orbisphere model 2104·01, Geneva, Switzerland) and a multichannel oxygen meter (Orbisphere model 2710). Details of the respirometer, test procedures and analysis of the polarographic records are given in Rombough (1988).

Subsamples of 10 individuals were preserved in 5% neutral buffered formalin at the end of each test. Individuals were weighed after a fixation period of at least 21 days (the time required for weights to stabilize) to provide estimates of total wet mass. All the alevins and five of the 10 embryos in each sample were dissected into tissue and yolk components. Components were weighed separately (yielding estimates of tissue and yolk wet mass) and then oven dried at 60 °C for 48 h to provide estimates of tissue and yolk dry masses.

Times to, and values for, maximum alevin (tissue + yolk) wet mass, maximum tissue wet mass (MTWM), maximum tissue dry mass (MTDM) and maximum metabolic rate ($M\mathrm{O}_2$ max) were estimated by solving polynomial equations relating each of the dependent variables to time from fertilization (Rombough 1985). Times to blastopore closure, eyeing and 50% hatch were estimated by visual inspection. Specific growth rate (g) was calculated as $(\ln m_2 - \ln m_1)(d_2 - d_1)^{-1}$, where m_1 and m_2 were wet tissue masses at sample periods d_1 and d_2, respectively. Mean metabolic intensities (wet mass-specific metabolic rates) were calculated for the equivalent half intervals.

Energy budgets were estimated for the period between fertilization and the time corresponding to the sample period closest to maximum tissue dry mass. The energy content of the yolk consumed during this period (C) was assumed to have been partitioned simply between tissue growth (G) and metabolism (R). Energy equivalents of 27·05 J mg^{-1} dry mass and 23·50 J mg^{-1} dry mass were used, respectively, for yolk and tissue (Rombough 1988). Total oxygen consumption was estimated graphically (as the area under the curve relating $M\mathrm{O}_2$ to time post-fertilization) and converted to its energy equivalent

using an oxycaloric value of 13·56 J mg^{-1} O_2 (Brett & Groves 1979).

Results

GROWTH AND DEVELOPMENT

Mortality was low (<5%) at all incubation temperatures. As expected, development proceeded more rapidly at higher temperatures. Estimates of times to selected developmental stages at each of the various incubation temperatures are given in Table 1.

Tissue growth followed a parabolic trajectory between blastopore closure and maximum tissue mass (Fig. 1). Tissue wet mass (TWM, mg) during this period can be predicted using the equation:

$$\ln TWM = -12{\cdot}630 + 2{\cdot}692 \ln d + 2{\cdot}838 \ln T$$
$$R^2_{adj} = 98{\cdot}7\%, n = 79 \qquad \text{eqn 3}$$

where d is the number of days post-fertilization and T is mean incubation temperature (°C). (R^2_{adj} is an unbiased estimate of the coefficient of determination for the multiple regression that takes into account degrees of freedom; Zar 1974.) Tissue dry mass remained a constant fraction of tissue wet mass (14·9%, 95% CI = 15·3–14·5%, n = 75) between blastopore closure and maximum tissue dry mass.

The maximum mass (total, wet tissue and dry tissue) attained by alevins tended to decrease with increasing incubation temperature (Table 1). For example, maximum tissue dry masses at 7·3, 10·0, 10·2 and 12·5 °C were only 97·7%, 89·1%, 80·3% and 62·4%, respectively, of that at 5·0 °C. Conversely, the amount of unconsumed yolk remaining at maximum tissue mass (both wet and dry) tended to be significantly greater at the higher incubation temperatures. For example, at 5·0 and 7·3 °C, it was estimated that only 6% and 2%, respectively, of initial yolk mass remained at MTDM. In contrast, 12%, 29% and 26%, respectively, of the original yolk mass remained at MTDM for the alevins incubated at 10·0, 10·2 and 12·5 °C.

