Persistent growth effects of temperature and photoperiod in Atlantic cod *Gadus morhua*

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Short-term environmental manipulations during the early juvenile stage have a large impact on harvesting size of Atlantic cod *Gadus morhua* nearly 3 years later. A group of juvenile Atlantic cod (initial mass 9·5 g) were reared for 3 months under simulated natural photoperiod or continuous light, and a range of temperatures (7, 10, 13 and 16° C, and a group called T-step, *i.e.* with temperature reduced successively from 16 to 13 and 10° C). After termination of the laboratory trial, the fish were moved to sea pens and reared at ambient conditions for 30 months before harvesting in June 2006. Observed growth gain from the 3 month laboratory trial was still persistent following the 30 months of sea-pen ongrowing. The T-step group displayed 15, 13, 1 and 10% superior mass gain respectively than the groups initially at 7, 10, 13 and 16° C at harvest in June 2006. Similarly, rearing under continuous light during the initial 3 month period during the early juvenile stage resulted in 1–9% larger size at harvesting compared to fish reared at simulated natural photoperiod. Gonado-somatic and hepato-somatic indices were similar in all groups. Contribution to the understanding of the mechanism behind size variation in adult fish can have wide range applications for Atlantic cod fisheries and aquaculture.

INTRODUCION

Many gadoids including Atlantic cod *Gadus morhua* L. experience a wide range of environmental conditions, including temperature and light conditions (Brander, 1995; Suthers & Sundby, 1999), in different parts of their distribution area. Variable and changing environmental conditions may affect growth and mortality and generate recruitment variability (Houde & Zastrow, 1993; Otterlei *et al.*, 1999; Buckley *et al.*, 2004; Baumann *et al.*, 2006). Positive

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correlations between increasing temperature and gadoid recruitment are usually found in cold northern waters, whereas negative relationships are observed in southern warmer waters and none found at intermediate temperatures (Planque & Frédou, 1999; Ottersen *et al.*, 2002; Buckley *et al.*, 2004). The relationship may also be seasonal as Baumann *et al.* (2006) found that the correlation between temperature and recruitment in Baltic Sea sprat *Sprattus sprattus* (L.) showed a clear seasonal trend with the strongest positive correlation found in August. Many attempts to relate recruitment variations to environmental conditions, however, have failed because of the interactions of covarying factors (*e.g.* fish size, temperature and food availability), which makes it difficult to disentangle such models and to evaluate the effect of each factor separately. Such attempts have also been criticized for the statistical approach because by scrutinizing many environmental factors one may ultimately find a relationship which is statistically significant due to chance alone, but probably spurious. One way to avoid this is to test these hypotheses under controlled and standardized environmental conditions in the laboratory and then track possible long-term effect when the fishes are reared under ambient conditions.

Variation in catch of the north-east Arctic cod (*G. morhua*) has always been large. Godo (2003) discussed three major causes of variation: (1) stock reduction through exploitation, (2) environmental influences on recruitment and (3) species interaction effects on maturation, growth and mortality. Godo (2003) used long-term time series to explain fluctuations in catch and stock abundance and compare those with changes in recruitment, size, age and growth. The analysis showed that substantial long-term variation might underlie short-term variability, and more importantly, that long-term changes roughly coincided with similar fluctuations in the environment. The current knowledge of short- and long-term effect of photoperiod and temperature on growth dynamics in early juvenile Atlantic cod and its interrelation with size and maturation incidence at harvest is inadequate. In wild populations of Atlantic cod, seasonal variations in growth rate have been demonstrated (Schwalme & Chouinard, 1999), although the changes caused by photoperiods *per se* are difficult to isolate from other concurrent changes in environmental factors such as temperature and food. Earlier studies have addressed the effect of continuous light on survival and growth of Atlantic cod larvae (Puvanendran & Brown, 2002), short-term effects on 1–2 g juveniles (Folkvord & Otterå, 1993) and on sexual maturation and growth of adult fish (Hansen *et al.*, 2001; Karlsen *et al.*, 2006; Taranger *et al.*, 2006). Whether, and how, environmentally related size enhancement within 0 year group of Atlantic cod is manifested in adult fish has previously not been studied.

