Journal of Fish Biology (2007) **70,** 584–599
doi:10.1111/j.1095-8649.2007.01331.x, available online at http://www.blackwell-synergy.com

Phenology and North Sea cod *Gadus morhua* L.: has climate change affected otolith annulus formation and growth?

G. M. Pilling*, R. S. Millner, M. W. Easey, D. L. Maxwell and A. N. Tidd

The Centre for Environment Fisheries and Aquaculture Science (Cefas), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, U.K.

(Received 27 February 2006, Accepted 9 October 2006)

Timing and rate of seasonal zone formation in southern North Sea cod *Gadus morhua* otoliths was studied. Samples were taken from two time periods, representing low and high temperature regimes. Opaque zones were laid down between January and June, in contrast with the pattern described in other published studies. Translucent zone formation started earlier in the warmer period, corresponding to peak annual sea surface temperatures, and a period of slow body growth and low metabolic activity. Translucent zone formation, however, continued once temperatures decreased and growth rate increased. It is hypothesized that translucent zone formation is triggered at a threshold of metabolic stress, and that the combined energetic requirements of reproduction, growth and migration may maintain translucent zone formation even if feeding conditions improve. Higher temperatures had a significant negative effect on the rate of translucent zone deposition, but caused a slight increase in opaque zone formation rate. The findings of this study indicate that historical otolith collections could provide key inputs into future phenological studies to improve the understanding of climate change impacts and the dynamics of otolith structure. © 2007 Crown copyright

Key words: Atlantic cod; *Gadus morhua*; North Sea; otolith; phenology.

INTRODUCTION

Cod *Gadus morhua* L. is a commercially important species in the North Sea. It is under considerable fishing pressure as well as being affected by environmental changes (Bannister, 2004). Cod biology is affected by temperature (Björnsson & Steinarsson, 2002; Brander & Mohn, 2004) while notable changes in water temperature in the North Sea have occurred in recent years, linked to the fluctuations in the North Atlantic Oscillation (NAO) (Dickson & Meincke, 2003).

Phenology, the study of annually recurring life cycle events, can provide particularly sensitive indicators of climate change. The decoupling of phenological

*Author to whom correspondence should be addressed. Tel.: +44 (0)1502 527730; fax: +44 (0)1502 524511; email: graham.pilling@cefas.co.uk

© 2007 Crown copyright

relationships has potentially serious ramifications for ecosystems (Edwards & Richardson, 2004). Since fish otoliths act as bio-recorders, storing information on life-history events, they have the potential to be used as direct phenological markers. Phenological changes may therefore be noted in the timing and rate of annuli formation in otoliths. A single annulus within an otolith has been defined as 'one of a series of [annual] concentric zones on a structure that may be interpreted in terms of age' (Kalish *et al.*, 1995). An annulus is composed of a translucent and an opaque zone. The translucent zone 'allows the passage of greater quantities of light than an opaque zone'. In sectioned otoliths under reflected light, the opaque zone appears light, and the translucent zone dark.

Deposition of opaque zones in otoliths of fishes from the northern hemisphere in the latitude of the North Sea (defined as 'subpolar' by Beckman & Wilson, 1995) occurs mainly during summer and autumn, between April and May and September and October (Williams & Bedford, 1974; Beckman & Wilson, 1995). A wide range of abiotic and biotic factors has been suggested as influencing the formation of translucent and opaque zones (Wright *et al.*, 2002). These include photoperiod (Wright *et al.*, 1992), feeding (Geffen & Nash, 1995), reproduction (Morales-Nin *et al.*, 1998) and spawning period (Morales-Nin & Ralston, 1990), although Beckman & Wilson (1995) found no clear link between spawning period and zone formation across a range of species. Panella (1980) suggested that environment might also play a key role with regular seasonal variances in water temperature affecting otolith formation. The relationship between otolith zone type and temperature remains unclear, however. For example, opaque zone formation has been linked to low environmental temperature (Reay, 1972), but the review of Beckman & Wilson (1995) indicated that opaque zones tended to form during the period of seasonally high temperatures.

The relationship between zone type and somatic growth also remains unclear. Opaque zone formation has been linked to periods of high metabolic activity and accelerating or maximum growth (Brothers, 1979; Kimura *et al.*, 1979), and translucent zone formation associated with periods of low metabolic activity (Williams & Bedford, 1974). Mina (1968) and Smith & Deguara (2003), however, reported opaque zone formation during a decrease in the rate of fish growth, and others correlated translucent zone formation with rapid growth periods (Buxton & Clarke, 1989). As Beckman & Wilson (1995) point out, this range of interpretation indicates that otolith growth and zone formation may be under the control of a combination of factors, which may vary among species.

The timing of seasonal zone formation in the otoliths of southern North Sea cod was explored in this study. The opaque or translucent zone width at the margin of otoliths from two different time periods, representing two periods of differing temperature regimes, was measured. General linear models (GLM) were then used to examine the relationship between covariates and both the timing and rate of opaque and translucent zone formation. Using those models, the impact of changes in these covariates on formation of annual increments in North Sea cod otoliths, and its relation to timing of growth in cod is discussed.

MATERIALS AND METHODS

Sagittal otoliths were selected from cod caught in the southern North Sea [International Council for the Exploration of the Sea (ICES) sub-area IVc; Fig. 1]. The area is relatively shallow (5–40 m deep), resulting in considerable water mixing (MAFF, 1981), and limited formation of thermoclines. Sea surface temperature (SST) data are therefore representative of actual temperatures experienced by demersal cod. In addition, reduced thermal 'buffering' results in a greater temperature signal than in other areas of the North Sea.

