Interpopulation differences in growth rates and food conversion efficiencies of young Grand Banks and Gulf of Maine Atlantic cod (*Gadus morhua*)

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Abstract: Geographically separated Atlantic cod (*Gadus morhua*) stocks in the northwest Atlantic exhibit life history variation and have been shown to differ genetically. The genetic and environmental contributions to phenotypic differences, however, have not yet been measured. We used common environment experiments to evaluate the importance of temperature on the observed growth variation between Grand Banks (GB) and Gulf of Maine (GOM) cod stocks. Larvae from the GB grew faster than GOM larvae at both 7 and 12°C. Growth rates of juveniles were not different, but GB juveniles had higher food conversion efficiencies than those from the GOM (at both ambient and warm temperatures). The results indicate that faster growth of GOM cod in the wild is not due to a higher genetic capacity for growth rate in GOM than in GB fish. The findings give evidence of genetically based phenotypic variation, which is in agreement with molecular studies on population differentiation in cod, and support the theory of countergradient variation in growth rates of larval fish.

Résumé : Des stocks de la Morue franche (*Gadus morhua*) du nord-ouest de l'Atlantique, provenant de régions géographiques distinctes, ont des démographies particulières et possèdent des différences génétiques. Les contributions relatives des gènes et de l'environnement aux différences phénotypiques n'ont cependant pas encore été déterminées. Des montages expérimentaux classiques ont permis d'évaluer l'effet de la température sur les différences de croissance que l'on observe entre les stocks des Grands Bancs (GB) et ceux du golfe du Maine (GOM). Les larves GB croissent plus vite que les larves GOM tant à 7°C qu'à 12°C. Les taux de croissance des juvéniles ne diffèrent pas, mais les juvéniles GB ont une meilleure efficacité de conversion de la nourriture que les juvéniles GOM aussi bien aux températures ambiantes que chaudes. Ces résultats indiquent que la croissance plus rapide des morues GOM en nature n'est pas due à une capacité génétique de croissance supérieure à celle des poissons GB. Il s'agit donc d'une variation phénotypique qui est basée sur des facteurs génétiques; cela s'accorde bien avec les études moléculaires de différentiation des populations chez la Morue franche et confirme la théorie de l'existence d'une variation à contre-gradient des taux de croissance chez les larves de poisson.

[Traduit par la Rédaction]

Introduction

Atlantic cod (*Gadus morhua*) are found from Baffin Island (~63°N) to Cape Hatteras (~35°N) in the western north Atlantic (Scott and Scott 1988). A large amount of life history variation exists in cod, generally with faster growth rates and younger ages at maturity occurring in warmer water (Brander 1994). In recent years, genetic differences among cod stocks have been found using molecular techniques. Studies such as those using nuclear DNA, microsatilite DNA, mitochondrial DNA, and allozymes vary in their sensitivity to detect population differences (reviewed in Ruzzante et al. 1999).

The importance of "clarifying the relationships among cod stocks" towards management of the species has been addressed by Rice (1997). Genetic differentiation based on molecular studies provides no information on phenotypic and thus life history variation among stocks. Another approach is to examine highly selected traits, such as growth rates, using common environment experiments. Here, differences in growth rates would suggest ecologically important genetic differences among the populations. This also allows for tests of patterns in genetic variability, such as countergradient variation (Conover et al. 1997).

There have been several common environment experiments conducted on different populations of cod (e.g., Hunt von Herbing et al. 1996; Puvanendran and Brown 1998; Otterlei et al. 1999). However, we are aware of only two studies (Hunt von Herbing et al. 1996; Puvanendran and Brown 1998) that have examined growth of larval northwest Atlantic cod under common environments and none that have investigated juvenile or older fish. Both of these studies compared a fall–winter spawning stock with a spring–summer spawn-

