Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*

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ABSTRACT: The relationship between the somatic growth rate (G) and feeding level (unfed, intermediate, and maximum rations) of age-0 juvenile cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* was quantified at different temperatures. Laboratory trials were conducted using 2 size-classes of cod (3.6 to 5.6 cm standard length [SL], and 8.1 to 12.4 cm SL) at 5, 8, 12, and 15°C, and 1 size-class of haddock (6.0 to 9.6 cm SL) at 8 and 12°C. The shape of the growth-feeding relationship was well described by a 3-parameter asymptotic function for cod and by a linear function for haddock (R^2 range = 0.837 to 0.966). The growth rate and scope for growth were maximum at 12°C, whereas growth efficiency was greatest (26.0 to 32.2%) at temperatures between 5 and 8°C. Juvenile cod held at 15°C exhibited reduced rates and efficiencies of somatic growth compared to fish at other temperatures. Biochemical-based growth indicators for age-0 juveniles were calibrated from measurements of the amounts of RNA, DNA, and protein in white muscle samples. A multiple linear regression using RNA:DNA and temperature as independent variables explained a significant portion of the variability observed in G of juvenile cod (R^2 = 0.716) and haddock (R^2 = 0.637). This relationship may be useful in estimating recent growth of age-0 juvenile cod and haddock in the field.

KEY WORDS: Age-0 juvenile · Cod · Haddock · Feeding · Growth · RNA:DNA

INTRODUCTION

Since the 1960s, low spawning stock numbers and variable year-class success in Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and other groundfish species on Georges Bank have led to extensive research efforts aimed at understanding how biotic and abiotic factors affect the growth and survival of these fish. Field data collected for cod and haddock in the NW Atlantic suggest that factors operating dur-

ing the early juvenile period influence year-class success in some years (Campana et al. 1989, Werner et al. 1999). Of special importance is the protracted habitat transition from the pelagic to demersal environment (settlement) which occurs in young-of-the-year (YOY) juveniles of both species at ~4 to 8 cm standard length (SL) (Lough & Potter 1993). The somatic growth rate of fish (age 90 d) shortly after this year-0 juvenile settlement phase has been positively correlated to year-class success in Atlantic cod (Campana 1996). However, dif-

ficulties both in the successful rearing of juvenile gadids in the laboratory, and the live capture and transport from the wild, have hampered efforts to evaluate the environmental factors that affect growth during this early juvenile period. Recent advances in the culture of cod and haddock now enable us to study the factors affecting growth and survival of year-0 juveniles of both species in greater detail.

Quantifying the relationship between rates of feeding and growth in an organism can provide considerable ecological insight. The growth-feeding relationship of juveniles of a variety of marine fish species has been studied via laboratory trials (e.g. Elliott 1975b, Fonds et al. 1992, Malloy & Targett 1994, Buckel et al. 1995) in an effort to increase the efficiency of aquaculture and to address ecological questions. Of particular ecological relevance are data collected on (1) rates of food consumption required for maintenance of existing tissues (C_{main}), (2) maximum consumption rates (C_{max}), (3) gross growth efficiency (GGE) (Brett & Groves 1979) and (4) optimal temperatures for growth.

Although previous studies have evaluated the growth-feeding relationship in large juvenile and adult cod (e.g. Edwards et al. 1972, Jones 1978, Jones & Hislop 1978, Hawkins et al. 1985), relatively little research has been conducted on this relationship in age-0 juvenile cod. Our understanding of the growth-feeding relationship in age-0 juvenile cod has been advanced by studies conducted at cold temperatures (Brown et al. 1989) and maximal feeding levels (Otterlei 2000, Purchase & Brown 2000). Extending these analyses to include a wider range in both temperatures and feeding levels would provide additional ecologically relevant data, since age-0 juvenile cod are found over a wide temperature range (Fahay et al. 1999) and feeding may be sub-maximal due to limited prey resources (Buckley et al. unpubl. data) or foraging limits imposed by competition (Tupper & Boutilier 1995) and/or predation risk (Clark & Green 1990). To our knowledge, only 1 study (Jones 1978) has provided information on the growth-feeding relationship of haddock.

Gaining reliable field estimates of growth rate and condition of an organism is an essential step toward understanding the factors that influence growth and survival. In early life stages of marine fish, biochemical-based indicators of growth, including measuring the quantities and/or ratios of nucleic acids (RNA and DNA) and protein in the whole body or specific tissues (e.g. Write & Martin 1985, Malloy & Targett 1994, Rooker & Holt 1996, Kuropat et al. 2002), have been used to generate field growth estimates. These indicators have been successfully applied to field-caught cod and haddock larvae (Buckley 1984) and have been measured in larger juvenile cod (Foster et al. 1993) but have not been calibrated for age-0 juvenile cod or haddock.

The primary objective of the present research was to quantify the relationship between rates of feeding and growth in age-0 juvenile cod and haddock. We conducted growth-feeding trials over a wide range of temperatures and feeding levels in an effort to understand how these factors influence growth and perhaps survival of both species during the age-0 period in the field. Specifically, we measured the growth rates of juvenile cod at 5, 8, 12, and 15°C, and haddock at 8 and 12°C that were either (a) unfed, (b) fed intermediate rations, or (c) fed maximum rations. A second research objective was to measure white muscle RNA, DNA, and protein in fish from these laboratory trials in an effort to evaluate and calibrate biochemical-based indicators of growth for future use on field-caught age-0 juveniles.

MATERIALS AND METHODS

Laboratory fish rearing. Several batches of juvenile Atlantic cod and haddock (2 to 3 mo, 2 to 3 cm SL) were obtained from an aquaculture research center (University of Maine, Orono, ME) and transported to the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA NMFS), Narragansett Laboratory. Juvenile haddock were the progeny of wild-caught adult broodstock spawned in captivity at either of 2 locations, the NOAA NMFS Narragansett Aquarium (fish from Great South Channel off the coast of Cape Cod, Massachusetts, USA) or Memorial University, Newfoundland, Canada (Nova Scotia and Newfoundland fish). Juvenile cod were the progeny of NOAA NMFS broodstock. Once transported to our laboratory, the juveniles were held in temperature-controlled, flow-through, circular tanks (91.4 and 121.9 cm diameter) receiving filtered (20 µm) Narragansett Bay seawater (1 to 3 l min^{-1}). The salinity was 29 to 32‰ and light levels were 0.5 to 1.0 µmol m^{-2} s^{-1}. Fish were fed an artificial diet (BioKyowa™, C-500, or C-1000 µm pellet) 1 to 3 times daily, depending upon fish size, prior to experimentation.