To further study the interrelation between early stage environmental exposure and achievable size at harvest, individually tagged fish were reared at different environmental conditions during their first year, and then subsequently under identical conditions. This allowed size variation in adult fish to be retraced its original sources. Hence, the purpose of this study was to investigate the possible long-term effect of rearing juvenile Atlantic cod at different temperatures and photoperiods during the juvenile stage on growth and maturation of fish at harvesting size.

MATERIALS AND METHODS

FISH MATERIAL AND REARING CONDITIONS

The broodfish were caught wild in the area around Bømlo (western Norway; 59°50′ N; 5°10′ E) in 2003 and reared in 40 m^3 tanks at simulated natural photoperiod and temperature of 6–8° C (sea water pumped from 160 m depth). The mean mass of the broodfish was *c.* 7 kg (range 5–18 kg). The eggs hatched on 28 March and the larvae were subsequently transferred to a 500 l tank with a constant temperature of 7·8° C. The larvae were reared under continuous light, fed fresh filtered natural zooplankton (gradually increasing size fraction from 80 to 1000 μm) and weaned on a commercial formulated feed (Marin 030 and 050; Ewos AS, Bergen, Norway) containing 60% protein, 12% fat and 12% carbohydrates. On 20 June 2003, the juveniles were brought to the Industrial and Aquatic Laboratory at the Bergen High Technology Centre and reared at 10° C and simulated natural photoperiod (60° N) until the start of the study.

The fish were distributed randomly into 16 experimental tanks. The 1 m^2 square, grey, covered fibreglass experimental tanks had a rearing volume of 400 l and a bottom outlet. Sea water with a salinity of 33·5, range ± 0·2, was pumped from 90 m depth. Water flow was set to 10 l min^{-1} for all experimental tanks. Oxygen saturation was measured weekly in the effluent (*i.e.* bottom outlet) water of all tanks and was >80% on each occasion. A 36 W fluorescent daylight tube integrated in the tank-cover provided light. Photon irradiation measured at the bottom of the tanks was *c.* 5 μmol m^{-2} s^{-1}. Both during the acclimation period and the experiment, the juveniles were fed a commercial dry diet (Marin 10 and 20; Ewos AS; 55% protein, 12% fat and 11% carbohydrate; gross digestible energy 20·4 MJ kg^{-1}). Feed was provided in excess for 2 h daily (0800–0900 and 1400–1500 hours). Pellet size (2 and 3 mm) was adjusted during the experiment, depending on fish size, with an introduction of 3 mm pellets from 14 October.

LABORATORY STUDY

The laboratory growth study was carried out from 8 September until 12 December 2003. On 25 August 2003, in preparation for the study, a sub-group within each tank (n = 18–30 in each tank, n_{total} = 224) were tagged intraperitoneally with Trovan® passive transponder tags, and gradually acclimated over 1 (7 and 13° C) or 2 days (16° C) or kept at 10° C. At three temperatures, *i.e.* 7, 10 and 13° C one group was exposed to simulated natural photoperiod for Bergen (60°25′ N) generated by a computer programme, including twilight periods, whereas the other group was exposed to continuous light. Each photoperiod and temperature regime consisted of two replicate tanks. The group reared at 16° C and at stepwise temperature were only exposed to natural photoperiod. The stepwise declining temperature regime (T-step) was as follows: 16° C from 9 September to 7 October, 13° C from 8 October to 19 November and 10° C from 20 November to 12 December. This group was supposed to mimic temperature conditions found in Norwegian waters in late summer and autumn (Anon., 2005). The mean rearing temperature in this group was 13·2° C. The temperature in all groups was measured twice daily, and remained within ± 0·2° C (s.d.) of that prescribed. A detailed description of the growth and feed utilization during the laboratory trial can be found in Imsland *et al.* (2005, 2006). As the two-way experimental set up (*i.e.* temperature and photoperiods) contains missing blocks (*i.e.* continuous light at 16° C and T-step) results are presented separately for the temperature part (all five temperatures) and the photoperiod period (7, 10 and 13° C reared at natural photoperiod and continuous light). But it must be stressed all presented data come from a single laboratory trial.

