

(not to be cited without permission of author)

Inter-individual differences in rates of routine energy loss and growth in early juvenile Atlantic cod (*Gadus morhua*)

Myron A. Peck^{1*}, Lawrence J. Buckley², and David A. Bengtson³

¹Graduate School of Oceanography, University of Rhode Island
South Ferry Rd, Narragansett, Rhode Island, 02882, USA

²URI-NOAA CMER Program, Graduate School of Oceanography
University of Rhode Island, South Ferry Rd, Narragansett, Rhode Island, 02882, USA

³Department of Fisheries, Animal and Veterinary Science, University of Rhode Island
Kingston, RI, USA, 02881, USA

*Corresponding Author Present Address
Department of Fisheries and Biological Oceanography
Institute of Hydrobiology and Fisheries Science
University of Hamburg
Olbersweg 24
D-22767
Hamburg
Germany

mpeck@gso.uri.edu

Tel +49(0) 40 42 838-6601

Fax +49(0) 40 42 838-6618

ABSTRACT

Young juvenile cod, *Gadus morhua*, within the same cohort exhibit marked growth variability, the physiological mechanisms of which are poorly understood. We evaluated whether differences in routine energy loss by juvenile Atlantic cod contributed to observed growth differences. The rates of respiration (O_2 consumption, CO_2 production) and ammonia (TAN) excretion were measured for 64 individual juveniles of the same cohort within a narrow size range (25 to 40 mm standard length, L_S , ages 79 to 112 days-post-hatch) growing at different rates. The relationships between body size and rates of O_2 consumption, CO_2 production, and TAN excretion were determined via regression analysis. Residuals from some of these regressions were significantly related to growth rate such that faster-growing juveniles had relatively lower rates of routine energy loss. Fish condition factor, weight (L_S)⁻³, also significantly decreased with increasing growth rate. Results of this study indicated differences in both the rates of routine energy loss and the patterns of growth allocation among individuals within the same cohort. Since these physiological attributes were positively correlated with growth rate, they may be indicative of “survivors” in field populations.

KEYWORDS

Juvenile cod, growth rate

INTRODUCTION

The somatic growth rate of Atlantic cod, *Gadus morhua*, during the early juvenile period has been positively correlated with survival and year-class success in both the Northwest (Campana 1996) and Northeast Atlantic (Ottersen and Loeng 2000). In the Northwest Atlantic on Georges Bank, otolith analysis of pelagic juvenile cod (90 days old, ~ 35 to 40 mm total length, L_T) indicated that length-at-age and year-class success were positively correlated (Campana 1996). Tupper and Boutilier (1995), studying newly settled cod (30 to 60 mm L_T) in coastal areas of Nova Scotia, observed that the largest and earliest settling cod had a competitive advantage over, and maintained higher growth rates than, smaller later-settling conspecifics. In the Northeast Atlantic, positive correlations between growth and survival have been found for cod within this year-0 juvenile settlement phase (Ottersen and Loeng 2000). The results of these studies on cod mirror those of other studies supporting the presence of size-selective mortality during the early juvenile stage in a variety of marine fish species (see review by Sogard 1997).

Positive correlations between rates of growth and survival in early stages of marine fish species mandate thorough investigation of the factors promoting inter-individual variability in growth rates. The growth rate of young juvenile fish is affected by an amalgam of influences from environmental sources (e.g., extrinsic differences in prey availability and temperature), as well as from physiological differences among individuals (e.g., intrinsic differences in metabolic rates and efficiencies). Although the fisheries literature is replete with examples of studies evaluating the environmental effects, far less research has been conducted on the contribution of inter-individual differences in physiology. Recent studies suggest a relationship between individual differences in metabolic rate (respiratory and exercise physiology) and growth rate in salmonids (Cutts et al. 1998, Gregory et al. 1998) and in a cyprinid (Kolok and Oris 1995). Linkages between inter-individual differences in rates (or efficiencies) of metabolism and growth have not been thoroughly examined in Atlantic cod, a species for which marked differences in growth are commonly observed and positive correlations exist between rates of growth and food availability during early life (Buckley and Lough 1987, Lough et al. 1996).

