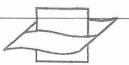
Fish Otoliths and their Relevance to Archaeology: An Analysis of Medieval, Post-Medieval, and Recent Material of Plaice, Cod and Haddock from the North Sea

Wim Van Neer, Anton Ervynck, Loes J. Bolle, Richard S. Millner and Adriaan D. Rijnsdorp

Abstract

The growth increments were investigated of late medieval, post-medieval and modern otoliths of plaice, cod and haddock from the North Sea. Thin-sectioned otoliths were used to age all the analysed individuals and to reconstruct their growth patterns. In addition, fish lengths of the archaeological specimens were calculated after the relation between otolith width and fish length was established using modern material. The age and fish length distribution, and the growth patterns obtained on the archaeological material allow inferences about fish trade, market strategies and consumption behaviour on producer sites (coastal sites) and consumer sites. Differences in growth patterns were observed between the archaeological and recent populations of the three demersal species analysed which may be related to a change in fishing pressure through time. However, diachronic changes in species distribution, temperature, food availability and selection of catch in function of market strategies may have played a role as well. Age and body size data allow some inferences about the exploited fishing grounds, but the growth patterns are of limited use in this respect.

Keywords: Otoliths, Growth, Fisheries, Archaeozoology



Vlaams Instituut voor de Zee Flanders Marine Institute

Introduction

The incremental structures in fish bones and otoliths from archaeological sites have been reported to have a high potential for the interpretation of fisheries in the past (e.g., Desse and Desse-Berset 1992; Hales and Reitz 1992; Van Neer *et al.* 1999; Higham and Horn 2000). Possibilities of interpretation would include the identification of the former fishing grounds, seasonality determination, reconstruction of fishing techniques and marketing practices. In addition, the archaeological material has potential for present-day fishery studies since it allows a comparison of fish growth between the pre-industrialised fishing era and the present period of

high fishing pressure. This input of archaeozoological material is vital for the study of the increased fishing effort since the mid-19th century and its effect on biomass and population dynamics, especially because the systematic collecting of fish otoliths from the catch of research vessels and from market samples only started during the period that fishing pressure was already high. Moreover, it is often not realised within recent fishery research that the effects of increasing fishing pressure may well have become apparent long before the Industrial Era. Historical sources suggest that at the beginning of the postmedieval period restrictive rules were already proclaimed in order to protect the coastal fishery

Received June 2001, revised manuscript accepted January 2002.

Authors' Addresses: Wim Van Neer, Royal Museum for Central Africa, B-3080 Tervuren, Belgium, and Katholieke Universiteit Leuven, Laboratory of Comparative Anatomy and Biodiversity, Ch. de Bériotstraat 32, B-3000 Leuven, Belgium, Email: vanneer@africamuseum.be; Anton Ervynck, Institute for the Archaeological Heritage of the Flemish Community, Doornveld Industrie Asse 3, n° 11 box 30, B-1731 Zellik, Belgium; Loes Bolle and Adriaan Rijnsdorp, Netherlands Institute for Fisheries Research, Haringkade 1, Postbus 68, NL-1970 AB IJmuiden, The Netherlands; Richard Millner, Centre for Environment, Fisheries and Aquaculture Science, CEFAS Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK.

(Hovart 1985). It would thus be no surprise if the impact of over-fishing would already be visible on archaeological material from that period.

It was decided to explore the possibilities of interpretation for both the former and present-day fisheries in the North Sea by setting up a common project in which archaeozoologists and fishery biologists took part. From the growth increments observed on the otoliths of three commercially important demersal fish species (plaice, cod and haddock), age profiles, body size reconstructions and growth rate calculations were made. From the biological point of view, the aim of the joint study was to analyse the possible processes regulating fish growth in the pre-industrial and industrial periods (Bolle et al. 2000; in prep.). The archaeological perspective was to see how the information provided could be maximally explored in order to reconstruct former fishing practices and market strategies. In this paper, attention is focused on these archaeological applications. Modern otolith samples, from fishes captured on a monthly basis, allowed methodological inferences on the validity of marginal growth increment studies for seasonality determinations on archaeological otoliths. However, because of the length of the discussion, the aspect of seasonality will be presented in a future contribution.

Material and Methods

The sites

Usually, the number of otoliths or 'earstones' discovered during excavation is low and on most sites they are totally lacking, either because they are overlooked or because of the poor preservation chances of these aragonite structures which are physically less stable than the hydroxy-apatite of bone (Carlson 1988). However, within the medieval and post-medieval archaeology of Flanders (the northern, Dutch-speaking part of Belgium), it is the experience that otoliths can be preserved in meaningful numbers in suitable, waterlogged contexts such as cesspits or large, deep refuse pits. Most probably, in these structures, alkaline conditions and the absence of (acid) rain percolation permit the survival of the aragonite remains. However, in order to obtain a large sample of otoliths, not only preservation conditions need to be favourable. An adequate recovery method is also needed, implying that sieving has to be applied during the excavation and that the sieved volumes need to be large enough. Often, the volume needed to obtain a satisfactory sample of fish bones only yields a small number of otoliths. The ideal situation is that sieved samples are taken in excess, and that residues are kept as a

sort of archive. On the excavations of the Institute for the Archaeological Heritage of the Flemish Community it is not uncommon to sieve a cesspit or other refuse context completely, on sieves with a mesh width of 0.5 mm.