Specific growth rate appears to be dependent on temperature as well as on stage of development during the period between blastopore closure and MTWM (Fig. 2). Both nested ANOVA (the appropriate parametric test for evaluating both factors simultaneously; Zar 1974) and Kruskal–Wallis non-parametric tests with resultant P values corrected for experiment-wide error rate using the sequential Bonferroni method (Rice 1989) indicated that the effect of either variable on specific growth rate was highly significant (P<0·01). [Both parametric and non-parametric tests were conducted because of uncertainty over whether specific growth rates were normally distributed. D'Agostino's D statistic (D = 0·19, P = 0·051) suggested growth rates were normally distributed; the D'Agostino–Pearson Omnibus K^2 statistic (K^2 = 6·3, P = 0·04) suggested they were not.] Specific growth rates were highest near blastopore closure. Thereafter, values declined in a roughly exponential fashion as the animals aged. Growth rates consistently appeared to be somewhat depressed (i.e. less than one would expect from the overall trend) shortly before hatch. At any given stage of development, growth rates were higher at higher temperatures. Mean rates (±SD, expressed on a wet mass basis) for the period between blastopore closure and MTWM were 3·5±2·9% day^{-1} (n = 15), 5·0±4·2% day^{-1} (n = 18), 6·5±8·0% day^{-1} (n = 12), 7·0±4·7% day^{-1} (n = 15) and 7·3±6·0% day^{-1} (n = 14), respectively, at 5·0, 7·3, 10·0, 10·2 and 12·5 °C.

Table 1. Time and size relationships for chinook embryos and alevins incubated at 5·0, 7·3, 10·0, 10·2 and 12·5 °C. Stages were identified using the system of Vernier (1969)

	Temperature (°C)				
	5·0	7·3	10·0	10·2	12·5
Whole egg wet mass at fertilization (mg) (mean±SD, n = 30)	340±9	341±36	340±9	341±36	341±36
Yolk dry mass at fertilization (mg) (mean±SD, n = 30)	126·2±3·7	122·8±13·2	126·2±3·7	122·8±13·2	122·8±13·2
Time to blastopore closure (stage 17) (days)	26·7	18·4	13·4	13·1	10·6
Time to 'eyeing' (stage 24) (days)	51·5	35·1	25·0	24·4	19·2
Time to 50% hatch (days)	112·8	76·5	54·0	53·0	40·1
Time to maximum alevin wet mass (days)	199·1	137·5	95·7	87·7	58·7
Maximum alevin wet mass (mg)	514·9	539·3	463·6	471·0	409·7
Time to maximum tissue dry mass (days)	199·3	141·6	101·7	90·8	69·0
Maximum tissue dry mass (mg)	74·5	72·8	66·4	59·8	46·5
Time to maximum tissue wet mass (days)	206·3	140·9	104·6	92·3	71·4
Maximum tissue wet mass (mg)	472·3	508·7	433·0	426·2	299·7
Time to maximum metabolic rate (days)	196·7	136·3	97·3	91·3	67·1
Maximum metabolic rate (μg O_2 h^{-1})	102·4	151·6	151·8	145·6	147·2

