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Using otolith microstructure to analyse growth of juvenile Baltic cod *Gadus morhua*

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ABSTRACT: Pelagic and demersal juvenile Baltic cod *Gadus morhua* L. were collected on the slope and the top of Rønne bank in the Baltic Sea during 2 cruises in November and December 1998. The growth, age at settling and vertical migration pattern were studied by otolith microstructure analysis. The relationship between fish and otolith size were found to change at settling, with an increase of fish size in relation to otolith size after settling. This change was more pronounced on the slope compared to the top of the bank. The timing of first settling at the 2 localities did not differ with respect to fish age. At both localities, fish that hatched early in the season spent a shorter time in the pelagic stage than late-hatched fish. However, significant differences in growth rate during the pelagic stage were observed, where fish captured on the slope grew faster. On the bank, individuals with fast otolith growth rates before settling continued to grow fast after settling. On the slope, no relationship between growth before and after settling was found. These results indicate that the different settling habitats occupied by juvenile Baltic cod have different potential for settling and nursery areas.

KEY WORDS: Baltic Sea · Juvenile cod · Otolith microstructure · Growth · Settling behaviour

INTRODUCTION

During their first year of life, Baltic cod *Gadus morhua* L. undergo a series of life stages, from the egg to yolk-sac larva, and larva to the pelagic and demersal juvenile stages. During these early life stages, mortality is extremely high in gadoid fish, decimating numbers by as much as 99.9% (Houde 1987, Rice et al. 1993, Cushing & Horwood 1994). Baltic cod have an extended spawning period, from March through to September (Bagge & Thurow 1993, Wieland & Zuzarte 1996). From the Bornholm Basin, Denmark, cod larvae and pelagic juveniles can be transported into nearshore areas below the Ekman layer, where they make the transition to the demersal life stage (Hinrichsen et al. 1997, 2001, Voss et al. 1999).

During the transport from spawning to juvenile nursery areas, survival is determined primarily by predation, the temporal match between larval hatching and the production of their zooplankton prey, as well as advection and retention of fish in favourable environments (e.g. Hjort 1914, Cushing 1972, Lasker 1981, Sissenwine 1984, Bailey & Houde 1989, Miller 1997). For Baltic cod, hatching and the early larval stage have been identified as two of the most critical periods (Köster et al. 2001), where density-independent processes like predation, cannibalism and food availability control larval survival (Cushing 1983, Fortier & Villeneuve 1996).

However, variability in the density-independent component of early life mortality is small (Myers & Cadigan 1993b), and abundances of eggs and larvae are seldom a good predictor of recruitment (Sissenwine 1984, Smith 1985, Peterman et al. 1988, Campana 1996). While the mechanisms regulating survival of larvae and pelagic juveniles may be predominantly density-independent, density-dependent mechanisms seem to take over during and after settling (Sundby et al. 1989, Myers & Cadigan 1993a).

In coral reef fishes, as in the demersal stage of a wide range of species, strong density-dependent competition for territories with shelter and favourable feeding

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conditions at settling is well known. This competition either affects survival of newly settled fish directly (e.g. Sissenwine 1984, Forrester 1990, Tupper & Hunte 1994, Carr & Hixon 1995, Tupper & Boutilier 1995a,b, Van der Veer et al. 1997), or regulates the size of the adult population by affecting the time until juveniles reach maturity (Jones 1987). Survival of pre-recruits is thus determined by an interaction of predation with other processes, such as competition for food and suitable habitat. A number of studies show that as fish grow, they pass through prey fields of various predators (e.g. Folkvord & Hunter 1986, Post & Evans 1989a), and that both the number of potential predators and the mortality they cause decrease with increasing fish size (Zijlstra et al. 1982, Van der Veer et al. 1996, Miller 1997).

The key driving force behind enhanced survival success, according to these theories, is growth. Even small changes in growth rate may affect survival considerably (Houde 1987, Rice et al. 1993, Campana 1996, Meekan & Fortier 1996). Analyses of growth patterns may thus provide insight into the mechanisms regulating survival of fish, as well as the suitability of different habitats as nursery areas.

