Growth changes in plaice, cod, haddock and saithe in the North Sea: a comparison of (post-)medieval and present-day growth rates based on otolith measurements


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Abstract

Fishing effort has strongly increased in the North Sea since the mid-19th century, causing a substantial reduction in the population size of exploited fish stocks. As fisheries research has developed simultaneously with the industrialisation of the fisheries, our knowledge of population dynamics at low levels of exploitations is limited. Otoliths retrieved from archaeological excavations offer a unique opportunity to study growth rates in the past. This study compares historical and present-day growth rates for four commercially important demersal fish species. A total of 2532 modern otoliths (AD 1984–1999) and 1286 historical otoliths (AD 1200–1925) obtained from archaeological excavations in Belgium and Scotland were analysed. Comparison of the growth patterns between eras revealed a major increase in growth rate of haddock, whereas growth changes were not observed in saithe and only in the smaller size classes of plaice and cod. Comparison of our results with literature data indicates that the observed growth rate changes in plaice and cod occurred within the 20th century. Apparently the onset of industrialised fisheries has not greatly affected the growth of plaice, cod and saithe populations in the North Sea. This result contradicts the expectation of density-dependent limitation of growth during the era of pre-industrialised fishing, but is in agreement with the concentration hypothesis of Beverton (Neth. J. Sea Res. 34 (1995) 1) stating that species which concentrate spatially into nursery grounds during their early life-history may ‘saturate’ the carrying capacity of the juvenile habitat even though the adult part of the population is not limited by the adult habitat.

Keywords: Pleuronectes platessa; Gadus morhua; Melanogrammus aeglefinus; Pollachius virens; Otoliths; Back-calculation; Archaeological excavations; Density-dependent growth; Concentration hypothesis

1. Introduction

Knowledge of population dynamic processes is important in creating a scientific basis for sustainable
exploitation of fisheries resources. Growth is one of these processes and changes in growth have a profound impact on the productivity of a fish stock. For instance, the increase in haddock landings in the 1960s has been partly ascribed to increased growth rates (Jones and Hislop, 1978). Similarly, changes in plaice landings coincided with changes in growth rates (Bannister, 1978; Rijnsdorp and Van Beek, 1991). Besides a direct effect on the biomass of fish stocks, changes in growth affect the reproductive output, because both maturation and egg production are affected by growth (Rothschild, 1986; Rijnsdorp, 1993a; Grift et al., 2003).

Examining the response of marine fish populations to heavy exploitation has been severely hampered by the lack of data from the pre-industrialised fishing era (Pope and Macer, 1996; Rijnsdorp and Millner, 1996). Among archaeozoologists there is a growing interest to analyse fish remains from excavations. Thanks to the systematic use of sieves during the last two decades, the number of fish remains available for study has increased dramatically (Van Neer and Ervynck, 1993). Many archaeological sites have yielded thousands of fish remains, but otoliths are often underrepresented due to the unstable nature of otoliths in comparison to fish bones. Favourable conditions for the preservation of otoliths are found in waterlogged contexts such as cesspits and deep refuse pits. Archaeozoologists have mainly focused on using otoliths to establish seasonal patterns in fishing (Monks and Johnston, 1993; Van Neer et al., in press). However, the growth patterns laid down in these archaeological otoliths offer fisheries biologists a unique opportunity to study growth rates in the past. Although growth rates as such are not directly relevant to the archaeological interpretation of the sites, the reconstruction of age and fish length distributions of landings based on growth patterns in otoliths allows inferences about fish trade and marketing strategies (Van Neer et al., 2002).

From studies of heavily exploited fish populations the general pattern emerges that growth during the adult phase is not related to population size, whereas growth in the juvenile phase may be density dependent (Cushing, 1981; Valiela, 1984; Daan et al., 1990; Van der Veer et al., 1994; Rijnsdorp, 1994). The question arises whether or not these patterns also apply to less heavily exploited populations, as density-dependent processes may become more pronounced at reduced levels of exploitation. The increase in growth observed in several flatfish species since the beginning of the 20th century is potentially related to increased exploitation (Rijnsdorp, 1994). Furthermore, growth rates of adult plaice were reduced after World War II, coinciding with the build-up of biomass as a consequence of reduced fishing during the war (Beverton and Holt, 1957; Rijnsdorp and Van Leeuwen, 1992). The response to changes in exploitation may differ between species in relation to their life history and their position within the food web. Increased exploitation results in a decrease of larger fish, but the number of small fish may increase in response to the reduction of predation pressure (Rice and Gislason, 1996; Daan et al., 2003). However, the abundance of adults is less likely to affect the juveniles of species that utilise sheltered nursery areas such as plaice and saithe.