LONG-TERM STUDY

After termination of the laboratory trial, all individually tagged fish were acclimated to 10° C and transported by lorry on 15 January 2004 to the production site of Marine

Harvest at Tustna (western Norway, 63°08′ N). Here, the fish were held in land-based open tanks (8 m diameter, 85 m^3) with a mean temperature of 9° C and reared under natural photoperiod until 25 May 2004 when they were transferred to a sea-pen (40 m in diameter, 7 m deep, 1000 m^3 in volume) at Smøla (western Norway, 63°31′ N). Here, the fish were reared at ambient temperatures (range mean temperatures, maximum 15° C in August, minimum 5° C in March) and natural photoperiod (no additional light), together with an additional 7500 other (untagged) Atlantic cod. Mean mass at start (all fish) was 172 g. The fish were hand-fed five times a week using a commercial formulated feed, Dan-Ex 1562, containing 15% fat and 58% protein (Dana Feed, Horsens, Denmark). From August 2005 the fish were reared at continuous light, with light intensity of 5·6 W m^{-2} sea-pen surface, by using two 1000 W lamps and two 100 W blue diode light (Idema Aqua AS, Haslum, Norway) on 5 m depth in the sea pens.

DATA ANALYSIS AND STATISTICAL METHODS

All fish were anaesthetized (metacain, 0·05 g l^{-1}), weighed (M) individually to the nearest 0·1 g at start and at termination of the laboratory experiment (after 95 days). On 29 May 2005, the mass of 82 tagged fish from the laboratory study was measured, and on 16 June 2006 M, gonad (M_G) and liver (M_L) masses of 147 tagged fish from the laboratory study were measured. Analysed fish during the sea-pen trial were randomly chosen as only a part of all the fish in the sea-pen were weighed. Specific growth rate (G) was calculated according to the formula: $G = 100 (e^g - 1)$, where $g = (\ln M_2 - \ln M_1) (t_2 - t_1)^{-1}$ and M_2 and M_1 is wet mass (g) at days t_2 and t_1, respectively. The liver index (hepato-somatic index, I_L) was calculated as: $I_L = 100 M_L M^{-1}$. The gonado-somatic index (I_G) was calculated as: $I_G = 100 M_G M^{-1}$.

In the laboratory trial, a nested ANOVA (where the replicates are nested within the experimental variables) was applied to calculate the effect of different temperatures (two-way nested ANOVA) and photoperiods and temperatures (three-way nested ANOVA) on mean masses. Significant ANOVAs were followed by a Student–Newman–Keuls multiple comparison test to locate differences among treatments (Zar, 1984). For mass, I_G and I_L data of fish in the sea-pen a one-way ANOVA was applied, followed by a Tukey HSD unequal N-test to locate differences among groups as the number of fish was unequal between the groups. Individual growth (G) trajectories were analysed using a growth curve analysis model (GCM; Chambers & Miller, 1995), which is an extension of the multivariate repeated measurements analysis of variance (MANOVA) model. The model equation of the GCM for the temperature data had the form:

$$\boldsymbol{Y}(n \times p) = \boldsymbol{X}(n \times q)\boldsymbol{B}(q \times p) + \boldsymbol{E}(n \times p)$$

where $\boldsymbol{Y}(n \times p)$ are the growth at age vectors $\boldsymbol{y} = (y_1, y_2, \ldots, y_p)$ for each p (age) measurements on n individual fish, $\boldsymbol{X}(n \times q)$ is the design matrix or the set of extraneous variables measured for each individual, *i.e.* $q = \text{age}_p + \text{temperature}_i$; ($i = 7$, 10, 13, 16° C and T-step); $\boldsymbol{B}(q \times p)$ is the matrix of parameters estimated by the model and $\boldsymbol{E}(n \times p)$ is the matrix of deviations for each individual from the expected value of $\boldsymbol{Y} = \boldsymbol{XB}$.

For the photoperiod data, the model equation is the same apart from $i = $ natural photoperiod and continuous light.