In the Baltic, the biomass of the primary copepod prey species of pelagic cod increases steadily from <100 mg m^{-3} in January to ca. 900 mg m^{-3} in July, and decreases dramatically during August/September, down to levels found in winter (Möllmann et al. 2000). Depending on hatch date, transport conditions and settling habitat, the individuals experience widely different environmental conditions, providing the foundation for widely varying growth and survival rates.

The main objectives of this study were to examine growth of juvenile Baltic cod from the pelagic stage through the transition to the early demersal stages, using otolith microstructure analysis. Particularly, the timing of settling in relation to hatch date and growth during the pelagic stage and the effect of pelagic growth rate on growth during the demersal stage was investigated. The effect of settling habitat on growth was also evaluated by comparison of growth between a deep locality with a temperature-stratified water column on the slope of the Bornholm Basin and a shallow, vertically mixed locality on the Oder bank.

MATERIALS AND METHODS

Field samples. A total of 82 pelagic juvenile Baltic cod were collected with RV 'Solea' on 3 to 5 November, of which a subsample of 20 fish was selected (see also Hüssy et al. 2003, this issue). In all, 169 demersal juvenile Baltic cod were collected with RV 'Dana' on 8 December in a shallow area on Oder bank (density: 0.3 ind. m^{-2}) and 105 juveniles in a deeper area on the slope of the Bornholm Basin (density: 0.2 ind. m^{-2}) (see Hüssy et al. 2003). For analysis, a random subsample of 50 fish was selected from each area.

On the bank, the water column was mixed virtually throughout the year, with temperatures decreasing from approximately 14 to 4.5°C in the investigated time period. Data were not available from Day of Year 334 onward, but were extrapolated linearly to measured values from the December cruise. On the slope, a strong thermocline developed around Day of Year 120, with 14°C in the surface and 5°C at the bottom and persisted approximately until Day 290. After Day of Year 320, an inverse thermocline, with cold water above warmer bottom water, developed and persisted until the day of capture. A detailed description of the geographical location, water depth and hydrography on these localities, hereafter called bank and slope, is given in Hüssy et al. (2003). The same random subsample of 50 fish from that study was also used in the present work.

After capture, the fish were immediately frozen at –20°C. Upon thawing, standard length (SL) was measured to the nearest 0.5 mm, and fish weighed to the nearest 0.01 g after drying at 60°C for 48 h (dry weight; DW). Sagittal otoliths, hereafter called otoliths, were extracted, rinsed in water and stored in labelled plastic bags.

Otolith treatment. After weighing to the nearest µg (otolith weight; OW), otoliths were ground and polished to a thickness of approximately 80 µm following the method described in Hüssy et al. (2003). Otoliths were analysed using an image analysis system (Image Pro, Version 4) with a microscope coupled to a monitor screen by a CCD camera and a frame grabber. The digitised images were saved as TIFF-files in black and white. Total length from the nucleus to the edge (otolith length; OL) was measured along the longest distance from the nucleus to the tip of the rostrum at a magnification corresponding to 6.4 µm $pixel^{-1}$. Measurements taken at different positions in the frontal lobe were scaled to total rostral length. Increment widths were analysed along a profile of grey values increasing from 0 (pure black) to 255 (pure white), with the 'caliper' tool of Image Pro using a profile width of 50 µm and a magnification corresponding to 2.2 µm $pixel^{-1}$. This tool identifies recurring patterns based on the residuals from a running average. The start of an increment was defined as the point at which the grey values changed at the fastest rate towards higher values (higher transparency). Increments were measured, and numbered, from the formation of the accessory primordia towards the edge (terminology see Campana & Neilson 1985). The daily formation periodicity of incre-

ments obtained using this method could not be rejected (Hüssy et al. 2003), and increments were therefore assumed to be daily.