In this study we evaluated whether differences in routine energy loss contributed to observed differences in rates of growth among individual year-0 juvenile Atlantic cod. Measurements of routine (non-feeding) metabolism were made on similar-sized fish that were growing at different rates. Routine energy loss (REL) was estimated from measurements of the rates of respiration (O_2 consumption, CO_2 production) and total ammonia nitrogen (TAN) excretion. Inter-individual differences in the rates of REL were analyzed with respect to differences in growth rates. We envisioned three hypothetical relationships between rates of REL and juvenile growth (Figure 1). Differences in the rates of REL among individuals could be: 1) negatively correlated to growth rate implying lower energy loss and increased metabolic efficiency in faster-growing individuals (Fig. 1A&B), 2) positively correlated to growth rate implying increased metabolic rates in faster-growing individuals (Fig. 1E&F), or 3) uncorrelated suggesting that inter-individual differences in routine metabolism were unrelated to growth rate (Fig. 1C&D). We evaluated these three competing hypotheses in an attempt to assess whether differences in routine metabolism contributed to differences in rates of growth among juvenile Atlantic cod.

MATERIALS AND METHODS

LARVAL AND JUVENILE REARING

One batch of Atlantic cod eggs was collected from group-spawning adult broodstock fish maintained at the U.S. National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA NMFS) Narragansett Laboratory (Narragansett, Rhode Island, USA). The eggs were incubated and hatched, and larvae and juveniles were reared within a semi-static 127-l oval tank at $8.0 \pm 0.5^\circ C$, $31 \pm 0.5\%$, with a 14-hr photoperiod. Larvae and juveniles were fed wild zooplankton (primarily copepods, *Acartia* sp.) collected daily from a nearby estuary. The size fraction of zooplankton offered to fish increased with fish age: 60 to 210, 210 to 330, 330 to 800, and 330 to 1200 μm fractions were offered at 0 to 5, 5 to 8, 8 to 12 and > 12 weeks post-hatch, respectively. Laboratory-cultured rotifers (*Brachionus plicatilis*) and brine shrimp (*Artemia* sp.) were also provided during the rearing period.

Juveniles within the same cohort and reared in the same tank were used in trials. Trials were conducted on eight separate occasions within a 33-d period using fish between 79 and 112 days-post-hatch (dph). On each occasion, fish within a similar range in sizes (~ 25 to 40 mm L_S) were selected for use in a trial. Fish sampled at 79 dph were among the largest and fastest growing fish in the tank (except for several cannibals which were removed), while those sampled at 112 dph were among the smallest and slowest growing. This sampling protocol enabled us to use fish that were within the same size range but had different growth rates and ages.

DUAL GAS RESPIROMETER

Measurements of routine energy loss were made using a closed circuit respirometer (Micro-Oxymax System, Columbus Instruments, Columbus, Ohio, USA) designed to simultaneously measure metabolic performance of multiple subjects. The system monitored O_2 , CO , and CO_2 concentrations (detected via paramagnetic sensors) in up to ten, 250-ml water chambers. The principle of operation and the sensitivity of this system were outlined by Czekajewski et al. (1994). Briefly, a known flow of air is forcibly ventilated through the head space of sealed chambers and the difference in gas concentrations along with flow information is used by a micro-computer controller to calculate oxygen consumption and carbon dioxide production. This system has been

commonly used in studies of microbial respiration rates (e.g., Berdalet et al. 1995), and was well suited for our work on small juvenile cod.

MEASUREMENT PROTOCOL

The rate of routine energy loss due to respiration (O_2 consumption, CO_2 production), and total ammonia nitrogen (TAN) excretion of individual juvenile cod were measured during eight, 36-hr trials. In each trial, ten respirometer chambers were used. Each of the ten chambers contained 250-ml of 0.3 μm filtered Narragansett Bay seawater (31 ‰). Eight chambers held a single juvenile fish and two chambers were blanks (no fish). Fish were placed into chambers between 18:00 and 21:00 hours, after which rates of O_2 consumption and CO_2 production in each chamber were measured once every two hours for 36 hours. Weighted mean rates for the two blanks were subtracted from rates calculated for chambers with fish at each bi-hourly measurement interval. Initial and final water samples were collected for determination of [TAN] using a spectrophotometric assay (Bower and Holm-Hansen 1980). Trials were conducted at 8.0 ± 0.2 °C at a light level of 1.0 μE (14-hr photoperiod). The respirometer was isolated within a laboratory which effectively shielded fish from external stimuli.

At the conclusion of each trial, the standard length (L_S , ± 0.1 mm) and wet weight (W_W , ± 0.1 mg) of each juvenile were measured and fish condition factor, $CF = 1000 (W_W) (L_S)^{-3}$, was calculated. Ages of the fish were known and growth rates ($mm\ d^{-1}$, or $mg\ d^{-1}$) were calculated from the lengths- and weights-at-age.