Monthly averages of SST for the southern North Sea were calculated across the ICES rectangles constituting sub-area IVc, using SST data from the ICES oceanographic database. Relatively low average SSTs were observed during the period 1980–1987, followed by a rapid increase in temperature of *c.* 1–2° C. SST then remained relatively constant during the period 1988–1995 (Fig. 2). Otoliths were selected from the end of the two periods of contrasting temperature: 1985–1986 and 1994–1995. These periods will subsequently be called the cold period and warm period. Selection of years at the end of these cold and warm periods ensured that fish had experienced the relevant temperature regime throughout their lives. Differences in average annual temperature were largely attributable to increased temperatures during the first half of the year (Fig. 3).

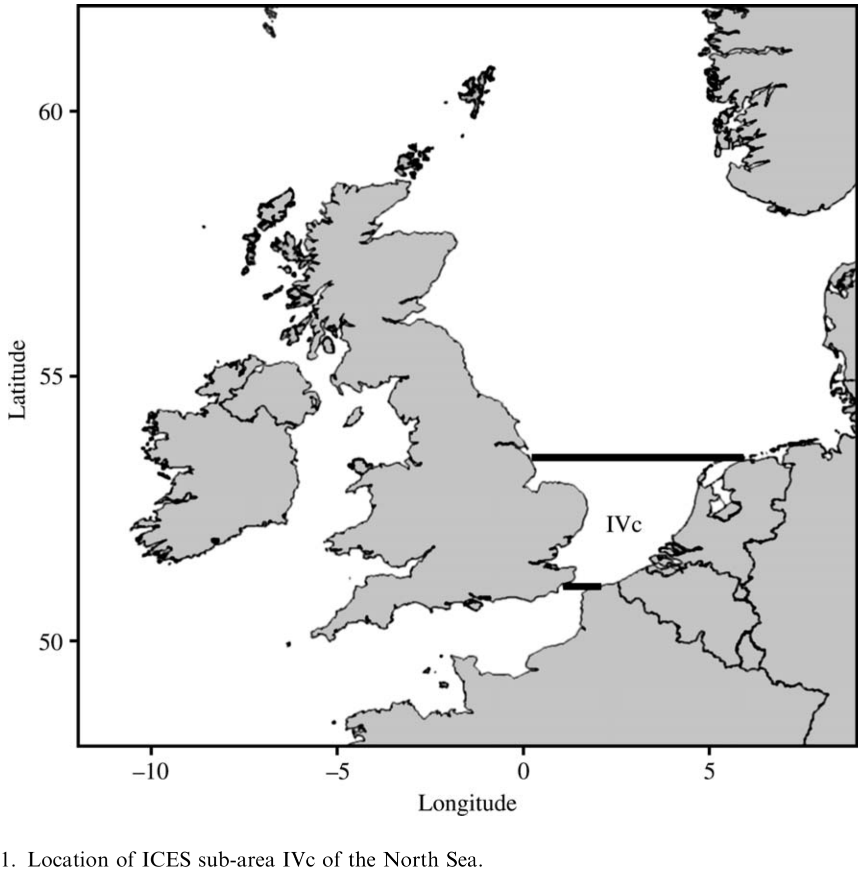

Fig. 1. Location of ICES sub-area IVc of the North Sea.

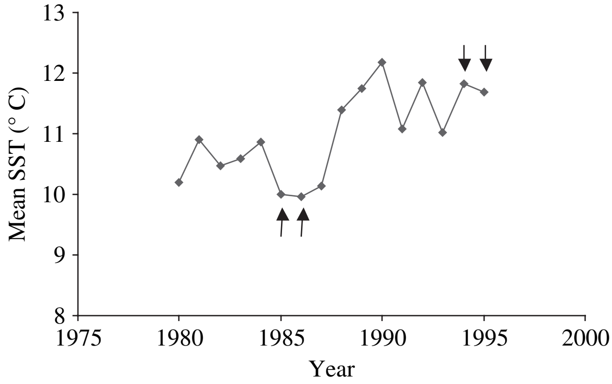

FIG. 2. Mean annual sea surface temperature (SST) in ICES sub-area IVc from 1980 to 1995. Arrows denote years selected for analysis.

MEASUREMENT

Analyses were restricted to ages 2–4 years, due to the small sample numbers of individuals caught at older ages, and the fact that age 1 year fish only recruited to the fishery part way through the year. Cod sagittal otoliths were selected by month and age, to attain between 20 and 30 otoliths in a particular month and age combination. Otoliths were sectioned using the technique described in Bedford (1983). Sections were then examined for their suitability. If zones were unclear, or if the section was not taken through the nucleus, the otolith was discarded. For all other otoliths, the width of the zone (opaque or translucent) at the margin of the otolith (marginal increment) was noted. Measurement of the width of the marginal increment was made using Optimas v5.0 software (Media Cybernetics, Atlanta, GA, U.S.A.), under reflected light at ×10 magnification. Lighting and magnification were kept constant for all measurements. Measurements were taken along the main growth axis of the ventral lobe to minimize variation, from the inside edge to the ventral edge of the marginal zone (Fig. 4). When both translucent and opaque zones of an incomplete annual increment were present at the margin, the width of each zone was measured. Three measurements of individual marginal increments were taken in each of a random sub-sample of 100 otoliths of age 3 year otoliths to assess measurement variability. The resulting average coefficient of variation (CV) was 4·6%.

