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A common garden experiment with larval Northeast Arctic and Norwegian coastal cod cohorts in replicated mesocosms

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ABSTRACT

A replicated mesocosm experiment was carried out to evaluate differential effects of feeding conditions for larval Northeast Arctic (NA) cod and Norwegian coastal (NC) cod. The two populations were (1) reared together with a 6-day older NA cohort (mixed) in high (HC) and low prey concentration (LC; 2000 and 200 prey/L initially), and (2) reared separately in HC treatments (non-mixed) to be able to evaluate both the effect of feeding conditions and possible effects of size interaction within mesocosms. The larvae were fed natural zooplankton, and the two stocks were identified in the mixed mesocosms by otolith marking. NA larvae hatched at a larger size, had higher growth rates, and survived better than NC larvae in both mixed and non-mixed mesocosms in the HC treatment. The second cohort clearly survived better in the non-mixed than in the mixed mesocosms, indicating the presence of an interaction effect before cannibalism could occur. We found a significant higher weight-at-length between NC and NA larvae (<12 mm), which was bigger than the effect difference due to feeding conditions. Furthermore, a positive relation between survival and initial growth within mesocosms was found. We suggest that lower growth at early larval stages was accompanied by lower survival, and suggest that this was further enhanced when larvae interacted with older and larger larvae.

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1. Introduction

Common garden experimentation is a popular method to evaluate potential population differences in growth and mortality in both adult and larval fish (Conover and Present, 1990; Otterlei et al., 1999). However, common garden experiments assume no biological interaction (i.e. competition for food, antagonistic behaviour, cannibalism, etc.) between populations within the experimental enclosure. To reveal such interference effects, it is necessary to compare common garden with concurrent single-population treatments (Laurence et al., 1981).

Norwegian coastal (NC) cod and Northeast Arctic (NA) cod are among the two most important commercial cod stocks along the coast of Norway and in the Barents Sea, and are defined genetically as separate populations (Bergstad et al., 1987; Sarvas and Fevolden, 2005). Earlier work has demonstrated population-specific growth differences during early life stages (ELS) with NC larvae growing faster than NA larvae in different light and temperature regimes (Otterlei et al., 1999; van der Meeren and Jørstad, 2001).

Earlier works on cod larvae in different prey levels have demonstrated that growth will be affected directly through concentration of prey (Puvanendran and Brown, 1999; van der Meeren and Moksness, 2003), and that the larvae increase their swimming activity at lower prey levels (Munk, 1995). Furthermore, recent studies have suggested that not only concentration, but also body size and composition of zooplankton will have an effect on larval survival in the sea (Beaugrand et al., 2003). Thus it seems evident that localized adaptations to prevailing prey fields could possibly explain some of the observed differences between the two populations.

We designed a common garden experiment with contrasting feeding regimes for larval NA and NC cod in replicated outdoor mesocosms. The two populations were co-reared with a 6-day older cohort to evaluate potential interaction effects at different size and developmental stages. In addition, each population was reared separately to be able to evaluate the effect of common rearing. The objective of this work was to (1) evaluate population-specific differences in size and condition, and (2) evaluate how these differences would manifest themselves in different feeding conditions when interacting with an older and larger cohort.

2. Material and methods

2.1. Larval background and incubation

Larvae used in this experiment came from two stocks raised at Real Seafood AS installations at Fana, Norway. Larvae of both the NA and NC population were offspring of first-generation-selected cod based on a broodstock of 25–30 families that was produced at

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Akvaforsk, Sunndalsøra in 2002. Families from the NA population were based on wild fish from Vesterålen (68°N, 14°E), while families from the NC population were based on wild fish from different fjords from north of 61°N along the Norwegian coast. Most of the wild broodstock were second-time spawners. There were, however, some cases of first-time spawners, especially in the NC broodstock. Incubation temperature was stable around 6 °C throughout the incubation period (Ivar Holmefjord, Real Seafood A/S, pers. com.).

2.2. Experimental design

The experiment was conducted outside at Espegrend Marine Biological Station (60°16′N, 5°13′E), in 12 land-based circular plastic mesocosms each with a volume of 2500 L. These were kept in groups of four in larger 32,000-L plastic tanks used as thermal baths. Each mesocosm had a lid with a small (0.21 m^2) opening in the middle. Eggs were collected at two different dates to obtain two different aged cohorts separated by 6 days. On 21.04.05, a NA group (NAI) was added to eight common rearing mesocosms (mixed), while on 27.04.05, NA and NC cod of a second cohort (NAII and NCII, respectively) were added to the same eight mesocosms in addition to being added in two separate rearing mesocosms each (non-mixed; Table 1, Fig. 1). The groups from the second cohort that were added to the mixed mesocosms were marked with a 100 mg/L alizarin complexone solution for 12 h in the incubators 8 days (NA) or 3 days (NC) prior to hatching. Lowercase letters abbreviate marked (m) and unmarked (um) groups, and thus also indicate whether they were reared in mixed (m) or non-mixed (um) tanks. At start-up, eggs were added directly to the mesocosms, where hatching took place within 1–2 days. Non-feeding trials were set up in 5-L buckets in the laboratory to analyse the quality of the egg groups.

Table 1
Experimental setup.

Treatment	Replicates	Cohort 1		Cohort 2	
		NA	NC	NA	NC
HC	4	13,500 (NAI)		6250 (NAIIm)	6250 (NCIIm)
LC	4	13,500 (NAI)		6250 (NAIIm)	6250 (NCIIm)
HC	2			25,000 (NAIIum)	
HC	2				25,000 (NCIIum)

Mean egg number added to the mesocosms for the different cohorts and stocks. Cohort 1 was added on 21.04.05 while the 6 days younger cohort 2 was added on 27.04.05. Names of the groups are indicated in parentheses.