Sufficient numbers of archaeological otoliths to examine growth rates are available for four commercially important demersal fish species: plaice (Pleuronectes platessa), cod (Gadus morhua), haddock (Melanogrammus aeglefinus) and saithe (Pollachius virens). These species differ in their current distribution within the North Sea. Haddock and saithe inhabit the deeper waters to the north, plaice is mainly caught in the southern and central areas and cod occurs throughout the North Sea (Knijn et al., 1993). Because these species occupy different niches within the ecosystem, they may differ in their response to increased exploitation. Inter- and intra-specific interactions through competition for food or predation may only occur in size-classes that overlap in distribution (Rijnsdorp and Van Beek, 1991). The species studied comprise the whole spectrum of spatial overlap. Juveniles of plaice and saithe are concentrated in coastal nursery grounds that are spatially segregated from the adult distribution area (Wimpenny, 1953; Daan et al., 1990). On the other side of the spectrum, we find haddock where juveniles and adults co-occur in the same areas. Cod occupies an intermediate position (Hislop, 1984; Daan et al., 1990; Munk et al., 1999).

Our objective is to compare growth rates in recent years with those prior to the onset of industrialised fishing. It is hypothesised that the substantial increase in exploitation since the mid-19th century has brought
the population size of exploited fish stocks below a level where density-dependent regulation occurs. Therefore, present-day growth rates of the adults are expected to be higher in all four species. Changes in the juvenile phase are expected to differ among species. For species of which the juveniles are subject to high predation mortality (cod and haddock), increased exploitation of the larger fish may result in increased density of the juveniles and hence lower growth rates. Such an inverse relationship between the population size of adults and juveniles is not expected to exist in plaice and saithe.

2. Materials and methods

2.1. Archaeological excavations

Otoliths (sagittae) were obtained from several excavation sites (Fig. 1 and Table 1) in Belgium (Raversijde, Mechelen, Ostend and Bruges) and one site in Scotland (Robert’s Haven). Species identifications were based on descriptions and images of otoliths (Chain, 1936; Härkönen, 1986; Nolf and Steurbaut, 1989) and on comparisons with a reference collection. Among at least 18 marine fish species encountered on these sites, otoliths of four commercially important demersal fish species (plaice, cod, haddock and saithe) were selected for growth analysis. Approximately 5% of the otoliths were a priori excluded because identification was uncertain or because the surface was severely eroded.

The archaeological material refers to three main periods (Table 1). Late-medieval otoliths were available from Raversijde (1425–1475), Bruges (1350–1450) and Robert’s Haven (1200–1400), post-medieval material (Mechelen 1700–1800; Bruges 1650–1750 and Ostend 1650–1700) originated from the period prior to the era of industrialised fisheries, and two samples (Mechelen and Bruges 1875–1925) refer

![Fig. 1. Map showing the regions within the North Sea and the locations of the archaeological excavation sites.](image-url)
to the period roughly corresponding with the onset of industrialised fisheries. The samples were dated by cultural artefacts (mainly ceramics types) found in the same contexts and by the stratigraphic position of these contexts. At the Raversijde excavation site, a single depositional event was discovered, where all otoliths (129 plaice otoliths) probably originate from a single fishing trip. In all other cases, the samples were derived from contexts accumulated over several decades (Van Neer and Pieters, 1997; Van Neer et al., 2002).

Robert’s Haven and Raversijde were coastal villages. The fish remains from Robert’s Haven represent fish that was landed by the inhabitants themselves and probably caught in local coastal waters. In the case of Raversijde, historical sources indicate that plaice and haddock were probably caught in local coastal waters, whereas the cod remains may partially represent fish that was caught in more northern waters. Without doubt, the majority of the marine fish consumed at Ostend came from its own harbour or from smaller fishing villages nearby. The towns Bruges and Mechelen are located inland and the remains of marine fish represent imported specimens. During the early post-medieval period, the Flemish (Belgian) fishery suffered from political troubles and marine fish marketed in inland towns probably originated from the southern part of the Netherlands. After the revival of the Flemish fishery around 1900, fish sold on inland markets may have come from either Flemish or Dutch fishing villages along the Southern Bight and English Channel (Van Neer et al., 2002).

