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Growth histories derived from otolith microstructure of three Norwegian cod stocks co-reared in mesocosms; effect of initial size and prey size changes

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Specific growth rates and survival were not significantly different among the pelagic juveniles of three electrophoretically distinguishable stocks of Norwegian cod (*Gadus morhua*), co-reared in four replicate 5.2 m^3 mesocosms, from hatch to day 38 or day 43 post-hatch. Arcto-Norwegian cod (AC, the main commercial cod stock which spawn in Lofoten and are distributed in the Barents Sea, mostly north of 70°N), were compared with a nearby coastal stock (Balsfjord cod, BC – from a fjord near Tromsø at 69°30′N), and a more southern coastal cod stock (CC, from near Bergen at 60°N). The increment width series of the lapillus – otolith growth history – and the relative daily growth rate were not significantly different among stocks within any mesocosm. Although AC larvae were larger, being derived from larger brood stock, they did not exhibit consistently greater otolith growth during the experiment. Larger size at harvest was correlated with growth during the latter part of rearing (>fourth week), which is when most differences in size at age are generated. Decreases in daily increment widths occurred in all stocks within 1–2 days, when the zooplankton food supply was changed from nauplii and copepodites to adult copepods, and when the average AC cod began to exhibit greater daily growth. Increment widths of reared AC cod at 37 days post hatch (>8 μm) were 2–3 times greater, and ontogenetically more variable than those of similar sized cod previously sampled from the Barents Sea (3–4 μm). Average otolith growth histories of pelagic juvenile cod reveal a substantial range in growth potential that is not apparent from more conservative comparisons of weight, and reveal a temporal sensitivity useful for the assessment of environmental fluctuations in the rearing process.

Key words: otolith, growth history, larval cod, electrophoresis, stocks, mesocosm, rearing, feeding.

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Introduction

Genetic studies of cod, *Gadus morhua*, in Norwegian waters have revealed a mosaic of stocks within the coastal cod group (Møller, 1968; Jørstad and Nævdal, 1989), which are also genetically distinct from the major, commercial stock – the Arcto-Norwegian cod (Møller, 1966; Dahle and Jørstad, 1993; Fevolden and Pogson, 1995, 1996). Differences among these stocks in larval growth and survival are of prime concern for determining the relative influence of prey abundance, prey size, and day length, and for aquaculture and sea ranching research. The examination of such processes has been facilitated by rearing different broods of young cod in mesocosms and enclosed ponds (e.g. Pedersen *et al.*, 1989; Blom *et al.*, 1991; Olsen *et al.*, 1991; van der Meeren and Næss, 1993; Folkvord *et al.*, 1994), in an attempt to simulate their environment at sea, while controlling for predation or temperature. Some of these stocks exhibit differences in larval growth, but the results

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have largely been equivocal (Gamble and Houde 1984; Jørstad and Nævdal, 1994; van der Meeren *et al.*, 1994), partly because the differences were often specific to each replicate mesocosm or because there were age differences within the comparisons. Also, when ration is constant, variable survival within an enclosure may change the relative prey availability per larva, which may account for growth differences (van der Meeren *et al.*, 1994).

The development of a genetically marked strain derived from wild coastal cod in western Norway (Jørstad *et al.*, 1987; Jørstad *et al.*, 1991) has enabled different stocks to be reared within the same enclosure, ensuring that the stock comparisons are made under the environmental conditions prevailing within each mesocosm.

The relative survival and growth of each stock is usually measured at the termination of the experiment, but the individual daily growth trajectory is unknown. The growth history of each individual fish, as indicated by the width of daily growth increments, can indicate events or dates during each larva's early life history that influenced the otolith growth rate, e.g. metamorphosis (Campana and Neilson, 1985). Numerous studies have shown how the increment width series in the larval and pelagic juvenile stages is influenced by temperature and/or prey abundance (e.g. Govoni *et al.*, 1985; Bailey, 1989; Campana and Hurley, 1989; Karakiri *et al.*, 1989; Hovenkamp, 1990; Suthers, 1996), as well as by storms and turbulence (Maillet and Checkley, 1991; Gallego *et al.*, 1996) and even dissolved oxygen (Sepúlveda, 1994). Suthers and Sundby (1993) showed how the increment widths of pelagic juvenile cod raised in a mesocosm decreased by about 20% during the transition from natural zooplankton prey to dry feed.

We compared the increment width series of the Arcto-Norwegian cod (AC, or Northeast Arctic cod) and two coastal cod stocks, co-reared within four replicate mesocosms. Since the growth rate of wild AC pelagic juvenile cod is almost twice that of similar stage Canadian cod (Suthers and Sundby, 1996), we wished to determine if the otolith growth history of AC stock differs from that of a nearby coastal stock, and a more southern coastal stock, when raised within the same mesocosm. We also examined the average daily growth histories for any critical times or events in the rearing procedure, and in relation to their final size at harvest, and in relation to those of wild cod.

Materials and methods

Brood stock and genetic identification of offspring

At the Institute of Marine Research, Austevoll Aquaculture Research Station (Norwegian west coast, 60°N), a genetically tagged broodstock of local coastal cod (CC), developed in the late 1980s (Jørstad *et al.*, 1991), has been used in a variety of controlled experiments (Blom *et al.*, 1994; Svåsand *et al.*, 1996) and release studies (Jørstad *et al.*, 1994). Other cod broodstocks such as Arcto-Norwegian cod (AC, spawning in Lofoten at 68–69°N), and coastal cod from Balsfjord (BC, situated at 69°30′N) have also been established at Austevoll. All the potential broodstock fish have been individually tagged and biopsy samples of white muscle have been analysed for a number of polymorphic enzymes (see references above).

Offspring from three different broodstocks were used. The genetically marked coastal cod were GPI-1*30/30 homozygotes and originated from the CC stock in the Austevoll region (Jørstad *et al.*, 1991). Broodstock of both sexes (232 individuals: 117 females of average 3.8 kg) from this strain were transferred to a separate 175 m^3 plastic bag enclosure and allowed to spawn naturally (Huse and Jensen, 1983; Holm and Andersen, 1989).

To distinguish between AC and BC stocks, the *LDH-3** system was used. Only genotype *LDH-3*70/70* for both sexes were selected from the AC stock, and for the BC stock only individuals of genotype *LDH-3*100/100* were selected. The selected fish were transferred to spawn in separate (20 m^3) plastic bags, one for AC (11 individuals: five females of average 10.6 kg) and one for BC (13 individuals: five females of average 2.7 kg). The number of broodstock in the AC and BC groups were low, and when two AC females died before egg collection two AC females of genotype *LDH-3*70/100* were added to the spawning pen. With only males of genotype *70/70*, offspring from crosses from these females would be of *70/70* (50%) and *70/100* (50%), which can be distinguished from offspring from the BC strain (*100/100*).