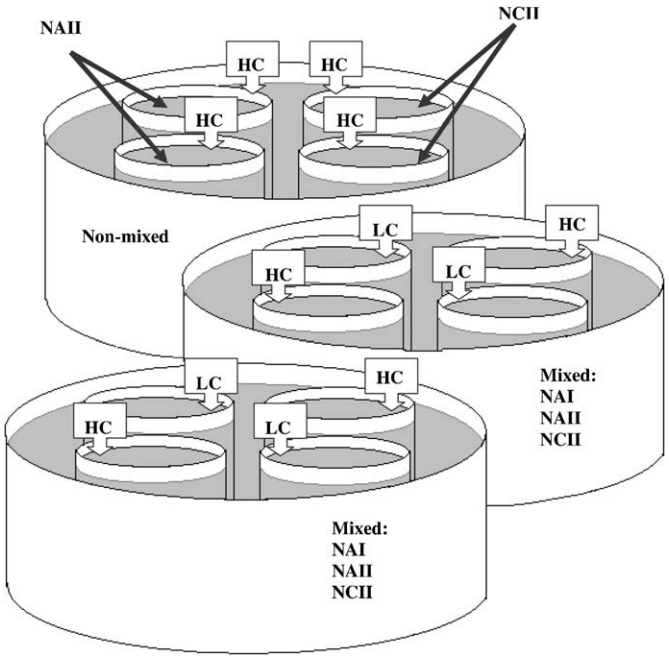

Fig. 1. Illustration of tank setup. Mixed and non-mixed abbreviate mesocosms with common rearing and single groups, respectively. HC and LC indicate high-concentration and low-concentration food level.

Table 2
Concentration of prey in HC and LC treatments on different dates (prey/L).

	27.04.05–17.05.05	18.05.05–26.05.05	27.05.05–03.06.05	04.06.05–15.06.05
HC	2000	1500	1000	500
LC	200	150	100	50

A measurement device of the type WTW Conductivity Meter LF 330 was used to measure temperature daily and salinity weekly, while WTW Oxi 340i was used to measure oxygen weekly.

The larvae were fed live natural zooplankton collected by filtering seawater using a Hydrotech filter generating different size fractions of zooplankton. The mesh size was changed twice during the experiment from an initial size spectrum of 80–250 to 120–400 μm at 25 dph, and further to 120–1000 μm at 32 dph. Zooplankton density was monitored daily and adjusted around noon. The mixed mesocosms were split up into two different zooplankton size treatments, where one received 100% from the smallest size fraction and the other an addition of 10% from a larger size fraction. This was done due to a parallel experiment that analysed the effect of size and concentration of prey on larval cod (Seljeset, 2006). The results indicated that the two different treatments did not have significant effects on growth or survival. Since this treatment did not have any effect on our comparison of groups, it was decided to pool the two treatments in this study to increase the replicates and facilitate graphical presentations. Four of the mixed mesocosms received high prey concentration (HC), while the remaining four received low prey concentration (LC). The design was to feed in excess in HC mesocosms and to have a suboptimal feeding regime in LC mesocosms (Table 2). Non-mixed treatments were replicated only at HC.

Plankton composition in the filtrates varied throughout the experiment with increasing amounts of bigger copepods and decreasing amounts of nauplii with time. There was a high amount of non-edible plankton from the start of the experiment, which increased proportionally in the LC mesocosms. The non-edible was not counted when quantifying the prey concentration treatments. The larvae ate successively bigger prey through the experiment with a mean of 0.2 mm at 18 dph to a mean of 0.6 mm at 46 dph. For more details on the prey size and species composition see Seljeset (2006).

2.3. Sampling and analysis

Sampling of larvae was carried out once every week, with a sample of 15 larvae from non-mixed mesocosms and 30 larvae from mixed mesocosms. Three sampling techniques were used: (1) sampling with a sampling tube (75 mm width) with an open/close function at the bottom, (2) sampling larvae with a fine-mesh dip net, and (3) sampling with a ladle. Sampling techniques 2 and 3 were applied only when concentrations of fish were low and sampling technique 3 was used only as long as there were no indications of larval avoidance. Mixed mesocosms were terminated on 08.06.05, while non-mixed mesocosms were terminated

on 15.06.05. On termination the mesocosms were drained and surviving fish counted, and an end sample of 50 and 100 larvae from the non-mixed and mixed mesocosms were sampled, respectively.

All larvae were photographed (Olympus Camedia 5050 zoom camera connected to a Nikon model C-DS dissecting microscope) and frozen individually in Eppendorf tubes, for later examination. Standard length (SL) and myotome height (MH) were measured from the photos using Image-J®. The frozen larvae were rinsed in freshwater, dried (Termax oven) at 60 °C for 24 h and weighed (Sartorious micro M3P micro weight) before they were dehydrated and four otoliths dissected out (sagittae and lapilii). The otoliths were mounted on crystal bond and checked for fluorescent marks in a microscope (model Axioskop 2 plus) without the need for further polishing (Meekan and Fortier, 1996; Otterlei et al., 1999). The larvae could be identified to group by differentiating between mark sizes, since the two marked larval groups had been marked with a 5-day difference.

2.4. Data analysis

All analysis and graphs were done using R 2.1.1. Overall survival was estimated from the numbers of eggs put into the mesocosm at start-up and the number of surviving larvae counted out in addition to subtracting the number of larvae sampled on each sampling day. All data on size (SL, DW) were log transformed before growth and morphometric analysis, and the data analysed for heterogeneity of variance and checked for normality using diagnostic plots. Outliers were analysed by analysing SL–DW and SL–MH plots. Outliers were excluded from the main sampling if they were found to be 4.5 SD from the mean (1 NCIIm, 1 NAIIum). In total, 3399 larvae were sampled during the experiment. Nested ANOVAs, with DW and SL as response variables and mesocosms as random effect, were used to test the effect of stock and concentration for every sampling date.