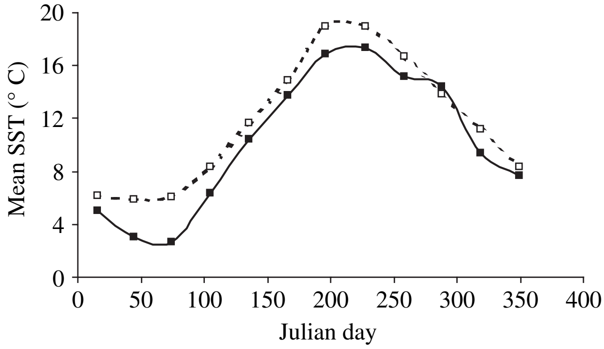

FIG. 3. Average monthly sea surface temperature (SST) in ICES sub-area IVc from 1985–1986 (-■-) and 1994–1995 (--□--).

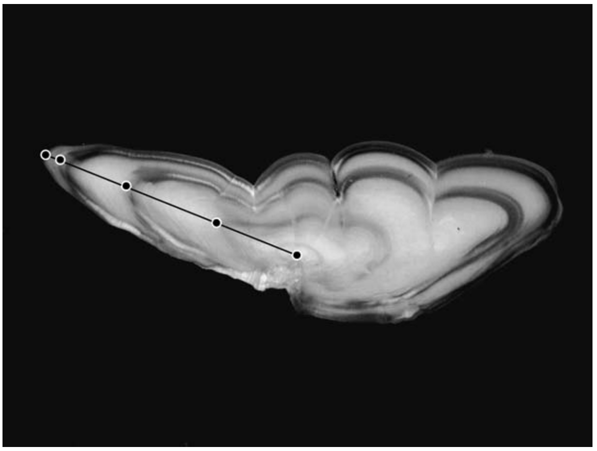

FIG. 4. Sectioned otolith from North Sea cod (age 3 years) caught in August. Otolith viewed under reflected light at ×10 magnification. Line shows axis of measurement, points show position of annual rings (complete opaque and translucent bands) and width of incomplete opaque zone at the edge of the otolith.

STATISTICAL ANALYSIS

Linear models were used to investigate timing of the onset of zone formation and rate of zone deposition: 1) onset of zone formation, the type of zone (translucent or opaque) present at the edge of the otolith of each fish was assessed by year, month and age, and examined graphically. Linear statistical models were then applied to population average incremental width data. Using model estimates, timing of the onset of zone formation was estimated for the cold and warm temperature periods (1985–1986 and 1994–1995); 2) rate of zone formation, the rate at which opaque and translucent marginal zones were formed was examined for the two temperature regimes. Models were developed on the basis of individual zone width measurements (*i.e.* not population average values). The influence of temperature on the rate of zone formation was examined.

The models used under stages 1) and 2) shared a common approach. Appropriate error structures for each model were first developed. Examination of the data indicated that the relationship between time and zone width was non-linear, while residuals showed that ln-transformation was required. This error structure is appropriate since zone width is bounded at zero. Zone width was ln-transformed following addition of a constant, as identified using the Box–Cox procedure (Box & Cox, 1964; Venables & Ripley, 2002) for both models. Linear models were then fitted to the transformed data through stepwise procedures within the R-software (Chambers & Hastie, 1992; R Development Core Team, 2003). The 'best' model was selected on the basis of the Akaike information criterion (AIC) value, and through examination of residual patterns and linearity of the quantile-quantile plot.

For each model, the covariates assessed were: (1) year (1985, 1986, 1994, 1995) or year group (1985–1986, 1994–1995, representing cold and warm years, respectively), as a factor; (2) age, as a factor; (3) Julian day of the time of capture, the number of days from 1 January of each year, as a continuous variable; (4) degree days (SST), the cumulative SST experienced over time (sum of daily SST), taken from the 1 January, as a continuous variable; (5) total length (L_T; cm), as a continuous variable. Models under stages 1) and 2) were first fitted with Julian day as the measure of time (no effect of temperature). Once the 'best fit' model based on Julian day was identified, the process was repeated using degree days (SST), which incorporates both a measure of time and of varying temperature over time. If the inclusion of degree days improved the model (based upon the AIC score), this was taken as the 'best fit' model.

When modelling translucent zone formation (syntax of the S programming language; the upper model examined the effects of individual covariates and their interactions), the initial upper model was: ln(translucent zone width + constant) ~ factor(year) × factor(age) × Julian day × L_T. In contrast, formation of the opaque zone begins late in the year, and finishes early in the next. The pattern of formation was therefore examined within a cohort across 2 years, rather than by age within a year. The initial upper model was therefore: ln(opaque zone width + constant) ~ factor(year group) × factor (cohort) × Julian day × L_T.

RESULTS

EXAMINATION OF DATA

Marginal increments from a total of 2 453 cod otoliths (ages 2–4 years) were measured, spread across the 4 years and all months (Tables I and II).

ONSET OF ZONE FORMATION

The proportion of individuals with each edge type is presented in Fig. 5 by month, year group and age. In warmer years (1994–1995), otoliths showed the formation of translucent edges earlier, in June, while in colder years (1985–1986) translucent edges were first found in July at most ages (Fig. 5). Examining the data further, otoliths of fish caught in the warmer years started forming translucent edges between the 1 and the 14 June, dependent upon age, while in the colder years they were found between the 19 June and 10 July. These dates corresponded to SSTs of 14·9° C (1994–1995), and between 13·7 and 17·3° C (1985–1986) respectively. Samples from both temperature regimes exhibited the onset of opaque zone formation in October (dependent upon age, between the 3 and 31 October in warmer years, and between the 6 and 13 October in colder years). The exception was age 4 year otoliths in warmer years (1994–1995) where

Table I. Number of North Sea cod otoliths measured by year and month

	Year			
Month	1985	1986	1994	1995
January	42	18	111	66
February	54	57	40	60
March	67	47	37	57
April	51	69	34	98
May	55	54	60	48
June	52	39	51	46
July	52	40	48	29
August	37	49	47	21
September	30	65	45	30
October	47	38	59	84
November	32	50	75	82
December	33	59	43	45
Total	552	585	650	666

TABLE II. Numbers of North Sea cod otoliths measured by year and age

	Year			
Age (years)	1985	1986	1994	1995
2	238	120	229	373
3	136	393	383	134
4	178	72	38	159
Total	552	585	650	666

opaque zones were first found in November (14). These dates corresponded to SSTs of between 11·4 and 12·7° C (1994–1995) and 13·7° C (1985–1986).