DATA ANALYSIS AND STATISTICS

Information regarding the metabolic substrate used by the fish was obtained by expressing the rates of O_2 consumption, CO_2 production and TAN excretion in two atomic ratios, calculated for each individual: respiratory quotient, $RQ = (\mu g\ CO_2) (\mu g\ O_2)^{-1}$, and $O:N = (\mu mol\ O_2) (\mu mol\ N)^{-1}$ (Brett and Groves 1979, Cetta and Capuzzo 1982, Finn et al. 1991).

Regression analyses were performed using SAS statistical software (SAS 1989) to determine the relationship between fish W_W (independent variable) and the mean hourly rates of O_2 consumption, CO_2 production, and TAN excretion (dependent variables). Residuals (observed-predicted) from these regressions were calculated and regressed against juvenile growth rate in L_S ($mm\ d^{-1}$) and W_W ($mg\ d^{-1}$). Values for RQ, O:N, and fish CF were also regressed against growth rate. Predictive regressions were used and the significance level was set at the $\alpha = 0.05$ level.

RESULTS

GROWTH RATE

The lengths- and weights-at-age of the 64 fish used in the present study implied ranges in linear growth rates equal to 0.27-0.47 $mm\ d^{-1}$ (Fig. 2) and 1.52-7.94 wet $mg\ d^{-1}$, respectively. The coefficient of variation ($CV = 100 \times \text{mean } SD^{-1}$) of growth rates was equal to 31.2% (GR_W , $mg\ d^{-1}$) and 14.0% (GR_L , $mm\ d^{-1}$). Rates of GR_L and GR_W were significantly related based upon the following regression:

$$GR_W = 17.22(\pm 1.86)GR_L - 2.63(\pm 0.70) \quad n = 64, R^2 = 0.58$$

where mean ($\pm SE$) parameter estimates are provided, $p < 0.0001$.

MORPHOMETRICS & CONDITION FACTOR

Fish condition factor was significantly negatively related to growth rate such that faster-growing juvenile cod (in length-at-age) tended to weigh less than slower-growing

individuals of the same length (regression 12 in Table 1, Fig. 3); at a given length, W_w decreased ~ 19 mg with every 1 mm d^{-1} increase in growth rate.

ROUTINE ENERGY LOSS AND ATOMIC RATIOS

Each of the three components of routine energy loss (rates of O_2 consumption, CO_2 production, TAN excretion) increased with fish size (Fig. 4A,D,&G) and was related to W_w by the equation: $\text{rate} = a (W_w)^b$ (Table 1). Rates of CO_2 production increased with body weight more quickly than did rates of O_2 consumption or TAN excretion ($b = 0.89$, 0.81 , and 0.56 , respectively) (Table 1). In each case, residuals from these regressions tended to be negatively correlated with individual growth rate (Table 1). Residuals from the regression of O_2 consumption versus body size were significantly negatively correlated to growth rate in length (GR_L) (Fig. 4C), supporting our first hypothesis (Fig. 1A&B), but were not correlated to growth rate in weight (GR_w) (Fig. 4B), supporting our second hypothesis (Fig. 1C&D). Residuals from the regression of CO_2 production and body size were significantly negatively correlated to both GR_L and GR_w (Fig. 4E&F), supporting our first hypothesis (Fig. 1A&B). Residuals from the TAN regression were not significantly related to growth rate (Fig. 4H&I), supporting our second hypothesis (Fig. 1C&D). Positive correlations between routine energy loss residuals and growth rate were not observed; our third hypothesis (Fig. 1E&F) was not supported.

Respiratory quotient (RQ) values, which ranged from 0.86 to 1.03, and O:N values, which ranged from 12.2 to 23.9, were lowest for individuals with the lowest growth rates and increased with increasing growth rate (Table 1). The change in these atomic ratios with growth rate was significant in some cases, depending upon whether growth rate was expressed in length or weight units (regressions 13 & 14 and 15 & 16, respectively, Table 1).

DISCUSSION

In this study, inter-individual differences in the rates of growth of 64, young juvenile Atlantic cod were significantly correlated to differences in rates of routine energy loss. Inter-individual differences in the rates of growth and routine energy loss were related such that faster-growing fish had lower than predicted energy loss compared to slower-growing conspecifics within the same cohort. Our findings suggest that growth rate difference among individuals were due, in part, to inter-individual differences in metabolic efficiency (our hypothesis 1, Fig. 1A&B). The energy savings afforded to faster-growing fish (outlined below) was, in part, a function of their decreased wet weight at length (lower condition factor).