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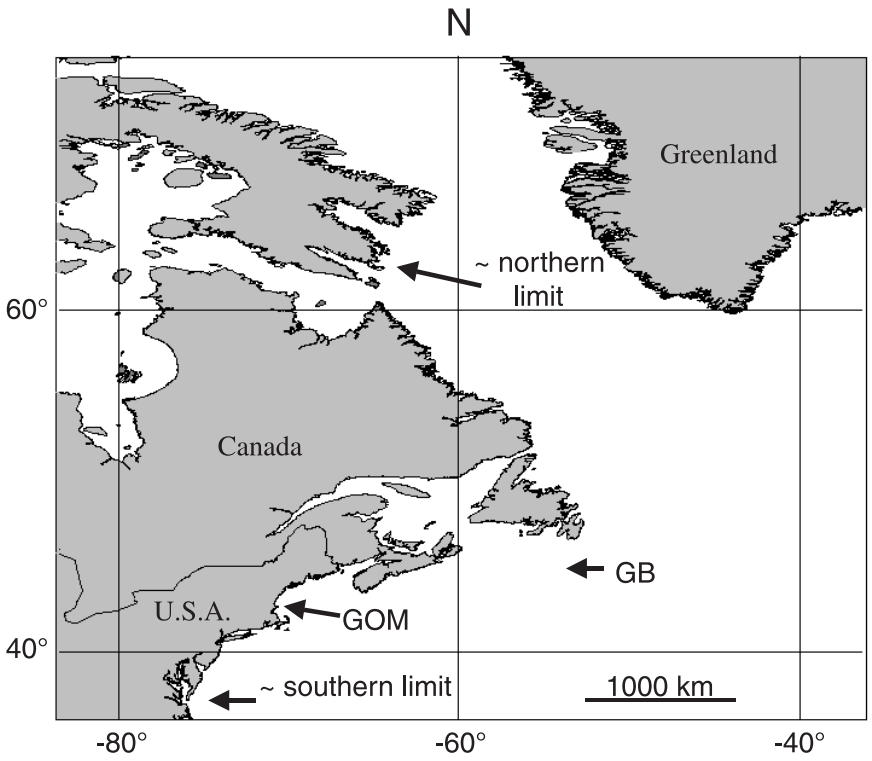
Fig. 1. Map of the northwest Atlantic Ocean showing approximate northern and southern limits of the distribution of Atlantic cod and locations of the GB and GOM collection sites.



ing stock, which may have compromised conclusions about growth rates.

This study was conducted to determine the genetic and environmental contribution towards differences in growth rates between cod stocks. We compared growth rates and food conversion efficiencies of young of the year cod from two areas (Grand Banks (GB) and Gulf of Maine (GOM)) under identical conditions, at two temperatures. We hypothesized that countergradient variation in growth rates and food conversion efficiencies exists in northwest Atlantic cod. Therefore, we predicted that at both temperatures, the more northern of the two populations would have faster growth rates and better food conversion efficiencies than the southern population.

Materials and methods

Larval experiment

Collection of gametes and egg incubation

Atlantic cod oocytes and sperm were obtained from spawning adults at sea. Collections were made from the GB (45°N, 55°W) in the Northwest Atlantic Fisheries Organization's (NAFO) division 3Ps and the GOM (42°N, 70°W) in NAFO division 5Y (Fig. 1). These two stocks differ genetically (Taggart et al. 1998), experience different temperatures, and exhibit life history variation, including differences in growth rates (Brander 1994). The GB sample was collected on 28 April 1998 and consisted of gametes from two females and seven males. Oocytes from the first female were fertilized with milt from four males, and the other three males were used to fertilize oocytes from the second female. Fertilized oocytes were pooled a short time later. The GOM sample was collected on 28 June 1998 and consisted of gametes from three females and nine males. Gametes from all 12 individuals were mixed together.

Embryos were brought to Memorial University of Newfoundland's Ocean Science Centre. Embryos from both populations arrived before formation of the blastula. Incubation was conducted in 300-L conical tanks at a temperature of 8 ± 1°C (±SD).

Experimental design

At 100% hatch, larvae from each population were placed in three 30-L black glass aquaria at 7 and 12°C and stocked at densities of 40 larvae·L^{-1}. Each aquarium was provided with filtered (to 10 μm), unsterilized seawater (salinity 32‰) at a rate of 50 mL·min^{-1} in a flow-through design. Light intensity was 1500 lx at the water's surface, and lights were on 24 h·day^{-1}.