2.2. Present-day otolith samples

Present-day otoliths (sagittae) were selected from material collected during ongoing research vessel surveys and market sampling programmes. Cod and plaice samples covered a wide range of fishing grounds, while haddock samples were more restricted in area coverage due to the current distribution pattern of haddock. As the historical saithe material was limited in number and quality, a correspondingly smaller sample of present-day saithe otoliths was included, from the northern North Sea only (Fig. 1 and Table 1).

With the exception of haddock from region VIa (1984–1995), all otolith samples were collected between 1995 and 1999. Samples were restricted to the spawning season (approximately January – March) and the summer (July – September). The target was to sample the full size range evenly for each region and season (10 plaice, 3 cod, 8 haddock and 8 saithe per 5-cm size class), but fish smaller than the minimum landing size were not always available. The plaice samples were also stratified by sex. Only one of the pair of sagittal otoliths of each fish was included in the growth analysis.

2.3. Otolith preparations and measurements

All otoliths were embedded in black polyester resin and transverse sections were cut through the nucleus, exposing the annual ring structure (Bedford, 1983; Bolle et al., 2003; Millner et al., ms. in prep.). For the accuracy of the analysis it is essential that the plane of section is as close to the primordial core as possible since deviations will affect the measurements. Images of the sectioned otoliths were digitised with a camera
attached to a binocular microscope. The width of the otolith and the annuli were measured using image analysing software. An experienced age reader marked the translucent-opaque transition at the outermost tips of each annulus. The X–Y coordinates of these annotations and the greatest width of the whole otolith were recorded. The X–Y measurements were then converted to annulus diameter. The direction of otolith growth changes with age from posterior-anterior (increase in otolith width) to dorso-ventral (increase in otolith thickness). This is illustrated for a plaice otolith in Fig. 2. The annulus diameter was calculated for the main axis of growth, which was defined as the greatest width axis. Therefore, the X–Y coordinates of the tips of each annulus were projected on the main axis of growth (A–A in Fig. 2). The distance between the projected tips of annulus i is the otolith diameter at age i.

2.4. Measurement errors

Interpreting otolith structures is a difficult and complex task involving knowledge of the life history of a species and experience in age reading. Because different age readers were involved, training and calibration exercises were carried out at the start of the project. Furthermore, duplicate measurements were carried out subsequently to estimate measurement errors induced by different interpretations. A total of 211 plaice, 213 cod, 199 haddock and 20 saithe otoliths were re-aged and re-measured by an independent second reader without prior knowledge of the first results.

The readers agreed on the age and the position of the annuli in the majority of otoliths. In some cases, a different interpretation of the structure caused substantial differences in increment measurements, while in others disagreement on age (for example, whether or not an annulus had been laid down on the edge) barely affected increment measurements. Despite differences at the level of the individual fish, on average the differences were insignificant (P < 0.05 in paired t-test for each species and annulus). Consequently, the conclusion was drawn that there is no reader-induced bias in the growth analyses.

2.5. Growth analyses

Growth patterns were examined in almost all otoliths listed in Table 1. A small number of otoliths (12 historical and 8 modern) were rejected because the growth checks were poorly visible. Another 41 modern otoliths (33 plaice and 8 haddock) were excluded because these fish were in their first year of life, providing no information on annual growth.

The basic comparisons of growth patterns were carried out using the direct otolith measurements instead of back-calculated fish length, because these are less prone to error. First, we calculated the mean diameter for each annulus giving a reconstruction of the otolith width at age. The increase in diameter between two consecutive annuli is referred to as the annual increment. Because these increments decrease with otolith size, just as the body size increments decrease with body size, they are plotted as a function of the otolith width at the beginning of the growing season. The mean increment per otolith size class was calculated for plotting purposes, while the individual estimates were used in the statistical analyses. Annual increments smaller than the range of a size class may lead to multiple entries for a single fish in a size class. To avoid this, the annual increment per size class was first averaged for individuals before the sample average was calculated.

If the estimation of growth rate is affected by age at capture then any differences between modern and historical growth rates may be merely due to differences in the age compositions of the samples compared. To correct for this potential sampling bias, measurements were weighted so that the effective age composition of the modern otoliths equalled that of the historical otoliths. For each age at capture, all measurements of modern otoliths were weighted by the sample size of historical otoliths divided by the sample size of modern otoliths. The measurements of historical otoliths were not weighted, but if an age at

![Fig. 2. Transversal section of a plaice otolith. Incremental measurements are projected on the main axis of growth A-A.](image-url)
capture was not represented in the modern samples then these measurements were excluded.