Polynomial stepwise regressions were carried out by starting with a simple linear model and then including higher-order polynomials if significant. Polynomials were fitted to size-at-age relations (using log DW (μg)). Specific growth rate (SGR) in % was estimated by differentiating the size-at-age models, and also between sampling weeks as follows:

$$\mathrm{SGR} = 100(e^{g} - 1) \quad (1)$$

$$g = (\mathrm{LN}(\mathrm{DW}_2) - \mathrm{LN}(\mathrm{DW}_1))/t \quad (2)$$

where g is the instantaneous SGR [$\mathrm{g\,g^{-1}\,d^{-1}}$], DW_1 the mean dry weight at a given sampling day, DW_2 the mean dry weight at the following sampling day, and t the time interval in days.

Size-independent indices were made by using residuals derived from a regression of weight at length as suggested by Suthers (1998). A second-degree polynomial was fitted with the same procedure as explained for the size-at-age relation. The effect of group and treatments on residuals was tested by means of ANOVAs to analyse population, group, and cohort differences.

A size- and temperature-dependent growth (STDG) model was applied to evaluate growth performance (Folkvord, 2005). This allowed us to compare the two cohorts and adjust for differences in ambient temperature between the two cohorts due to the 6-day difference. Since the model predicted the optimal growth at size and temperature for the two stocks, we assumed that negative residuals, calculated as observed values from the data minus expected values from the model, would be a response to food-limited growth conditions.

3. Results

3.1. Environmental conditions and initial group differences

The temperature was relatively stable in all mesocosms, and increased from a mean of 7.8 °C at the start of the experiment to a mean of 9.8 °C at the end. The salinity was generally low (mean = 29.8 ppt) with a tendency towards higher salinity at the bottom of the mesocosm. Oxygen was generally stable in all mesocosms (mean = 97.3%) with the lowest value at 93% and the highest at 105%.

The initial egg size was significantly different between the NA and NC groups in terms of both DW and egg diameter (ANOVA, $p<0.01$). There was, however, no significant effect of otolith marking (ANOVA, $p>0.05$), and no significant difference in size between the NA groups of the first and second cohort at 50% hatching (ANOVA, $p>0.05$).

The length-at-age measurements in the non-feeding trials displayed the same trends as the egg size, with the NC groups being significantly smaller (ANOVA, $p<0.05$) at a given sampling day, and no differences between the size-at-age of the NA larvae of the first or second cohort.

From the non-feeding trial we found no clear indications of survival differences between the groups except for a slight tendency of higher mortality rate in the unmarked NA group of the second cohort (NAIIum; Fig. 2).

3.2. Larval mortality in mesocosms

In general, NAII fish had higher survival (6.2% and 7.2%) than NCII fish (2.2% and 2.8%) in the non-mixed mesocosms. In mixed mesocosms NCII fish were completely missing after 5 dph, with only three observations in total. NAII fish survived somewhat better (ranging from 1.3% to 2.2% in HC mesocosms), but there were few observations of this group as well (Table 3).

In the HC treatment mesocosms NAI fish had a much higher survival (ranging from 15.8% to 24.6%) than NAII fish in both mixed and non-mixed treatments (see above), while in LC mesocosms the only fish left at the end of the experiment were NAI (ranging from 2.8% to 6.5%; Table 3). The highest survival of NAI fish was observed in mesocosm 9 (24.6%). This was also the mesocosm with the highest survival of the NAII group (2.2%).

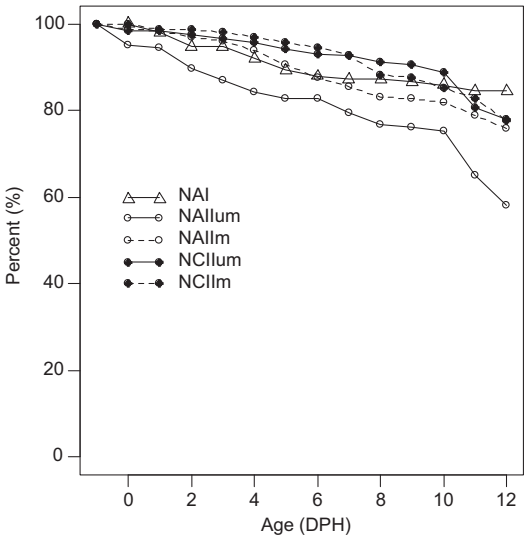

Fig. 2. Survival with age for unfed larvae of different groups. Dotted lines indicate groups marked with alizarine.

The highest estimated number of survivors of the second cohort based on weekly subsamples was found in the LC mesocosms at 5 dph. The second cohort disappeared, however, from the LC mesocosms on the following two sampling days, and at 19 dph, survivors of the second cohort were found only in the HC mesocosms.

3.3. Differences in growth and size-at-age in stocks and tanks

NCII larvae in the mixed mesocosms were excluded from the growth analysis since there were only three observations in total.

NAII larvae were heavier and longer than NCII larvae throughout the experiment (non-mixed; Fig. 3). This was, however, significant only for both SL and DW in the fifth week of sampling (32 dph). The NAI larvae were significantly heavier in the HC treatment compared to the LC treatment from the second to the sixth sampling week, and significantly longer from the fourth to the sixth sampling week. NA groups in different treatments showed a similar tendency of having the highest SGR at earlier dph than the NC group (Fig. 4A).