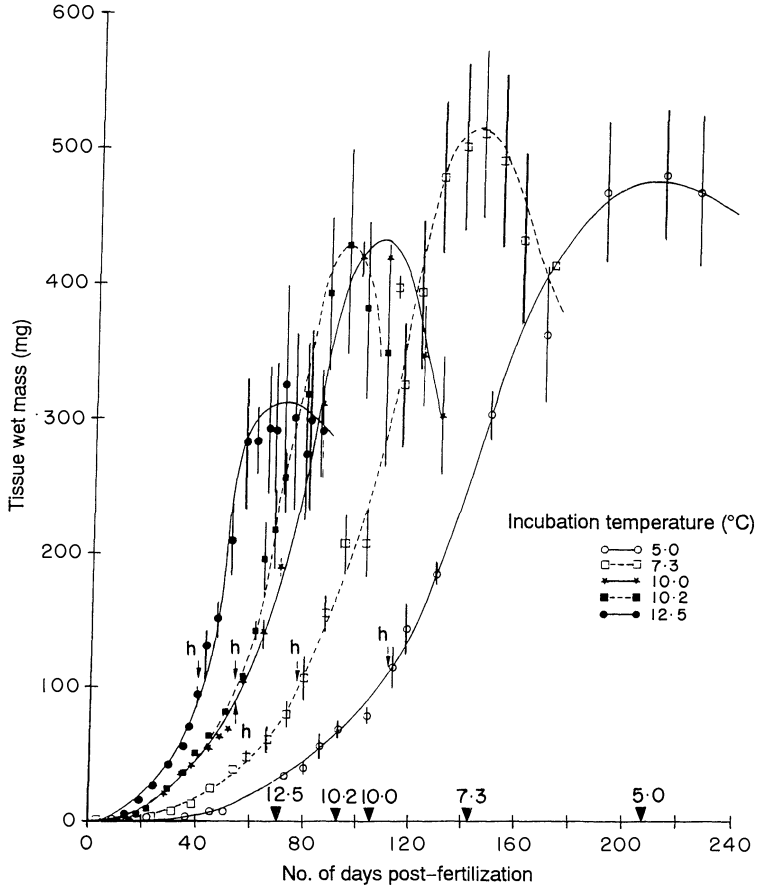

Fig. 1. Changes in tissue wet mass during the course of embryonic and larval development at each of five incubation temperatures. Vertical arrows indicate 50% hatch. Error bars indicate 95% confidence limits.

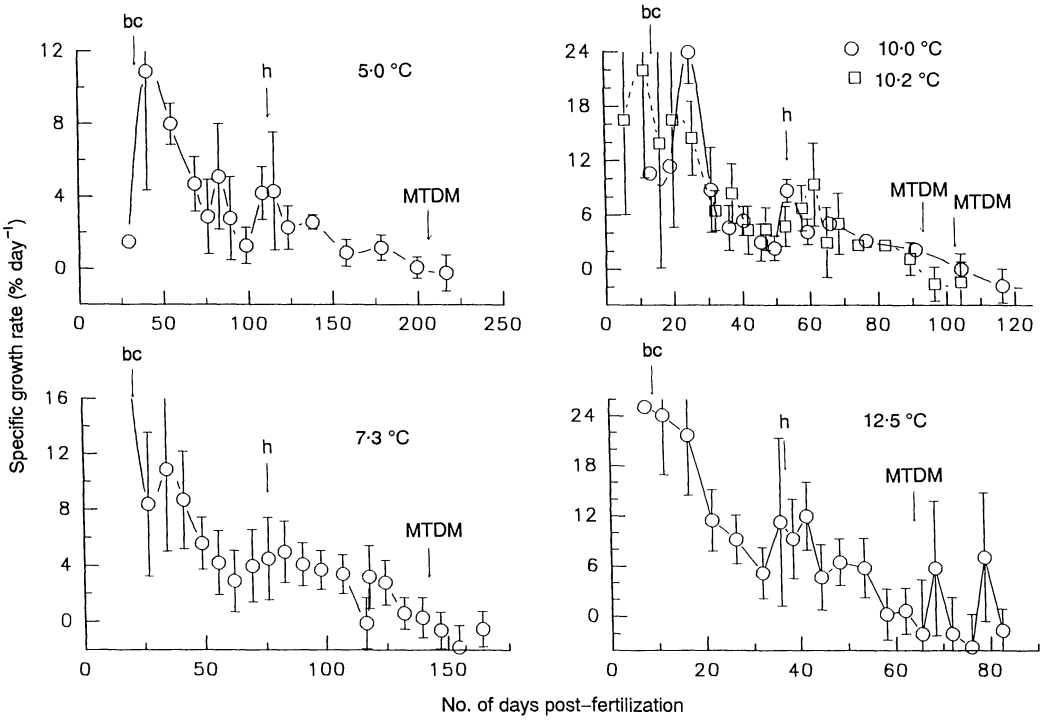

Fig. 2. Specific growth rate as a function of time after fertilization at each of five incubation temperatures. Vertical arrows indicate times to selected developmental stages. bc, blastopore closure; h, 50% hatch; MTDM, maximum tissue dry mass. Error bars indicate 95% confidence limits.