An equal volume of cultured algae (*Isochrysis galbana* (Tahitian strain) and *Nannochloropsis oculata*) was given to each tank twice daily. Larvae were fed cultured (enriched with Algamac 3010) rotifers (*Branchionus plicatilis*) with a target prey density of 4000·L^{-1}. Light aeration ensured that prey were equally distributed throughout the tank. Twice daily, prey concentration was measured (using three 5-mL aliquots) and adjusted as necessary. At day 21, a mixture of rotifers and *Artemia salinia* nauplii (enriched with Algamac 3010 and DHA selco on alternative days) was supplied (total prey density 4000·L^{-1}) to the larvae for 1 week, and then, only *Artemia* were given. This feeding regime resulted in food always being present in the tanks and was based on previous growth experiments on larval cod (Puvanendran and Brown 1999). The growth experiments ran from 18 May 1998 to 29 June 1998 for the GB stock and from 9 July 1998 to 20 August 1998 for the GOM stock. Experimental conditions for both stocks were identical.

Sampling

Larvae were starved for 12 h prior to sampling. Ten larvae were sampled randomly from each tank at the start of the experiment (30 per treatment) and five (15 per treatment) weekly thereafter for

6 weeks. Each larva was killed using MS 222, placed on a depression slide, and videotaped under a dissecting microscope. Total length (L_T), myotome height (M_H, at the anus), and eye diameter (E_D, along the body axis) were recorded to the nearest 0.1 mm for each larva using an image analysis system. The M_H was used as a means of measuring body depth. At week 6, the L_T of larvae was measured directly using a dissecting microscope. These larvae were then placed on separate preweighed pieces of aluminum foil for determination of dry weight (W_D). The E_D and M_H were not recorded. Values of W_D (±0.00001 g) were obtained using an electronic balance after drying individuals at 60°C for 24 h.

Data analysis

Relationships between L_T versus W_D, L_T versus E_D, and L_T versus M_H were first compared for differences between populations at the two temperatures using analysis of covariance (ANCOVA, covariate = L_T) and then were analyzed using linear regression. Comparisons of growth rates between populations and temperatures were carried out by ANCOVA. The growth model contained terms representing the effects of population, temperature, age, and all interactions, with age as the covariate. Each datum in the analysis was the average length of the five (10 at week 0) larvae sampled per tank per week, which gave a sample size of $N = 60$ (12 tanks × 5 sampling dates, see Results). Transformation or randomization was not required to meet the assumptions of the tests (except the length to weight relationship which was ln transformed), as residuals were found to be homogenous and normal in distribution. To account for multiple response variables in population comparisons, a Bonferroni correction was applied (Rice 1989). This gave a comparison-wide α of 0.05/4 = 0.0125, which preserved an experimental-wide α of 0.05.

Juvenile experiment

Collection of fish

Juvenile cod were siblings of fish used in the larval experiment. Larvae not used in the first experiment were mass reared in 300-L conical tanks, following similar procedures as used in the larval experiment, at ~12°C. Shortly after metamorphosis, juveniles were transferred to 3000-L tanks, where they were weaned onto food pellets. Fish were kept under continuous lighting and fed ab libitum until transfer to the experimental setup.

Experimental setup

All fish were kept in two rectangular raceways, each measuring 80 × 400 × 62 cm. Each raceway was divided into 10, ~200-L compartments using framed netting, which served as experimental "tanks." Triplicate compartments for each population were set up in both raceways in an altering manner and seeded with 10 juvenile cod each ($N = 120$). Mean L_T at the start of the experiment was 11.3 cm (range 9.1–15.6 cm) for the GB cod and 8.4 cm (range 6.7–11.1 cm) for the GOM cod. The initial sizes were different because the eggs from the two stocks hatched more than a month apart, and the GB cod grew faster as larvae (see Results).

Water entered and exited each raceway in two places, and aeration was supplied to each compartment to ensure substantial mixing of water. Temperatures (daily) and dissolved oxygen (weekly) were monitored throughout the experiment and did not differ among compartments in each raceway. Temperature was ~6°C in both raceways when the experiment started (9 December 1998). Temperatures were gradually changed in the two raceways over the first 2 weeks of the experiment. One raceway received filtered heated seawater (mean temperature over entire experiment ~12°C, range 6.4–14.0°C) and the other raceway received filtered ambient seawater (mean temperature over entire experiment ~3°C, range 1.2–6.1°C). Lighting was provided by flourescent tubes, and photoperiod was adjusted fortnightly to approximate day lengths at 44°N (intermediate between both populations). Twilight was simulated with incandescent light for 0.5 h before and after flourescent lighting. Light intensity was measured at the water's surface and was 1500 lx under full lighting and 2 lx during the twilight period.