Even though the HC treatments produced larger- and faster-growing larvae than the LC treatments (Fig. 4B), there were also noticeable variations between mesocosms of the same treatment. A significant tank effect for several of the sampling weeks for weight- and length-at-age between the mesocosms of the same treatment was found after the third sampling week (ANOVA, $p<0.05$), reflecting the divergence of similar initial systems with time.

The end sample, taken from the tank on termination, was not significantly larger from the main sampling in any of the mesocosms (ANOVA, $p>0.05$), indicating no major problem of avoidance of larger individuals. However, there were observations of exceptionally large individuals in the end sample in some of the LC mesocosms, indicating possible occurrence of cannibalism. This was also confirmed in the stomach analysis from the last samples (Seljeset, 2006).

The growth during each week and survival at end of the experiment for each mesocosm were contrasted to find if there was any connection between survival and growth and how this related to each other throughout the larval period (Fig. 5). We found a significant positive correlation between average population growth and survival in the first 2 weeks ($r_s = 0.89$, $p<0.01$; Fig. 5A). There was also a significant negative correlation between growths in the first week and last week of the experiment ($r_s = -0.74$, $p<0.05$; Fig. 5B).

Table 3
Average weight and survival at termination for the different groups NAI, NAIIm, and NCIIm (collected on 21 April 2005), and NAIIum and NCIIum (collected on 27 April 2005).

Mesocosm setup	Mixed mesocosms						Non-mixed mesocosms			
Cohort	First cohort		Second cohort							
Group name	NAI		NAIIm		NCIIm		NAIIum		NCIIum	
Egg diameter. (mm)	1.442 (0.055)		1.435 (0.067)		1.350 (0.051)		1.438 (0.076)		1.350 (0.055)	
Egg weight (μg)	78.9 (16.7)		71.6 (12.7)		57.3 (7.9)		81.8 (14.9)		51.4 (9.4)	
Prey concentration	HC	LC	HC	LC	HC	LC	HC	LC	HC	LC
Survival (%)	17.6	4.6	1.6	–	–	–	6.7	–	2.5	–
Age at termination (DPH)	46	46	40	–	–	–	47	–	47	–
Final weight (μg)	5975 (4321)	4382 (3091)	3099 (1206)	–	–	–	7022 (2699)	–	5303 (2192)	–
SGR (%)	11.2	10.1	11.9				11.2		11.0	

Initial stock densities are based on mL egg with an average egg density of 500 egg/mL. SD is given in parenthesis. Survival is calculated from end sample and sampled larvae throughout the experiment. SGR is the averaged specific growth rate between the first and last samplings.

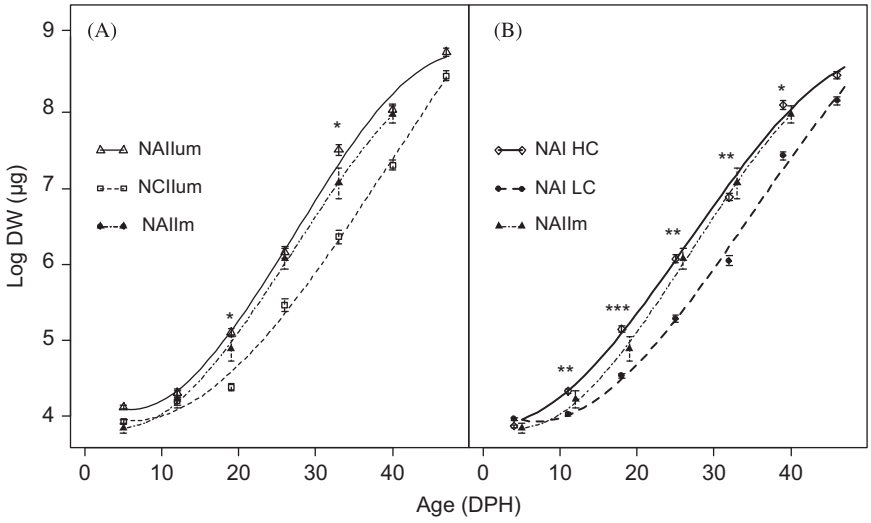

Fig. 3. Size-at-age models and mean (±2SE) DW for NAIIum, NCIIum, and NAIIm (A), and NAI for HC and LC mesocosms and NAIIm (B). The groups are indicated by solid and dotted line, respectively, and significance levels from nested ANOVA are indicated as follows: $^{*}<0.05$, $^{**}<0.01$, and $^{***}<0.001$. NCIIm is not included in the analysis.

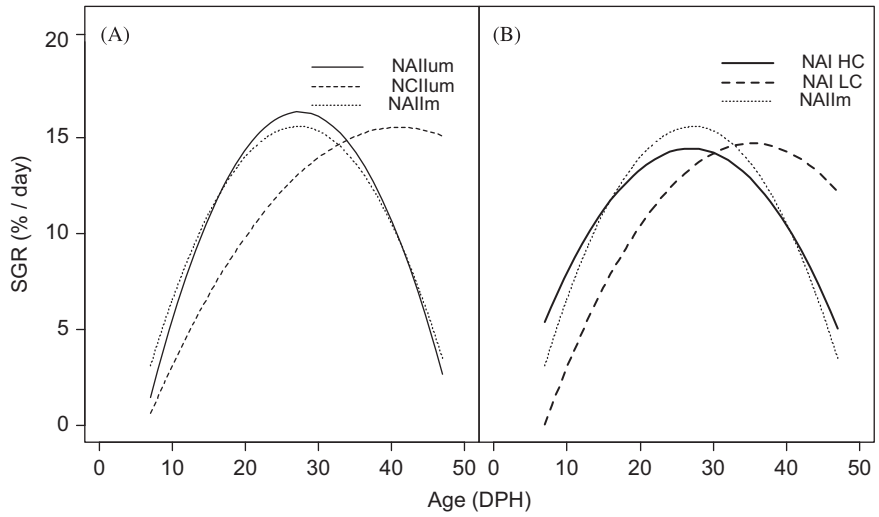

Fig. 4. Specific growth rate (SGR) estimated from differentiating size-at-age models plotted against age for NAIIm, NAIIum, and NCIIum (all HC) (A) and for NAI in HC and LC mesocosms and NAIIm (HC) (B).