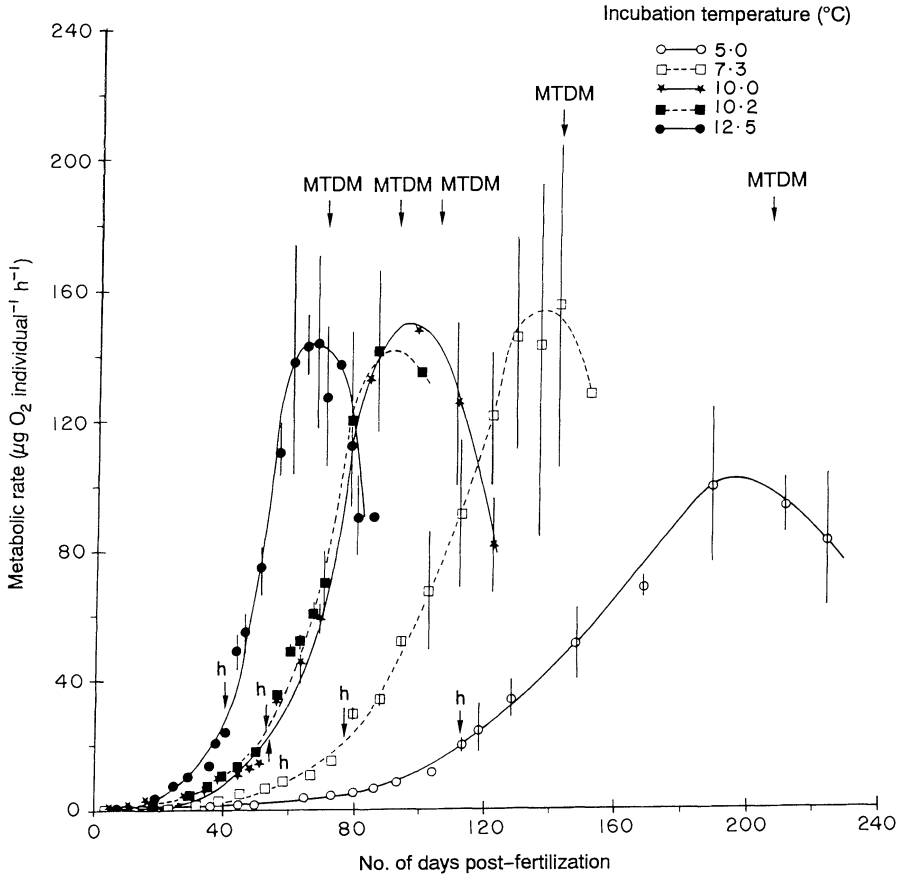

Fig. 3. Metabolic rate as a function of time after fertilization at each of five incubation temperatures. Vertical arrows indicate time to selected developmental stages. h, 50% hatch, MTDM, maximum tissue dry mass. Error bars indicate 95% confidence limits.

METABOLISM

Metabolic rate, like tissue mass, followed a parabolic trajectory during most of embryonic and larval development (Fig. 3). Metabolic rates (M_{O_2}; $\mu g\,h^{-1}$) during the period between blastopore closure and maximum metabolic rate can be predicted using the equation:

$$\ln M_{O_2} = -16{\cdot}897 + 2{\cdot}873 \ln d + 3{\cdot}840 \ln T$$
$$R^2_{adj} = 96{\cdot}3\%,\ n = 75 \qquad \text{eqn 4}$$

where d is the number of days post-fertilization and T is incubation temperature (°C). It was interesting that while an increase in temperature from 5·0 to 7·3 °C resulted in a significant increase in maximum metabolic rate, further increases in temperature had no additional effect on maximum metabolic rate (i.e. M_{O_2} max at 7·3, 10·0, 10·2 and 12·5 °C were virtually identical; Fig. 3).