Intervals of similar increment structure were identified using the method based on the difference between running averages of consecutive increment widths described in Hüssy et al. (2003, see 'Increment structure in field samples', p 246): average(IW_{i-10} to IW_i) – average(IW_i to IW_{i+10}). The first change in increment patterns was assumed by these authors to be correlated with time of settling, because: (1) juveniles caught in November did not have a change in increment widths, (2) the fish from the December sample that had settled before the November cruise, and therefore could not be caught with pelagic trawls, had a change in increment width (see 'Results'), (3) the back-calculated fish size at first pattern change in the December sample corresponded well with observed fish sizes at settling (see Hüssy et al. 2003). Increments between the accessory primordia and this first change in increment structure were called pelagic increments; those formed after the change were called demersal increments. Numbers of increments within the 2 intervals were recorded. OL at formation of accessory primordia was calculated as OL – $\sum(IW_i)$ and OL at increment pattern change as OL – $\sum(IW_{demersal})$.

Since all fish were assumed to originate from the same cohort, samples were pooled to result in a better model for fish DW:

$$\ln(DW) = a + b \cdot \ln(OW) + c \cdot \ln(OW)^2 \quad (1)$$

where $a = -2.025$, $b = 0.924$ and $c = 0.094$ (df = 119, r^2 = 0.96). Correspondingly, fish length was best described by the model:

$$\ln(SL) = d + e \cdot \ln(OL) + f \cdot \ln(OL)^2 \quad (2)$$

where $d = 7.550$, $e = -1.776$, $f = 0.182$ (df = 119, r^2 = 0.97). Fish size at settling ($SL_{settling}$) was therefore back-calculated assuming a proportional relationship between otolith size and fish size over time:

$$\ln(SL_{settling}) = \ln(SL_{catch}) \times \frac{d + e \cdot \ln(OL_{settling}) + f \cdot \ln(OL_{settling})^2}{d + e \cdot \ln(OL_{catch}) + f \cdot \ln(OL_{catch})^2} \quad (3)$$

Statistical analysis. Measurements of fish length and weight, OL and OW of the field sample were tested for normality using the Kolmogorov-Smirnov 1-sample test. Normally distributed data of fish length and weight and OL and OW were then compared using 1-way ANOVA, while non-normally distributed data were analysed using Wilcoxon rank sum test for equality of means. The frequency distributions of fish ages were compared using Wilcoxon signed rank test for paired observations. Regression coefficient and intercepts of regressions were compared using ANCOVA. Significance levels were set at p = 0.05. The number of observations were 20 for the November sample and 50 for both slope and bank of the December samples.

Table 1. *Gadus morhua*. Summary of fish and otolith measurements (mean ± SD). Pelagic days = days from the accessory primordia to the first change in increment pattern, juvenile days = days from the accessory primordia to the edge. Day of Year 290 = day of thermocline breakdown. Significance levels of comparison between slope and bank samples: ***p < 0.001, **p < 0.01, *p < 0.05, ns: not significant

Parameter	Demersal		Pelagic
	Slope	Bank	
Sample number	50	50	20
Fish length (mm)	69.22 ± 21.26	61.64 ± 26.16***	41.30 ± 8.10
Dry weight (g)	0.71 ± 0.72	0.64 ± 1.36***	0.09 ± 0.05
Juvenile days	68 ± 22	66 ± 32 ns	31 ± 13
Otolith weight (mg)	3.85 ± 2.78	3.60 ± 5.38***	0.55 ± 0.36
Otolith total length (µm)	1379 ± 363	1200 ± 552***	620 ± 185
Otolith length at settling (µm)	793 ± 160	731 ± 242**	
Pelagic days	28 ± 9	27 ± 11 ns	
Otolith length on Day 290 (µm)	793 ± 327	649 ± 242**	

RESULTS

Differences between localities at catch

The analysis of fish length, DW, OL and OW of the December samples showed significant differences between the 2 localities: juveniles from the slope were larger/heavier (both p < 0.001, df = 98), and had larger/heavier otoliths than juveniles from the bank (both p < 0.001, df = 98). Their age distributions (age from accessory primordia to edge), however, did not differ (p = 0.72, Table 1). Subtracting the 34 d between the 2 cruises from the number of juvenile days and the sum of the outermost 34 increments from OL of fish from the December samples yielded an age distribution that did not differ significantly from the November sample (p = 0.70) (Fig. 1). Juveniles from the 2 cruises can therefore be assumed to be derived from the same cohorts of fish.