Growth-feeding trials. Fifteen growth-feeding trials were conducted, 5 using smaller (~4.5 cm SL) juvenile cod (cod$_S$, n = 174), 6 trials using larger (~9.0 cm SL) juvenile cod (cod$_L$, n = 225), and 4 using (~7.0 cm SL) juvenile haddock (n = 135). Prior to a trial, fish were acclimated to the experimental temperature (5, 8, 12, or 15°C) for at least 10 d (Table 1). Trials lasted from 8 to 13 d (depending upon fish size and water temperature) and contained 6 to 17 tanks (10 l semi-static, $^3/_4$ water replacement d^{-1}) with 3 randomly selected juvenile fish in each tank. Preliminary trials indicated that isolated fish had reduced food consumption compared to groups of 2 or 3 fish. In each trial, 2 replicate tanks were main-

tained at each of 3 feeding rates: (1) no food (unfed), (2) intermediate rations, and (3) maximum rations. A total of 4 intermediate rations (~1.5, 3.0, 5.0, and 7.5% fish dry body weight) was used, with 1 to 3 intermediate ration levels included in each trial. Fed fish were provided pre-weighed rations of an artificial diet (Bio-Kyowa™ C-1000 µm pellet), over the course of at least 2 daily feedings. To calculate the weight of food consumed, uneaten pellets were collected on each day, counted, and their weight estimated (1 pellet = 0.91 ± 0.02 mg). Due to the large difference between the percentage of water in the food (4.7%, n = 10) and the fish (78.3% cod, 81.7% haddock, Peck et al. 2003, unpubl. data), food consumption rate by fish was expressed on a dry weight basis with fish wet weight converted to dry weight using equations in Peck et al. (2003, unpubl. data). The BioKyowa™ diet used in this study was 55% protein, 10% fat, 4% fiber, and 17% ash (manufacturer's data). The energy content of the artificial diet was 20.82 ± 0.31 (SE) Joules (mg dry weight)$^{-1}$ (n = 15, Gentry, Phillipson Micro-bomb calorimeter).

At the beginning and end of each trial, fish were anaesthetized (MS 222, 0.7 mg l^{-1}) and the wet weight of each fish was measured (±0.01 g, Sartorius LC 2200 S electronic balance). At the end of each trial, fish SL was measured (±0.1 mm, Measy #5921 caliper). At the end of 10 of the trials (Table 1), a white muscle sample was dissected from the dorsal region anterior to the first dorsal fin of each fish and stored at –80°C until biochemical analyses were performed. A total of 333 muscle samples were collected and analyzed, 207 from cod and 126 from haddock.

Fish growth. The specific growth rate (G, % d^{-1}) was calculated based on the formula:

$$G = 100(e^g - 1) \tag{1}$$

where g = instantaneous growth coefficient equal to:

$$g = (\ln W_t - \ln W_0)/t \tag{2}$$

where W_t and W_0 equal the final and initial mean wet weight of the 3 fish within a replicate tank and t = time (d) between measurements. Gross growth efficiency (GGE) was calculated as:

$$GGE = 100(G/C) \tag{3}$$

where C = food consumption rate (% dry body weight fish^{-1} d^{-1}). In our calculations of GGE using Eq. (3), we used predicted values for G (determined from regression analyses performed on growth-feeding data) and observed values for C. Observed C (% d^{-1}) was the mean value of daily consumption estimates equal to the dry weight of food consumed in a day, divided by total dry weight of fish in the tank on that day (initial weight + daily increase determined from Eq. 1) multiplied by 100.

Table 1. *Gadus morhua* and *Melanogrammus aeglefinus.* Summary data for laboratory growth-feeding trials conducted using age-0 juvenile Atlantic cod (2 size groups, cod$_S$ and cod$_L$), and haddock at different temperatures. Mean ± SE final size (wet weight [wet wt] and standard length [SL]) of fish used in each trial are provided. Days = trial duration; DM = dissection of muscle for biochemical analyses; Y = yes; N = No. n = 3 fish per tank

Growth-feeding trial				Age-0 juvenile fish final size	
Species (ID) T (°C)	Tanks (n)	Days	DM	Wet wt (g) Mean ± SE	SL (cm) Mean ± SE
Cod$_S$					
5	13	13	Y	1.14 ± 0.10	5.22 ± 0.19
8	10	9	Y	0.65 ± 0.02	4.13 ± 0.04
12	13	8	Y	0.53 ± 0.03	3.99 ± 0.06
12	8	9	Y	0.59 ± 0.11	3.96 ± 0.21
15	14	9	Y	1.72 ± 0.18	5.58 ± 0.31
Cod$_L$					
5	16	13	N	8.60 ± 0.68	9.51 ± 0.24
8	15	10	N	5.24 ± 0.32	8.11 ± 0.15
8	8	11	N	8.52 ± 0.87	9.57 ± 0.33
12	13	10	N	7.44 ± 0.44	8.90 ± 0.17
12	6	11	N	7.70 ± 0.86	9.29 ± 0.35
15	17	11	Y	6.51 ± 0.42	9.45 ± 0.21
Haddock					
8	11	11	Y	4.06 ± 0.44	7.19 ± 0.29
8	6	10	Y	4.13 ± 0.95	6.91 ± 0.56
12	6	10	Y	2.61 ± 0.13	6.22 ± 0.12
12	10	11	Y	4.41 ± 0.45	7.24 ± 0.27