Metabolic expansion appears to be essentially isometric (i.e. more or less directly dependent on tissue mass) up to maximum metabolic rate. The metabolic mass exponent ($b = 1{\cdot}049$, SE = 0·022) of the equation relating metabolic rate (M_{O_2}; $\mu g\,h^{-1}$) to tissue wet mass (TWM; mg):

$$\ln M_{O_2} = -3{\cdot}340 + 1{\cdot}049 \ln \mathrm{TWM} + 0{\cdot}805 \ln T$$
$$R^2_{adj} = 97{\cdot}0\%,\ n = 75 \qquad \text{eqn 5}$$

was slightly greater than unity ($b = 1{\cdot}00$). The corresponding exponent for tissue dry mass ($b = 1{\cdot}012$, SE = 0·031, $n = 75$), however, was not significantly different from unity.

Given the large number of potential sources of error (e.g. errors in estimating yolk and tissue masses, the energy contents of yolk and tissue, the total amount of oxygen consumed and the oxycaloric equivalent), energy budgets balanced extremely well (Table 2). This was particularly true at 5·0, 10·0 and 10·2°C, where estimates of total oxygen consumption based on measurements of oxygen uptake rates (R) were within 10% of values estimated from changes in yolk (C) and tissue (G) masses [energy budgets are in complete balance if $R\,(C\text{-}G)^{-1} = 100\%$]. Cumulative growth efficiency up to MTDM showed a moderate but consistent decrease with increasing incubation temperature between 5·0 and 10·2°C (from 57·0% to 53·7%; Table 2) and a rather sharp decrease between 10·2 and 12·5°C (from 53·7 to 44·6%).

Metabolic intensity (mass-specific metabolic rate) varied significantly ($P < 0{\cdot}01$, using nested ANOVA) both with stage of development and with temperature (Fig. 4). At any given temperature, there was about a threefold variation in metabolic intensity during the course of embryonic and larval development. Metabolic intensities were consistently highest just prior to

Table 2. Energy utilization by chinook embryos and alevins incubated at 5·0, 7·3, 10·0, 10·2 and 12·5 °C. Energy budgets were calculated on the basis of data for the sample period closest to maximum tissue dry mass. Gross conversion efficiency was calculated as dry mass of tissue formed divided by dry mass of yolk consumed

	Temperature (°C)				
	5·0	7·3	10·0	10·2	12·5
Day sampled	188·8	135·8	97·8	92·8	69·7
Per cent of initial yolk mass remaining	13·4	9·8	15·8	17·0	23·9
Total dry mass of yolk consumed (mg) (mean ± SD, $n=5$)	109·3 ± 9·7	110·8 ± 19·2	106·3 ± 6·8	101·9 ± 23·7	93·4 ± 18·7
Dry mass of tissue formed (mg) (mean ± SD, $n=5$)	71·7 ± 8·4	70·9 ± 6·0	66·1 ± 2·7	63·0 ± 6·9	47·9 ± 10·3
Gross conversion efficiency (%)	65·6	64·0	62·2	61·8	51·3
Energy equivalent of yolk consumed (C) (J)	2956	2997	2875	2756	2526
Energy equivalent of tissue formed (G) (J)	1685	1666	1553	1480	1125
Cumulative growth efficiency ($G\,C^{-1}$) (%)	57·0	55·6	54·0	53·7	44·6
Cumulative amount of O_2 consumed (mg)	102·0	123·0	103·4	93·9	78·4
Energy equivalent of O_2 consumed (R) (J)	1382	1667	1402	1273	1063
Balance $R(C–G)^{-1}$ (%)	108·7	125·2	106·1	99·8	75·9

blastopore closure. Values declined following blastopore closure, reaching a minimum during the early- to late-eyed stage. Metabolic intensities increased during the late embryonic and early- to mid-larval stages to reach secondary maxima just prior to MTDM. Values declined following MTDM, particularly at the higher temperatures, as yolk supplies became exhausted. Metabolic intensities increased as the temperature increased. Mean values (±SD) for the period between blastopore closure and maximum metabolic rate were 171 ± 50 ($n=18$), 270 ± 98 ($n=20$), 287 ± 113 ($n=14$), 309 ± 108 ($n=17$) and 385 ± 114 ($n=20$) μg O_2 g^{-1} wet tissue h^{-1}, respectively, at 5·0, 7·3, 10·0, 10·2 and 12·5°C.