Conversion of otolith sizes into fish lengths was required to be able to reconstruct the length of the fish at capture in the case of the archaeological samples and to compare our results to fish length at age observations reported in previous studies. For all four species the relationship between otolith width and fish length was best described by a power function (Rijnsdorp et al., 1990; Bolle and Rijnsdorp, 2000):

$$e^\log(FL) = \alpha + \beta e^\log(OW)$$

where FL is fish length (cm) and OW is otolith width (mm) at the time of capture. The parameter estimates are presented in Table 2 and can be used to reconstruct the fish length according to following derivatives of formula (1):

$$L_i = E^\alpha(O_i)^\beta$$

$$L_i = FL^\alpha(O_i/OW)^\beta$$

where $L_i$ is fish length and $O_i$ is otolith width at the time of annulus formation of the ith annulus.

If fish length at time of capture is known then the proportionality method (3) can be used. Fish length at capture is registered for all modern otoliths, but is unknown for otoliths retrieved from archaeological excavation sites. For historical otoliths the reconstruction of fish length can only be done using (2). In some cases otolith type (left or right), sex, season and/or region may have a minute, though statistically significant effect on the relationship between otolith width and fish length (Bolle and Rijnsdorp, 2000). As so many factors have no or only marginal effects on the fish - otolith size relationship, it seems unlikely that it has changed much over time.

3. Results

3.1. Age and size distributions

Fig. 3 presents the age and fish length distributions for each species and era. The observed fish length is plotted for the modern specimens, whereas the reconstructed fish length is presented for the historical otoliths. The age and length distributions of the historical otolith samples presumably reflect those of historical catches. This is not the case for the modern otolith samples, as these were stratified by fish length. Therefore the age distributions of present-day landings were included in Fig. 3 (ICES, 2003). The present-day catches showed a clear shift towards younger fish in the case of haddock and cod, a small shift towards younger fish for plaice and a shift towards older fish for saithe.

The age and size distributions of the modern and historical otolith samples were different. The youngest age groups and smallest size classes of all species except saithe were over-represented in the modern samples compared to the historical samples (Fig. 3). Furthermore, the larger size classes of plaice and haddock, and the older age groups of plaice were relatively over-sampled in the modern samples.

The age and size distributions also differed between excavation sites, especially in cod. Most of the cod landed in Raversijde and Robert’s Haven were 40–70 cm and 2–4 years old, whereas most of the cod marketed in Mechelen corresponded to larger (>80 cm) and older (6+) fish. Such differences between sites were probably related to trade: fishermen consumed the smaller fishes themselves and exported the larger ones to the inland markets (Van Neer et al., 2002). Differences between regions also occurred in the modern otoliths samples, but these were less pronounced than in the historical samples (Bolle and Rijnsdorp, 2000).

3.2. Geographic variations in growth rates

The modern otolith samples of cod and especially plaice covered a large part of the North Sea and

<table>
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<th>N</th>
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<th>β</th>
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<td>1.279</td>
<td>1.456</td>
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<tr>
<td>Haddock</td>
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<td>1.107</td>
<td>1.521</td>
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<tr>
<td>Saithe</td>
<td>109</td>
<td>0.93</td>
<td>0.806</td>
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</table>
Fig. 3. The age and size distributions of the modern and historical otolith samples and the age distributions of present-day landings for (a) plaice, (b) cod, (c) haddock, and (d) saithe.
adjacent waters (Table 1 and Fig. 1), allowing an analysis of the geographic variation in growth (Fig. 4). The annual growth increments were largest in cod from the English Channel (region VIIId) and smallest in the northern North Sea (region IVa). Small plaice also showed the highest growth rates in region VIIId and the lowest rates in region IVa, while larger plaice grew fastest in the southern North Sea (region IVc) and slowest in region Vla. The annual growth increments of haddock did not differ between the three regions sampled.

3.3. Comparison of growth rates between eras

Growth rates in the era of pre-industrialised fisheries were compared with present-day growth rates by plotting the mean annual increments for each species and era (Fig. 5). The means were weighted by the age distributions of the samples (Section 2.5). As latitudinal trends in growth were observed (Fig. 4), a distinction was made between southern and northern samples.