Ln-transformed population average translucent zone width was related to Julian day through linear modelling. Average population translucent zone width increased with time, until the otoliths had started to lay down opaque zones. At this point, average population translucent zone width started to fall, because cod with an opaque zone had a zero translucent width on that Julian day. To simplify analysis, data were constrained between the start of the period of translucent zone formation and mid-September (Julian day = 260), the time of capture at which 100% of otoliths had a translucent zone on their edge (Fig. 5). The resulting model is described in Table III. There was no significant difference in the average population translucent width during the selected

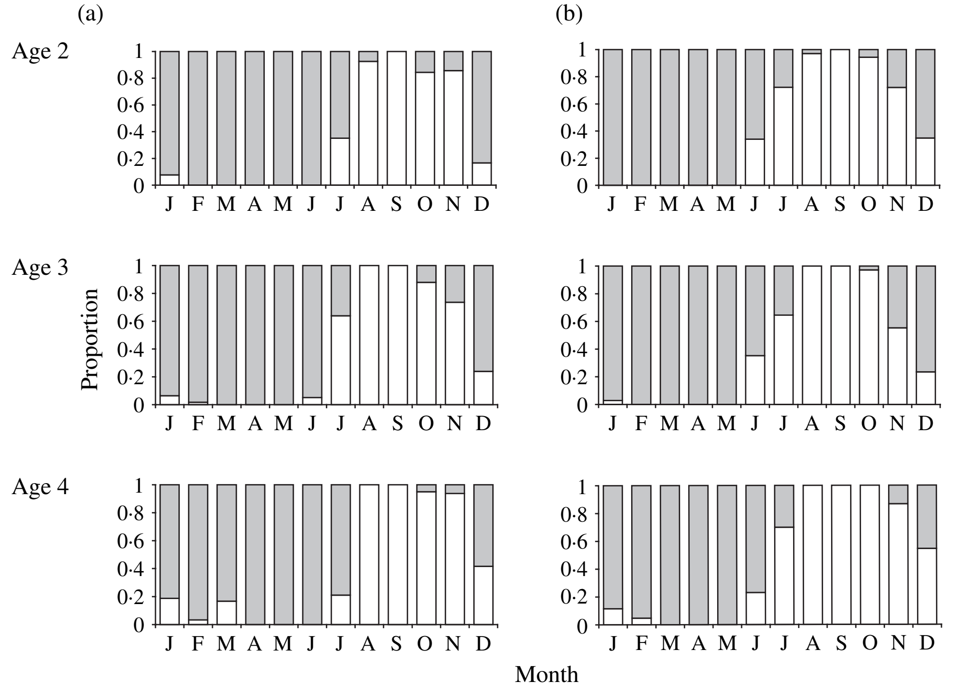

FIG. 5. Proportion of North Sea cod otoliths with a translucent (□) or opaque (▒) margin by month in the two temperature periods (a) 1985–1986 and (b) 1994–1995 by age.

TABLE III. ANOVA statistics and parameter estimates based on the linear model for the population average translucent zone width (W_{TZ}) [$\ln(W_{TZ} + 0{\cdot}03)$] in North Sea cod otoliths

Coefficients	d.f.	SS	MS	P	Estimate	S.E.
Julian day	1	19·76	19·76	<0·001	0·019	0·002
Year group 2 (1994–1995)	1	0·17	0·17	0·120	1·009	0·448
Julian day:year group 2	1	0·29	0·29	0·042	−0·004	0·002
Residuals	96	6·56	0·07			
Constant						
$r^2 = 0{\cdot}75$					−6·248	0·349

period between ages; addition of age in the model did not significantly improve the fit (age coefficient $P > 0{\cdot}05$).

Although translucent zone width increased with time (Julian day), the interaction with year group shows that in warmer years (year group 2, 1994–1995), the gradient was significantly lower than in cooler years (represented by the base model). This was examined further in the modelling of individual zone widths. The model explained 75% of the variation in (transformed) translucent zone width. The predicted translucent width for the two temperature periods from the model, and the corresponding data, are presented in Fig. 6.

Model results supported the observation that translucent zone formation began earlier in warmer years than in the colder ones. Model parameters indicated that the warmer (1994–1995) model for translucent growth would cross the *x*-axis on Julian day 125 (5 May), whereas the colder (1985–1986) model crossed the *x*-axis on day 150 (29 May). This is earlier than indicated by the actual data and may result from the difficulty in correctly identifying very small amounts of translucent zone growth at the otolith edge, which may have started formation (as expected by the model) in May.