A control sample of cod larvae from the CC spawning pen demonstrated that some additional spawners had been mixed with the genetically marked fish of genotype *GPI-1*30/30*. The analyses showed that 13% of the offspring from this pen were of other *GPI-1** genotypes, mainly other heterozygotes for the rare allele **30*. Based on the control sample and the genotype distributions for the two loci used, it was possible to identify those individuals belonging to the CC stock in the offspring mixture where all three stocks were represented. Only one of 575 sampled individuals from the experimental bags could not be identified to stock origin.

Fertilized eggs were collected in parallel from all three spawning systems, and the eggs were incubated separately for hatching. After hatching, larvae from each stock were mixed and transferred to each of four plastic bag enclosures (mesocosms) for comparisons of all three strains in the same mesocosm.

Mesocosm rearing system

The experiments were carried out at Austevoll Aquaculture Research Station. Cod larvae were reared in 5.2 m^3 enclosures of black three-layer woven PEL plastic, supported by a floating PEH plastic ring tied to a raft system (van der Meeren *et al.*, 1994). The four mesocosms were sited in a 20 000 m^3 seawater pond used for zooplankton production and temperature stabilization (Naas *et al.*, 1991). The enclosures were initially filled with seawater collected from the fjord outside the pond, and filtered through 80 µm plankton net by a UNIK 900 wheel filter (van der Meeren, 1991a). This water was also used for renewal in the bags, entering the cone bottom through a flexible tube. A daily exchange rate of approximately 7–10% was used for the first 10 days after larval stocking, after which it was increased gradually to 50% per day after day 35 post-hatch. Temperature, oxygen saturation, and salinity were measured at two depths (0.5 and 2.5 m) in two of the enclosures throughout the experiments. Light could not penetrate the plastic wall of the enclosures. Thus, the enclosures were equally illuminated from above by natural light. For analysis, temperature data were used from the water intake pipe to the mesocosms, and light levels were recorded by the Meteorological Institute in Bergen as global radiation (both sky and indirect, MJ m^{-2}), expressed here as the number of hours of sunlight.

The four mesocosms are referred to hereafter as Bags 1, 2, 3, and 4. Into each were released exactly 300 larvae of each stock (i.e. 900 larvae per bag). Bag 1 contained larvae that hatched on 13 April 1994 while Bags 2, 3, and 4 contained larvae from a separate brood hatched on 18 April 1994. All mesocosms were harvested on 26 May, resulting in 38-day-old larvae in Bags 2, 3, 4 and 43-day-old larvae in Bag 1. Subsequent references to age (Day) are in terms of post-hatch.

Zooplankton, mainly nauplii, juvenile, and adult stages of the copepod *Eurytemora affinis*, was collected from the pond by a UNIK 900 wheel filter placed on the raft system (van der Meeren, 1991a; van der Meeren and Naas 1997). The filter concentrated plankton retained on plankton nets of 80 and 250 µm mesh sizes. The 80–250 µm fraction was further filtered through plankton nets of either 120 µm (before Day 5 in Bag 1 and before Day 8 in Bags 2, 3, 4), or 150 µm (Day 6–17 in Bag 1 and Day 10–12 in Bags 2, 3, 4), and the filtrate fed to the larvae. The >250 µm fraction was additionally used after Day 23 (Bag 1) and Day 26 (Bags 2, 3, 4) .

The replicate Bags 2, 3, and 4 received equal daily rations. Feeding was calculated from a theoretical energy model for turbot larvae (van der Meeren, 1991b), with substitution of respiration values for cod (Laurence, 1978). An average specific growth rate of 15% D^{-1} (weight) was used in the calculations. The plankton were counted and categorised into three groups: copepod nauplii, copepodites, and copepods. To simplify the feeding procedure, average values for energy content of typical sizes of the different plankton groups were used. These were 0.0054, 0.037, and 0.259 J ind^{-1} for nauplii, copepodites, and copepods, respectively (calculated from Böttger and Schnack, 1986; Blom *et al.*, 1991; van der Meeren, 1991b).

Treatment of post-larvae at harvest

Each mesocosm was drained, and the surviving cod were counted. A subsample of 143 or 144 cod individuals from each mesocosm was weighed (wet weight to the nearest 0.1 g), numbered and frozen for genetic identification (Table 1). Before freezing, the heads were preserved in alcohol for otolith analysis. Due to time constraints when working with fresh material, length was not recorded.

Individual tissue samples were analysed by starch gel electrophoresis and stained for glucosephosphate isomerase and lactate dehydrogenase. All larvae were genotyped for the two loci (*GPI-1** and *LDH-3**) used as markers and identified to the respective strain of cod, generally based on the following: *GPI-1*30/30* – CC; *LDH-3*70/70* – AC; *LDH-3*100/100* – BC (Fig. 1).

Both sagittae and lapilli were removed under polarized light and glued to microscope slides with commercial nail polish (n>40 per mesocosm, except Bag 4 due to the loss of some labelling, Table 2). The lapilli were affixed to separate slides, and one of each pair was polished to the nuclear plane with 10 µm and 1 µm lapping film (Suthers *et al.*, 1989). Otoliths were viewed under oil with the 100 × objective, and aged by counting the number of daily growth increments (as the increment counts did not necessarily equal 38 or 43, Table 2). Counts were repeated until the same age was determined at least twice. The increment width series for each fish was then measured along the longest radius using a video system connected to a digitizer (Anderson and Moksness, 1988). The narrow (<1 µm) increments in the perinuclear region were measured in blocks of four to six in relation to landmarks seen directly down the microscope, rather than to measuring them only from the video screen. The measurement series was accepted if the number of measured increments was close to the known age (2–3 days less or 1 day more). We assumed that any minor aging errors occurred when resolving the increment width series during the larval period and the measurement series was shifted with the outmost increment set to Day 37 (or 42). Between 0–5% of otoliths from the 12 stock × bag combinations were discarded as unreadable. In approximately half the otoliths, the last two increments were difficult to measure, and were estimated from the preceding increments. The

Table 1. Averaged data on final day, 26 May 1994 for the four mesocosms, Bag 1 (hatched on 13 April 1994, sampled on Day 43) and Bags 2, 3, 4 (hatched on 18 April 1994, sampled on Day 37). Initial stocking densities were 300 larvae of each stock per mesocosm and n-sample is the number of each stock in the final subsample of 144 individuals (or 143 in Bag) from all the survivors. Survival (%); SGR, specific growth rate (% weight increase per day, corrected for mortality, see Methods); final dry wt., (mg) estimated from wet weight by conversion factor of 0.18; initial dry wt., (mg) from freeze dried individuals. Numbers in parentheses are standard deviations (s.d.).