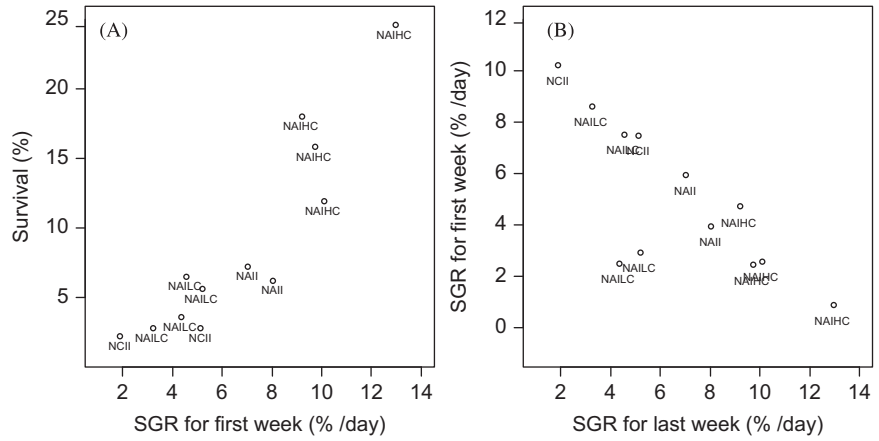

Fig. 5. SGR (%/d) against survival (%) in the different mesocosms for the first 2 weeks (A), and growth in the first 2 weeks against growth in the last week (B). SGR is based on average weight between samplings, while survival is based on final count on termination. In the mixed mesocosms, growth and survival are based only on the older cohort (NAI), while the second cohort is represented only from the non-mixed mesocosms (NAII and NCII).

3.4. Larval morphometry and condition

NC offspring were on average 7.3% heavier at a given length than NA larvae (ANOVA, $p<0.001$; Figs. 6A and B), while no difference was found between the two cohorts of NA larvae or between mixed and non-mixed tanks (HC; ANOVA, $p>0.05$). This was also the case when looking at larvae under 12 mm, defined as the size of initiation of metamorphosis (Otterlei et al., 1999; ANOVA, $p<0.01$). The larvae in HC mesocosms were heavier at length compared to those in the LC mesocosms (ANOVA, $p<0.05$). This difference was a result of lighter larvae at length in the second and third sampling week in the LC mesocosms creating a difference of up to 3%.

3.5. Realised growth relative to maximum growth potential

Both of the two populations in the non-mixed mesocosms (Fig. 7A) grew initially sub-optimally compared to predicted STDG potential. However, NAII fish had near-optimal growth the following weeks, while the NCII fish were estimated to have a suboptimal growth throughout the experiment with the exception of 26 dph. In the HC mesocosms, NAI fish (Fig. 7B) coincided well with the modelled growth trajectory for the first sampling weeks in the HC treatments and then appeared to fall behind on the consecutive sampling days. In the LC treatments, NAI larvae had suboptimal growth in the first three sampling weeks, but had a more optimal growth from the fourth sampling week and onwards compared to the HC mesocosms. The NAII fish in the mixed treatments (HC; Figs. 7A and B) was the group of the second cohort that coincided best with the expected growth trajectory from the first sampling week. There was a general trend of suboptimal growth towards the end of the experiment for all the groups.

3.6. Relative size variation of groups within mesocosms

An increase in CV of weight corresponded to an exponential increase in size in the first 2–3 weeks for all groups (Figs. 8A and B). When looking at CV of weight relative to average population weight, the CV of the LC treatment diverged noticeably from the HC treatment at an average larval size of approximately 150 μg for NAI larvae. The two treatments seemed to have variance plateau around 50% and 70% for HC and LC treatments, respectively (Fig. 8B). While LC decreased somewhat the HC was relatively

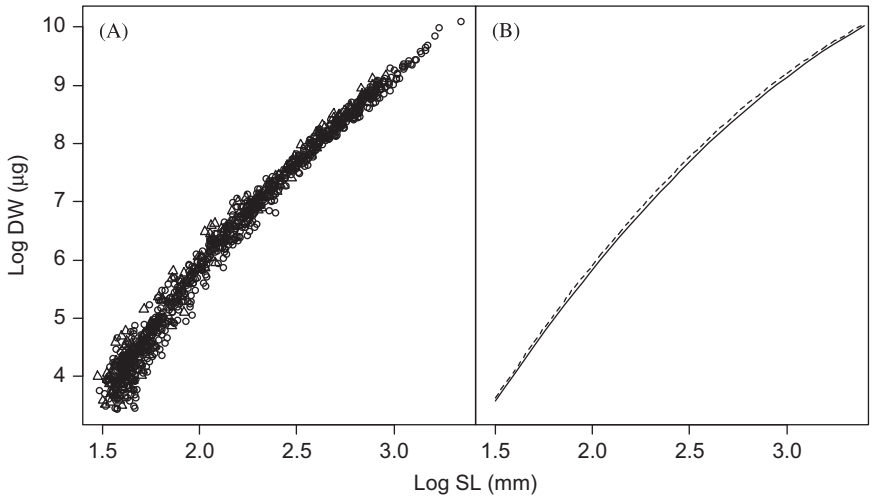

Fig. 6. (A) Weight-at-length (natural log) for all observations from HC. NA larvae are denoted with circles and NC larvae are denoted with triangles. (B) Second-degree polynomials for NA larvae (solid line) and NC larvae (dashed line), fitted for graphical purposes.