The within-year trend in cod body size was also examined across the years examined. A lowess smoother (span 0·3) was fitted to individual L_T-at-capture, by Julian day. The resulting pattern showed a decrease in the rate of growth

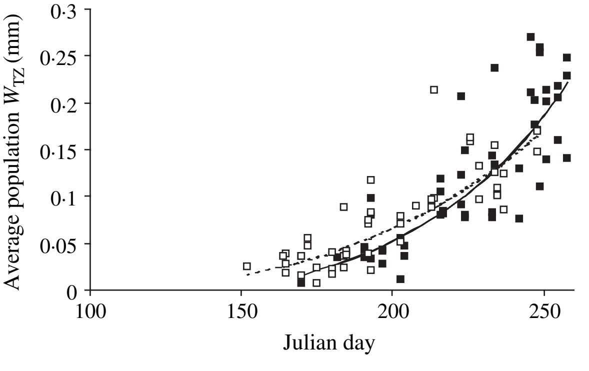

FIG. 6. Average population translucent zone width (W_{TZ}) over time for the two temperature periods [1985–1986 (-■-) and 1994–1995 (-□-)] and corresponding model fits to the data.

during the period Julian day 180–240, *i.e*. end of June to end of August [Fig. 7(b)]. This period of slow growth corresponded with the period when fish started to lay down a translucent zone at the otolith edge, and the period of highest temperatures. This pattern of lower somatic growth rate in summer was consistent between years, based on additional samples collected between 1984 and 1999 through port sampling in England (unpubl. data).

RATE OF ZONE FORMATION IN COD OTOLITHS

Evolution of opaque and translucent zones in North Sea cod otoliths by Julian day was examined. There appeared to be little difference between the

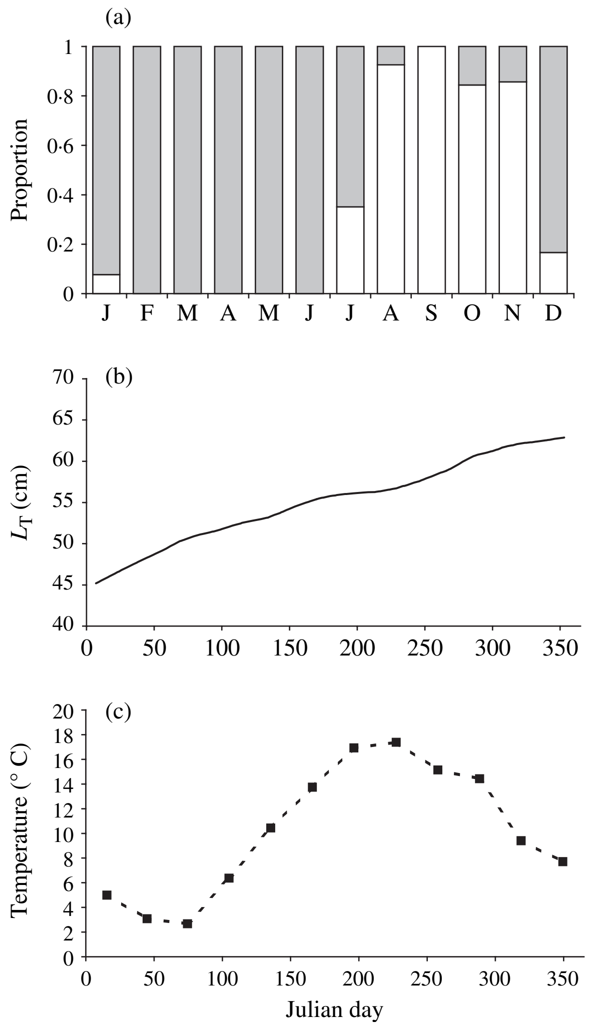

FIG. 7. (a) Pattern of translucent (□) and opaque (■) grey zone formation for age 2 year individuals, (b) lowess smoother fit to total length-at-age data from 1985–1986 over time (Julian day) and (c) mean monthly temperature regime in 1985–1986.

rates of opaque zone formation between the two temperature periods (Fig. 8). In contrast, there appeared to be a difference in the rate of translucent zone formation between periods. Translucent zone widths in the colder years (1985 and 1986) appeared generally larger than those in the warmer years (1994 and 1995). The difference in width increased with increasing Julian day (Fig. 8).

The linear model for the rate of translucent zone formation is presented in Table IV. Degree days, rather than Julian day, was a better descriptor of the pattern of translucent zone formation (based on the AIC value). The interaction term with year indicated that, in warmer years (1994–1995), the growth rate of the translucent zone was significantly lower than in colder years. Note that this year-group effect may be driven in part by the stronger 1986 effect, however, and that the coefficients are similar for 1985, 1994 and 1995. This is in contrast to the pattern shown in Fig. 8, where the translucent zone radius in both 1985 and 1986 are generally greater for a given Julian Day than those in 1994 and 1995. Within the model, increasing age significantly decreased the width of the translucent zone. The year effect was also significant. The model explained 65% of the observed variation.

The results of the linear model of the rate of opaque zone formation are presented in Table V. The model showed that Julian day, rather than degree days, was the best predictor of opaque zone width (based on the AIC value). The interaction term suggested that both larger fish of a given age and older fish (cohort) had smaller opaque zones. The year-group term suggested that cod otoliths in warmer years laid down their opaque zones slightly faster than in

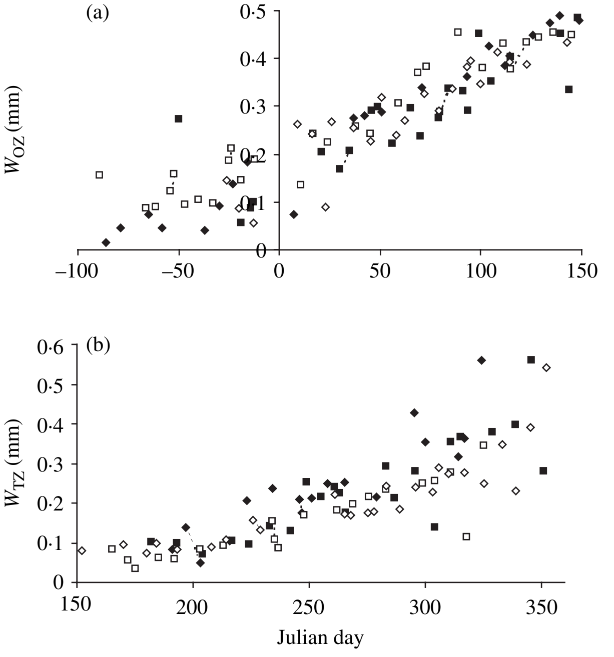

FIG. 8. Evolution of (a) opaque zone width (W_{OZ}) and (b) translucent zone width (W_{TZ}) over time, by year: 1985 (■), 1986 (◆), 1994 (□) and 1995 (◇).