	Balsfjord cod (BC)	Coastal cod (CC)	Arcto-Norwegian (AC)
(a) Bag 1 (42 days)			
n-sample	44	90	10
Survival %	44.5	91.0	10.1
SGR	14.0 (0.5)	13.4 (0.8)	13.4 (0.4)
Final dry wt.	13.6 (2.8)	9.9 (3.7)	16.1 (3.5)
Initial dry wt. (Day 3)	0.061 (0.003)*	0.057 (0.008)	0.078 (0.008)
(b) Bag 2 (37 days)			
n-sample	38	57	49
Survival %	33.4	50.1	43.1
SGR	16.6 (0.6)	16.5 (0.9)	16.6 (0.8)
Final dry wt.	15.2 (4.0)	12.3 (5.1)	20.2 (6.0)
Initial dry wt. (Day 2)	0.067 (0.003)	0.055 (0.008)	0.083 (0.005)
(c) Bag 3 (37 days)			
n-sample	51	41	52
Survival %	38.1	30.7	38.9
SGR	17.0 (0.8)	16.9 (0.6)	16.7 (1.0)
Final dry wt.	18.9 (4.5)	15.9 (5.7)	20.8 (6.7)
Initial dry wt. (Day 2)	0.067 (0.003)	0.055 (0.008)	0.083 (0.005)
(d) Bag 4 (37 days)			
n-sample	59	46	38
Survival %	64.0	49.9	41.2
SGR	15.3 (0.8)	16.0 (0.9)	15.9 (0.9)
Final dry wt.	10.6 (3.1)	11.9 (4.0)	18.1 (6.8)
Initial dry wt. (Day 2)	0.067 (0.003)	0.055 (0.008)	0.083 (0.005)

*Estimated from egg diameter distribution by: dry wt. $=0.145*(\text{diameter}/2)^{1.834}$ ($n=59$, $R^2=0.86$).

incomplete final increment (Day 38 or 43) was excluded from any further analysis.

Analysis

Stock survival (%) in each mesocosm was calculated from the number of each stock, as identified genetically, divided by the total subsample analysed (144 or 143), multiplied by the total number of survivors (N) to the end of the experiment divided by 3. Specific growth rate (SGR) was calculated with an exponential model (Ricker, 1958) from the difference between the final weight and the mortality-corrected initial weight distribution (assuming that most of the mortality occurred in the smaller larvae, which are thus excluded from the initial weight distribution, van der Meeren, 1991a; van der Meeren *et al.*, 1994). For convenience, wet weights were converted to dry weights (DW) by a factor of 0.18 (van der Meeren *et al.*, 1994). Due to varying numbers of each stock retrieved from each mesocosm, one way ANOVAs for each mesocosm were used to compare the calculated dry weights among stocks.

The otolith growth history was compared among stocks and mesocosms by the relative recent growth (RGR, Hosn *et al.*, 1997), as 100*increment width on Day n/radius on Day $(n-1)$. Absolute growth could not be back-calculated as length was not recorded at harvest. Relative recent growth was calculated at 5-day intervals prior to Days 17, 22, 27, 32, 37 (and Days 22–42 in Bag 1). Statistical comparisons were made $\geq$Day 15 (Bags 2, 3, 4) or $\geq$Day 20 (Bag 1) when the larvae had clearly metamorphosed (Pedersen and Falk-Petersen, 1992; Kjørsvik *et al.*, 1991), so that otolith growth was compared within the pelagic juvenile stage (Hare and Cowan, 1995). Each 5-day RGR was compared among stocks by a separate 1-way ANOVA for each mesocosm. All 5-day RGRs were then examined by Canonical Discriminant Analysis (level of significance set at 0.05), to determine if there were periods of growth characteristic of each stock.

Individual 5-day RGRs were also compared by Principal Component Analysis (PCA, with varimax rotation), to determine if fish had a characteristic growth pattern with respect to the final weight (i.e. overall

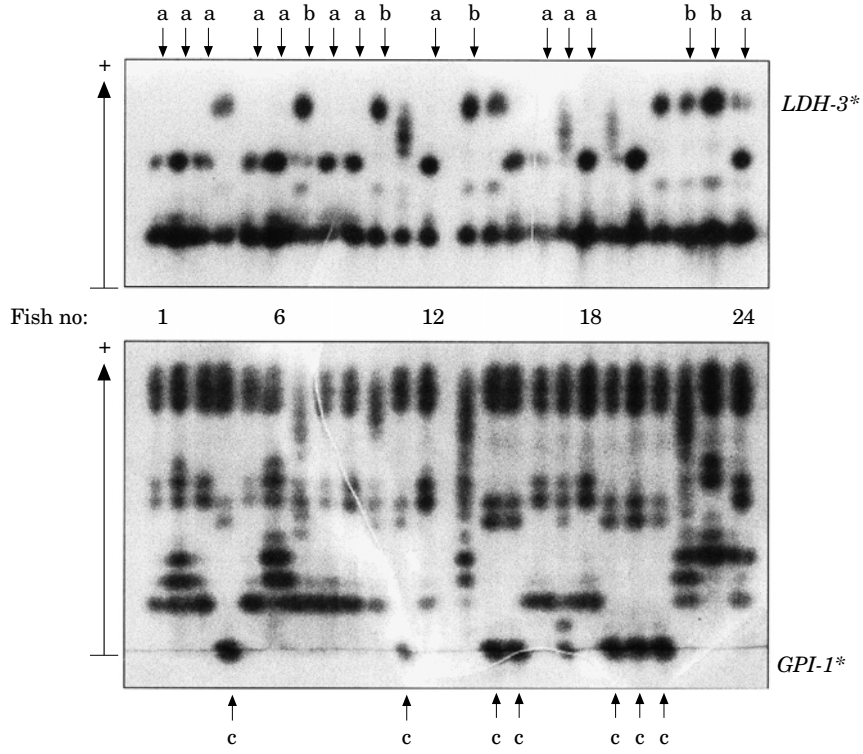

Figure 1. Identification of cod strains based on starch gel electrophoresis and staining for glucosephosphatate isomerase (GPI) and lactate dehydrogenase (LDH). Arcto-Norwegian cod (a): (*LDH-3* 70/70*) fish no. 1, 2, 3, 5, 6, 8, 9, 12, 16, 18, and 24, (*LDH-3*70/100*) fish no. 17; Balsfjord cod (b): (*LDH-3*100/100*) fish no. 7, 10, 13, 22, and 23; Coastal cod (c): (*GPI-1*30/30*) fish no. 4, 11, 14, 15, 19, 20, and 21.

growth). Varimax rotation re-distributes factor loadings among the RGRs such that each RGR tends to be associated with one factor, to aid in interpretation of the factors (rows–fish, columns–time, using Systat version 6). Interpretation of the two factors was made by the relative magnitude of each factor loading with the 5-day RGRs. For this comparison, analyses were conducted for all fish in Bags 2, 3, and 4 combined, and in Bag 1.

To examine the growth history with respect to ration, 1-day RGRs of all fish combined from each mesocosm were compared by PCA to determine general daily patterns of growth for all fish in each mesocosm (rows–days, columns–fish). The first two derived factor scores for each day, representing the overall daily RGR, were interpreted by correlation with temperature, light, Day post-hatch, logarithm of (daily energy ration of nauplii and copepodites) and logarithm (daily energy ration of adult copepods).