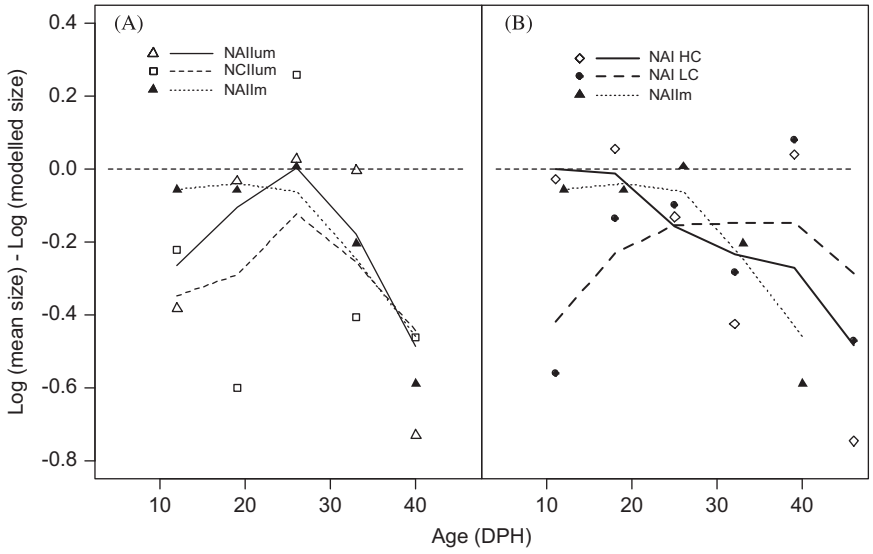

Fig. 7. Difference between estimated weight-at-age (natural log) from a size- and temperature-dependent growth (STDG) model for NAIIm, NAIIum, and NCIIum (all HC) (A) and for NAI in HC and LC mesocosms and NAIIm (HC) (B). The STDG model is taken from Folkvord (2005). Straight dotted line indicates zero deviance from the model, indicating optimal growth according to the model.

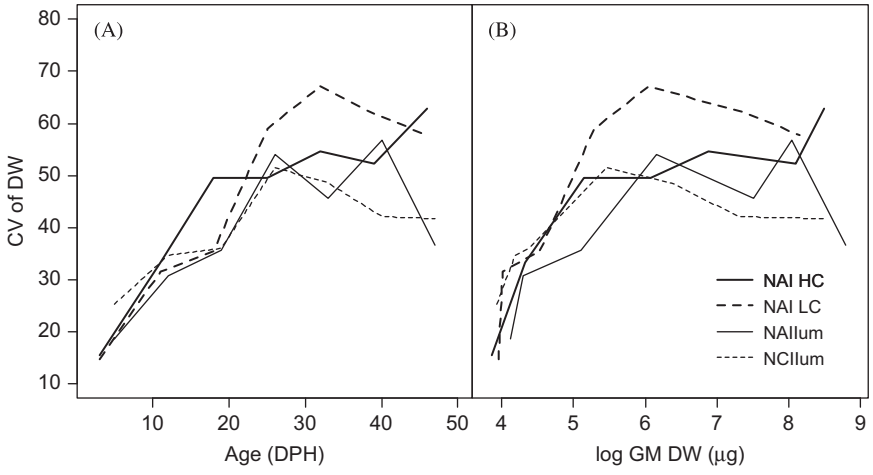

Fig. 8. Coefficient of variation (CV) of dry weight versus (A) age and (B) geometric mean weight for all groups with sufficient data (natural log).

stable and had a sharp increase at the end of the experiment. Larvae from the second cohort (non-mixed) seemed to have a general decrease in variance after 26 dph.

4. Discussion

First, we discuss the population-specific differences on an ecological basis and compare our results with earlier findings. Then, we discuss the advantages of size, development, and growth in the different feeding conditions, and how these relate to possible biological interactions within our specific experiment.

4.1. Population differences

The two cod populations reared in this experiment were affected differently by the different rearing conditions. In contrast to earlier findings (van der Meeren et al., 1994; Svåsand et al., 1996; Otterlei et al., 1999; van der Meeren and Jørstad, 2001). NA larvae had a higher growth than NC larvae throughout most of our experiment in the non-mixed mesocosms. According to the model comparison the NC larvae clearly grew sub-optimally in our rearing conditions. Otterlei et al. (1999) pointed to the fact that their findings of stock-specific difference in growth were small, compared to the effect of temperature, while Suthers et al. (1999) did not find any stock-specific differences between the populations. Confounding factors like initial size and maternal effects (Chambers and Waiwood, 1996; Clemmesen et al., 2003), together with difficulties of getting a representative sample from the populations, can easily affect the results when variance in size and growth is large. In addition, relatively high mortality rates, as observed in our experiment, may affect the growth estimates and either inflate or deflate observed differences between larval groups through selective mortality (Tian et al., 2007). Even so, the suboptimal growth of NC larvae from our experiments highlights the point that this stock-specific growth difference seems to be small compared to the growth variance within populations during ELS.