TABLE IV. ANOVA statistics and parameter estimates based on the linear model for the rate of translucent zone width (W_{TZ}) formation [ln (W_{TZ} + 0·02)] in North Sea cod otoliths

Coefficients	d.f.	SS	MS	*P*		Estimate	S.E.
Factor (age)	2	8·179	4·089	<0·001	(age 3)	−0·113	0·024
					(age 4)	−0·326	0·030
Factor (year)	3	8·405	2·802	<0·001	(1986)	−0·087	0·133
Year group	1	2·044	2·044	<0·001	(1994)	−0·075	0·131
Year	2	6·361	3·181	<0·001	(1995)	0·141	0·133
Degree days SST	1	124·950	124·950	<0·001		0·0006	0·00004
Factor(year):DD.SST	3	3·925	1·308	<0·001	(1986)	0·001	0·00005
Year group	1	2·410	2·410	<0·001	(1994)	−0·00006	0·00005
Year	2	1·515	0·758	<0·001	(1995)	−0·0001	0·00004
Residuals	874	75·666	0·087				
Constant							
$r^2 = 0·65$						−3·104	0·108

cold years. The term incorporates both year-group effects and year effects, which were difficult to separate. The term also contrasts with the effect on the translucent zone, and with the similarity in opaque width over time shown on Fig. 8. The model explained 63% of the variation.

The results suggest that width of the translucent zone was smaller in warmer years, even though growth started up to a month earlier, whereas that of the opaque zone was wider.

To examine the overall effect of zone deposition rate differences between the year groups, the L_T and otolith radius relationship was calculated for each (all ages combined), using robust regression. The gradients (Table VI) were significantly different [GT-2 test, $P < 0·05$, (Sokal & Rohlf, 1995)]. For a given L_T, otolith radius in warmer years was significantly smaller than that for cod caught in the colder years. Any compensatory effect of the opaque zone increase in warmer years appears insufficient to compensate for the smaller translucent zone. Note that there was no significant difference in the

TABLE V. ANOVA statistics and parameter estimates based on the linear model for the rate of opaque zone width (W_{OZ}) formation [ln (W_{OZ} + 0·1)] in North Sea cod otoliths

Coefficients	d.f.	SS	MS	*P*		Estimate	S.E.
Julian day	1	62·694	62·694	<0·001		0·007	0·001
Factor (cohort)	2	24·200	12·100	<0·001	Cohort 2	−0·119	0·030
					Cohort 3	−0·329	0·044
Factor (year group)	1	1·510	1·510	<0·001	Year group 2	0·128	0·022
L_T	1	0·707	0·707	<0·001		0·014	0·004
Julian day:L_T	1	1·112	1·112	<0·001		−0·00004	0·00001
Residuals	811	51·733	0·064				
Constant							
$r^2 = 0·63$						−3·756	0·029

L_T, total length.

TABLE VI. Slope (*b*) of the robust regression of total North Sea cod total length and total otolith radius, by year group

	1985–1986	1994–1995
b	0·047	0·044
S.E.	0·005	0·000

L_T-at-age of individuals in the two temperature periods, although mean L_T values did tend to be larger in warmer years.

DISCUSSION

Temperature (or a related covariate) influences the onset of opaque and translucent zones. The initial period of translucent zone formation coincides with peak seasonal temperatures experienced within the southern North Sea. Changes in environmental temperature are likely to influence metabolic rates and life-history processes (Campana & Hurley, 1989), and the onset of translucent zone formation does indeed correspond with a period of reduced growth rate in North Sea cod. Björnsson & Steinarsson (2002) showed that cod in the laboratory exhibit an optimum temperature for growth (under food-unlimited conditions). At the elevated temperatures seen in the southern North Sea, where cod are at the southern limit of their distribution, a decrease in growth rate attributable to higher temperatures might therefore be expected. Cod in the North Sea do not generally live in a food-unlimited environment, however, but there are seasonal patterns to food availability (Reiss & Kröncke, 2005). Electronic data storage tag studies have revealed reduced activity in cod in the North Sea between June and August (Julian day 180–240; Righton *et al.*, 2001). This period corresponds with both the period of reduced growth and start of translucent zone formation. Turner *et al.* (2002) thought that this reduced activity corresponded to 'sit and wait' behaviour to conserve energy when prey are not abundant. The finding supports both the experimental work of Hüssy & Mosegaard (2004), who noted that increased metabolic stress caused by reduced feeding resulted in a switch to translucent growth, an effect more pronounced at increased temperatures, and the opinion of Hüssy *et al.* (2004) that translucent zones form during unfavourable growth conditions.