Results

Comparison of stocks at harvest

There were no consistent differences in stock survival, or stock specific growth rates, among the replicate mesocosms (Table 1, Fig. 2). Differences among mesocosms appeared greater than among stocks. Stock survival and to a lesser degree SGR, varied within a mesocosm (particularly in Bag 1), ranging between 10–91% survival and 13.4–17.0% SGR for the different cod stocks. In general, survival and SGR were negatively correlated (Fig. 2, $r = -0.25$, including the particularly low survival and SGR of AC cod in Bag 1).

The final individual dry weights of CC tended to be the lowest and those of AC cod the greatest (Table 1). AC were significantly heavier than CC in Bags 1, 2, and 3 ($p<0.05$), and not different from the BC stock. In Bag 4 a single large AC individual prevented any formal analysis, but there was a similar trend. The AC cod came from larger broodstock (see Methods) which is reflected in the trend for a heavier initial dry weight (Table 1). Although the females of the CC broodstock were heavier than the BC broodstock, the initial CC dry weight was lower than the initial BC dry weights.

Rearing conditions and otolith growth profiles

There were some days when the cod could not be fed, and they were therefore given additional food on the

Table 2. Summary of otolith data: n-otoliths, number of otoliths examined; n-rings, age estimated from number of daily growth increments; hatch diameter (μm), size of otolith at hatching (μm); initial dry wt. (mg). Numbers in parentheses are standard deviations (s.d.).

	Balsfjord cod (BC)	Coastal cod (CC)	Arcto-Norwegian (AC)
(a) Bag 1 (42 days)			
n-otoliths	17	19	7
n-rings	38.4 (2.1)	39.1 (2.0)	38.6 (1.2)
Hatch diameter	20.3 (1.7)	21.3 (1.7)	22.0 (1.6)
Final radius	110.3 (6.3)	105.4 (13.1)	114.9 (6.0)
(b) Bag 2 (37 days)			
n-otoliths	15	16	9
n-rings	36.5 (2.1)	35.7 (1.8)	36.1 (1.2)
Hatch diameter	20.4 (1.9)	21.3 (2.2)	21.9 (2.3)
Final radius	113.2 (10.1)	107.3 (1.9)	123.5 (10.7)
(c) Bag 3 (37 days)			
n-otoliths	16	16	12
n-rings	36.7 (1.3)	36.9 (1.0)	37.6 (0.7)
Hatch diameter	21.0 (1.7)	22.1 (1.7)	19.7 (2.3)
Final radius	122.2 (13.7)	118.6 (10.2)	126.2 (10.2)
(d) Bag 4 (37 days)			
n-otoliths	7	6	4
n-rings	37.9 (0.9)	38.5 (1.2)	36.3 (1.0)
Hatch diameter	20.0 (1.1)	22.2 (1.7)	25.1 (1.0)
Final radius	110.2 (13.6)	113.8 (10.2)	130.7 (16.0)

preceding days, in accordance with the feeding model (Fig. 3). Overall, the feeding regime in both experiments provided more than the calculated energy requirements. In addition, the prey size changed suddenly during the rearing. The food was dominated by nauplii up until Day 27–28 in Bag 1 (Fig. 3a,b), and Day 25 in Bags 2, 3 and 4 (Fig. 3c,d), but changed to the larger size fraction (adult copepods) on Day 26 (Day 26 and Day 30 in Bag 1).

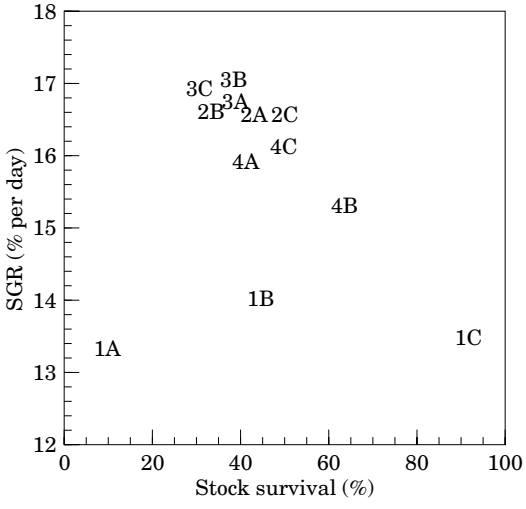

Figure 2. Scatterplot of specific growth rate on survival, from the four mesocosms. Numerals (1, 2, 3, 4) denote the mesocosm; A=Arcto-Norwegian cod, B=Balsfjord cod, C=coastal cod.

Water temperature in all mesocosms gradually increased from approximately 8 to 15°C during the rearing, while the light index varied from 0 to 15 h of incident sunlight (Fig. 3).

Over all mesocosms, ln(dry weight) was linearly related to the lapillus radius, and while there was no significant difference in slope among stocks (ANCOVA, $p>0.3$), there were significant differences in intercepts, with CC cod having a proportionally smaller dry weight with respect to radius (Bonferoni test, $p<0.01$, Fig. 4). The adjusted least square mean of CC dry weight with respect to radius was approximately 1.5 mg less than BC or AC cod.

In general, the average growth profile for each stock in each mesocosm shows an exponential increase in the daily average increment width after Day 15 (Bags 2, 3, 4: Fig. 5b,c,d) and Day 20 (Bag 1: Fig. 5a) for all three stocks. On Days 28 and 33 (Bag 1), Day 27 (Bag 2), Day 26 (Bag 3), and Day 28 (Bag 4), a distinct levelling of this trend occurred, although AC cod in Bags 2 and 4 did not show the same decrease in daily increment width. After 4–6 days, the increment widths generally returned to the earlier growth.

A canonical discriminant analysis among stocks of the five, 5-day RGRs revealed no significant differences (Bag 1, $p=0.5$; Bag 2, $p=0.1$; Bag 3, $p=0.1$; Bag 4, $p=0.4$), i.e. there was no characteristic pattern in RGR with respect to stock. Using only the four largest fish from each stock