Metabolic intensity was independent of specific growth rate at all temperatures [i.e. the slopes of the lines relating the two variables were not significantly different ($P>0·05$) from zero]. The two variables were independent whether one looked at the data for the embryonic period only, for the larval period only or for the combined embryonic–larval period. This was true whether metabolic intensities and specific growth rates were expressed on a wet mass basis (Fig. 5) or on a dry mass basis.

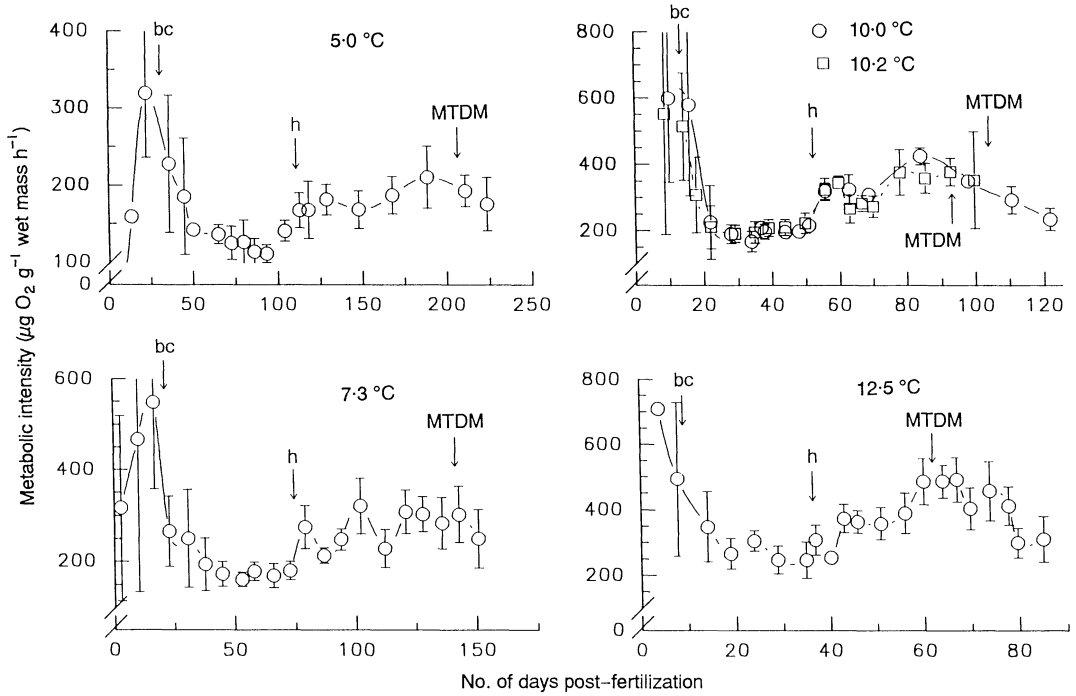

Fig. 4. Changes in metabolic intensity during the course of embryonic and larval development at each of five incubation temperatures. Vertical arrows indicate time to selected developmental stages. bc, blastopore closure; h, 50% hatch; MTDM, maximum tissue dry mass. Error bars indicate 95% confidence limits.