All fish were fed pellet food (Moore Clarke) to satiation once daily, and the amount eaten by each tank of fish was recorded. The pellets were easily consumed by all fish (i.e., observations indicated that food was not rejected by the fish) and were delivered one at a time by hand. Pellets were given to a tank until the fish stopped immediately consuming them. This was a direct measure of food consumption and eliminated estimation of actual amount of food consumed from the amount of food remaining in the tank. More specific information concerning the experimental design can be found in Purchase (1999).

Sampling and data analysis

All fish were measured (L_T to the nearest 0.1 cm) and weighed wet (to the nearest 0.01 g) at the start of the experiment, at week 5, and at week 14. Juvenile condition factors and other indices of nutritional status are presented elsewhere (Purchase and Brown 2000). The mean weight of food eaten by each fish in a tank was used for determination of gross food conversion efficiency (GFCE):

$$\mathrm{GFCE} = W_G/W_{FE}$$

where W_G is mean weight gain of each fish in a tank and W_{FE} is mean weight of food eaten by each fish in a tank. Gross specific growth rates (GSGR) were calculated as

$$\mathrm{GSGR} = (\ln W_F - \ln W_I)/\mathrm{time} \times 100$$

where W_F is the mean final fish ln weight, W_I is mean initial fish ln weight, and time is in days.

GSGR and GFCE were analyzed using three-way analysis of variance (ANOVA). The Bonferroni correction gave a comparison-wise α of 0.05/2 = 0.025. The variables in the model were population, temperature, sampling period, and all interaction terms. Residuals were found to be homogeneous and normal in distribution.

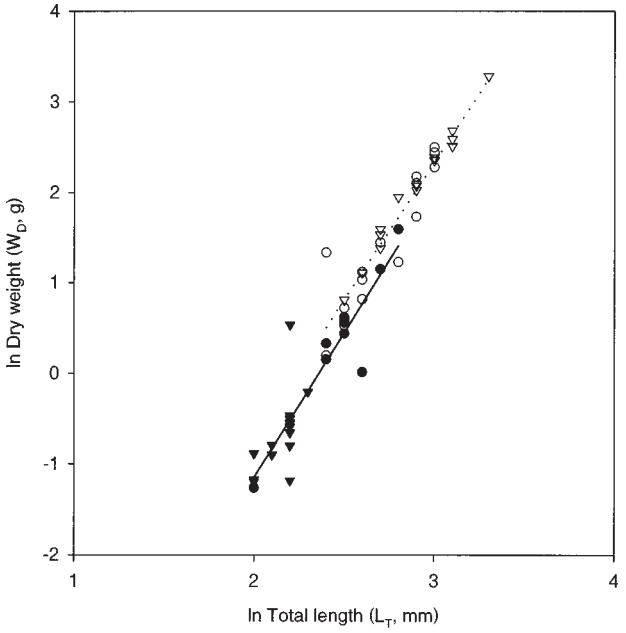
Results

Larval experiment

The slope of the W_D to L_T relationship was similar for both Atlantic cod populations and temperatures (ANCOVA; $F_{1,47} = 0.03$, $p = 0.866$); however, temperature had a significant effect on the intercept (ANCOVA; $F_{1,51} = 7.49$, $p = 0.009$) (Fig. 2). The slope of the relationship of E_D to L_T was also not significantly different between GB and GOM larvae at either temperature (ANCOVA; $F_{1,247} = 1.88$, $p = 0.172$), but a significant temperature and L_T interaction term (ANCOVA; $F_{1,247} = 11.76$, $p < 0.001$) was present (Fig. 3*a*). The slopes of the regression lines for M_H and L_T were significantly different (ANCOVA; $F_{1,246} = 6.56$, $p = 0.011$), and the analysis was conducted at each temperature. At 12°C, no significant difference in slopes (ANCOVA; $F_{1,132} = 0.02$, $p = 0.877$) or intercepts (ANCOVA; $F_{1,133} = 0.36$, $p = 0.550$) of the M_H and L_T relationship between GB and GOM larvae was found. There was a significant difference in slopes between the two populations at 7°C (ANCOVA; $F_{1,114} = 19.06$, $p < 0.001$) (Fig. 3*b*).