Between the 2 localities of the December sample, significant differences were found in the intercept and regression coefficient of the ln(DW) = $a + b \times$ ln(OW) relationship (p < 0.05, df = 96). Significant differences were also found between the regression coefficients of the 2 demersal samples and the pelagic November sample (both p < 0.001, df = 66) (Fig. 2). This is probably caused by an ontogenetic change in the otolith

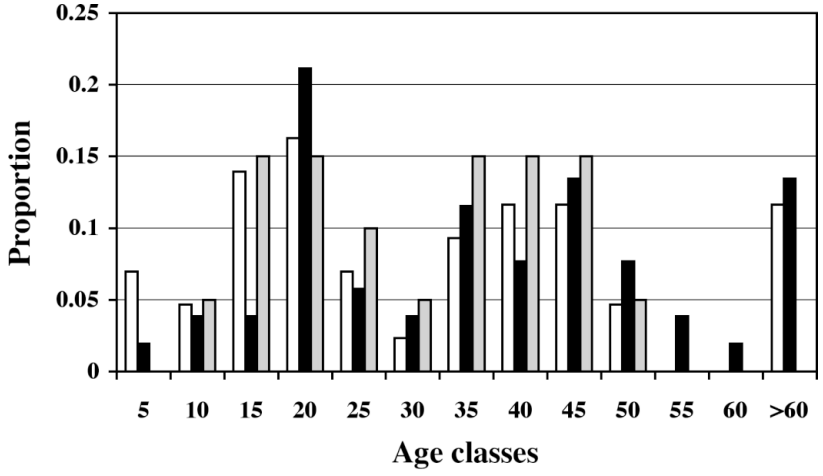

Fig. 1. *Gadus morhua*. Frequency distributions of fish age from the accessory primordia to the edge at capture of the November sample (grey columns), and the December samples, back-calculated to the date of the November sample (black columns: slope; white columns: bank)

size–fish size relationship, resulting in higher somatic growth in relation to otolith growth after settling to the demersal habitat.

Pelagic life-stage and settling period

The 2 areas did not differ with respect to OL at formation of accessory primordia ($p = 0.55$). The number of days from the accessory primordia to settling and the corresponding otolith growth rates were analysed in relation to average date of pelagic increment formation. The pelagic phase duration (number of days in first increment pattern interval) was significantly and positively correlated with average Day of Year of increment formation, showing that early spawned juveniles settled at a younger age than those which were late spawned. Intercept and slope of these regressions did not differ significantly between the 2 localities (both < 0.05, df = 49) (Fig. 3).

Since the number of days in the pelagic stage did not differ between the 2 localities, the corresponding average increment widths were regressed on average Day of Year of increment formation. This revealed a significant, negative correlation for the bank locality ($p < 0.001$, df = 49). Excluding the 6 latest settled individuals, whose increments may have been affected by an ontogenetically determined decrease in width, from the analysis did not change the result ($p < 0.001$, df = 43). This means that the earlier in the season that fish are spawned, the wider their increments. On the slope locality this correlation was also negative, but not significant ($p = 0.056$, df = 49). In the context of this paper, this presumably temperature-induced decline in increment width is not interesting. More importantly, comparisons showed that throughout the pelagic stage, increments of fish caught on the bank were significantly smaller than fish caught on the slope ($p < 0.01$, df = 96) (Fig. 4).

These results indicate that early spawned fish settle at a younger age than fish spawned later in the year. On the slope, fish settled at the same age as those on the bank, but had faster otolith growth rates. The settling pattern of the 2 localities is shown in Fig. 5, represented as proportion of settled individuals in relation to date, days after formation of accessory primordia, and fish size in mm (Fig. 5a,b and c, respectively).