The growth patterns recorded in plaice otoliths from Belgian excavation sites were compared with modern growth patterns in the southern North Sea and the English Channel (Fig. 5a). Because the increase in fishing effort already started in the second half of the 19th century, the otoliths dated 1875–1925 were excluded. Modern growth rates were significantly higher in the smaller size classes. No growth changes were observed in the larger size classes.

Fig. 5b compares the growth patterns of cod otoliths found at Belgian excavation sites with modern growth patterns in the southern North Sea and the English Channel. This comparison showed a significant difference in the smaller size classes. However, it was uncertain whether all of the archaeological otoliths from Belgium represent fish caught in local coastal waters. The difference in growth rate was smaller but still significant if the Belgian otoliths were compared with modern samples from the northern North Sea. Cod otoliths from Robert’s Haven were compared with present-day otoliths from regions Vla and IVa (Fig. 5c). Although the growth rates appeared to be similar in all size classes, the differences in the smallest size classes were significant.

The majority of gadoid otoliths found at the Belgian excavation sites were haddock otoliths. Haddock is
scarce in the southern North Sea and English Channel at present, so the archaeological samples were compared with modern otoliths from regions IVa and IVb (Fig. 5d). The growth rates of all size classes are currently much higher than in the past.

All historical saithe otoliths were from Robert’s Haven, and all modern saithe otoliths were caught in region IVa. Current growth rate appeared to be slightly lower than in the 13th–14th century samples but the difference was insignificant (Fig. 5e).

A general linear model was used to examine the significance of the observed differences between modern and historical growth rates. A linear decline in growth rate (annual increment) with size was assumed, and age at capture was included in the model. The analyses were carried out using otolith measurements rather than back-calculated fish length. In all species except saithe, the difference between modern and historical growth rates was significant (Table 3). To examine the significance of era in the larger size classes, the model was re-run several times, stepwise dropping the smaller size class (ANOVA tables not presented). Modern and historical growth rates did not significantly differ in the larger size classes of plaice (otolith >3.5 mm, fish length >25 cm), northern cod (otolith >3 mm, fish length >18 cm) and southern cod (otolith >6 mm, fish length >50 cm). The difference was significant in all size classes of haddock.

The age at capture significantly affected the growth rate estimation in all species (Table 3), which means that the size of an otolith increment was partly dependent on the age at capture and comparisons between samples could be biased by different age compositions. This potential bias was minimised because the measurements were weighted by the age distribution. Furthermore, modern and historical growth rates were compared within age groups (age at capture). This was only possible for a small number of age groups because of the limited number of otoliths. The observed patterns within age

![Fig. 5. Comparison of modern and historical growth patterns for (a) plaice, (b) southern cod, (c) northern cod, (d) haddock, and (e) saithe. The weighted mean annual increment is plotted as a function of otolith size class. The weighting procedure is described in the text. The number of observations for each era and size class, and the standard deviation of the mean are presented in the plots.](image-url)
groups were similar to the overall patterns (not presented).

4. Discussion

4.1. Fishing patterns

Although present-day fisheries exploit the whole North Sea, historical fisheries were probably concentrated in coastal waters (Van Neer et al., 2002) where younger age groups are generally more abundant. Despite these differences, comparison of the catch compositions showed a clear shift towards younger fish in the present-day catches of cod and haddock and to lesser extent in the plaice catches, which corroborates the presumed lower level of exploitation in the pre-industrial era. The relatively low number of 10 year and older plaice in the historical catches is probably related to seasonal migration and fishing patterns. Older plaice are only abundant in the southern North Sea during the spawning period between December and February, while plaice fisheries in the 16th century along the Dutch coast started in February-March and lasted for about two to three months (Egmond, 1997). The historical saithe sample showed a bimodal age distribution with a peak on age groups 3 to 5 and 9 to 10+, but it is doubtful whether this pattern reflects the historical catch composition because of the small sample size.

4.2. Methodology growth analyses

The reconstruction of growth patterns in fish populations based on the analysis of increments in otoliths may be subject to bias. Firstly, sampling bias can occur if growth rates are estimated using only market samples (Rijnsdorp and Van Leeuwen, 1992). Growth rates of the youngest age groups (age at capture), which are only partially recruited to the exploited population, will be overestimated because only the fastest growing fish will have reached marketable sizes. This bias cannot have occurred in the modern growth rate estimates (with the exception of saithe), because survey and market samples were used. The historical otoliths, however, can be considered to represent a historical market sample. This source of bias probably affects plaice more than the gadoid species, because the latter

<table>
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grow faster and fewer age groups are only partially recruited to the fisheries. However, comparisons of growth rates estimated for fully recruited age groups, which are insensitive to this bias, confirm the overall differences in growth rate observed.