Developmental observations indicated that the yolk sac, representing the source of endogenous energy, was absorbed by all fish at 1 week of age. Similarly, all groups of larvae had inflated gas bladders by 1 week of age. However, only the GB larvae at 12°C had visible fin rays at 4 weeks post-

Fig. 2. Relationship of W_D to L_T of GB (circles) and GOM (triangles) Atlantic cod (at 6 weeks posthatch) reared under identical laboratory conditions at 7°C (solid symbols, solid line) and 12°C (open symbols, dotted line). Each symbol represents one fish larva. Regression equations: 12°C, ln W_D = –6.62 + 2.96 ln L_T ($p < 0.000001$, $r^2 = 0.92$); 7°C, ln W_D = –8.01 + 3.40 ln L_T ($p < 0.000001$, $r^2 = 0.85$).



hatch. These were present in the 12°C GOM larvae 1 week later.

Growth rates were compared from hatch (week 0) to week 4. Survival to week 4 was similar for all treatments and averaged 13% (range 7.3–15.0%). Data from week 4 to week 6 were not included in the growth rate analysis due to increased mortality after week 4, which resulted in substantially different densities among tanks. Fish at 12°C grew significantly faster than those at 7°C (ANCOVA; $F_{1,54}$ = 211.60, $p < 0.001$) (Fig. 4). GB larvae had significantly faster growth rates than GOM larvae at both temperatures (ANCOVA; $F_{1,54}$ = 25.00, $p < 0.001$) (Fig. 4).

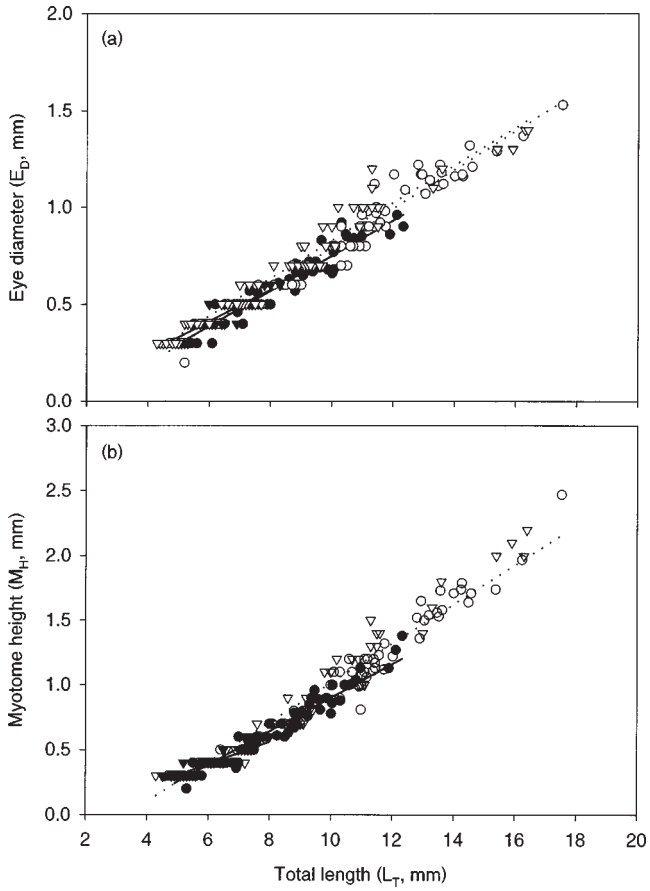
Juvenile experiment

Mortality was low in all groups (range 0–13%) and populations were not statistically compared. At warm temperatures, GSGR (ANOVA; $F_{1,24}$ = 291.44, $p < 0.001$) and GFCE (ANOVA; $F_{1,24}$ = 80.25, $p < 0.001$) were significantly higher than at ambient temperatures (Fig. 5). GSGRs were not significantly different for the two populations of cod at either temperature (ANOVA; $F_{1,24}$ = 1.72, p = 0.202) (Fig. 5*a*), but GB cod had significantly higher GFCE than GOM cod at both temperatures (ANOVA; $F_{1,24}$ = 11.74, p = 0.002) (Fig. 5*b*).