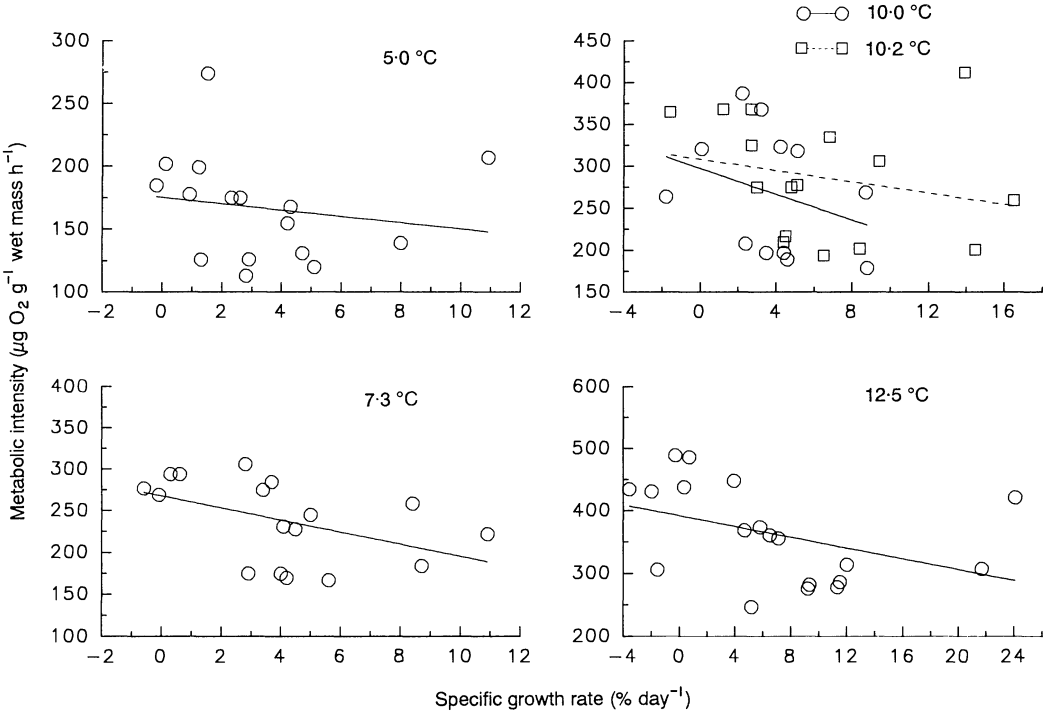

Fig. 5. Mass-specific metabolic rate (metabolic intensity) as a function of specific growth rate at each of five incubation temperatures. Lines of best fit are shown. None of the slopes is significantly different from zero.

Discussion

The total lack of correlation between metabolic intensity and specific growth rate during chinook embryonic and larval development was unexpected. The accepted paradigm in animal energetics is that there is a positive relationship between rate of energy expenditure and rate of growth (Brody 1945; Kleiber 1961; Jobling 1985). It has been assumed that this relationship applied to early life stages as well as to juvenile and adult fish (Smith 1957; Kiørboe & Møhlenberg 1987). However, the results of this and several other recent studies (Wieser *et al.* 1988; Wieser 1989; Wieser & Medgyesy 1990a,b; Wieser, Laich & Medgyesy 1992) challenge this premise.

Wieser *et al.* (1988) were the first to suggest that there might be a dissociation between metabolic and growth rates during early life. They noted that while the growth rate of roach (*Rutilus rutilus*) larvae varied with ration size there was no corresponding change in average metabolic rate. Unfortunately, metabolic and growth rates were not measured simultaneously so there was some question as to the significance of this result. The result was intriguing enough, however, for Wieser & Medgyesy (1990a,b) to conduct a series of more carefully controlled experiments in which ration size, growth rate and oxygen consumption were measured simultaneously in larvae of roach (Wieser & Medgyesy 1990a) and whitefish, *Coregonus wartmanni* (Wieser & Medgyesy 1990b). In both species, metabolic intensity was found to be independent of specific growth rate in young, rapidly growing ($g > 8\%$ day^{-1}) larvae. There is some suggestion that this is also the case in rapidly growing larvae of pike, *Esox lucius* (Wieser *et al.* 1992) and herring, *Clupea harengus* (D. F. Houlihan, personal communication).