While elevated temperature and a lower feeding rate correspond to the start of the translucent zone period, temperature declines before translucent zone completion in December and January. Turner *et al.* (2002) noted that cod become highly active in October and November as they migrate south to spawning grounds in the eastern English Channel and Southern Bight (Daan, 1978). Fish examined in the current study were relatively young, 2–4 year olds. At age 3 years, ICES stock assessments assume that only 23% of individuals are mature (ICES, 2005). Fish tagged in the study of Turner *et al.* (2002), however, included those of age 3 years, suggesting that mature or not, cod of that age may follow the migration pattern. Decreasing temperatures in October may therefore allow energy to be directed from maintenance back into growth (and ovary development in mature cod), in readiness for migration. If the hypothesis that translucent zone formation relates to metabolic stress is extended and if it is assumed that there is a threshold for metabolic stress, the temperature and lack of food in summer, and later in the year the combined requirements of reproduction, growth and migration, may cross this threshold (despite increasing feeding rates), leading to continued translucent zone formation.

The rate of translucent zone (and to a lesser extent opaque zone) formation, as well as the timing, was different between years. Models indicated that higher temperatures had a significant negative effect on the rate of translucent zone formation. While modelled opaque zone width was slightly larger in warmer years, year and temperature effects could not be separated (as degree days was not a significant covariate in the model). Certainly, there was no obvious difference indicated by the plots of opaque width in the 2 year groups. In general, overall otolith accretion rate is expected to increase with temperature (Mosegaard *et al.*, 1988), although some studies do support the negative influence of temperature on zone width found in this study, for example Ralston & Howard (1995), and Hüssy *et al.* (2004) noted that otolith matrix incorporation is inversely related to temperature.

The relationship between total otolith width and L_T suggests that in colder periods, otoliths were larger than in the warmer period. This may largely be a result of the reduction in translucent zone size in warmer years, which does not appear to have been compensated for by any increase in opaque width suggested by the model. Changes in the size of otoliths may therefore represent changes in the formation of a single otolith zone type, rather than an overall change in otolith accretion rate.

In southern North Sea cod, opaque zones are present on the otolith edge from October to August, with 100% of cod laying down an opaque zone from January to June. This is in marked contrast to the findings of both Williams & Bedford (1974) for North Sea cod otoliths from the mid-1950s, and Beckman & Wilson (1995) for a wide range of species, which both indicated that opaque zones were deposited during summer and autumn. Unfortunately, Williams & Bedford (1974) do not specify from where in the North Sea their samples were taken. Cod caught in more northern areas of the North Sea lay down opaque zones later in the year than in the southern North Sea (Wright *et al.*, 2002), which may contribute to some of the difference. Also, the method used to examine otoliths at that time (breaking and reading using transmitted light) may also mean that the onset of a particular zone was not identified as readily as in sectioned otoliths. It seems unlikely, however, that these factors account for all the considerable differences seen. Increasing temperatures within the North Atlantic since the 1960s (Fromentin & Planque, 1996) could explain the earlier onset of translucent zone formation in recent years. The period of translucent zone formation is also longer in the current study (*c.* 7 months) than that shown by the 1955 cohort (5 months for age 2 year cod). This may suggest that higher water temperatures, and related factors such as ecosystem changes, may have lengthened the duration of the metabolically stressful period for North Sea cod since the 1950s.

It must be noted that this study is based upon data from a relatively limited, if representative, range of years. Between-year variability can be high, as found during this study. In turn, other unmeasured differences between the years selected might have influenced otolith zone formation. The examination of additional years of data, which was outside the scope of the current study, are required to determine the generality of the influence of water temperature.

The chronological abilities of otoliths and their use as recorders of historical environmental and physical conditions have become key areas of study (Campana & Thorrold, 2001). With the existence of historical otolith collections and fossil otoliths, and given the potential impacts of climate on growth identified here, the ability of otoliths to act as an easily referenced library could provide a key input into future phenological studies.

This paper was prepared with support provided by the Commission of the European Communities Directorate General for Fisheries (DG XIV) under contract (IBACS; Integrated approach to the biological basis of age estimation in commercially important fish species), and the U.K. Department for Food, Environment and Rural Affairs (under contract C1473). Thanks to two anonymous reviewers and to A. Payne for very helpful and constructive comments on an earlier version of this manuscript.

References

Bannister, R. C. A. (2004). The rise and fall of cod (*Gadus morhua*, L.) in the North Sea. In *Management of Shared Fish Stocks* (Payne, A. I. L., O'Brien, C. M. & Rogers, S. I., eds), pp. 316–338. Oxford: Blackwell Publishing.

Beckman, D. W. & Wilson, C. A. (1995). Seasonal timing of opaque zone formation in fish otoliths. In *Recent Developments in Fish Otolith Research* (Secor, D. J., Dean, J. M. & Campana, S. E., eds), pp. 27–44. Columbia, OH: Belle W. Baruch.

Bedford, B. C. (1983). A method for preparing sections of large numbers of otoliths embedded in black polyester resin. *ICES Journal of Marine Science* **41,** 4–12.

Björnsson, B. & Steinarsson, A. (2002). The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 494–502.

Box, G. E. P. & Cox, D. R. (1964). An analysis of transformations (with discussion). *Journal of the Royal Statistical Society B* **26,** 211–252.

Brander, K. & Mohn, R. (2004). Effect of the North Atlantic Oscillation (NAO) on recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1558–1564.

Brothers, E. B. (1979). Age and growth studies on tropical fishes. In *Stock Assessment for Tropical Small-scale Fisheries* (Saila, S. B. & Roedel, P. M., eds), pp. 119–136. Kingston, RI: University of Rhode Island International Center for Marine Research Development.

Buxton, C. D. & Clarke, J. R. (1989). The growth of *Cymatoceps nasutus* (teleostei: Sparidae) with comments on diet and reproduction. *South African Journal of Marine Science* **8,** 57–65.