Discussion

In the larval experiment, although the slopes were similar, the relationship of W_D to length showed a higher intercept for Atlantic cod larvae reared at 12°C than at 7°C, indicating that larvae from both populations were heavier at length at

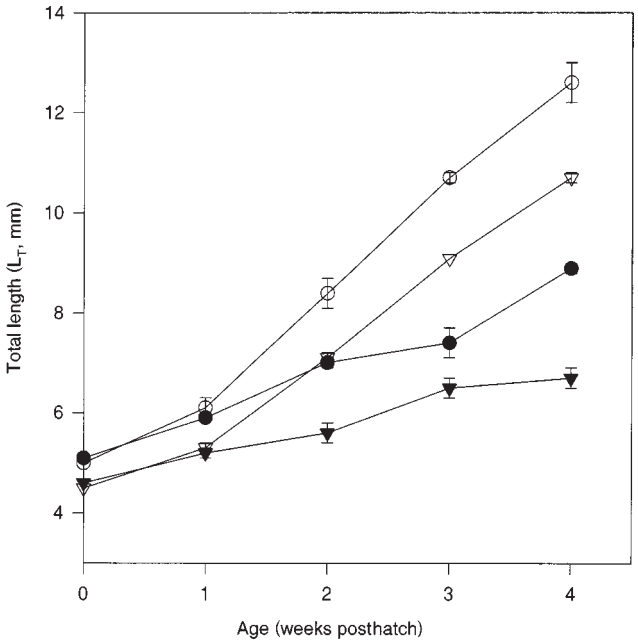
Fig. 3. Relationship of (*a*) E_D and (*b*) M_H to L_T of larval Atlantic cod from the GB (circles) and GOM (triangles) reared under identical laboratory conditions at 7°C (solid symbols, solid lines) and 12°C (open symbols, dotted lines). Each symbol represents one fish larva. All p values are <0.000001. Regression equations: (*a*) 12°C, GB, E_D = –0.20 + 0.10 L_T ($r^2 = 0.98$); 12°C, GOM, E_D = –0.18 + 0.10 L_T ($r^2 = 0.95$); 7°C, GB, E_D = –0.14 + 0.09 L_T ($r^2 = 0.94$); 7°C, GOM, E_D = –0.07 + 0.08 L_T ($r^2 = 0.79$); (*b*) 12°C, GB and GOM, M_H = –0.45 + 0.14 L_T ($r^2 = 0.95$); 7°C, GB, M_H = –0.31 + 0.11 L_T ($r^2 = 0.93$); 7°C, GOM, M_H = –0.09 + 0.08 L_T ($r^2 = 0.78$).



12°C. Therefore, in addition to faster growth in terms of length, the larvae had relatively higher energy reserves at 12°C. This suggests that cod larvae are able to acquire or assimilate energy more effectively at warmer temperatures (under unlimited food). The change in body proportions (E_D and body depth) with length differed between the two populations. The ecological significance of this result is unclear.

Larval and juvenile cod from both populations grew faster under warmer water temperatures. Faster growth at higher temperatures is well documented for larval and postlarval cod (e.g., Hunt von Herbing et al. 1996; Otterlei et al. 1999). Using commercial catch data for cod, Brander (1994) reported that from age 1 to age 4, each 1°C increase in environmental temperature results in a 29% increase in weight. In our study (larvae and young juveniles), after only 4 weeks, GB larvae were 71% longer and GOM larvae 67% longer at 12°C than at 7°C. This amounted to a 14.2% difference in length for each 1°C for GB larvae and a 12.6% difference