Demersal life stage

Average growth rates during the demersal stage were calculated as $(SL_{catch} - SL_{settling})$/days in demersal stage. The proportional distribution of demersal growth rates shows that during the demersal stage, fish on the bank experienced slower somatic growth than those on the slope (Fig. 6). At settling, fish from the

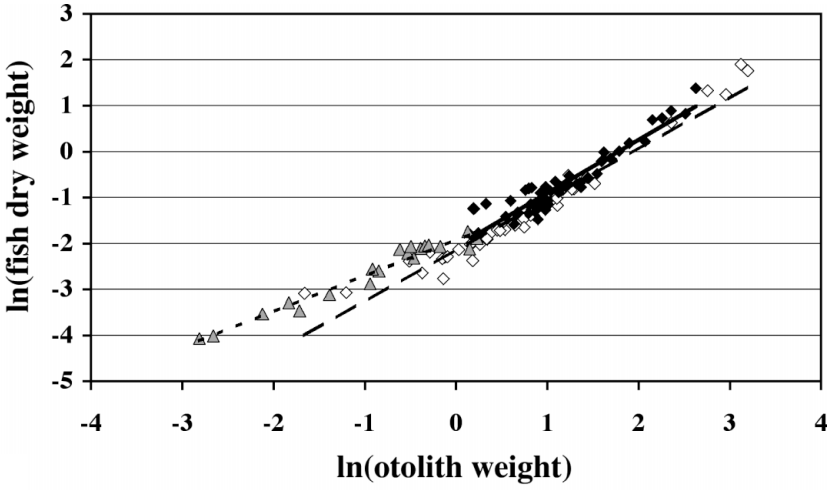

Fig. 2. *Gadus morhua*. Relationship between fish dry weight (g) and otolith weight (mg). △: pelagic stage; ◇: bank; ◆: slope; dotted line: pelagic stage, $\ln(DW) = -1.91 + 0.78 \cdot \ln(OL)$, $r^2 = 0.96$, $p = < 0.001$; solid line: slope, $\ln(DW) = -2.33 + 1.48 \cdot \ln(OL)$, $r^2 = 0.91$, $p < 0.001$; broken line: bank, $\ln(DW) = -2.14 + 1.09 \cdot \ln(OL)$, $r^2 = 0.95$, $p < 0.001$

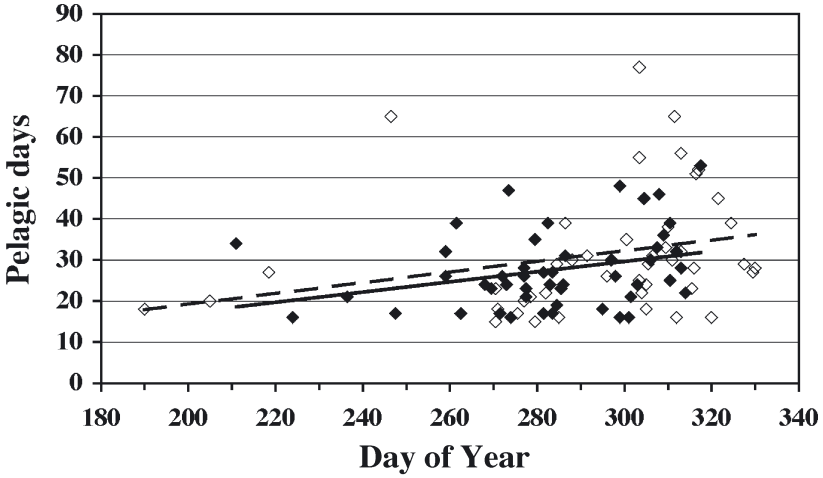

Fig. 3. *Gadus morhua*. Number of days spent in the pelagic stage in relation to average date of increment formation. ▲: slope; ◇: bank; solid line: slope, Pelagic Days = −7.562 + 0.124 × Day of Year, r^2 = 0.096, p = 0.026; broken line: bank, Pelagic Days = −7.441 + 0.132 × Day of Year, r^2 = 0.054, p = 0.043. Common regression: Pelagic Days = −9.755 + 0.136 × Day of Year, r^2 = 0.09, p = 0.003

slope had significantly larger otoliths than fish from the bank, although they were of similar age. The observed difference in otolith size between the 2 localities increased from the time of settling (average of 62 µm) to capture (average of 179 µm).

A significant difference in OL back-calculated to Day of Year 290 (breakdown of thermocline) was observed between the 2 localities (average of 144 µm, p < 0.01, df = 96). However, this difference between OL at the 2 localities was similar to the one observed at catch (average of 179 µm, see Table 1). Growth rates of slope cod otoliths must therefore have been faster than bank cod otoliths during the time before the breakdown of the thermocline.