The weight-at-length difference found during ELS between the two stocks is an indication that there are already, from early larval stages, differences in morphological characteristics. Earlier work has reported population-specific difference at pre-juvenile stages (>12 mm) (Otterlei et al., 1999), while our work suggests that this population-specific difference is already present from a larval stage (<12 mm). Differences in morphology can possibly reflect differences in prevailing physical and biological conditions at early life stages for the two stocks. Small survival advantages for morphologically adapted larvae might create enough selective pressure at ELS to create population-specific differences. Interestingly though, the heavier NC fish did not have an advantage in the mixed mesocosms, disappearing already after 5 dph. Population differences in morphology at adult stages have long been common knowledge among fishermen (Svåsand et al., 1996). The stout and smaller NC cod is often easy to separate from the thinner and more elongated NA cod. These morphological differences may reflect the migratory behaviours of the two stocks, with NA cod migrating considerably more than NC cod. A more elongated body form has been documented in salmonids, which have long migrating patterns (Fleming and Gross, 1989), while adaptations in body form in relation to environment have recently been documented in cod during juvenile stages (Marcil et al., 2006). If the more elongated body, observed already at larval stages, is an effect of selection for migratory life cycle, this indicates that selection occurring at subsequent stages can affect the growth, energy allocation, and form of the larva.

4.2. Size versus mortality during ELS

Size is important in relation to food availability because it increases prey search- and capture ability (Blaxter, 1986). The apparent disadvantage of initial size of the second cohort manifested itself as increased mortality when interacting with the other larval groups. Even in HC mixed mesocosms the second cohort had lower survival than in the non-mixed mesocosms, indicating interference effects under feeding conditions that have been considered earlier as adequate (e.g., van der Meeren and Jørstad, 2001). Blom et al. (1994) demonstrated that food limitation at early juvenile stages in a marine pond induced a differential size-selective mortality between groups with a 4-day difference in age, and suggested that this was a result of density-dependent food competition during the early juvenile stage. This might have been the case in our setup already from an early larval stage. This is further supported by the complete disappearance of second cohort larvae in the LC mesocosms. Cannibals were not observed in our experiment until the last part of the experiment (Seljeset, 2006), and the two cohorts were not sufficiently different in size at early stages (Folkvord, 1997). Both cohorts had a strong selection for nauplii in the first part of the experiment (Seljeset, 2006), which could have led to an inter-cohort-specific competition for suitable prey. It thus seems likely that food availability was the most determining factor for the observed difference. However, other interference effects (i.e. antagonistic behaviour) cannot be ruled out.

Size-selective mortality in predator free environments is generally explained as either (1) changes in food availability, which favours a certain size (Folkvord et al., 1994a), (2) cannibalism (Folkvord and Otterå, 1993), or (3) social hierarchies, where lower ranked individuals suffer (Koebele, 1985). Decreasing variance in size distribution of the second cohort coincided with the change from 1500 to 1000 prey/L and increase in added average prey size. This could have led to a size-selective mortality favouring larger individuals. Furthermore, there was evidence of cannibalism in the tanks at the end of the experiment from observations from stomach analysis (Seljeset, 2006). However, CV actually increased in the last weeks in the NAI group in the HC. One possible explanation is that the cannibalism was inter-specific (Folkvord et al., 1994b), i.e. smaller individuals being removed were the larvae of the second cohort. In this case larger individual would increase growth (and CV) due to a piscivore diet, whilst smaller individuals of the cohort would not be removed. This is further supported by the fact that CV of the NAII fish in the non-mixed mesocosms decreased towards the end of the experiment, even though they surpassed the NAI in size, indicating cohort specific cannibalism.

We found a positive relationship between survival and growth between mesocosms. Since no predation/cannibalism was evident in the first weeks of sampling (Seljeset, 2006), high survival was probably correlated with sufficiently available prey to sustain required growth rates during early larval stages. This is further supported by the fact that the mesocosms with high survival of NAI larvae were also the mesocosms with the highest survival of the second cohort, and the fact that the faster-growing NA cod survived better in the mixed tanks than the slower-growing NC cod. This is in line with earlier findings from laboratory experiments (Buckley et al., 1993), and indicates that fast growth is not necessarily directly related to survival, but is a typical feature of a cohort with high survival in the first 2 weeks of their lives.

There was a clear indication of a negative correlation between growths in the first week and last week of the experiment within mesocosms. This could reflect the intrinsic dome-shaped growth progression of cod larvae (present study; Otterlei et al., 1999; van

der Meeren and Moksness, 2003). In addition, larvae grow and die at different rates within each experimental unit, which subsequently creates differently experienced feeding conditions. This growth progression can be a confounding factor when working with population-specific growth differences, and necessitates either the use of otolith microstructure to derive individual growth histories (Suthers et al., 1999; van der Meeren and Moksness, 2003) or a frequent sampling scheme to map out actual differences in early larval growth.

4.3. Final remarks

Our results contradict earlier findings of population-specific growth differences, but support findings of morphological differences. We suggest that lower growth during early larval stages was accompanied by lower survival, and that this was further enhanced when larvae interacted with older and larger larvae. Common garden experiments that seek to study the relevance of feeding conditions should thus be accompanied by additional single groups to be able to evaluate whether growth and survival differences are due to differences in intrinsic factors or an artifact of the imposed interference effects between groups in closed environments. To further evaluate whether growth differences are really a result of food-limited growth conditions, the comparison with STDG models that predict optimal growth is recommended.

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References

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426 (6967), 661–664.

Bergstad, O.A., Jørgensen, T., Dragesund, O., 1987. Life history and ecology of the Gadoid resources of the Barents Sea. Fisheries Research 5, 119–161.

Blaxter, J.H.S., 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Transactions of the American Fisheries Society 115 (1), 98–115.

Blom, G., Svåsand, T., Jørstad, K.E., Otterå, H., Paulsen, O.I., Holm, J.C., 1994. Comparative survival and growth of two strains of Atlantic cod (*Gadus morhua*) through the early life stages in a marine pond. Canadian Journal of Fisheries and Aquatic Sciences 51, 1012–1023.