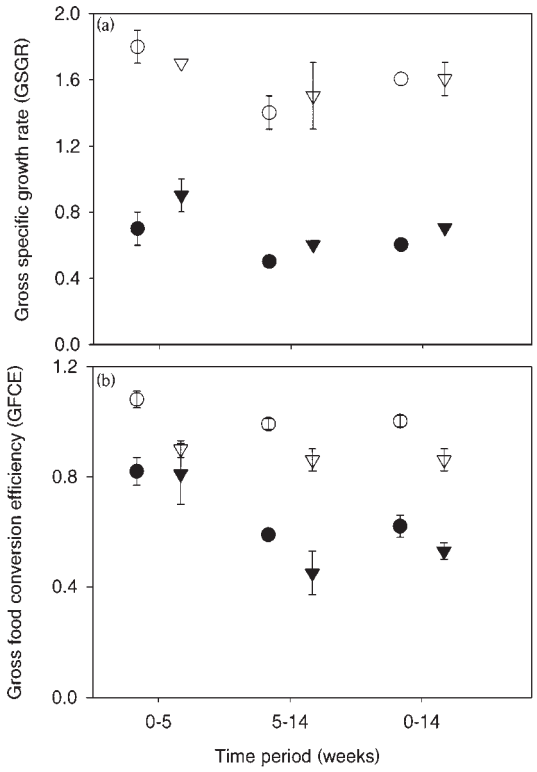
Fig. 4. L_T at age of GB (circles) and GOM (triangles) Atlantic cod reared under identical laboratory conditions at 7°C (solid symbols) and 12°C (open symbols). $N = 3$ (tank averages) per sample; vertical bars indicate standard error (may be smaller than the symbol).



for GOM larvae. At the start of the juvenile experiment, both temperature groups contained fish of equal average weight (7.5 g). The average weight of both populations at the end of the experiment was 13.7 g at ambient temperatures and 34.8 g at warm temperatures. This accounted for a 2.56-fold difference in weight after only 14 weeks. The warm temperatures totaled 1197 degree-days compared with 282 degree-days for the ambient temperatures. The result was a 2.3% increase in weight for every 100 degree-days.

In the wild, GOM cod grow faster than those on the GB (see Campana et al. 1995). The average weight of 4-year-old cod on Georges Bank (near the GOM) has been reported to be 3.47 kg, while on the southern GB, it is 0.85 kg (Brander 1994). In this study, at common temperatures, GB larvae grew faster than those from the GOM, while there was no difference in growth rates of juveniles from the two populations. The faster growth rate of larval GB cod may have been due to increased food consumption, increased food conversion efficiency, or both. Present and Conover (1992) found that both factors contributed to the increased growth of northern populations of larval Atlantic silverside (*Menidia menidia*). Food conversion efficiency was not measured in the larval experiment, but juvenile GB cod had better food conversion efficiencies than GOM cod in our study. Overall, GB cod had 1.2 times higher food conversion efficiencies than GOM cod. Better food conversion efficiency in a northern population was also found by Nicieza et al. (1994*a*) in Atlantic salmon (*Salmo salar*). They proposed that higher latitude populations may evolve improved food conversion efficiencies in order to better exploit periods when temperatures allow for rapid growth. Presumably, there are trade-offs associated with higher food conversion efficiencies; otherwise, one would expect all populations to show the highest possible.

Fig. 5. (*a*) GSGR and (*b*) GFCE of juvenile Atlantic cod from the GB (circles) and GOM (triangles) reared at warm (open symbols) and ambient temperatures (solid symbols). Each symbol is the mean of the tank means; error bars indicate standard error (may be smaller than the symbol).



The results suggest that genetically based population differences in the capacity for growth rates and food conversion efficiencies exist between GB and GOM cod. These results support those of molecular studies, which indicate genetic differences in neutral characters among cod stocks (Bentzen et al. 1996; Ruzzante et al. 1996). The fact that there seems to be genetic variation in highly selected traits, such as larval growth rates, suggests that ecologically important genetic differences exist between GB and GOM cod.

However, it is premature to conclude that population differences seen in this study are completely genetic in origin, for two reasons. First, gametes were collected from wild adults and parental effects (e.g., maternal investment) may have been present. Kjesbu (1989) reported that a single female cod may have eggs of different sizes from successive batches throughout a single spawning season. Therefore, one must be careful when relying on sizes of eggs to suggest individual variations in maternal investment. Gametes were collected during the peak spawning period on the GB but toward the end of the spawning season in the GOM. It is therefore possible that the GOM gametes may have been of lower quality than the stock average. GB larvae were larger at hatch than GOM larvae, which may have been a result of different egg sizes. Unfortunately, egg diameters were not measured. However, we feel that parental effects were unlikely to be the cause of the differences in growth rates in the larval experiment. Growth was compared well beyond the absorption of the yolk sac, an important maternal influence, and the size difference between the two populations