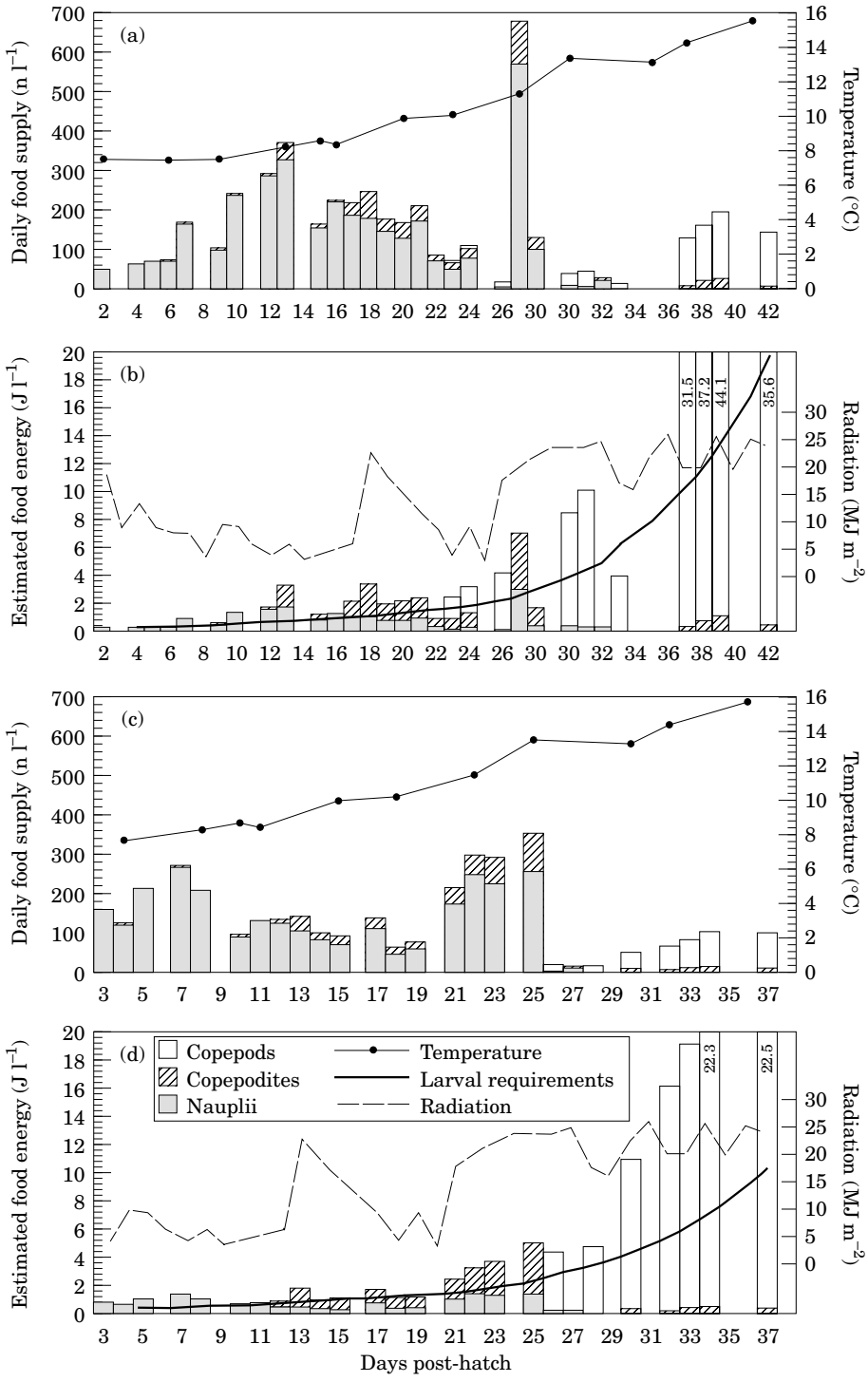

Figure 3. Summary plot of environmental conditions in the mesocosms showing the daily prey provided (no. litre^{-1} and J litre^{-1} of the three size fractions of copepods, using energy conversion provided in Methods), temperature, daily light levels as global radiation (both sky and direct sunlight), and the larval energy requirements estimated for 15% specific growth rate. (a) and (b): Bag 1; (c) and (d): Bags 2, 3, and 4.

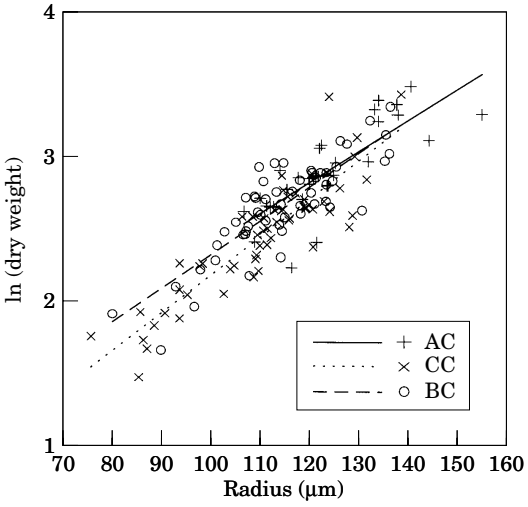

Figure 4. Scatterplot of fish size (ln dry weight) on otolith radius (measured from the hatch check) of the Arcto-Norwegian cod (AC), Balsfjord cod (BC), and Coastal cod (CC) stocks, lnDW=1.39+0.0259*radius, n=144, r^2=0.77.

(i.e. the fastest growers of each stock), a separate canonical discriminant analysis for each mesocosm also detected no significant difference among stocks ($p>0.4$). Alternatively, individual ANOVAs on each RGR revealed only two significant differences among stocks in the 5-day relative growth rate; for the period prior to Day 32 in Bag 2 (AC>CC) and Day 27 in Bag 3 (AC>CC, ANOVA $p<0.02$).

The first two factors of the PCA of the five, 5-day RGRs in Bags 2, 3, and 4 accounted for over 70% of the total variance (Table 3). Factor 1 was a contrast of the earlier and later periods of growth, while Factor 2 was significantly correlated with middle periods (RGR22, 27). The interpretation of factors derived for Bag 1 was similar, except that the last period (RGR42) was significantly negatively correlated with Factor 2. Inspection of the scatter plot of the first two factors, using symbol size as proportional to log weight, indicates large final weights were associated with faster RGR during the last half of the rearing (Bags 2, 3, and 4, Fig. 6b), but less so for Bag 1 (Fig. 6a).

The PCA reduced the individual daily RGR profiles of all fish in each mesocosm to two dimensions, accounting for >70% of the total variance (Table 4, Fig. 7). By plotting each day's standardized factor scores, the overall trajectory of the mesocosm's RGR reveals an abrupt change in RGR in Bag 1 after Day 28 and Day 31/32 (Fig. 7a), in Bag 2 after Day 25 (Fig. 7b), in Bag 3 after Day 24 (Fig. 7c), and after Day 25 in Bag 4 (Fig. 7d). The two factors were strongly correlated with environmental variables (temperature, light), day (over the last 20 days of rearing), and sometimes copepods (energy content of adults), but the influence of these variables was modified by nauplii (which was negatively correlated with the two factors, Fig. 7).

Discussion

There was no consistent difference in overall survival or growth among stocks at harvest (Fig. 2), once the SGR calculation had accounted for the larger initial and final weights of the AC stock. The negative relationship between SGR and survival was surprising, as it is typically a positive relationship in the ocean (Houde, 1989). Under the rearing conditions, however, we were unable to incorporate the mesocosm specific survival rates into the calculated daily feeding ration of 15% SGR, and therefore individuals in mesocosms with low survival received an enhanced ration (van der Meeren *et al.*, 1994). Within a mesocosm, the among stock differences were only dramatically different in Bag 1, which had the lowest SGR, and where the AC and BC stocks had comparatively low survival (for unknown reasons).