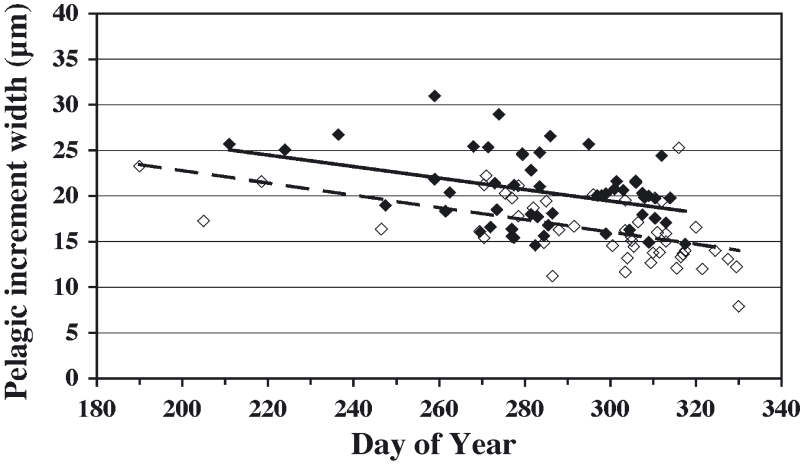

Fig. 4. *Gadus morhua*. Average increment widths (mm) of the pelagic stage in relation to average date of formation. ◆: slope; ◇: bank; solid line: slope, average IW = 32.87 − 0.044 × Day of Year, r^2 = 0.07, p = 0.0563; broken line: bank, average IW = 36.47 − 0.068 × Day of Year, r^2 = 0.24, p = 0.00064

Coupling between growth rates at settling and size at catch

The effect of fast growth during the pelagic stage on fish size at capture was assessed using the residuals from the increment width–day of formation regression (Fig. 6), assuming that fish with positive residuals had experienced fast otolith growth and fish with negative residuals slow otolith growth. The residuals from the 2 localities ($resid_{bank}$ and $resid_{slope}$) were regressed against fish DW at capture. A significant, positive correlation was found for the bank sample: $resid_{bank}$ = −0.6955 + 3.6012 × DW (p < 0.01, df = 49, r^2 = 0.17), while growth rate before settling had no effect on fish size at capture on the slope: $resid_{slope}$ = −0.8591 + 1.4176 × DW (p = 0.17, df = 49, r^2 = 0.04).

DISCUSSION

In the present study, early spawned Baltic cod were found to make the transition to the demersal habitat at a younger age than their late-spawned conspecifics. Fish with the best match between hatch-date timing and maximal zooplankton biomass may thus experience the fastest growth rates, which leads to early settling and promotes better survival according to the 'match-mismatch' (Cushing 1972) and 'stage duration' hypotheses (Houde 1987). The spawning date/age-dependent settling pattern was the same at both localities. However, fish settling on the slope had wider pelagic increment widths throughout the season, indicating that these fishes had grown faster. These results suggest growth-rate-related differences in settling habitat, mediated by either preferences in settling habitat, differential size-specific mortality rates, or an interaction between growth and mortality.

Preferences in settling habitat

Baltic juvenile cod have been observed to undertake exploratory migrations into deeper water layers as early as at the pelagic stage (Böttcher et al. 1998). The observed segregation