continued to increase with age. The analysis used to compare growth rates assumes linearity of growth. Growth rates varied from linearity (especially at 12°C), and thus, more variation was present in the model, reducing its statistical power. Even with this deceased ability to detect significant differences, the analysis indicated that GB larvae grew faster than GOM larvae. Furthermore, nongenetic effects are less likely to have persisted in the juvenile experiment, where there were still differences between the populations (also Purchase and Brown 2000). Second, the small sample size of adults contributing gametes in this study may not accurately represent the whole population. There were, however, seven possible crossings in the GB sample and 27 in the GOM sample.

Growth rates of both populations responded positively to temperature in our experiments, and GB larvae grew faster than GOM larvae at the same temperature. Therefore, the faster growth of wild GOM cod must arise from environmental differences between the two areas. The GOM experiences higher yearly average temperatures (50 m, 6.4°C) than the GB (50 m, 1.8°C) (deYoung et al. 1994). As expected in countergradient adaptation, the negative effect that colder temperatures on the GB have on growth of larval cod is reduced by their capacity for faster growth rates. Contrary to the countergradient variation hypothesis, the faster growth rate of GB larvae was more pronounced at the lower temperature (7°C). This may indicate that GB cod are better adapted to growth at low temperatures than GOM cod. Other studies also suggest greater capacities for growth rates from higher latitudes (or colder environments) in adult (Brander 1995), juvenile (Suthers and Sundby 1996), and larval cod (Hunt von Herbing et al. 1996; but see Svåsand et al. 1996; Otterlei et al. 1999). In temperature-controlled studies, faster growth rates in northern populations have also been found in other species of fish, including largemouth bass (*Micropterus salmoides*) (Williamson and Carmichael 1990), Atlantic salmon, (Nicieza et al. 1994*b*), and striped bass (*Morone saxatilis*) (Conover et al. 1997).

The disadvantages of small size are thought to select for countergradient variation; faster growing fish may outgrow potential predators. It is generally assumed that size-selective mortality is highest during the earliest periods of life, and therefore, it has been predicted that countergradient variation would be most significant in the larval stage (Conover 1992). This hypothesis has been supported in this study, as larval GB cod had higher capacities for growth rates than those from the GOM, but juveniles (same sibling group as larvae) had similar growth rates.

The results of this study support the findings of Hunt von Herbing et al. (1996), where larval Newfoundland cod grew faster than those from Nova Scotia. In their study, faster growth of Newfoundland cod was associated with a more developed intestinal tract than that of cod from Nova Scotia. This may have influenced growth rates and may explain the higher food conversion efficiencies of GB cod in our study. In both studies, the northern population outgrew the southern population, suggesting that northwest Atlantic cod larvae likely exhibit countergradient in growth rates.

In recent years, many cod stocks in the northwest Atlantic have been severely depleted, with the largest decline taking place off northeastern Newfoundland. If the observed growth rates in these studies are genetic in origin, and are representative of their respective populations, it could have significant implications for the recovery of cod stocks. The capacity for faster growth rates in larval cod from northern populations may indicate that cod from southern areas would not be effective at rebuilding stocks if they immigrated to the north. For example, larvae from southern populations might reach a smaller size at the end of the first growing season in northern environments, and size-selective winter mortality has been reported in many fish species (Shuter and Post 1990; Conover 1992). Thus, offspring of cod from southern areas may be less likely to survive in areas farther north. The capacity for faster growth in the northern population is also significant for the development of cod aquaculture. Traditionally, one would choose a stock with the fastest growth rates to culture. However, if countergradient variation is present, northern populations (possibly the slowest growing in their natural environment) may be the best suited for domestication (Williamson and Carmichael 1990).

In summary, the results of this study suggest that environmental factors in the northwest Atlantic that likely result in slower growth of cod in northern areas have also resulted in the evolution of higher maximum growth rates and better food conversion efficiencies in northern cod. Thus, there seem to be genetic differences among stocks in these highly selected traits, in accordance with observed genetic differences found by researchers using molecular techniques.

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