Earlier findings showed that the AC strain had lower SGR than the CC when reared together under similar conditions (van der Meeren *et al.*, 1994). This was also confirmed in another rearing experiment in 14 enclosures with AC and CC larvae from the present broodstock (same spawning as Bag 1, unpubl. results). It is difficult to believe that addition of another group of larvae (BC) would affect growth differences between AC and CC larvae. The apparent lack of a consistent growth difference may have been due to low female numbers of the AC spawning stock, resulting in low larval diversity and possible effects on AC larval growth related to genetic or maternal (e.g. egg-batch, size of female, size of eggs and larvae) differences between individual spawners.

Comparison of stock growth history

The growth history of reared AC cod during the first 5–6 weeks was not significantly different from that of the two coastal stocks, despite the greater mean increment widths of the AC stock observed in Bags 2 and 4 during the final 10 days due to individual variance (Fig. 5). Similarly, in terms of 5-day RGR, there was no characteristic pattern of growth (from the Canonical Discriminant Analysis), although we did observe two instances of significantly greater 5-day RGR by AC compared to CC (ANOVA; Bag 2, Day 32; Bag 3, Day 27). Consistent with these observations was the fact that CC had proportionally larger otoliths with respect to dry weight (Fig. 4), such that similar increment widths could have translated into greater daily somatic growth by BC and AC stocks, had we measured length at harvest and not wet weight.

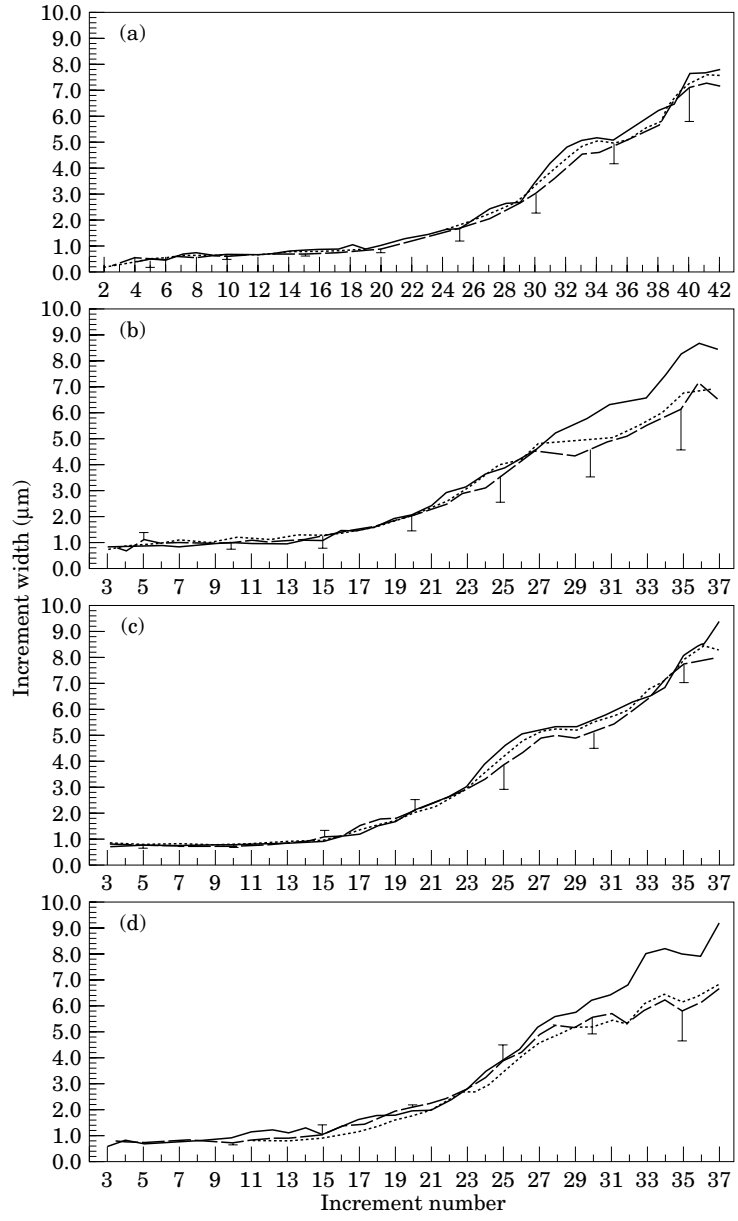

Figure 5. Profile of daily increment widths (μm) for the three stocks in (a) Bag 1, (b) Bag 2, (c) Bag 3, and (d) Bag 4. Error bars at 5 day intervals are standard deviation. - - -, Balsfjord cod; — —, coastal cod; ——, Arcto-Norwegian cod.

We hypothesized that the AC should exhibit faster growth than the CC, because pelagic juvenile AC from the Barents Sea showed almost double the growth rates of a more southern, Canadian stock (Suthers and Sundby, 1996). This was related to the day length, and the need for faster growth in the short northern summer for over-winter survival. The effect of day length on growth of Norwegian cod stocks is currently being investigated. It is possible that our rearing experiment was terminated before resolvable differences in growth could be realized. The exponential nature of growth curves for pelagic juvenile cod (Suthers and Sundby, 1996) also shows that differences between growth curves become obvious after 6 weeks, and shows that significant differences may be difficult to detect before 4 weeks. It would have been interesting to have extended the rearing period to 10 or 12 weeks, although difficulties with cannibalism may have arisen (Folkvord, 1991).

We also observed that the final weight at harvest was in general related to the relative growth rates in the latter

Table 3. Factor score loadings of the first two principal components of each mesocosm (percent of total variance explained) of the 5-day RGRs, used to interpret the axes in Figure 6. n=43 in Bag 1; n=101 in Bags 2, 3, 4 combined. *; $p<0.01$.

Factor	RGR17	RGR22	RGR27	RGR32	RGR37	RGR42
1I (43%)	—	−0.74*	−0.75*	0.45*	0.82*	0.40*
1II (25%)	—	−0.12	0.37*	0.80*	0.03	−0.67*
2,3,4I (43%)	−0.71*	−0.51*	0.19	0.80*	0.85*	—
2,3,4II (28%)	0.28	0.67*	0.87*	0.33*	0	—

half of the rearing period (PCA, Fig. 6b), rather than earlier growth changes (although there was no distinctive period of RGR when the larger fish attained their size advantage). This may indicate that ontogenetic changes such as improving digestive capacity, together with increasing availability and suitability of larger prey after the third week, may determine growth levels among individuals in a larval population. Small differences in RGR of older (and thus larger) individuals may add much more weight in absolute terms compared to similar differences in young larvae.

The AC larvae were initially larger, being derived from the larger brood stock (Table 1), yet, surprisingly, they did not demonstrate a consistent growth or survival advantage over the other two stocks with smaller larvae. According to predator field theory (the "bigger is better" hypothesis, *sensu* Leggett and Deblois 1994), larger larvae in the open sea may benefit from their size through increased relative survival probability (Bailey and Houde, 1989). In the sea, where prey may be temporally and spatially scarce, big larvae also have greater yolk reserves to enhance transition success at start of exogenous feeding. In contrast, neither scarcity of food at initiation of exogenous feeding nor presence of predators were characteristics of the mesocosms. Therefore, being initially big may not necessarily be advantageous in such systems.