A second source of bias may be introduced through mortality. In every population a certain variation in growth rate will occur. Each size class consists of relatively young, fast-growing fish as well as older, slower-growing fish, but the proportion of the initial growth rate types changes with increasing size. If mortality is independent of size, the probability that fish survive to a certain size class will be higher for fast-growing fish than for slow-growing fish. If size-selective mortality occurs certain growth types may be selectively removed from the population. In exploited fish populations the fast-growing fish of a year class will be caught first, and it may take several years before the slowest-growing fish are subject to fishing mortality (Ricker, 1969). Fishing mortality usually causes selective removal of fast-growing fish, but the direction of selectivity may vary if a dome-shaped selection pattern occurs in which intermediate-sized fish are more vulnerable to fishing mortality than large fish (Sinclair et al., 2002a). Sinclair et al. (2002b) examined the relative importance of size-selective mortality, density and temperature using an integrated statistical model and concluded that size-selective mortality was the dominant effect in the growth analyses of cod in the Gulf of St. Lawrence, Canada. A simulation study (Rijnsdorp, 1999) showed that size-selective mortality bias in back-calculation studies is strongest when growth rates are estimated using otoliths of large fish that are close to their maximum size, whereas the bias is insignificant when otoliths of smaller fish are analysed. In the present study only very few fish close to their maximum size were analysed. Assuming an unchanged selection pattern, the comparison of growth rates within an age group (age at capture) will be unbiased. To minimise age effects due to sampling bias or size-selective mortality, the growth rates were weighted for the age distribution of the samples. Furthermore, the growth rates were also compared within age groups and these results confirmed the overall patterns. Age was included in the statistical analyses and the differences in growth rates corrected for age effects is significant in plaice, cod and haddock.

4.3. Changes in growth

Given the above considerations, we may conclude that an increase in growth rate has occurred in cod, haddock and plaice since the pre-industrialised era. In cod and plaice, the increase was restricted to the smaller size classes, whereas in haddock an increase in growth occurred over the full size range. The question now arises of whether the increase in growth took place in the period of the expansion of the fisheries in the second half of the 19th century, when stock biomass probably showed its sharpest decline as can be inferred from the decline in catch rates (Sahrhage and Wagner, 1978; Rijnsdorp and Millner, 1996), or in the course of the 20th century. The results of our study are compared with growth curves for different time periods during the 20th century taken from the literature (Fig. 6). These comparisons show that the sizes at age estimated for the pre-industrialised era are strikingly close to those recorded for the first half of the 20th century.

Growth in haddock in the 1926–1939 period was slightly lower than in the pre-industrialised era (Fig. 6d). The archaeological otoliths (1425–1800) were obtained from Belgian excavations sites and historical evidence suggests that these fish were caught in a local fishery (Van Neer et al., 2002). As latitudinal differences in growth rates have been reported (Parry and Jones, 1952; Jones, 1962), it is probable that these specimens will have exhibited higher growth rates than contemporaneous specimens from the central and northern North Sea. The rather high numbers of haddock otoliths found at Belgian excavation sites indicate that this species must have been quite numerous in the southern North Sea in the (post-)medieval period, whereas nowadays haddock only occurs in the central and northern North Sea. This interpretation is supported by an analysis of trade and tax archives (Holm and Bager, 2001). Between the 1920s and the 1950s the growth increased coinciding with an overall decrease in abundance (Jones and Hislop, 1978). In the 1960s, the growth rates of the two extremely abundant year classes of 1962 and 1967 as well as those of the following two weak year classes born in 1963 and 1968 were retarded, indicating a density-dependent response (Jones, 1983). In the long term, there has been an increase in mean lengths at age, and the lengths at age of the 1961 and 1966
year classes which preceded the strong 1962 and 1967 year classes were the highest recorded since the 1920s (Jones, 1983). Growth rates have continued to increase in the 1980s (Wagner and Dethloff, 1985), and current growth rates as revealed by back-calculations appear to be the highest ever reported for the North Sea. Since the gadoid outbursts in the 1960s population size has decreased, and during the last two decades population size is more or less stable with occasional peaks corresponding to the maturation of above-average year classes (Hislop, 1996; ICES, 2003). The changes in haddock growth rates appear to be closely related to changes in population size. Density-dependent growth was also reported for other haddock stocks (Marshall and Frank, 1999).