For example, the daily rate of routine energy loss by a 35-mm cod growing at 0.40 mm d^{-1} is predicted to be 7% less than that for the same length cod growing at 0.25 mm d^{-1} ($1 \text{ mg } O_2 = 13.598 \text{ Joules}$, Brett and Groves 1979, regressions 1, 4, & 6 Table 1). Our findings for juvenile cod agree with those of Danzmann et al. (1987) who observed lower rates of routine energy loss (O_2 consumption) by young juvenile rainbow trout (*Salmo gairdneri*) from a faster-growing strain compared to trout from a slower growing strain.

In the present study, inter-individual differences in growth were also associated with other physiological differences including the use of metabolic substrates as revealed through atomic ratios (RQ and O:N). The range in the values of these ratios (RQ = 0.86-1.03, and O:N = 12.2-23.9) indicated that young cod catabolized a mixture of metabolic substrates (Cetta and Capuzzo 1982, Finn et al. 1991, Brett and Groves 1979) and that the use of specific substrates may shift with growth rate (e.g., lower O:N values indicated a higher proportion of protein use in relatively slow-growing individuals, Table 1).

In general, the strength of the correlation between growth rate and values measured on individuals in this study (e.g., CF, O:N, and RQ values, and residuals of O₂, CO₂, and TAN) was variable and depended upon how growth was expressed. Correlations between various parameters and growth rate which were significant when growth was expressed in length units, were often not significant when growth was expressed in weight units or vice versa (e.g., regressions 5 & 6, 11 & 12, 13 & 14, 15 & 16 in Table 1). The disparity of the results was due to growth-rate dependent changes in fish morphology; fish condition factor declined with increasing growth rate.

The significant decrease in condition factor with increasing length-specific growth rate of fish in this study was an unexpected finding. A similar correlation between growth rate and fish condition factor was observed by Svåsand et al. (1996) who compared the growth dynamics of different cod populations. In that study, Norwegian coastal cod were found to have a significantly higher growth rate and lower condition factor than Arcto-Norwegian cod (Svåsand et al. 1996). Results of the present study are the first to indicate a similar relationship between growth rate and condition factor among individuals within the same population and cohort. Although fish growth during early juvenile ontogeny is preferentially allocated to length as opposed to weight (Ricker 1979), the potential costs and tradeoffs of this juvenile growth strategy likely depend upon the level of prey resources. For example, a lower condition factor translates to a smaller energy reserve and a greater likelihood of mortality due to starvation within depauperate prey environments. Cod in poor condition have been encountered, at times, within poor prey environments in the field (e.g., Buckley and Lough 1987, Lough et al. 1996). However, in areas with abundant prey resources, the cubic relationship between increases in axial length and weight confers an advantage to preferential length increase. At the present time, the influences of prey resource history and fish growth history on specific patterns of energy allocation to growth remains largely unexplored.

CONCLUSIONS

In the decades of research on Atlantic cod, the early juvenile period (3 to ~13 cm SL) has received relatively little attention owing to difficulties in both the successful rearing of juvenile gadids in the laboratory and the live capture and transport from the wild. Consequently, few measurements of routine energy loss in young, small (3 to 4 cm L_S) juvenile cod have been obtained. This study utilized a closed-circuit respirometer that measured both O₂ consumption and CO₂ production. Rates of O₂ consumption measured in this study using the MicroOxymax™ system agreed well with those measured for similar-sized cod at similar temperatures using a standard flow-through respirometer (Peck et al. Submitted) (Fig. 5).

Previous studies on young juvenile Atlantic cod have compared the physiology and growth of different stocks (Svåsand et al. 1996, Otterlei et al. 1999, Purchase and Brown 2000), as well as the influence of different genotypes on growth rate and physiology within a stock (Nævdal et al. 1992, Salvanes and Hart 2000). Results of this study indicated that differences can exist in both the rate of routine energy loss and patterns of growth allocation among individual juvenile cod from the same cohort. Since both the former and latter were correlated with growth rate, these physiological attributes may be indicative of “survivors” in field populations. Inter-individual differences in physiological traits influencing energy acquisition (e.g., rates of food consumption, assimilation efficiency, and swimming activity) will likely have the greatest consequences to differences in growth rate and are the topic of future investigations.

ACKNOWLEDGEMENTS

This research benefited from discussions with E. Caldarone. We would like to thank J. Hawk for help with data collection. We are especially indebted to M.-L. Dickson at URI GSO for allowing us to conduct research using the Micro-Oxymax respirometer. Finally, we would like to thank the employees of the NOAA NMFS Narragansett Laboratory for access to and use of their facility. This research was funded by NOAA / University of Rhode Island Cooperative Marine Education and Research grant # NA77FE0494 and by University of New Hampshire Open Ocean grant # NA16RP1718.