Buckley, L.J., Smigielski, A.S., Halavik, T.A., Burns, B.R., Laurence, G.C., 1993. Growth and survival of the larvae of three temperate marine fish species at discrete prey densities. II. Cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and silver hake (*Merluccius bilinearis*), In: Walthers, B.T., Fyhn, H.J., (Eds.), Physiology and Biochemistry of Fish Larval Development. University of Bergen, Bergen, pp. 183–195, ISBN 82-992402-0-4.

Chambers, R.C., Waiwood, K.G., 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences 53, 186–2003.

Clemmesen, C., Bühler, V., Carvalho, G., Case, R., Evans, G., Hauser, L., Hutchinson, W.F., Kjesbu, O.S., Mempel, H., Moksness, E., Otterå, H., Paulsen, H., Thorsen, A., Svåsand, T., 2003. Variability in condition and growth of Atlantic cod larvae and juveniles reared in mesocosms: environmental and maternal effects. Journal of Fish Biology 62 (3), 706–723.

Conover, D.O., Present, T.M.C., 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83 (3), 316–324.

Fleming, I.A., Gross, M.R., 1989. Evolution of adult female life-history and morphology in a pacific samlon (Coho, *Oncorhunchus-kisutch*). Evolution 43 (1), 141–157.

Folkvord, A., 1997. Ontogeny of cannibalism in larval and juvenile fish with special emphasis on cod, *Gadus morhua*. In: Chambers, L.R.C., Trippel, E.D. (Eds.), Early Life History and Recruitment in Fish Populations. Chapman & Hall, London, pp. 251–278.

Folkvord, A., 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences 62 (3), 1037–1052.

Folkvord, A., Otterå, H., 1993. Effects of initial size distribution, day length and feeding frequency on growth, survival and cannibalism in juvenile Atlantic cod (*Gadus morhua L.*). Aquaculture 114 (3–4), 243–260.

Folkvord, A., Blom, G., Dragesund, O., Johannessen, A., Nakken, O., Nævdal, G., 1994a. A conceptual framework for enhancing and stabilizing recruitment of marine fish stocks. Aquaculture and Fisheries Management 25, 245–258.

Folkvord, A., Øiestad, V., Kvenseth, P.G., 1994b. Growth patterns of three cohorts of Atlantic cod larvae (*Gadus morhua* L.) studied in a macrocosm. ICES Journal of Marine Science 51, 325–336.

Koebele, B.P., 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. Environmental Biology of Fishes 12, 181–188.

Laurence, G.C., Smigielski, A.S., Halavik, T.A., Burns, B.R., 1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer 178, 304–311.

Marcil, J., Swain, D.P., Hutchings, J.A., 2006. Countergradient variation in body shape between two populations of Atlantic cod (*Gadus morhua*). Proceedings of the Royal Society B—Biological Sciences 273 (1583), 217–223.

Meekan, M.G., Fortier, L., 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Marine Ecology Progress Series 137 (1–3), 25–37.

Munk, P., 1995. Foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and hunger. Marine Biology 122 (2), 205–212.

Otterlei, E., Nyhammer, G., Folkvord, A., Stefansson, S.O., 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal Fisheries and Aquatic Sciences 56 (11), 2099–2111.

Puvanendran, V., Brown, J.A., 1999. Foraging, growth and survival of Atlantic cod larvae reared in different prey concentrations. Aquaculture 175 (1–2), 77–92.

Sarvas, T.H., Fevolden, S.E., 2005. Pantophysin (Pan I) locus divergence between inshore v. offshore and northern v. southern populations of Atlantic cod in the north-east Atlantic. Journal of Fish Biology 67 (2), 444–469.

Seljeset, O., 2006. Importance of abundance and prey size spectra for growth and survival in larval cod. M.Sc. Thesis, Department of Biology, University of Bergen.

Suthers, I.M., 1998. Bigger? Fatter? Or is faster growth better? Considerations on condition in larval and juvenile coral-reef fish. Australian Journal of Ecology 23 (3), 265–273.

Suthers, I.M., van der Meeren, T., Jørstad, K.E., 1999. Growth histories derived from otolith microstructure of three Norwegian cod stocks co-reared in mesocosms; effect of initial size and prey size changes. ICES Journal of Marine Science 56 (5), 658–672.

Svåsand, T., Jørstad, K.E., Otterå, H., Kjesbu, O.S., 1996. Differences in growth performance between Arcto-Norwegian and Norwegian coastal cod reared under identical conditions. Journal of Fish Biology 49 (1), 108–119.

Tian, T., Fiksen, Ø., Folkvord, A., 2007. Estimating larval fish growth under size-dependent mortality: a numerical analysis of bias. Canadian Journal of Fisheries and Aquatic Sciences 64 (3), 554–562.

van der Meeren, T., Jørstad, K.E., 2001. Growth and survival of Arcto-Norwegian and Norwegian coastal cod larvae (*Gadus morhua* L.) reared together in mesocosms under different light regimes. Aquaculture Research 32 (7), 549–564.

van der Meeren, T., Moksness, E., 2003. Growth and mortality patterns evaluated from otolith microstructure in Atlantic cod *Gadus morhua* larvae reared on different feeding regimes in mesocosms. Marine Ecology Progress Series 264, 95–107.

van der Meeren, T., Jørstad, K.E., Solemdal, P., Kjesbu, O.S., 1994. Growth and survival of cod larvae (*Gadus morhua* L.): comparative enclosure studies of Northeast Arctic cod and coastal cod from western Norway. ICES Marine Science Symposium 198, 633–645.