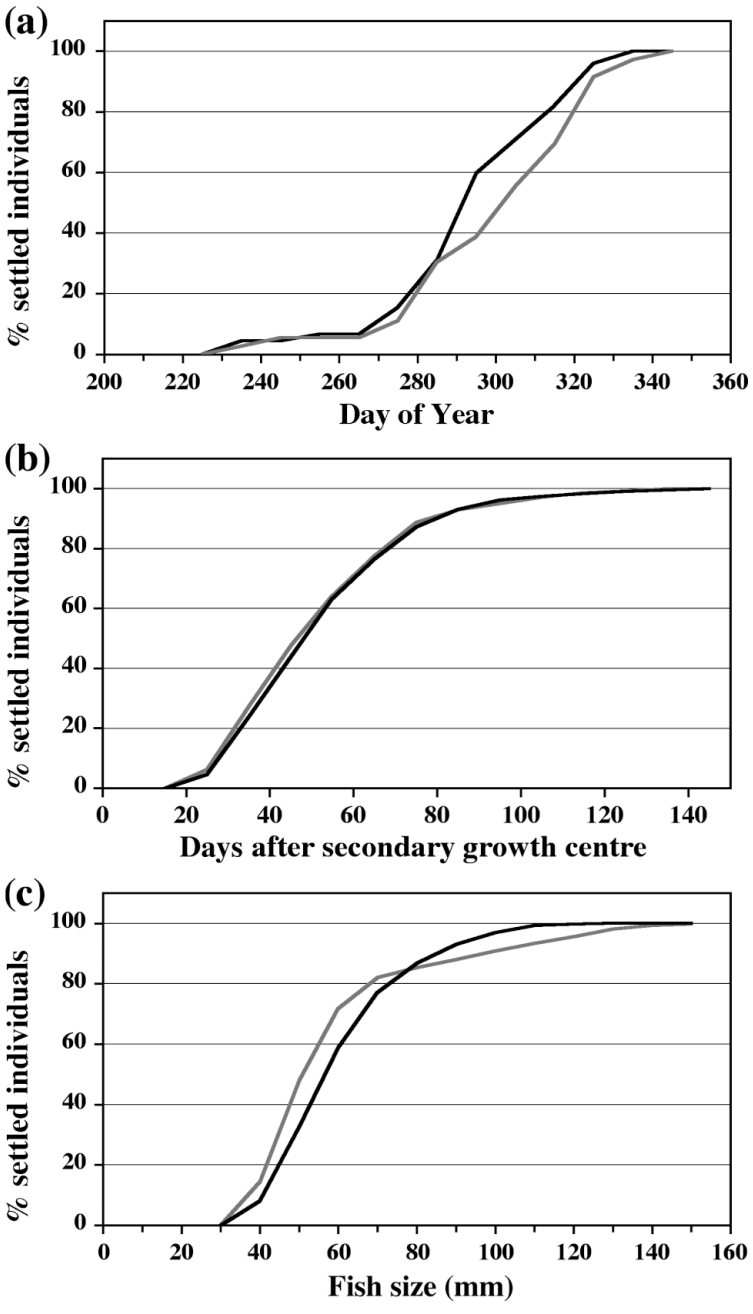

Fig. 5. *Gadus morhua*. Cumulative proportion of settled juvenile cod in relation to (a) Day of Year, (b) days after formation of the accessory primordia and (c) fish length. Black line: slope; grey line: bank

may therefore occur if juveniles with faster growth rates select different habitat types for settling, in this case the deeper slope.

Size-specific mortality

In Norwegian Atlantic cod, the relationship between predation-induced mortality and growth seems to be one of the driving forces regulating the timing of and size at settling (Salvanes et al. 1994). Due to changes in mortality and growth rates, the mortality:growth ratio increases with time and fish size, which may induce the juvenile fish to switch to a habitat with a lower mortality:growth ratio (Salvanes et al. 1994). Therefore, differential predation-induced mortality may have caused the observed settling patterns. In the juveniles examined in this study, no difference in time spent in the pelagic stage was observed, and predation-induced differences in the settling pattern would therefore have to occur during the demersal stage. However, the distributions of juvenile and adult cod, their only predator in the Baltic Sea, are spatially segregated (Aro 1989, Sparholt et al. 1991), and cannibalism is therefore limited (Uzars & Pliksh 2000). Predation-related mortality therefore seems an unlikely explanation for the observed settling pattern.

Interaction between growth and mortality

After settling, the fish size–otolith size relationship changed. Such changes have previously been associated with ontogenetic development from one life stage to another (Hare & Cowen 1995, Rogers et al. 2001) and may be caused by a stage-specific, more cost-effective, increase in prey size (Mittelbach 1983). At capture, fish and otoliths were significantly smaller on the bank, and the difference in otolith size between the 2 areas increased after settling. Also, the regression coefficient of the fish size–otolith size relationship was significantly smaller in the bank sample, indicating slower somatic growth compared to the slope (Secor & Dean 1989). At least 2 mechanisms may have caused these differences: differential temperature regimes or prey availability.