In cod, the mean size at age estimated for the whole North Sea in the early 20th century (Graham, 1934) did not differ from the medieval growth curve for the northern North Sea, and was slightly higher than the growth curve based on otoliths from Belgian excavation sites (Fig. 6b–c). Between 1930 and the 1970s, mean size-at-age has slightly increased due to growth rate changes in the smaller size classes. In the northern North Sea this difference is very small and almost non-existent if fitted Von Bertalanffy growth curves are compared (Daan, 1974, 1978). Houghton and Flatman (1981) examined annual weight gain in relation to VPA stock size estimates for the period 1963–1977 and concluded that growth in the western North Sea was density dependent. However, a critical re-examination by Daan et al. (1990) showed that alternative interpretations were possible. They concluded that a significant downward trend in annual weight gain existed only for 1-group cod, but that this trend was not significantly related to population density. Bromley (1989) investigated the evidence for density-dependent growth in gadoids using survey data for the period 1977–1987. He focussed on 1 and 2 group cod, haddock and whiting and found that in

Fig. 6. Comparison of fish length at age curves estimated for different time periods for (a) plaice, (b) southern cod, (c) northern cod, (d) haddock, and (e) saithe. The numbers between brackets in the legends refer to the following sources: (1) Fig. 3 in Rijndorp and Van Leeuwen (1992); (2) page 67 in Graham (1934); (3a) Table 3 in Daan (1974); (3b) Table 6 in Daan (1974); (4) Table 25 in Jones and Hislop (1978); (5) Fig. 39 in Wagner and Dethloff (1985); (6) Table 5 in Cieglewicz and Draganik (1969); (7) Tables 1–2 in Moguedet et al. (1987).
all but 1-group cod a negative correlation existed between size-at-age and density. However, most of the variation was caused by an area effect and evidence for density-dependent growth within areas was minimal. Brander (1999) ascribed most of the variability in cod growth rates to temperature effects. Overall, there appears to be little support for density-dependent growth in North Sea cod. For Barents Sea cod, an inverse relationship is observed between the abundance and the mean size-at-age of juveniles. Ottersen et al. (2002) argue that both abundance and mean size-at-age are mainly determined by abiotic density-independent mechanisms during the first half year of the fishes’ life.

The available data on saithe did not provide evidence for a change in growth since the pre-industrial era, since the back-calculated growth for the present and the pre-industrial era fall within the range of observations reported in the literature (Fig. 6e).

In plaice, the pre-industrial growth curve (1425–1800) was very similar to the 1930s growth curve, but well below the present-day growth curves (1970–1979 and 1995–1999, Fig. 6a). Rijnsdorp and Van Leeuwen (1996) showed that the growth rates of the smaller size classes increased in the 1960s and 1970s. These changes in growth were not related to temperature but coincided with an increase in nutrients in the coastal waters, which resulted in an increase in benthic productivity in the plaice nursery areas (Beukema, 1989; Beukema and Cadée, 1988). It also coincided with an increase in trawling impact on the benthos, which may have enhanced the productivity of opportunistic benthic species (Rijnsdorp and Van Beek, 1991; Rijnsdorp and Van Leeuwen, 1996). Therefore, the lower growth rate of juveniles before the 1960s is likely to have been caused by competition for food. Borley (1916) transplanted juvenile plaice from the crowded inshore nursery grounds to a shallow offshore bank where no small plaice occurred. Growth of the transplanted plaice increased to a level comparable to the rate observed in the 1970s and 1980s (Rijnsdorp and Van Leeuwen, 1992). A density-dependent reduction in growth has been reported for the juveniles of abundant year classes in the early 20th century, a phenomenon that still occurs today despite the improved feeding conditions (Rijnsdorp and Van Leeuwen, 1996; ICES, 2003). Evidence for changes in growth of adult plaice is not equivocal. A suggestion for density-dependent growth in the adult phase stems from the decrease in mean weight-at-age of adults during World War II, when fishing was substantially reduced and the biomass of plaice increased threefold (Beverton and Holt, 1957). Furthermore, the back-calculated length increment of adults was reduced at the end of the war and the years immediately following the war (Rijnsdorp and Van Leeuwen, 1992). However, this reduction may also have been due to the survival of slower growing fish that would have been selectively removed by the fishery if the fishery had continued during the war (Rijnsdorp, 1999). Given the similarity in growth rates of plaice larger than 30 cm between the pre-industrial era and the current time, it is concluded that density-dependent growth in adult plaice does not play a major role in the North Sea.