Biochemical-based indicators of growth. Nucleic acid content was quantified according to Caldarone et al. (2001), with the following modifications for work with juvenile fish. Samples of muscle tissue (~1 to 6 mg freeze-dried weight) were removed from a –80°C freezer, immediately freeze-dried (>12 h), weighed (±0.001 mg, Cahn microbalance) and immersed in 300 µl buffered 1% sarcosil. The sample was then sonicated for 5 s (Fisher Sonic Dismembrator 60, Level 5), shaken for 0.5 h (Fisher Vortex Genie 2, Level 3), diluted with tris-EDTA buffer (pH 7.0) to a volume of 1.5 ml, and centrifuged (11 000 × g, 15 min). The supernatant was removed and diluted to 0.1% sarcosil and the concentrations of RNA and DNA were estimated from the fluorescence in ethidium bromide before and after sequential treatment with RNase and DNase. Commercial preparations of 18s plus 28s rRNA (Sigma) and ultra-pure highly polymerized calf thymus DNA were used as standards. The concentration of protein in the homogenate was measured spectrophotometrically (Cambridge Instruments 7520 Microplate Reader) using the protocol of Smith et al. (1985) adapted for a 96-well microplate format. Samples or standards plus reagents were incubated at 60°C for 1 h to allow for complete color development. A serial dilution of bovine serum albumin was used as a standard. RNA, DNA, and protein

Table 2. *Gadus morhua* and *Melanogrammus aeglefinus.* Parameter estimates for 2 equations predicting growth (G, % weight d^{-1}) from daily food consumption (C, % weight d^{-1}). Parameter estimates are provided for 1 of 2 equations: (T1) a 3-parameter non-linear function, or (T2) a 2-parameter linear function. These equations predict G at food consumption rates between 0 (unfed) and C_{max} (mean ± SE rate of food consumption by fish provided maximum food rations, n = 2 to 5 tanks for each species at each temperature, 3 fish per tank). na = not applicable

| Species | T (°C) | C_{max} (% d^{-1}) Mean ± SE | Eq. | Parameter estimates Eq. (T1): $G = \Phi - a(\exp^{-C \times b})$ or Eq. (T2): $G = a + bC$ | | | | |
				Φ Mean ± SE	a Mean ± SE	b Mean ± SE	n	R^2
Cod$_S$	5	5.8 ± 0.3	(T1)	1.61 ± 0.55	2.98 ± 0.57	0.31 ± 0.13	13	0.90
	8	7.6 ± 0.1	(T1)	1.90 ± 0.35	3.69 ± 0.40	0.47 ± 0.18	10	0.97
	12	13.0 ± 0.1	(T2)	na	−1.30 ± 0.23	0.39 ± 0.04	21	0.86
	15	9.3 ± 0.6	(T1)	0.52 ± 0.30	2.06 ± 0.37	0.44 ± 0.18	13	0.84
Cod$_L$	5	4.9 ± 0.5	(T1)	2.19 ± 0.65	2.86 ± 0.62	0.25 ± 0.10	16	0.95
	8	6.3 ± 0.5	(T1)	1.21 ± 0.20	2.32 ± 0.22	0.42 ± 0.10	23	0.90
	12	7.7 ± 1.1	(T1)	0.76 ± 0.28	2.68 ± 0.31	0.38 ± 0.11	19	0.87
	15	6.7 ± 0.2	(T1)	0.44 ± 0.41	1.80 ± 0.41	0.33 ± 0.18	17	0.88
Haddock	8	9.6 ± 0.7	(T2)	na	−0.90 ± 0.11	0.37 ± 0.02	17	0.94
	12	10.5 ± 1.2	(T2)	na	−1.08 ± 0.20	0.34 ± 0.03	16	0.89

concentration were calculated based upon the freeze-dried weight of the muscle sample.

In one trial, unfed haddock at 8°C were sampled (wet weight and SL measured and muscle dissected) at the beginning (Day 0), in the middle (Day 3), and at the end (Day 10) of the trial in an effort to assess the time

Fig. 1. *Gadus morhua.* Growth rate (% body weight d^{-1}) versus water temperature for age-0 juvenile Atlantic cod (pooled data for cod$_S$ = mean 0.92 g, cod$_L$ = mean 7.30 g wet weight). Growth rates of fish held at different rates of food consumption are shown. Daily rates of food consumption are expressed as percentage of fish body weight, and include unfed, intermediate, and maximal (ad libitum) levels. Intermediate ration levels were partitioned into 4 separate groups for visual clarity. Values = mean ± SE

course of changes in white muscle RNA, DNA, and protein.

Statistics. Data collected in this study were analyzed via linear regression, multiple linear regression, and non-linear regression analyses, using SAS statistical software (SAS 1989). The significance level was set at $p \leq 0.05$.

RESULTS

Rates of food consumption and somatic growth

The observed maximum food consumption rate (C_{max}) ranged from 4.9 to 13.0 % d^{-1} and was highest for both species at 12°C (Table 2). Values for weight-specific growth rate (G) for cod$_S$ (~0.92 g wet weight), cod$_L$ (~7.33 g wet weight) and haddock (~3.80 g wet weight) ranged from −2.2 to 4.3, −2.4 to 1.6, and −1.6 to 3.8 % d^{-1}, respectively. Rates of G varied with both water temperature and feeding level. For example, G decreased at higher temperatures in unfed fish, whereas G increased with temperature in fish feeding maximally between temperatures of 5 and 12°C (Fig. 1). For each species, G increased with increased daily feeding level and in most cases for cod$_S$ and cod$_L$ appeared to approach a temperature-dependent asymptotic level at maximal rates of food consumption (Fig. 2). In most cases, the growth-feeding relationship for cod$_S$ and cod$_L$ at each temperature was described by a 3-parameter, asymptotic function:

$$G \%(d)^{-1} = \Phi - a(\exp^{(-C \times b)}) \qquad (4)$$

where Φ, a, and b are constants and C = % d^{-1} (Table 2). For haddock and cod$_S$ at 12°C, linear functions explained a similar proportion of the variability in
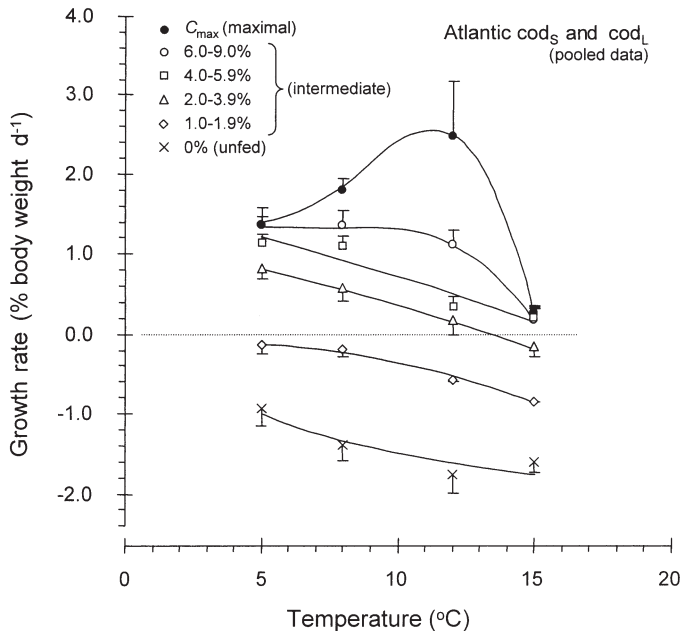
G with less variance around parameter estimates (Table 2). Values for G of cod_S and cod_L were relatively low at all feeding levels at 15°C (Fig. 2).

The linear growth-feeding relationships for haddock at 8 and 12°C could be combined into a multiple linear regression including food consumption (C) and temperature (T) as independent variables:

$$\text{Haddock } G = -0.3(\pm 0.4) + 35.1(\pm 2.0)\ C - 0.07(\pm 0.04)T$$
$$n = 34, \text{ R}^2 = 0.914 \qquad (5)$$

where mean ($\pm$ SE) parameter estimates are indicated. The addition of body size (wet weight) as an independent variable did not significantly increase the amount of variability explained by this regression.

Maintenance rations (C_{main}), calculated using parameter estimates listed in Table 2 and solving for $G = 0$, increased with temperature and were highest at 15°C in cod_S (Table 3, Fig. 3). The difference between C_{main} and observed C_{max}, or the scope for growth (SfG) (Elliott 1975a), was greatest at 12°C and reduced at 15°C, especially for cod_L (Fig. 3).

Growth efficiency

Gross growth efficiency (GGE), calculated from Eq. (3) using observed C and predicted G (G from equations and parameter estimates listed in Table 2), was influenced by both temperature and the rate of food consumption (Fig. 2). Maximal GGE for the smaller cod was greatest at 8°C, while that for the larger cod occurred at 5°C (Fig. 2, Table 3). GGE_{max} tended to de-

Table 3. *Gadus morhua* and *Melanogrammus aeglefinus.* Predicted rates of food consumption (C) and maximal gross growth efficiency (GGE_{max}) at different temperatures for age-0 juvenile cod and haddock. Maintenance consumption rates (C_{main}), GGE_{max}, and the consumption rate at GGE_{max} were calculated using equations in Table 2. Error estimates (SE) were equal to the difference between values calculated using the parameter error (+SE) estimates in those equations. GGE = G/C

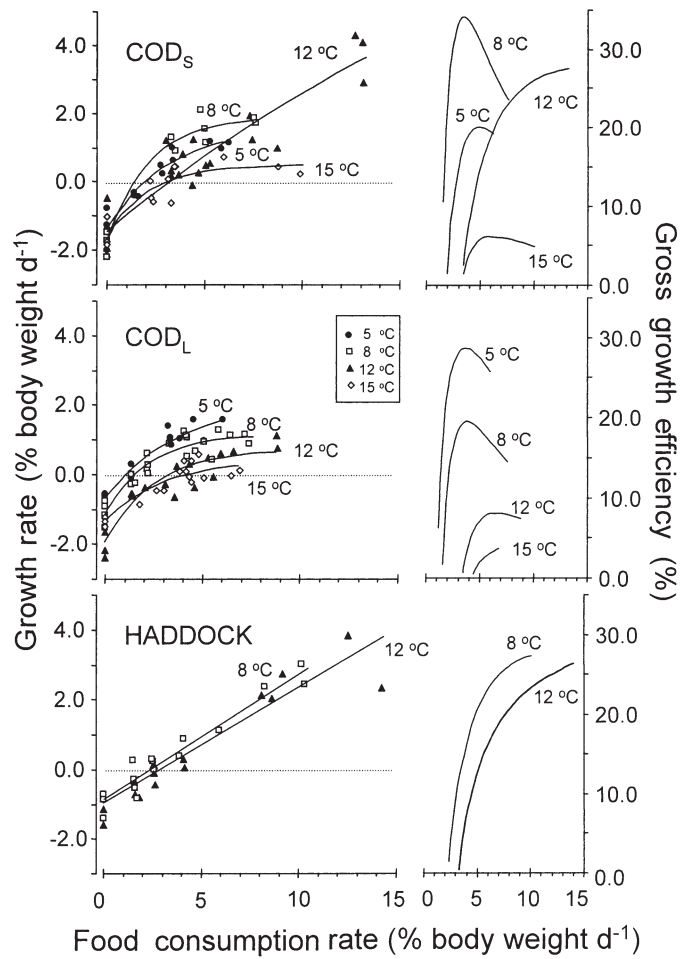| Species (wet wt)	T (°C)	Predicted rate of food consumption (C) (% body weight d^{-1})		GGE_{max} (%)
		C_{main} Mean ± SE	C at GGE_{max} Mean ± SE	
Cod$_S$	5	1.9 ± 0.8	4.9 ± 2.0	20.0
(0.92 g)	8	1.4 ± 0.5	3.7 ± 1.3	33.9
	12	3.3 ± 1.0	13.0 ± 0.1	28.6
	15	3.2 ± 1.4	6.1 ± 2.4	6.2
Cod$_L$	5	1.1 ± 0.5	3.7 ± 1.5	28.7
(7.33 g)	8	1.5 ± 0.4	3.9 ± 1.0	19.5
	12	3.3 ± 1.1	6.5 ± 2.0	8.1
	15	4.2 ± 2.3	6.7 ± 2.0	3.6
Haddock	8	2.5 ± 0.5	9.6 ± 0.7	27.2
(3.80 g)	12	2.8 ± 1.9	10.5 ± 1.2	23.7