REFERENCES

- Berdalet, E., T. Packard, B. Lagacé, S. Roy, L. St.-Amand, and J.-P. Gagné. 1995. CO₂ production, O₂ consumption and isocitrate dehydrogenase in the marine bacterium *Vibrio natriegens*. *Aquat. Microb. Ecol.* 9: 211-217.
- Bower, C.E., and T. Holm-Hansen. 1980. A salicylate-hypochlorite method for determining ammonia in seawater. *Can. J. Fish. Aquat. Sci.* 37: 794-798.
- Brett, J.R., and T.D.D. Groves. 1979. Physiological Energetics. In: Hoar, W.S., D.J. Randall, and J.R. Brett (Eds.) *Fish Physiology Vol VIII*. Academic Press, NY, pp. 279-352.
- Buckley, L.J., and R.G. Lough. 1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. *Can. J. Fish. Aquat. Sci.* 44: 14-25.
- Campana, S.E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 135: 21-26.
- Cetta, C.M., and J.M. Capuzzo. 1982. Physiological and biochemical aspects of embryonic and larval development of the winter flounder, *Pseudopleuronectes americanus*. *Mar. Biol.* 71: 327-337.
- Cutts, C.J., N.B. Metcalfe, and A.C. Taylor. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *J. Fish Biol.* 52: 1026-1037.
- Czekajewski, J., L. Nennerfelt, H. Kaczmarek, and J.F. Rabek. 1994. Application of a new generation of computerized apparatus for the study of oxygen uptake and production of CO and CO₂ during photo-(thermal) oxidation of polymers. *Acta Polymer.* 45: 369-374.
- Danzmann, R.G., M.M. Ferguson, and F.W. Allendorf. 1987. Heterozygosity and oxygen-consumption rate as predictors of growth and developmental rate in rainbow trout. *Physiol. Zool.* 60: 211-220.
- Finn, R.N., H.J. Fyhn, and M.S. Evjen. 1991. Respiration and nitrogen metabolism of Atlantic halibut eggs (*Hippoglossus hippoglossus*). *Mar. Biol.* 108: 11-19.
- Gregory, T.R., and C.M. Wood. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* 55: 1583-1590.
- Kolok, A.S., and J.T. Oris. 1995. The relationship between specific growth rate and swimming performance in male fathead minnows (*Pimephales promelas*). *Can. J. Zool.* 73: 2165-2167.
- Lough, R.G., E.M. Caldarone, T.K. Rotunno, E.A. Broughton, B.R. Burns, and L.J. Buckley. 1996. Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 43: 1875-1904.

- Nævdal, G., A. Folkvord, E. Otterlei, and S. Thorkildsen. 1992. Growth rate related to genotype of 0-group cod at three environmental temperatures. *Sarsia* 77: 71-73.
- Otterlei, E., G. Nyhammer, A. Folkvord, and S.O. Stefansson. 1999. Temperature- and size-dependent growth of larval and juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. *Can. J. Fish. Aquat. Sci.* 56: 2099-2111.
- Ottersen, G., and H. Loeng. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. *ICES J. Mar. Sci.* 57: 339-348.
- Peck, M.A., L.J. Buckley, and D.A. Bengtson. Submitted. The effects of body size and temperature on energy losses due to standard, routine, and feeding metabolism in early juvenile Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.*
- Purchase, C.F., and J.A. Brown. 2000. Interpopulation differences in growth rates and food conversion efficiencies of young Grand Banks and Gulf of Maine Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 57(11): 2223-2229.
- Ricker, W.E. 1979. Growth Rates and Models. In: Hoar, W.S., D.J. Randall, and J.R. Brett (Eds.) *Fish Physiology Vol VIII*. Academic Press, NY, pp. 677-743.
- Salvanes, A. G.V., and P.J.B. Hart. 2000. Is individual variation in competitive performance of reared juvenile cod influenced by haemoglobin genotype? *Sarsia* 85: 265-274.
- SAS Institute Inc. (1989). *SAS/STAT® User's Guide Version 6, Fourth Edition Volume 2*. SAS Institute Inc., Cary, NC, pp. 846.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bull. Mar. Sci.* 60(3): 1129-1157.
- Svåsand, T., K.E. Jørstad, H. Otterå, and O.S. Kjesbu. 1996. Differences in growth performance between Arcto-Norwegian and Norwegian coastal cod reared under identical conditions. *J. Fish Biol.* 49: 108-119.
- Tupper, M., and R.G. Boutilier. 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Mar. Ecol. Prog. Ser.* 118: 295-300.