Campana, S. E. & Hurley, P. C. F. (1989). An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. *Canadian Journal of Fisheries and Aquatic Sciences* **46,** 603–613.

Campana, S. E. & Thorrold, S. R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* **58,** 30–38.

Chambers, J. M. & Hastie, T. J. (1992). *Statistical Models in S*. New York: Chapman & Hall.

Daan, N. (1978). Changes in cod stocks and cod fisheries in the North Sea. *Rapports et Procès-verbaux des Réunions Conseils International pour l'Exploration de la Mer* **172,** 39–57.

Dickson, R. R. & Meincke, J. (2003). The North Atlantic Oscillation and the ocean's response in the 1990s. *ICES Marine Science Symposium* **219,** 15–24.

Edwards, M. & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430,** 881–884.

Fromentin, J.-M. & Planque, B. (1996). *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series* **134,** 111–118.

Geffen, A. J. & Nash, R. D. M. (1995). Periodicity of otolith check formation in the juvenile plaice *Pleuronectes platessa* L. In *Recent Developments in Fish Otolith Research* (Secor, D. J., Dean, J. M. & Campana, S. E., eds), pp. 65–73. Columbia, OH: Belle W. Baruch.

Hüssy, K. & Mosegaard, H. (2004). Atlantic cod (*Gadus morhua*) growth and otolith accretion characteristics modelled in a bioenergetics context. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1021–1031.

Hüssy, K., Mosegaard, H. & Jessen, F. (2004). Effect of age and temperature on amino acid composition and the content of different protein types of juvenile Atlantic cod (*Gadus morhua*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1012–1020.

Kalish, J. M., Beamish, R. J., Brothers, E. B., Casselman, J. M., Francis, R. I. C. C., Mosegaard, H., Panfili, J., Prince, E. D., Thresher, R. E., Wilson, C. A. & Wright, P. J. (1995). Glossary for otolith studies. In *Recent Developments in Fish Otolith Research* (Secor, D. J., Dean, J. M. & Campana, S. E., eds), pp. 723–729. Columbia, OH: Belle W. Baruch.

Kimura, D. K., Mandapat, R. R. & Oxford, S. L. (1979). Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*) using otoliths. *Journal of the Fisheries Research Board of Canada* **36,** 377–383.

MAFF (1981). *Atlas of the Seas Around the British Isles*. Lowestoft: Ministry of Agriculture, Fisheries and Food.

Mina, M. V. (1968). A note on a problem in the visual qualitative evaluation of otolith zones. *ICES Journal of Marine Science* **40,** 211–219.

Morales-Nin, B. & Ralston, S. (1990). Age and growth of *Lutjanus kasmira* (Forskal) in Hawaiian waters. *Journal of Fish Biology* **36,** 191–203. doi:10.1111/j.1095-8649.1990.tb05595.x

Morales-Nin, B., Torres, G. J., Lombarte, A. & Recasens, L. (1998). Otolith growth and age estimation in the European hake. *Journal of Fish Biology* **53,** 1155–1168. doi:10.1111/j.1095-8649.1998.tb00239.x

Mosegaard, H., Svedäng, N. G. & Taberman, K. (1988). Uncoupling of somatic and otolith growth rates in Arctic charr (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 1514–1524.

Panella, G. (1980). Growth patterns in fish sagittae. In *Skeletal Growth of Aquatic Organisms* (Rhoads, D. C. & Lutz, R. A., eds), pp. 519–560. New York: Plenum Press.

Ralston, S. & Howard, D. F. (1995). On the development of year-class strength and cohort variability in two northern Californian rock-fishes. *Fishery Bulletin* **93,** 710–720.

Reay, P. J. (1972). The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. *ICES Journal of Marine Science* **34,** 485–504.

Reiss, H. & Kröncke, I. (2005). Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. *Estuarine Coastal and Shelf Science* **65,** 253–274.

Righton, D., Metcalfe, J. & Connolly, P. (2001). Different behaviour of North and Irish Sea cod. *Nature* **411,** 156.

Smith, K. A. & Deguara, K. (2003). Formation and annual periodicity of opaque zones in sagittal otoliths of Mugil cephalus (Pisces: Mugilidae). *Journal of Marine and Freshwater Research* **54,** 57–67.

Sokal, R. R. & Rohlf, F. J. (1995). *Biometry: the Principles and Practice of Statistics in Biological Research*. New York: W. H. Freeman and Company.

Turner, K., Righton, D. & Metcalfe, J. D. (2002). The dispersal patterns and behaviour of North Sea cod (*Gadus morhua*) studied using electronic data storage tags. *Hydrobiologia* **483,** 201–208.

Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S*. New York: Springer-Verlag.

Williams, T. & Bedford, B. C. (1974). The use of otoliths for age determination. In *Ageing of Fish* (Bagenal, T. B., ed.), pp. 114–123. Old Working: Unwin Brothers.

Wright, P. J., Talbot, C. & Thorpe, J. E. (1992). Otolith calcification in Atlantic salmon parr, *Salmo salar* L., and its relation to photoperiod and calcium metabolism. *Journal of Fish Biology* **40,** 779–790. doi:10.1111/j.1095-8649.1992.tb02624.x

Wright, P. J., Panfili, J., Morales-Nin, B. & Geffen, A. J. (2002). Types of calcified structures: Otoliths. In *Manual of Fish Sclerochronology* (Panfili, J., Pontual, H., Troadec, H. & Wright, P. J., eds), pp. 31–56. Brest: Ifremer-IRD co-edition.

Electronic References

ICES (2005). *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak*. Available at http://www.ices.dk/reports/ACFM/2005/WENSSK/WENSSK2005.pdf

R Development Core Team (2003). R: A *Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at http://www.R-project.org.