Fig. 2. *Gadus morhua* and *Melanogrammus aeglefinus.* Growth rate (% body weight d^{-1}) and gross growth efficiency (%) versus food consumption rate (% body weight d^{-1}), for age-0 juvenile Atlantic cod and haddock. Data are shown for 2 size-classes of cod (cod$_S$ = mean 0.92 g, cod$_L$ = mean 7.30 g wet weight). Growth Crate regression lines are for the equations listed in Table 2

cline with temperature in both species with the highest values equal to 33.9% (8°C), 28.9% (5°C), and 27.2% (8°C), for cod$_S$, cod$_L$, and haddock, respectively (Fig. 2, Table 3). GGE_{max} occurred at intermediate feeding levels at most temperatures in cod and at maximal feeding levels in haddock. The feeding level at GGE_{max} increased with increasing temperature in cod$_L$ and haddock, but not in cod$_S$ (Fig. 2, Table 3). GGE of both cod groups at 15°C was relatively low at all ration levels compared to other temperatures with GGE_{max} equal to 6.2 and 3.6%, respectively (Fig. 2, Table 3).

Biochemical-based indicators of growth

Changes in the biochemical measures of white muscle of unfed haddock at 8°C with time indicated that
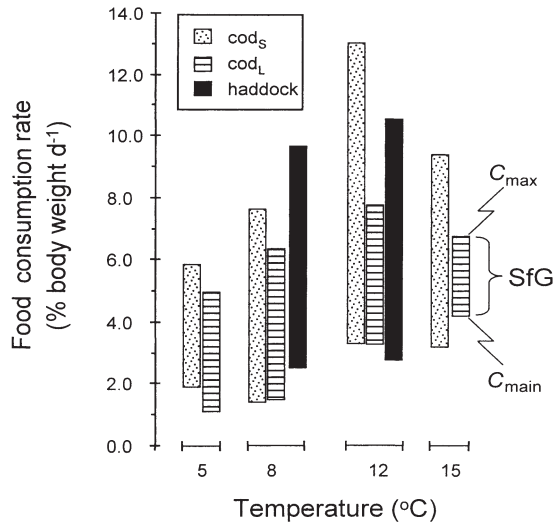
Fig. 3. *Gadus morhua* and *Melanogrammus aeglefinus.* Food consumption rate (% body weight d^{-1}) versus temperature for age-0 juvenile Atlantic cod$_S$, cod$_L$, and haddock. Maintenance (C_{main}) and maximal (C_{max}) food consumption rates are indicated. Bars indicate the scope for growth (SfG = $C_{main} - C_{max}$)

nucleic acids (e.g. RNA:DNA, R:D) responded within ~3 d to the cessation of feeding at this temperature, and changed little after an additional 7 d (Fig. 4). At temperatures between 5 and 12°C, white muscle R:D in unfed fish (5.91 to 7.42) was nearly half (64%) that of fish fed maximum rations (10.74 to 12.18) (Table 4, Fig. 4). Other biochemical measures including RNA: freeze-dried weight (R:W) and RNA:protein (R:P) also decreased with decreasing feeding level (values for unfed fish were ~77% of those measured in fish feeding maximally) (Table 4). For both species at each temperature, linear regressions using R:D as an independent variable explained the most variability in juvenile G (dependent variable) followed by R:W, R:P, and protein:freeze-dried weight (P:W) (Table 5).

Multiple linear regressions using R:D and water temperature (T) as independent variables explained a significant portion of the variability in G of cod and haddock:

$$\text{Cod } G = -7.14(\pm 0.79) + 0.65(\pm 0.06)$$
$$\text{R:D} + 0.23(\pm 0.04) \, T \quad (6)$$
$$n = 56, \, R^2 = 0.716$$

$$\text{Haddock } G = -6.05(\pm 1.15) + 0.59(\pm 0.08)$$
$$\text{R:D} + 0.16(\pm 0.08) \, T \quad (7)$$
$$n = 31, \, R^2 = 0.637$$

where mean (±SE) parameter estimates are indicated for both equations. The addition of body size (wet weight) as a variable did not significantly increase the variability explained by either of these regressions, nor did the addition of R:P (p > 0.10).

At 15°C, values of white muscle R:D, R:W, and R:P in cod, were 60, 52, and 51% of the mean values of the 3 lower temperatures averaged across the 3 feeding levels (Table 4).

DISCUSSION

Rates of food consumption and growth

Maximum rates of food consumption (C_{max}) and growth (G_{max}) in marine fish are typically related allometrically to body size (Brett & Groves 1979) and size-specific rates in the present study are in line with those of previous studies on this species. For example, rates of C_{max} in cod larvae, 0.90 g juveniles, 7.30 g juveniles, and 500 g adults have been measured to be ~55, 13.1, 8.9, and 1.9% d^{-1}, respectively (Edwards et al. 1972, see their Table 2; Karamushko & Reshetnikov 1994, present study). The allometric scaling of G_{max} with body size has been quantified at a variety of temperatures by Björnsson & Steinarsson (2002) for juvenile and adult cod and by Otterlei (2000) for young juveniles over a size range of 2 to 20 g. In the present study, our value of G_{max} for cod$_S$ (0.92 g) at 8°C was 2.1% d^{-1}, which agrees well with growth rates obtained in other laboratory studies using age-0 juvenile cod (Brown et al. 1989,
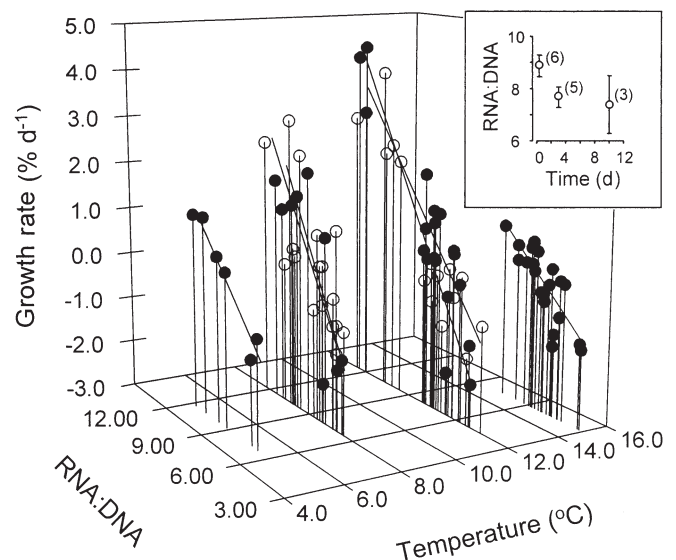