Table1: Summary data for rates of routine energy loss and growth in young juvenile Atlantic cod. Parameter estimates are provided from regression analysis of: 1) power functions relating rates of O₂ consumption, CO₂ production, and total ammonia nitrogen (TAN) excretion to fish wet weight (WW), as well as WW to standard length (SL), and 2) linear functions relating O₂, CO₂, and TAN residuals, as well as respiratory quotient (RQ) and condition factor (CF) to growth rate. Growth rates are expressed in both length (GRL, mm d⁻¹) and weight (GRW, mg d⁻¹) units.

Regression Equation and Variables		Regression Parameters				Regression Statistics			
		a value		b value		n	R ²	p-value	sig
		mean	± SE						
y = a(x) ^b									
1)	ug O ₂ (fish) ⁻¹ (h) ⁻¹ vs. mg W _W	1.210 ±	1.22	0.81 ±	0.03	64	0.90	< 0.0001	*
2)	ug CO ₂ (fish) ⁻¹ (h) ⁻¹ vs. mg W _W	0.740 ±	0.10	0.89 ±	0.04	64	0.89	< 0.0001	*
3)	ug TAN (fish) ⁻¹ (hr) ⁻¹ vs. mgW _W	0.160 ±	0.06	0.56 ±	0.08	38	0.57	< 0.0001	*
4)	mg W _W vs. mm L _S	0.010 ±	0.01	2.89 ±	0.07	64	0.97	< 0.0001	*
y = a + b(x)									
5)	Residual O ₂ vs. GR _W	7.29 ±	5.35	-1.79 ±	1.35	64	0.03	0.1892	
6)	Residual O ₂ vs. GR _L	22.92 ±	11.28	-60.12 ±	29.97	64	0.06	0.0492	*
7)	Residual CO ₂ vs. GR _W	15.14 ±	6.32	-3.83 ±	1.59	64	0.09	0.0191	*
8)	Residual CO ₂ vs. GR _L	49.65 ±	12.71	131.55 ±	33.77	64	0.20	0.0002	*
9)	Residual TAN vs. GR _W	0.58 ±	0.34	-0.14 ±	0.09	38	0.07	0.1120	
10)	Residual TAN vs. GR _L	0.81 ±	0.70	-2.03 ±	1.85	38	0.03	0.2779	
11)	Condition Factor vs. GR _W	8.56 ±	0.23	-0.09 ±	0.06	64	0.04	0.1161	
12)	Condition Factor vs. GR _L	10.47 ±	0.40	-6.06 ±	1.06	64	0.35	< 0.0001	*
13)	Respiratory Quotient vs. GR _W	0.92 ±	0.02	0.01 ±	0.01	64	0.01	0.0978	
14)	Respiratory Quotient vs. GR _L	0.87 ±	0.03	0.24 ±	0.09	64	0.11	0.0077	*
15)	O:N vs. GR _W	12.10 ±	1.40	1.40 ±	0.40	38	0.30	0.0003	*
16)	O:N vs. GR _L	12.71 ±	3.21	12.40 ±	8.45	38	0.06	0.1506	