Wieser (1989, 1991) has advanced two reasons why metabolic intensity might be independent of growth rate in rapidly growing fish larvae. If metabolic intensity is to be dependent on growth rate, two criteria must be satisfied: (1) the total cost of activities other than growth (a' in equation 2) must remain constant and (2) the unit cost of growth (b' in equation 2) cannot vary. Neither condition may hold during early life. Small animals such as fish embryos and larvae display high routine metabolic intensities compared with larger animals. Wieser (1989, 1991) suggested that one of the consequences of this is that very small animals have less ability to increase power output to support activities such as growth. He went on to speculate that fish larvae may circumvent the problem by suppressing other energy-consuming functions and reassigning the energy saved towards growth. If chinook embryos and larvae were to partition energy in such a compensatory fashion, rather than in the additive fashion that Smith's (1957) model assumes, it is not surprising that metabolic intensity was independent of growth rate. Any change in the amount of energy expended on growth would simply be compensated for by a corresponding increase or decrease in the amount of energy expended in another area. Wieser (1991) also pointed out that the unit cost of growth is not necessarily constant throughout life. Growth costs in juvenile and adult fish are typically in

the order of 35–45% of the energy content of the tissue formed (Jobling 1985; Jørgensen 1988; Wieser *et al.* 1988; Wieser & Medgyesy 1990a,b). This is 3–4 times the theoretical minimum cost of protein synthesis assuming 3–5 ATP are required to form one peptide bond (Wieser *et al.* 1988; Kelly & McBride 1990). Embryonic and larval growth costs could be significantly lower than those of older fish and still fall within theoretical limits. While empirical evidence pertaining specifically to fish embryos and larvae is lacking, recent studies of growth costs in isolated fish cells suggest that variation in COG during the course of development is possible. The net cost of protein synthesis in several types of cultured fish cells has been shown to be highly variable (up to 20-fold) and inversely related to growth rate (Pannevis & Houlihan 1992; Houlihan & Smith 1993). How significant such variation is in the intact organism (or whether it even occurs) is open to question but the results are intriguing. It may turn out that much of the variation in reported values for COG during early life (see Introduction) is actually the result of differences in growth rate.

At present, there is insufficient evidence to indicate which strategy (compensatory energy partitioning or variable growth costs) or combination of strategies, developing fish employ to meet the high costs associated with rapid growth. What the evidence does indicate is that energy allocation is more complicated than is generally appreciated. One cannot simply assume that the response one sees in older, more slowly growing fish necessarily applies during early life. Indeed, Wieser (1989) has argued that some assumptions, in particular that energy allocation is invariably additive with respect to routine metabolism, may not apply even in older fish on close examination.

Non-additive energy partitioning has implications for physiologists attempting to estimate the cost of activities other than growth. Typically, the cost of a particular activity (e.g. osmoregulation) is estimated from the relationship between metabolic rate and activity level. This approach assumes that other costs remain constant. However, if energy is allocated in compensatory fashion cost estimates, at the very least, may be seriously biased. Compensatory energy partitioning, in fact, may be the reason that attempts to estimate the cost of activities such as osmoregulation during fish development largely have been unsuccessful to date (Morgan, Jensen & Iwana 1992). Non-additive energy partitioning also has implications for those modelling growth. In particular, the von Bertalanffy (1960) growth model assumes that energy allocation is additive [von Bertalanffy's model can be derived rather simply from Smith's (1957) model by substituting the allometric relationship between metabolic rate and tissue mass for metabolic rate in equation 1]. The von Bertalanffy model is favoured by many biologists because it seems to have a physiological basis. This virtue disappears if energy partitioning turns out to be compensatory.

This study raises a number of questions that need to be addressed. In particular, if variations in growth rate are not responsible for stage-specific variations in metabolic intensity, what is? Stage-specific variations in metabolic intensity during chinook development were highly significant (≅threefold) and consistent across all temperatures. Variations of similar magnitude and timing have been reported in other salmonids (Hayes, Wilmot & Livingstone 1951; Smith 1957; Alderdice, Wickett & Brett 1958; Gruber & Wieser 1983). Such consistency suggests that some basic process is involved but precisely what is not clear. Another, and perhaps related, question is why the maximum rate of oxygen uptake of individual chinook alevins did not increase when the temperature was raised above 7·5 °C (Fig. 3). Based on a Q_{10} of 3·0 (the average at other stages), one would expect the maximum metabolic rate at 12·5 °C to have been about 1·8 times that at 7·3 °C. The fact that maximum metabolic rate did not increase suggests that some factor becomes limiting at higher temperatures. Again, precisely what limits maximum power output at higher temperatures is not clear.

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