RESULTS

SHORT-TERM EFFECT OF TEMPERATURE AND PHOTOPERIOD ON GROWTH

The overall initial mean mass ± S.D. was 9·5 ± 2·7 g and did not differ [three-way nested ANOVA, power $(1 - \beta) > 0·7$; Figs 1 and 2] between the
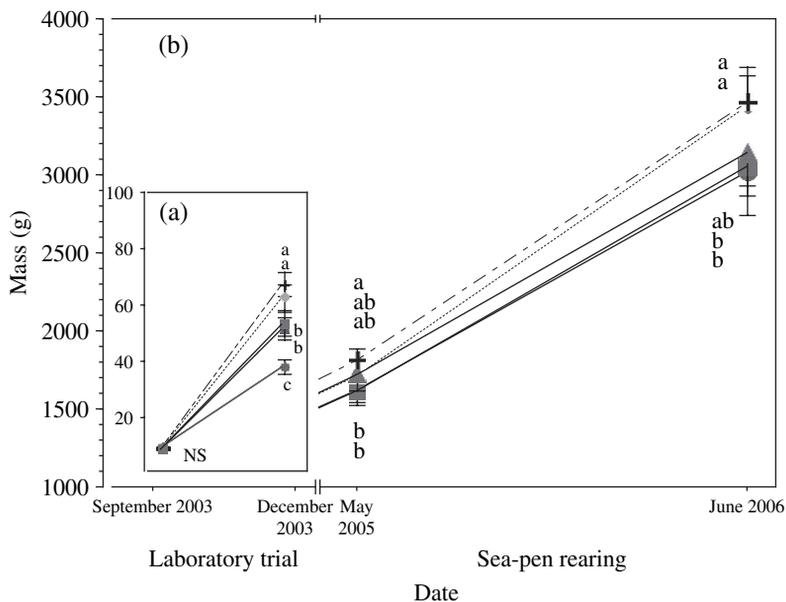
FIG. 1. Mean ± S.E.M. total body mass for individually tagged Atlantic cod reared at five different temperatures [7 (–●–), 10 (–■–), 13 (--◇--) and 16 (--△--) ° C, and T-step (--+--)] (a) for 95 days during the early juvenile period and (b) then reared at ambient conditions in sea pens for 914 days. Mean mass information is pooled for the sexes. Different lower case letters indicate statistical differences (one-way ANOVA, $P < 0.05$) between the experimental groups, with 'a' as the highest value; $n = 9$–42 for each mean value; NS, not significant.

temperature and photoperiod groups. At termination of the laboratory trial mean masses of the temperature groups (Fig. 1) differed significantly, as the final mean masses of the T-step and 13° C groups were between 18 and 22% higher than those of the other temperature groups. Significant differences were also found at the termination of the photoperiod trial (Fig. 2), the final mean masses in December 2003 of the continuous light groups at 13 and 10° C were 15 and 11% higher than those of the natural photoperiod group, whereas no difference was found at 7° C. The relative difference between mean mass at natural photoperiod and continuous light was similar at all temperatures. Hence, no significant interaction between temperature and photoperiod on size was found (two-way ANOVA, $P > 0.05$).