Fig. 4. *Gadus morhua* and *Melanogrammus aeglefinus.* RNA:DNA and growth rate data collected at 5, 8, 12, and 15°C for cod (n = 56, ●) and at 8 and 12°C for haddock (n = 32, ○). Each datum equals the mean RNA:DNA and growth rate for the 3 fish in each tank. Linear regression equations and statistics are provided in Table 5. Insert: mean ± SE RNA:DNA versus time since last feeding (d) at 8.0°C for 6.1 to 8.2 cm SL haddock. No. of fish sampled at each time is indicated in parentheses

Table 4. *Gadus morhua* and *Melanogrammus aeglefinus*. Biochemical attributes of white muscle tissue collected from age-0 juvenile cod and haddock maintained at different levels of food consumption for 9 to 14 d. Values are provided for RNA:DNA (R:D), RNA:freeze-dried weight (R:W), RNA:protein (R:P), and protein:freeze-dried weight (P:W). Ratio units = µg:µg. Three of the ratios (R:W, R:P, and P:W) were multiplied by 100 to express a percentage (%) for ease of presentation. Number of tanks at each level of food consumption is indicated (n)

| Ratio | Species | T (°C) | Rate of daily food consumption | | | | | |
| | | | Zero (unfed) | | Intermediate | | Maximum (C_{max}) | |
			Mean ± SD	n	Mean ± SD	n	Mean ± SD	n
R:D (µg:µg)	Cod	5	7.05 ± 0.31	2	9.49 ± 0.45	2	11.29 ± 0.58	2
		8	7.24 ± 0.67	3	9.23 ± 1.05	4	11.45 ± –	1
		12	5.91 ± 0.81	4	7.25 ± 0.73	13	12.18 ± 0.28	3
		15	4.56 ± 1.29	6	5.43 ± 0.84	12	5.62 ± 1.28	5
	Haddock	8	7.42 ± 0.88	4	8.51 ± 1.33	10	10.74 ± 1.35	3
		12	6.16 ± 1.06	3	7.36 ± 1.79	10	10.75 ± 1.17	2
R:W (%)	Cod	5	1.46 ± 0.10	2	1.63 ± 0.12	2	1.92 ± 0.13	2
		8	1.40 ± 0.22	3	1.74 ± 0.15	4	1.89 ± –	1
		12	1.35 ± 0.03	4	1.42 ± 0.10	13	1.91 ± 0.07	3
		15	0.81 ± 0.27	6	0.81 ± 0.17	12	0.90 ± 0.20	5
	Haddock	8	1.63 ± 0.11	3	1.92 ± 0.29	10	2.41 ± 0.49	3
		12	1.64 ± 0.04	2	1.76 ± 0.20	11	2.34 ± 0.19	2
R:P (%)	Cod	5	2.44 ± 0.16	2	2.75 ± 0.16	2	3.24 ± 0.42	2
		8	2.37 ± 0.48	3	2.83 ± 0.44	5	3.36 ± –	1
		12	2.21 ± 0.13	4	2.38 ± 0.21	12	3.04 ± 0.25	3
		15	1.39 ± 0.47	6	1.33 ± 0.34	12	1.44 ± 0.24	5
	Haddock	8	2.70 ± 0.23	3	3.31 ± 0.45	10	4.15 ± 1.01	3
		12	2.52 ± 0.05	2	2.78 ± 0.33	11	3.65 ± 0.34	2
P:W (%)	Cod	5	60.05 ± 0.17	2	59.90 ± 0.79	2	59.51 ± 3.51	2
		8	62.56 ± 6.07	3	62.72 ± 8.14	5	62.93 ± –	1
		12	57.99 ± 5.67	4	61.01 ± 2.93	13	62.85 ± 3.62	3
		15	59.55 ± 3.82	6	61.10 ± 3.47	12	62.90 ± 4.17	5
	Haddock	8	60.56 ± 2.92	3	58.17 ± 3.58	10	58.71 ± 3.86	3
		12	65.75 ± 1.03	2	64.15 ± 3.98	11	59.31 ± 3.75	2

Folkvord & Otterå 1993, Otterlei 2000, Purchase & Brown 2000). For example, a G_{max} of ~2.6 % d^{-1} was observed for 0.9 to 9.2 g juvenile cod feeding maximally at ~9.5°C (Folkvord & Otterå 1993). G_{max} for age-0 juveniles appears to be >2× G_{max} of 2 and 3 yr old juvenile cod at similar temperatures (e.g. ~300.0 g juveniles ~0.9 % d^{-1}, Hawkins et al. 1985, see their Fig. 8, 10°C).

Much less is known about maximal rates of food consumption and growth in haddock. The G_{max} for haddock at each temperature was greater than that for cod$_S$ and cod$_L$ at 8°C, and ~3× greater than that for cod$_L$ at 12°C. Unfortunately, relatively few data exist (Jones 1978) to compare to our observed rates of C_{max} (9.6 to 10.5 % d^{-1}) and G_{max} (3.0 to 3.1 % d^{-1}) at 8 and 12°C. Thus, the allometric relationship between fish size and rates of growth and food consumption in haddock remains largely unexplored. Similarly, comparisons of C_{max} and G_{max} rates measured in the laboratory and those estimated for field fish are hampered by a lack of data collected on rates of C_{max} or G_{max} for comparably sized early age-0 juvenile haddock (and cod) in the field. Additional field research targeting this somewhat elusive size range (see Lough & Potter 1993)

would permit a more detailed comparison of feeding and growth of laboratory and field fish.