Other factors such as the temperature regime (Brander, 1999), the overall productivity of the ecosystem (Cushing, 1982) or selective fishing (Stokes et al. 1993; Law, 2000; Heino and Godo, 2002) may also have influenced the changes in growth rates. Growth rate is positively correlated with temperature (Fonds et al., 1992) and the observed geographical variation in growth rates is likely to reflect the latitudinal trend in temperature. For haddock, no clear latitudinal pattern was detected in the present study because of the restricted sampling range, but geographic and latitudinal differences in growth rates were reported by Parrish and Jones (1952) and Jones (1962). On average temperatures have increased by about 1.5 °C since the Middle Ages (KNMI, 1999). The period between 1400–1700 AD was the coldest period since the last glacial and is referred to as the ‘Little Ice Age’ (Lamb, 1995). However, these temperature reconstructions refer to air temperatures in winter, whereas water temperatures in summer mainly determine growth rates of fish. Furthermore, within time frames corresponding to the precision of the dating of archaeological otoliths (50–200 years), variations in temperature regimes are indicated that often greatly exceed the long-term increase (KNMI, 1999). Decadal-scale changes in marine ecosystems have been reported in relation to climate forcing (Cushing, 1982), but the effect of changes in the overall productivity of the North Sea ecosystem on growth is difficult to evaluate. These uncertainties make it difficult to assess the effect of climate changes on
growth rate comparisons between eras. Nevertheless, it is unlikely that temperature rise alone can explain the growth rate changes in haddock, taking into account the relatively small growth rate changes observed in the other species.

Demersal fisheries in the North Sea only harvest fish above a certain minimum size and therefore may cause an evolutionary change in life-history traits, such as growth, maturation and reproduction (Stokes et al., 1993; Law, 2000; Heino and Godo, 2002). The reduction in the reproductive size and age observed in North Sea plaice and northeast Arctic cod has been shown to be partly due to such an evolutionary change (Rijnsdorp, 1993b; Heino et al., 2002; Grift et al., 2003). As maturation will channel energy resources from somatic growth to reproduction, a reduction of the size at first maturation is expected to result in a decrease in somatic growth. Also direct selection for certain growth types may occur, as shown experimentally by Conover and Munch (2002). If a fisheries-induced decrease in growth rate occurred, it may have confounded an increase in growth rate due to the release of the density-dependent competition.

In conclusion, an unequivocal interpretation of the observed changes in growth cannot be given. Nevertheless, our study lends support for the hypothesis of density-dependent growth in the adult phase in the case of haddock, and it indicates that growth in juvenile plaice may be related to density-dependent processes. Our results do not provide evidence for density-dependent growth in adult plaice, cod and saithe, nor do they support the hypothesis that growth of juvenile gadoids has decreased because of increased juvenile abundance related to reduced predation pressure.

The lack of density-dependent growth in the adult stages of plaice, cod and saithe may be related to the difference in habitat availability for the successive life history stages. Beverton (1995) hypothesised that marine species, which concentrate spatially into nursery grounds, may saturate the carrying capacity of the juvenile habitat, whereas the adult stage may not be limited by adult habitat (Beverton, 1995; Iles and Beverton, 2000). This hypothesis is related to the nursery size hypothesis put forward by Rijnsdorp et al. (1992) and the member/vagrant hypothesis presented by Sinclair and Iles (1989). As plaice, saithe and to a lesser extent cod concentrate during the juvenile phase (Daan et al., 1990), the ‘concentration hypothesis’ may explain why we did not find a change in growth during the adult life phase, whereas in haddock, a species that does not concentrate during the juvenile phase, an increase in growth rate was observed. Whether density-dependent processes occur in the adult phase depends on the relative size of the habitats available for the successive life history stages. In the Baltic, an enclosed sea basin with a relatively large zone of shallow nursery grounds compared to the size of the adult habitat, a large increase in adult growth was observed during the increase in fishing effort in the 20th century (Rijnsdorp, 1994).

Our study has shown that fish remains available from archaeological sources may play an important role in biological research of population dynamic processes. Further work may extend the analysis to other species and other areas to test whether our conclusion of the lack of density-dependent growth in the adult stages in species with limited nursery grounds holds true.

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