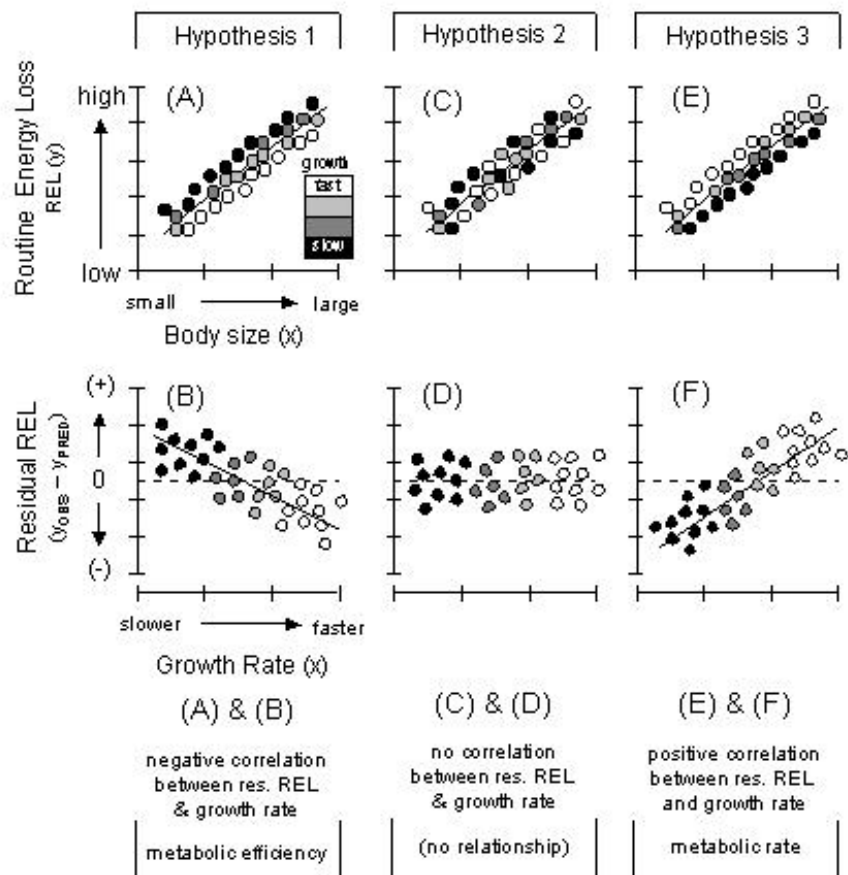


Figure 1: Three hypothetical relationships between inter-individual differences in rates of routine energy loss (REL) and growth. Circles represent individual fish, the degree of fill indicates their relative growth rate. Top panels = REL versus fish size. Bottom panels = residuals from top panel regression versus growth rate. A&B) Faster growing individuals have lower than predicted REL based upon residuals, implying increased metabolic efficiency. C&D) No correlation between REL and growth rate, rates of routine metabolism and growth are unrelated. E&F) Faster growing fish have higher than predicted REL, implying increased metabolic rate.

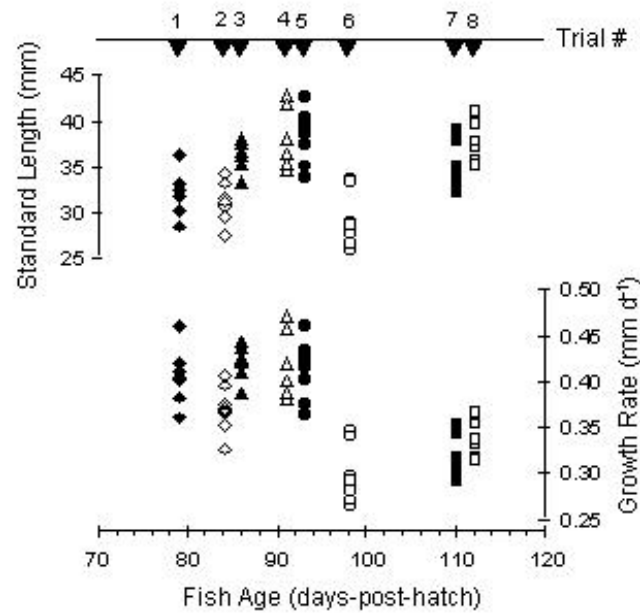


Figure 2: Standard length (mm), growth rate, mm (d)^{-1} , and fish age (days-post-hatch) of the 64 juvenile Atlantic cod sampled from the same rearing tank and used in trials. The routine energy loss by eight individuals was measured in each of eight trials.

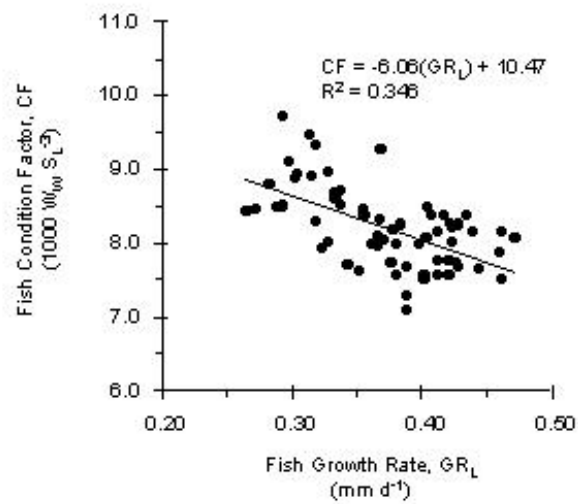


Figure 3: Juvenile Atlantic cod condition factor, $CF = 1000$ (wet weight, mg) (standard length) $^{-3}$, versus growth rate, $GR_L = (\text{mm}) (\text{d})^{-1}$, for 64 individual fish in the same cohort reared in the same tank.