Shape of the growth-feeding relationship

In the present study, the shape of the growth-feeding relationship varied between species and changed with temperature. At the lowest and highest temperatures, the relationship was non-linear and tended to reach a plateau in cod$_S$ and cod$_L$. At intermediate temperatures the relationship appeared more linear for haddock (8 and 12°C) and cod$_S$ (12°C), and no plateau was observed. The literature is equivocal with respect to the shape of the growth-feeding relationship in marine fish with both non-linear (asymptotic) (Elliott 1975b, Brett & Groves 1979) and linear (Staples & Nomura 1976, Malloy & Targett 1994) relationships observed in other species. Similarly, studies on cod have indicated both non-linear (asymptotic) (Edwards et al. 1972, Brown et al. 1989) and linear (Jones & Hislop 1978, Hawkins et al. 1985) growth-feeding relationships. Based upon a review of the literature on Atlantic cod,

Jobling (1982) considered the relationship between growth and feeding to be linear.

The shape of the growth-feeding relationship has also been observed to change with temperature in other species including juvenile brown trout *Salmo trutta* (Elliott 1975b), and age-0 juvenile summer flounder *Paralichthys dentatus* (Malloy & Targett 1994). Nevertheless, in a previous study using larger (100 g) juvenile cod, no differences were noted in the shape (linear relationship) among 4 different temperatures (Hawkins et al. 1985). Changes in the shape of the growth-feeding relationship with ontogeny (and/or size) and temperature indicate physiological changes with these factors, underscoring the importance of collecting basic physiological data on different life stages (and/or sizes) and at different temperatures for a species.

C_{main}, scope for growth, and optimal temperature for growth

The food consumption rate (% d^{-1}) required for maintenance of existing tissues, or maintenance consumption (C_{main}, C at $G = 0$), tends to decrease with increasing fish size and increase with increasing temperature (Elliott 1975a,b, Brett & Groves 1979, Hawkins et al. 1985). The decrease in C_{main} with increasing fish size can be attributed to the allometric scaling of metabolism with body size and has been previously observed in larger juvenile cod by Jones & Hislop (1978). Estimates of C_{main} in the present study (1.1 to 4.2% d^{-1}) were ~4× greater than those (0.3 to 1.4% d^{-1}) calculated for larger, 100 g juvenile cod at similar temperatures (Hawkins et al. 1985). The exponential increase in C_{main} with temperature in the present study mirrors the increase in routine metabolism with temperature measured for similarly sized juvenile cod between 4.5 and 15.5°C (Peck et al. 2003). An exponential increase in C_{main} with temperature has also been observed for larger (100 g) juvenile cod studied at 7, 10, 15, and 18°C (Hawkins et al. 1985). The range of consumption rates greater than C_{main}, or the scope for growth (SfG = $C_{max} - C_{main}$) also tended to increase with temperature, being greatest at 12°C for cod_S and haddock, and at 8°C for cod_L. SfG was greatly reduced at 15°C for both cod size-classes (Fig. 3).

Table 5. *Gadus morhua* and *Melanogrammus aeglefinus.* Parameter estimates (a and b) and regression statistics for the equation $G = a + b(X)$, estimating growth (G, % body weight d^{-1}) from various biochemical attributes (X, µg:µg or %) of white muscle tissue of juvenile Atlantic cod and haddock. Biochemical attributes: RNA:DNA (R:D), RNA:freeze-dried weight (R:W), RNA:protein (R:P), and protein:freeze-dried weight (P:W)

Biochemical Attribute (X)	Species	T (°C)	Parameter estimates: $G = a + b(X)$ a Mean ± SE	b Mean ± SE	n	Statistics R^2	p
R:D (µg:µg)	Cod	5	−4.41 ± 0.67	0.49 ± 0.07	6	0.921	0.002
		8	−6.25 ± 2.18	0.74 ± 0.24	8	0.576	0.018
		12	−4.80 ± 0.73	0.72 ± 0.09	20	0.774	<0.001
		15	−2.66 ± 0.50	0.46 ± 0.09	23	0.565	<0.001
	Haddock	8	−4.31 ± 1.36	0.54 ± 0.15	17	0.444	0.004
		12	−4.44 ± 0.77	0.63 ± 0.09	15	0.774	0.001
R:W (%)	Cod	5	−6.21 ± 1.78	3.83 ± 1.06	6	0.765	0.023
		8	−5.80 ± 2.72	3.79 ± 1.61	9	0.409	0.046
		12	−9.29 ± 1.78	6.77 ± 1.19	20	0.642	<0.001
		15	−1.72 ± 0.57	1.12 ± 0.42	23	0.232	0.016
	Haddock	8	−3.37 ± 1.40	1.95 ± 0.70	16	0.355	0.015
		12	−7.74 ± 1.96	4.56 ± 1.06	15	0.586	<0.001
R:P (%)	Cod	5	−5.34 ± 1.84	1.96 ± 0.65	6	0.696	0.039
		8	−4.19 ± 2.14	1.67 ± 1.06	8	0.261	0.159
		12	−8.60 ± 2.05	3.82 ± 0.83	19	0.539	<0.001
		15	−1.72 ± 0.57	1.12 ± 0.42	23	0.271	0.016
	Haddock	8	−3.35 ± 1.29	1.13 ± 0.38	16	0.389	0.010
		12	−7.27 ± 3.03	2.74 ± 0.70	15	0.539	0.002
P:W (%)	Cod	5	5.95 ± 17.98	−0.10 ± 0.30	6	0.025	0.764
		8	−0.11 ± 5.89	0.01 ± 0.09	9	0.001	0.916
		12	−10.45 ± 6.19	0.19 ± 0.10	20	0.163	0.087
		15	−5.81 ± 2.50	0.09 ± 0.04	23	0.184	0.041
	Haddock	8	5.10 ± 5.63	−0.08 ± 0.10	16	0.047	0.421
		12	5.87 ± 7.19	−0.08 ± 0.11	15	0.040	0.473

The growth dynamics of poikilotherms are, to a great extent, dictated by temperature. Consequently, a large body of research has focused on identifying the optimal temperature for growth in Atlantic cod. Results of a gastric evacuation study by Tyler (1970) were the first to suggest that the optimal temperature for growth in Atlantic cod was below 15°C. Subsequently, these results have been confirmed by a number of growth-feeding studies which indicated an optimum temperature for growth (G_{max}) between 12 and 15°C for YOY Atlantic cod (Otterlei 2000, Björnsson & Steinarsson 2002, the present study). Results of the present study in which YOY growth was maximal for cod_S at 12°C (and was relatively diminished in cod_S and cod_L at 15°C) agree with the previous growth studies. However, it should be kept in mind that the 'optimum' temperature for growth of juvenile cod may likely be lower than 12°C in the wild due to food limitation at such high temperatures (Buckley et al. unpubl. data). At the present time, a discussion of the temperature optimum for growth in age-0 juvenile haddock is premature, although changes in growth rates and growth efficiencies (discussed below) for haddock between 8 and 12°C were similar to those found for cod.