LONG-TERM EFFECT OF TEMPERATURE AND PHOTOPERIOD ON GROWTH AND MATURATION

There was a positive correlation between the size at the end of the laboratory trial and size at harvest 30 months later ($0.21 < r < 0.33$, $P < 0.05$). Mean individual growth trajectories were different (GCM, MANOVA$_{temperature}$, Wilk's $\Lambda_{20,280} = 0.25$, $P < 0.001$) between the five temperatures. Significant differences were also found in growth-at-age trajectories of the experimental groups (MANOVA$_{temperature \times age}$, Wilk's $\Lambda_{16,242} = 0.28$, $P < 0.001$) from early September 2003 to June 2006. The mean mass of fish reared at different
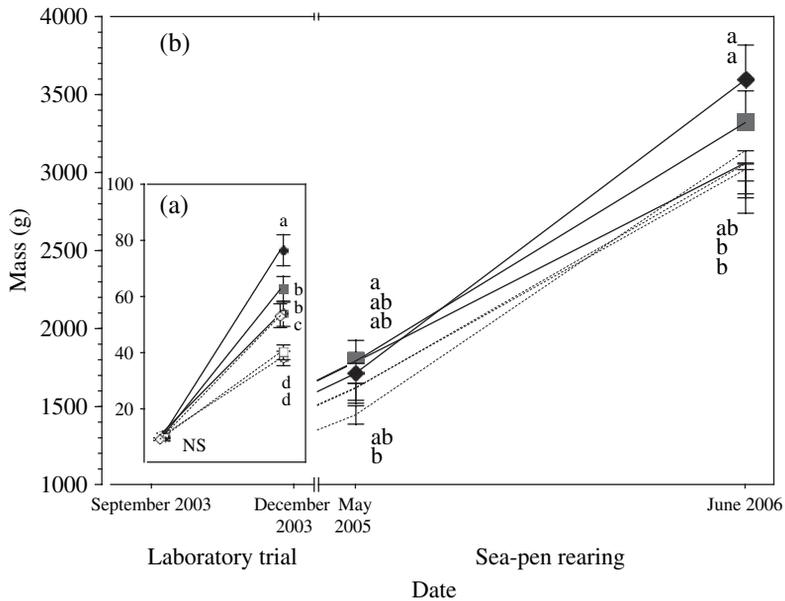
FIG. 2. Mean ± S.E.M. total body mass for individually tagged Atlantic cod reared at different photoperiods [natural photoperiod (- -, ○, □, ◇) and continuous light (——, ●, ■, ◆)] and temperatures [7 (○, ●), 10 (□, ■) and 13 (◇, ◆) ° C] (a) for 95 days during the early juvenile period and (b) then reared at ambient light and temperature conditions in sea pens for 914 days. Mean mass information given is pooled for the sexes. Different lower case letters indicate statistical differences (one-way ANOVA, $P < 0.05$) between the experimental groups, with 'a' as the highest value; $n = 9$–32 for each mean value; NS, not significant.

temperatures during the early juvenile stage differed after 30 months of open tanks on land and sea-pen rearing at ambient conditions (Tukey HSD unequal N-test, $P < 0.05$; Fig. 1). On 16 June 2006, the mean mass of the T-step fish was largest (3·48 kg, $n = 20$), followed by the 13° C fish (3·44 kg, $n = 22$), the 16° C (3·14 kg, $n = 15$), the 10° C (3·05 kg, $n = 11$), and with the smallest fish from the 7° C group (2·90 kg, $n = 21$).

Mean individual growth trajectories of fish reared at different photoperiods during the early juvenile stage were different (GCM, MANOVA$_{photoperiod}$, Wilk's $\Lambda_{5,136} = 0.77$, $P < 0.001$). Significant differences were also found in growth-at-age trajectories of the experimental groups (MANOVA$_{photoperiod \times age}$, Wilk's $\Lambda_{4,137} = 0.80$, $P < 0.001$) from early September 2003 to June 2006. Similarly, the mean mass of fish reared at different photoperiods and temperatures during the early juvenile stages differed following 30 months rearing period under ambient sea conditions (Tukey HSD unequal N test, $P < 0.05$; Fig. 2). On 16 June 2005, the mean masses of the fish previously reared on continuous light ($n = 58$) were between 5 and 9% larger than fish reared at simulated natural photoperiod ($n = 54$) during early juvenile period. The relative difference between mean masses of the groups reared at different photoperiods in the short-term laboratory trial did not vary between the temperatures in May 2005 or June 2006. Hence, no significant interaction between temperature and photoperiod on size was found (two-way ANOVA, $P > 0.05$).

Male I_G and I_L did not vary among groups (Figs 3 and 4), whereas for females, there was a stepwise increase in I_G with temperature, apart from the 7° C group [Fig. 3(a)]. A similar trend of higher I_G in the best growing and largest fish was found in the females reared at different photoperiods during the juvenile period, as fish initially reared under constant light had a 15% higher I_G [Fig. 4(a)]. For the I_L, no systematic trend was seen for the females in either trial, although I_L was slightly higher in fish reared at simulated natural photoperiod during the early juvenile period [Fig. 4(b)]. No interaction effects between previous temperature and photoperiod rearing regimes on I_G or I_L levels were found in either sex ($P > 0.05$).