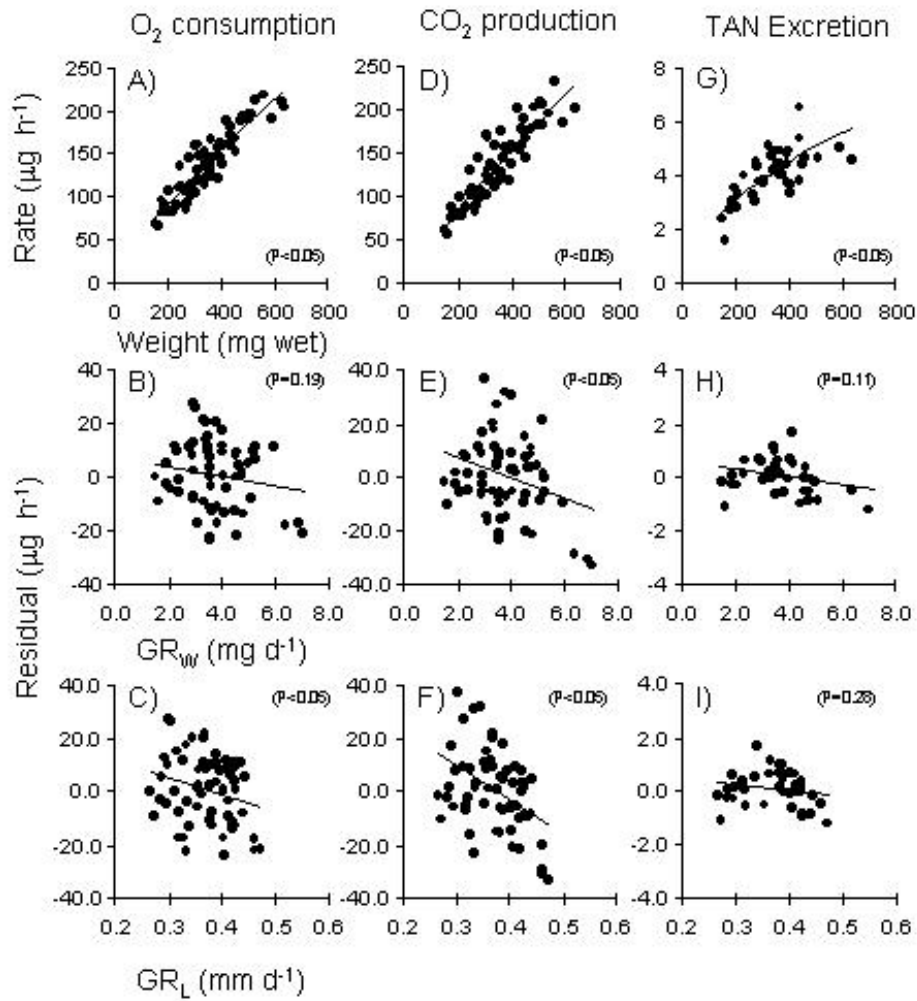


Figure 4: Rates of O₂ consumption, CO₂ production, and total ammonia nitrogen (TAN) excretion versus fish size (wet weight, mg) and residuals from these regressions versus growth rate in length (GR_L, mm d⁻¹) and weight (GR_w, wet mg d⁻¹). Panels A-C = O₂ consumption, panels D-F = CO₂ production, and panels G-I = TAN excretion. P-values for regressions are indicated within each panel. Regression equations are provided in Table 1.

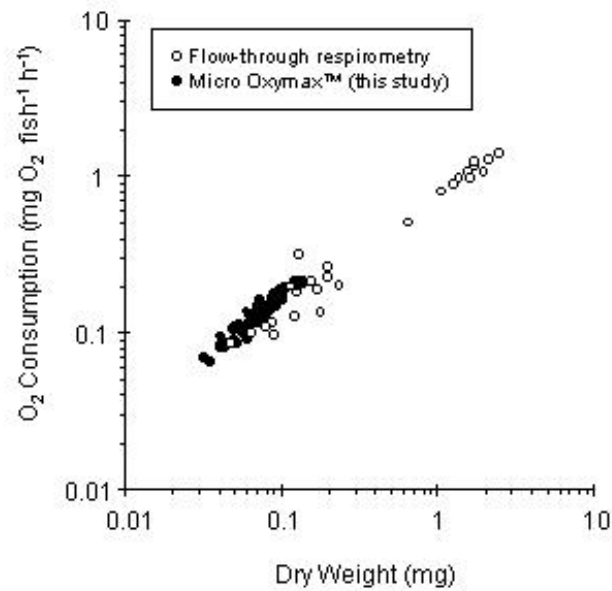


Figure 5: Rate of O₂ consumption versus fish wet weight for Atlantic cod juveniles. Data were obtained from trials conducted using a closed-circuit respirometer (this study), and via flow-through respirometry (Peck et al. Submitted) at 8°C.