Gross growth efficiency

The ranges in GGE_{max} values for cod_S and haddock at 8 and 12°C (23.7 to 33.9%), and for cod_L at 5 and 8°C (19.5 to 28.7%) in this study agree well with the ranges in GGE obtained in other young juvenile fish including: ~27 to 30% for 6 to 10 cm bluefish *Pomatomus saltatrix* (Buckel et al. 1995), 22 to 35%, and 29 to 31% for 4 to 8 cm plaice *Pleuronectes platessa*, and European flounder *Platichthys flesus*, respectively (Fonds et al. 1992). Of the various factors influencing GGE, feeding level, water temperature, and fish size are among the most important (Elliott 1975b). For example, GGE was greatly affected by ration level, with GGE_{max} occurring at intermediate levels of food consumption at each temperature for cod (except cod_S at 12°C) due to the non-linear (asymptotic) growth-feeding relationship observed in this study. GGE_{max} was also observed at intermediate ration levels for larger (500 g wet weight) Atlantic cod by Edwards et al. (1972), and in any species where the growth-feeding relationship is observed to be asymptotic (e.g. Elliott 1975b, Brett & Groves 1979). Our data indicate that GGE_{max} for cod_S and cod_L occurs at mean feeding rates of ~75 and 80% of maximal consumption, respectively. These percentages are in close agreement with that (80%) found by Elliott (1975b) for brown trout. This is in contrast, however, to GGE_{max} in juvenile haddock, which

occurred at maximal levels of food consumption (similar to that of cod_S at 12°C) due to the linear growth-feeding relationship.

GGE_{max} increased with decreasing temperature in cod_S, haddock, and most markedly in cod_L. The trend of increasing GGE_{max} with decreasing temperature has been previously observed by other researchers working on Atlantic cod age-0 juveniles (Brown et al. 1989) and larger juveniles (Hawkins et al. 1985), and seems to be an adaptive physiological characteristic of this predominantly cold-water species.

Biochemical-based indicators of growth

Results of the present study indicate that 1 biochemical-based indicator of growth, the R:D, can be used to predict growth and/or recent feeding level of age-0 juvenile cod and haddock at each of the temperatures examined. R:D explained the most variability in rates of G of cod and haddock, followed by R:W and R:P, with white muscle protein content (P:W) largely unrelated to short-term growth. Measurement of white muscle R:D, when combined with temperature in a multiple linear regression, explained a significant percentage of the variability in G for age-0 juvenile cod ($R^2 = 0.716$) and haddock ($R^2 = 0.637$). Our findings are similar to those of other investigations measuring concentrations of nucleic acids in early (larval and YOY) stages of marine fish (e.g. Buckley 1984, Write & Martin 1985, Malloy & Targett 1994, Rooker & Holt 1996, Kuropat et al. 2002). The response time of R:D to changes in feeding regime (~3 d, Fig. 4) is similar to that measured in other studies including 5 d in larger juvenile cod (Foster et al. 1993) and 1 d for early juvenile summer flounder (Malloy & Target 1994).

Results of the present study indicate that the R:D of white muscle tissue was a good indicator of recent growth in Atlantic cod and haddock at body sizes attained by fish undergoing habitat transition (settlement). At the present time, our laboratory results may be used as a coarse indicator of recent growth in field fish. For example, setting G equal to zero and solving for R:D in Eqs. (6) & (7) yields:

$$\text{Cod R:D}_{main} = 11.137 - 0.436(T), \quad T = 5 \text{ to } 15°C \tag{8}$$

$$\text{Haddock R:D}_{main} = 10.246 - 0.268(T), \quad T = 8 \text{ to } 12°C \tag{9}$$

where R:D_{main} equals the R:D at zero growth. These equations provide temperature-specific R:D values for age-0 juvenile cod and haddock delineating fish that, in the short term, were likely feeding and growing well from those which were likely feeding and growing poorly.

Summary

The growth rate of fish during the first year of life and its relationship to survival is a prominent feature in most hypotheses attempting to explain recruitment variability in marine fish. The confluence of 2 factors, feeding level and temperature, plays a dominant role in determining fish growth rate (Brett & Groves 1979) which, during the age-0 juvenile period, has been positively correlated to year-class success in Atlantic cod (Campana 1996). The latter correlation provided the impetus for the present laboratory study, as it underscored the importance of (1) understanding how various factors affect growth, and (2) obtaining accurate growth estimates of age-0 juvenile cod and haddock.

With regard to our first research objective, results of this study indicated that growth rates were markedly affected by feeding level with the observed range in growth rates as great as 6.5% d^{-1} separating fish that were unfed from those that were maximally feeding. By defining the shape of the growth-feeding relationship at different temperatures, we estimated how temperature influenced weight loss in unfed fish (endogenous metabolism), the daily rate (C_{main}) and range (scope for growth) of food consumption required to sustain positive growth, and the gross growth efficiency at which that growth occurs. These estimates should aid in the formulation of hypotheses regarding age-0 juvenile growth and survival on Georges Bank. For example, the marked decline in GGE$_{max}$ with temperature could serve to decrease the relative survival potential of juveniles undergoing the habitat transition later in the year (at warmer temperatures) on Georges Bank. With regard to our second research objective, results of this study indicate that measurements of white muscle nucleic acids can be used as a biochemical-based indicator of growth. Growth rates of age-0 juveniles in the field may be estimated directly from measurements of white muscle R:D and temperature. With growth estimates of field-caught juveniles in hand, it may be possible to, among other things, identify factors varying spatially (e.g. related to habitat suitability; Kuropat et al. 2002) that affect growth and survival, generate a relative biochemical-based index of year-class status, and/or buttress modeling efforts aimed at understanding the ecology and recruitment processes of Atlantic cod and haddock.

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