DISCUSSION

The data show that early environmental manipulation can have a long-term effect on growth in Atlantic cod, whereas the effect on maturation was limited. Although the experimental interval encompasses only a brief period of the life cycle, growth differences persist throughout the entire juvenile period up to adult sizes. Differences in size have been shown to persist in groups of wild
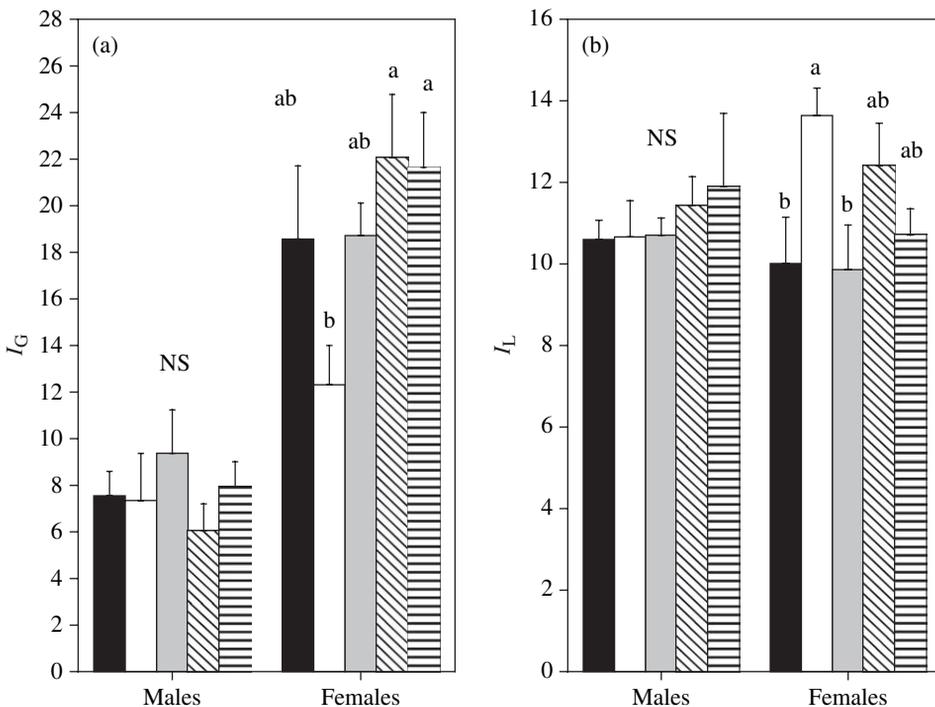

FIG. 3. Mean ± S.E.M. (a) gonado-somatic (I_G) and (b) hepato-somatic (I_L) indices for individually tagged Atlantic cod reared at five different temperatures [7 (■), 10 (□), 13 (▨) and 16 (◩), and T-step (▤)] for 95 days during early juvenile period and then reared at ambient conditions in sea pens for 914 days. Different lower case letters indicate statistical differences (one-way ANOVA, $P < 0.05$) between the experimental groups, with 'a' as the highest value; $n = 9–42$ for each mean value; NS, not significant.
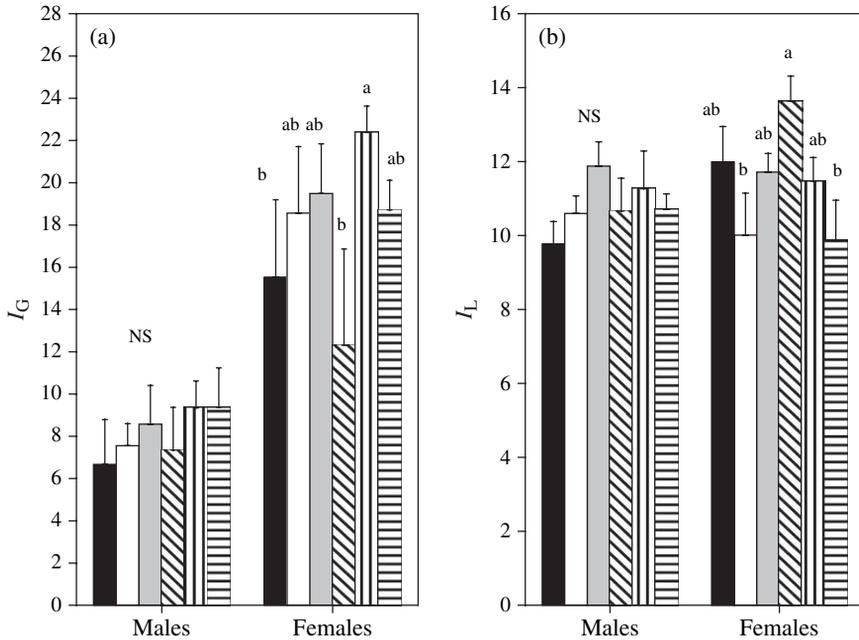
FIG. 4. Mean ± S.E.M. (a) gonado-somatic (I_G) (a) and (b) hepato-somatic (I_L) indices for individually tagged Atlantic cod reared at different photoperiods and temperatures [7° C and continuous light (■), 7° C and natural photoperiod (□), 10° C and continuous light (▨), 10° C and natural photoperiod (◩), 13° C and continuous light (▥) and 13° C and natural photoperiod (▤)] for 95 days during the early juvenile period and then reared at ambient light and temperature conditions in sea pens for 914 days. Different lower case letters indicate statistical differences (one-way ANOVA, $P < 0.05$) between the experimental groups, with 'a' as the highest value; $n = 9$–32 for each mean value; NS, not significant.