Temperature

Below the temperature for optimal growth, otolith growth rate increases proportionally with somatic growth rate (Marshall & Parker 1982, Mosegaard & Titus 1987, Mosegaard et al. 1988); higher temperatures lead to a decoupling between the 2 growth rates (Mosegaard & Titus 1987). However, a temperature-mediated decoupling during the demersal stage can be excluded, since temperatures never exceeded 14°C at both localities.

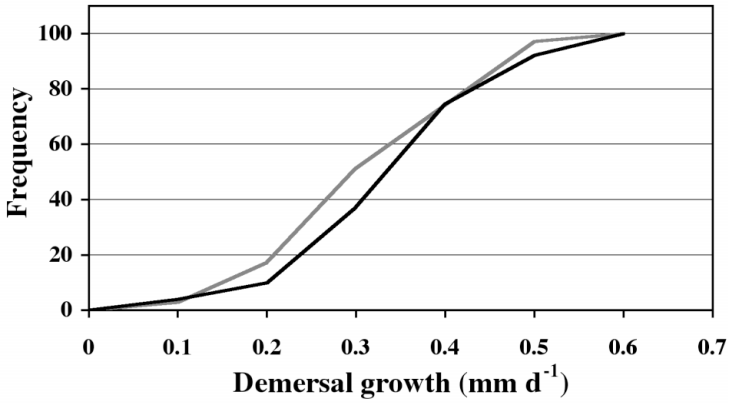

Fig. 6. *Gadus morhua*. Cumulative growth frequencies of juvenile Baltic cod during the demersal stage on the 2 localities investigated. Black line: slope; grey line: bank

Prey availability

The diversity of potential prey species in the Baltic Sea is limited, forcing newly settled cod to feed on the same size-range and species of prey as fish of a larger size (Hüssy et al. 1997). The major prey items during the first months of the demersal stage are benthic and semi-benthic invertebrates such as mysids and amphipods (Hüssy et al. 1997), whose highest densities are found below 25 m (Aschan 1988, Hansson et al. 1990, Rudstam & Hansson 1990). On the slope, feeding conditions may therefore have been more favourable than on the shallow bank due to greater variety and quantity of prey items, as suggested by Hüssy et al. (1997). Since the density of juvenile cod was also lower on the slope, and mortality due to predation is negligible (Uzars & Pliksh 2000), density-dependent competition for food may have been a mechanism responsible for the observed differences in growth.

Juvenile Atlantic cod become territorial after settling, defending territories in association with shelter sites (Tupper & Boutilier 1995a,c), which results in size-selective growth, mediated by strong density-dependent competition, not just for food resources but also for shelter sites (Tupper & Boutilier 1995a,c). No knowledge exists of the behaviour in demersal juvenile Baltic cod, but our results agree with the finding of Tupper & Boutilier (1995a,c): in Baltic cod, late-spawned fish experienced a prolonged pelagic stage, and fast pelagic growth entailed fast demersal growth on the bank, but not on the slope.

However, no differences in growth occurred between the 2 localities after the breakdown of the thermocline on the slope until capture, apparently linking the better growth conditions on the slope with the existence of the thermocline. Extensive daily vertical migrations are well known in juvenile Atlantic (Perry & Neilson 1988, Lough et al. 1989, Lough & Potter 1993) and Baltic cod (Böttcher et al. 1998). Comparison between observed otolith growth rates, with growth rates estimated under different assumptions of juvenile behaviour, indicated that juvenile cod from the slope were in fact undertaking daily vertical migrations (Hüssy et al. 2003). These migrations are thought to maximise consumption (Bromley & Kell 1995) and to regulate the fish's energy budget (Javaid & Anderson 1967, Mac 1985, Neverman & Wurtsbaugh 1994, Sogard & Olla 1996) and may promote differential growth rates.

Mortality during the first winter is highest in small fish of a variety of species (Post & Evans 1989b, Cargnelli & Gross 1996, Gotceitas et al. 1999). Attaining as big a size as possible before the onset of winter is therefore of vital importance for juvenile cod. The results from this investigation suggest that the time of hatch, growth during the pelagic stage and the habitat selected for settling are some of the key factors for survival of juvenile Baltic cod.

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