Temporal response of increment widths to food limitation

The otolith growth history did appear to be highly sensitive to daily changes in food ration, reflected in the averaged increment series within 1–2 days, as shown by the overall trajectories of average increment widths (Fig. 5) and in the factor scores in RGR (Fig. 7). All trajectories in Bags 2, 3, and 4 showed a distinct change on Days 24, 25, and 26 (Fig. 7b,c,d), when the food regime changed from nauplii and copepodites to mostly adult copepods (Fig. 3c), and the energy ration was temporarily reduced until Day 30 (Fig. 3d). The increasing water temperature also levelled at 13–14°C during this time (Day 25–30, 13–18 May), possibly perturbing the growth trajectory. It is unclear why the growth

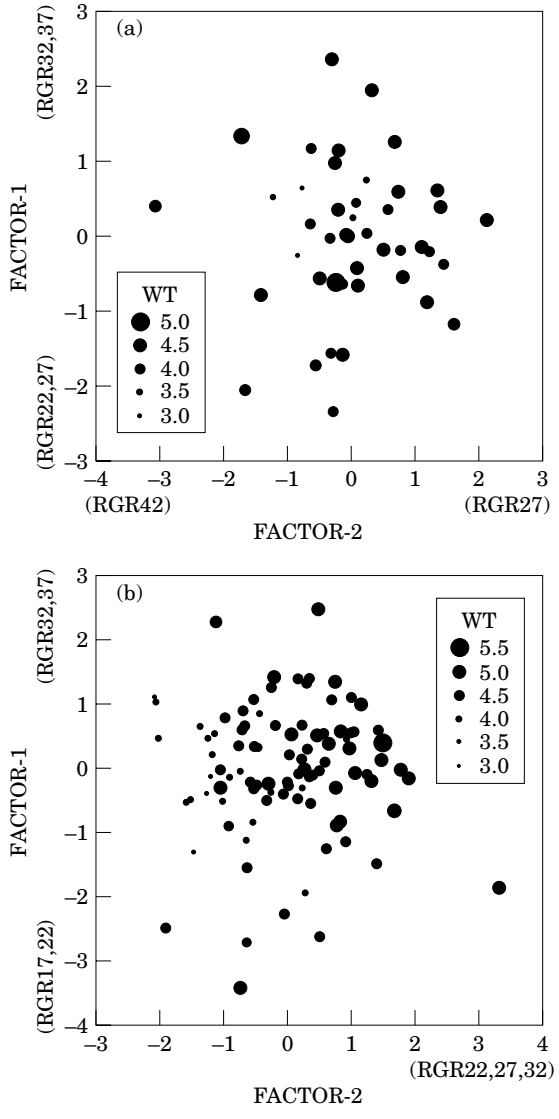

Figure 6. Plot of each fish's factor score loadings of its 5-day relative recent growth (RGR) profile for the last 23 days in (a) Bag 1 and (b) Bags 2, 3, 4 combined. Symbol size is proportional to the log(wet weight), WT. Significant correlations between each factor and the 5-day RGR are included on the axes (Table 3). Note that the largest fish at harvest had no characteristic period of growth.

Table 4. Pearson correlation coefficients between the daily factor score loadings of relative recent growth (RGR) (percent of total variance explained), derived from a PCA of all growth profiles from each mesocosm (see Figure 7) and the five environmental variables listed. Day, day post-hatch; Temperature, water temperature (interpolated from Figure 3 where necessary); Light, hours of incident sunlight; ln(naup+copepodites), ln(total daily energy content of nauplii+copepodites); ln(copepods), ln(total daily energy content of copepods). n=23 days. *; $p<0.05$.

Factor	Day	Temperature	Light	ln(naup+copepdites)	ln(copepod)
1I (50%)	0.86*	0.87*	0.71*	−0.54*	0.36
1II (33%)	0.50*	0.39	0.02	−0.21	0.27
2I (55%)	0.64*	0.72*	0.79*	−0.16	0.25
2II (15%)	0.72*	0.60*	0.11	−0.53*	0.51*
3I (42%)	0.92*	0.90*	0.57*	−0.49*	0.54*
3II (38%)	0.07	0.19	0.55*	0.23	−0.11
4I (49%)	0.89*	0.88*	0.65*	−0.37	0.70*
4II (32%)	−0.03	0.06	0.29	0.05	−0.23

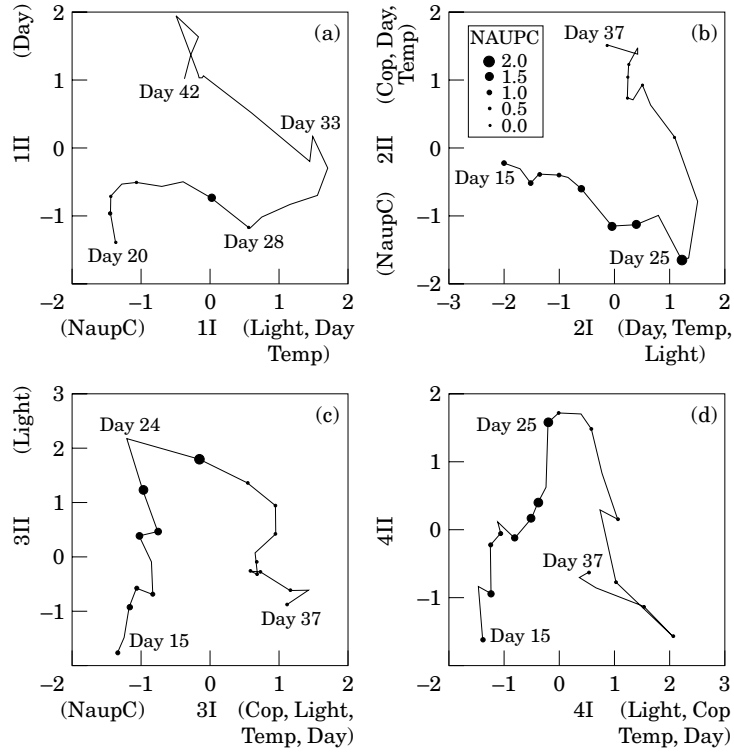

Figure 7. Plot of each day's factor score loadings of relative recent growth (RGR) derived from a PCA of all fish from each mesocosm. Largest significant environmental correlations with each component (Table 4) are included on each axis. (a) Bag 1, (b) Bag 2, (c) Bag 3, (d) Bag 4. Symbol size is proportional to the log transformed daily energy ration provided in the form of nauplii and copepodites, NaupC (i.e. excluding adult copepods). Note the dates when marked changes in growth trajectory occurred – but the sign (+ or -) of the factor loadings among analyses is arbitrary.

trajectory did not return to its initial orientation in two-dimensional space (Fig. 7), unless the energy yield of adult copepods was not as great as nauplii. The first factor in these plots is positively correlated with the physical variables of day, temperature and light, while the second factor was correlated with nauplii (Table 4, Fig. 7), suggesting that the nauplii contributed to the early high RGR.