fishes during short growth trials, *e.g. Menidia menidia* (L.) (Billerbeck *et al.*, 2000) and *Menidia peninsulae* (Goode & Bean), Yamahira & Conover, 2003, whereas this is first experimental study where growth persistence is studied on an individual level for nearly 3 years. These findings have both practical and theoretical implications. From a theoretical viewpoint, the data could be incorporated into contemporary recruitment models. It is important to gain better insight into the factors that govern size variation as variations in fish sizes within a population can have dramatic effects on the dynamics of a cohort (Chambers & Leggett, 1992; Rice *et al.*, 1993). The study shows that initial size difference is an important variable to include in recruitment models, as this can help to explain both short- and long-term size variability within a specific cohort. Long-term size correlations were found as size at termination of laboratory trial was positively correlated with size at harvest in all groups. Such long-term correlations have, as far as is known, not been reported for Atlantic cod before. Size correlations between year-classes have been observed for wild juvenile north-east Arctic cod where significant size correlations are documented between year-classes, and the basis for these relative size differences are formed during the first half year of life (Ottersen *et al.*, 2002). The long-term

correlation after 2·5 years (914 days) between initial and harvesting size seen here, however, surpasses those found in earlier studies. Short-term correlations between initial and final mass have also been shown in Atlantic cod larvae (Suthers *et al.*, 1999). Using otolith microstructure to study the growth history, Suthers *et al.* (1999) found that final mass at 42 days post-hatch (Ph) was related to growth rates from 4 weeks Ph and onwards. A long-term (534 days) effect in line with present findings was reported by Imsland *et al.* (1997). They reared juvenile turbot *Psetta maxima* (L.) at three different photoperiods: continuous light, 16L:8D and natural photoperiod for 5 months, and then pooled the fish and reared at natural photoperiod for 12 months. This is in line with the present findings as growth promoting effect of continuous light was found, and this effect persisted over time. In contrast with the present findings, however, Imsland *et al.* (1997) found lower maturation in female turbot reared at extended photoperiods during the early juvenile period.

A finding in this study that could have an important practical implication for the aquaculture sector is the advantage of rearing the fish at optimal temperatures and at continuous light during the juvenile period as size differences established at this stage may be maintained in the adult fish. Similar findings have been observed for wild juvenile north-east Arctic cod where significant size correlations are documented between year-classes and the basis for these relative size differences are formed during the first half year of life (Ottersen *et al.*, 2002). In the present study, the tagged fish were acclimatized to 10° C before transport to commercial ongrowing in north-west Norway, and moved to sea pens when sea temperature was *c*. 7° C. Size differences after 17 and 30 months in sea pens were slightly reduced, but the general picture was that differences in the juvenile stage can be traced throughout the adult stage. This long-term growth effect could have a positive effect on commercial aquaculture of Atlantic cod. By applying optimal combinations of temperatures and photoperiods during the juvenile phase in land-based farms, the farmer may be able to produce more biomass on a given time scale of a commercial size fish.