In Bag 1 the RGR trajectory altered direction on Day 28 and Day 33 (Fig. 7a), which corresponded to change in prey size on Day 28. The second growth trajectory changed on Days 31/32 in Bag 1,

corresponding to the 13–18 May period. It is possible that a factor other than diet or temperature change occurred, but our records do not indicate this.

Comparison of AC otolith growth to that from the Barents Sea

The increment width series of the reared AC cod (Fig. 5) is dramatically different to that obtained for a subset of similar size fish previously sampled from two areas in the Barents Sea (Lofoten and Tromsøflaket, sampled in July 1988, data from Suthers and Sundby, 1993). The selected wild fish were within the range of 17–28 mm SL and 46–51 days post-hatch, to overlap the estimated lengths of reared fish, and where necessary were adjusted to a common hatch date. The daily growth increments of cod from off northern Norway have a linear trajectory between Days 15–50, such that they are approximately double the width of reared cod at Day 15, and approximately half their width by Day 30 (Fig. 8a). Water temperature is undoubtably an important component as temperatures were consistently higher within the mesocosm than in the Norwegian and Barents Sea in July (Suthers and Sundby, 1993), and almost double that in the ocean after Day 30 (>12°C vs. <9°C). Prey abundance in mesocoms is usually more than double that found near Lofoten (Sundby, 1994). Thus the superior growth of AC in the mesocosms starting at the fourth week post-hatch (Fig. 8b) may be explained both by high temperature and good feeding conditions in the enclosures. Cod larvae at this stage may be able to exceed 20% daily increase in weight (van der Meeren and Næss, 1993; van der Meeren *et al.*, 1994), which is far higher than the growth rates reported from the open sea (Ellertsen *et al.*, 1987; Morse, 1989). The food and temperature contribution to this growth difference is substantial and confirms their role as regulatory mechanisms for growth rate and hence recruitment (Houde, 1989; Folkvord *et al.*, 1994; Ellertsen *et al.*, 1989; Sundby, 1994). Rapid growth will shorten the duration of the post-larval period, leading to reduced predation mortality and/or less cannibalism. According to Sundby *et al.* (1989), 40–90% of the early juvenile (post-larval) AC year class is concentrated north of the Tromøsflaket bank, one of the locations for the field-caught AC larvae in Figure 8. This area may therefore be of particular interest for evaluation of a "late critical period" in relation to availability of copepodite and adult *C. finmarchicus* stages to AC post-larvae (Folkvord *et al.*, 1994).

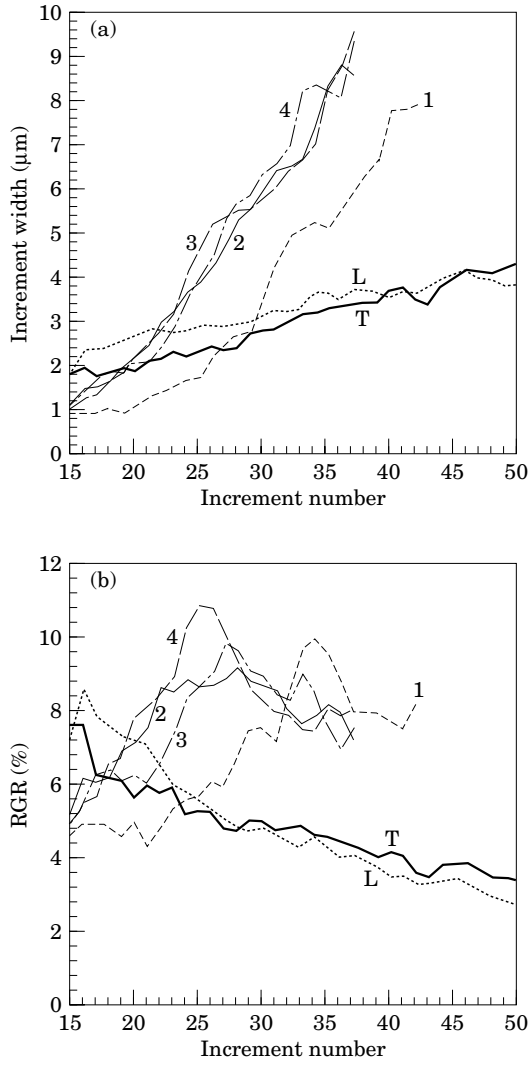

Figure 8. Comparison of mesocosm otolith growth with cod larvae from the sea. (a) Increment width profiles for days 15–50 post-hatch for Arcto-Norwegian cod (AC) from Bags 1, 2, 3, and 4 (from Fig. 5), and similar sized AC stock (17–28 mm SL, 46–51 days post-hatch) from the Barents Sea near Lofoten (L, n=10) and Tromøsflaket (T, n=7), sampled in July 1988 (data from Suthers and Sundby 1993). These cod are adjusted to a common hatch date where necessary. (b) Relative recent growth (RGR; relative growth rate as a percentage by each increment width of the otolith radius).

Conclusions

The technique of measuring the otolith growth history is limited to periods when increment widths are >1–2 µm. Prior to this i.e. up to 15–20 Days post-hatch, the larval growth is characterized by increments around 1 µm which often had to be measured in groups (see Methods). Our difficulty in resolving these increments, particularly in the slow-growing Bag 1, is reflected in the under-aging of these fish by an average of 1–3 days (Table 2). We assume that any possible inaccuracy in aging and increment width series occurred during this

larval period, and was one of the reasons for restricting our analyses to larvae >15 days old.

In this study, we used increment width as a proxy for actual daily fish growth but avoided converting it to daily changes in SL or dry weight (Campana, 1990), because we had no conversion data except wet weight at harvest (which covered only a narrow size range). Other published otolith size–fish size relationships were not amenable because our enclosure-reared cod probably had smaller relative otolith sizes due to their fast growth (Fig. 8, Mosegaard *et al.*, 1988; Secor and Dean, 1989; Wright *et al.*, 1990; Milicich and Choat, 1992). Our use of RGR is analogous to the somatic growth rate calculation (Hosn *et al.*, 1997), and the biological intercept back-calculation.

Our study shows the advantages of electrophoretically distinguishable stocks being co-reared within the same mesocosm, as mesocosm-specific effects are inevitable. The uncensused mortality during the experiment altered the theoretical ration, and therefore survival was negatively correlated with SGR, increasing the SGR up to 17%, compared with the modelled ration of 15% daily increase in weight. While we found no significant difference among stocks, the otolith growth history in pelagic juvenile cod demonstrates a remarkable fidelity to the feeding and environmental regime. Our study reveals enormous scope for growth rate variation, especially during the latter part of the pelagic juvenile stage.

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