In contrast to the present data, Sæther (2005) indicated that moving juvenile Atlantic cod from different rearing temperatures (between 8 and 15° C) to low (3° C) temperature will lead to growth reduction in all groups and obliterate the short-term gain of rearing juvenile Atlantic cod at elevated temperatures. In the present study, the tagged fish were acclimatized to 10° C before transport to commercial ongrowing in western Norway, and moved to sea pens in May when sea temperature was *c*. 9° C. Size differences after 30 months rearing under commercial scale conditions were slightly reduced, but the general picture was that differences in the juvenile stage can be traced throughout the adult stage. It is possible that the short duration of rearing at different temperatures (4 weeks) and the abrupt acclimation to very low temperatures in the study of Sæther (2005) may explain the disparity between the two studies. The changes that occur during thermal acclimation involve a series of adaptations at the enzymatic level that may lead to higher feed efficiency. There is some evidence that downward thermal acclimation (*i.e.* moving fishes from higher to lower temperature) may result in increased activities in enzymes involved in aerobic energy liberation and ion transport in muscle (Jobling, 1994) and increased digestive enzyme activity (Kuzmina *et al.*, 2003). Optimal temperature

for enzymatic activity can vary with size (Luczkovich & Stellwag, 1993). Accordingly, the fish in the T-step group in the present trial may have been reared closer to optimal temperatures for enzymatic activity during the early juvenile period than the fish in the constant temperature groups. Imsland *et al.* (2006) showed that feed conversion efficiency (E_c) was improved in line with reduced temperature in the T-step group. E_c increased from 1·0 to 1·2 to 1·35 when Atlantic cod were reared at 16, 13 and 10° C, respectively. In contrast, E_c remained stable throughout the trial in the other temperature groups (Imsland *et al.*, 2006).

Many fish species thermoregulate behaviourally through natural behaviour, *i.e.* seek out a temperature close to their optimal temperature for growth (Zinichev & Zotin, 1987; Hill & Magnuson, 1990; Wildhaber & Crowder, 1990). For several fish species, the final preferendum temperatures are suggested to coincide with the optimal temperature for growth (McCauley & Huggins, 1979) or alternatively near the optimal temperature for feed conversion efficiency (Larsson, 2005). The current study and the study of Imsland *et al.* (2006) have clearly shown that environmental related growth differences in 0 year group of Atlantic cod are mirrored in size differences at harvesting several years later. The effect is most profound at near-optimal temperature (13° C) and at a stepwise declining temperature, mimicking ontogenetic changes in optimal temperature for growth. If these findings are converted to stock level this means that maximum recruitment and biomass of a given Atlantic cod stock will tend to occur in temperature conditions near the stocks optimal temperature for growth and feed conversion efficiency. The global warming that is widely expected to occur over this century will not be confined to the atmosphere; the oceans would also get warmer (Hannesson, 2007). Over the next 50 years, temperatures in the north-east Atlantic, and especially the Barents Sea, are expected to rise by 1–3° C (Hannesson, 2007). In the light of the present findings such temperature change would indicate displacement of Atlantic cod catches, or alternatively that catches might increase in areas with more optimum temperature conditions as a result of temperature rise. Indeed, time series from Norway show that here is strong evidence that the catches of Atlantic cod in the North Sea are influenced by variations in temperature, with lower temperatures leading to increased catches and *vice versa* (Hannesson, 2007; Stenevik & Sundby, 2007). In contrast, the recruitment and catches of north-east Arctic cod was found to respond favourably to rises in temperature in the Norwegian Sea. The present findings of long-term environmental effect on size in adult Atlantic cod may help to understand and predict the threats and impacts of global warming on recruitment level and status of Atlantic cod stocks.

In conclusion, the present study shows that environmental related growth differences in 0 year group of Atlantic cod are mirrored in size differences at harvesting several years later. These findings will increase the understanding of size variation in natural and cultured stocks of Atlantic cod. Better understanding of the mechanism behind size variation can have wide range applications for fisheries and culture of the species.

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