Due to the extensive sieving practised since the early 1990's, important collections of otoliths from commercially important species have been recovered at a number of late medieval and post-medieval Flemish sites (Fig. 1). Large otolith samples from the late medieval period (15th century) are available from Raversijde. Postmedieval otoliths are present in considerable numbers from the period of preindustrial fisheries (Oostende, AD 1650–1700; Brugge, AD 1650–1750; Mechelen, 18th century) and from the era of industrial fishing (Brugge, AD 1875–1925; Mechelen, AD 1875–1925). The sites from which this material is derived are briefly described below.

Raversijde is a lost coastal village that was inhabited during the 15th century by a community of fishers and farmers. At the site, the remains were found of several houses and related structures (ditches, refuse pits, wells) (Pieters 1997). Because of the calcareous clay soil and a high groundwater level, the preservation of animal remains is excellent and fish remains are particularly abundant, including otoliths. The faunal analyses carried out thus far are published by Van Neer and Ervynck (1993; 1994a; 1994b), Pieters *et al.* (1994b; 1996) and Van Neer and Pieters (1997). The contexts from which the otoliths are derived all date to the period

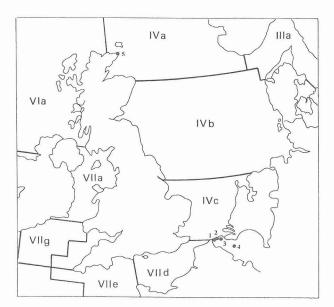


Figure 1. Location of the archaeological sites with abundant otoliths: 1, Raversijde; 2, Oostende; 3, Brugge; 4, Mechelen; 5, Robert's Haven. The ICES divisions of the North Sea from which modern otoliths were studied are also indicated.

AD 1425-1475. In one instance, an assemblage of plaice remains was found that represents a single depositional event (Van Neer and Pieters 1997). These remains were found in a small lens of sediment and represent only heads and tails of plaice that were processed for later consumption (local or elsewhere?). All other otoliths and bones are from general refuse contexts that were deposited over a period of several years or decades. A preliminary evaluation of the potential of the material from the single depositional event has already been published, including the analyses of both otoliths and vertebrae (Van Neer et al. 1999), but the present study must be seen as a complete revision. The chronological context situates Raversijde within the heyday of Flemish fishery, during which Flemish boats were not only active in the local coastal waters, but also on the fishing grounds off the East-English and Scottish coast (Degryse 1944; Van Uytven 1979; Asaert 1980). Whether the fishing campaigns went even further north, however, is not at all clear.

Urban archaeology at the coastal town of Oostende has yielded rich fish assemblages from early postmedieval date, derived from cesspits, refuse pits and refuse layers (Pieters et al. 1994a). From one such layer, dating from the second half of the 17th century, a collection of otoliths has been selected for the present analysis. Without doubt, the majority of the marine fish consumed at Oostende came from its own harbour, or from the smaller fishermen's villages nearby. At the same time, however, Oostende was an urban market place, and therefore the site shares the characteristics of both a consumer and a producer place. During the 17th century, the Flemish open sea fishery suffered heavily from political troubles and was virtually non-existent (Boelmans Kranenburg 1979; 1980). Therefore, it can be presumed that species caught in open sea and consumed within the town, came from foreign (i.e., Dutch) harbours. Fish caught in coastal waters could have come from Flemish harbours, including the town itself.

The town of Brugge is located inland, on the edge of the coastal plain. The otoliths studied from this town are derived from cesspits of urban households and represent accumulations of several years or decades (see, e.g. De Witte et al. 1995). Around 1700 AD, due to the condition of the Flemish fishery at that time (Boelmans Kranenburg 1979; 1980), marine fish perhaps merely arrived at the town's market via the coastal villages from the southern part of the Netherlands. Around 1900 AD, due to the revival of local open sea fishery, fish can have arrived at the site again via the Flemish harbours.

Post-medieval (18th to early 20th century) contexts (L. Muylaert, pers. comm.) yielded numerous otoliths at Mechelen, a town further inland, located in the basin of the river Schelde. Marine fish sold at

Mechelen's market during that period must have come from the fishermen's settlements near or in the estuary of the river Schelde, from the Flemish coast or from the southern part of the Dutch coast.

A large number of otoliths of commercially important species being available from sites in northern Belgium, material from other sites along the North Sea was sought for inclusion. Colleagues working on fish remains from The Netherlands, Great Britain, Germany and Denmark were contacted in an attempt to obtain additional otolith collections, but it appeared that numbers were usually too low and the time periods over which they accumulated too long to make an analysis worthwhile. The only exception found is the site of Robert's Haven from which almost 200 otoliths were put at our disposal. The site is a typical midden deposit located at the eastern coast of Scotland, Caithness. Artefacts and radiocarbon dates suggest that the deposition took place during the 13th-14th centuries AD. The analyses of the intra-skeletal distributions of the cod and saithe remains, as well as of the cutmarks, seem to indicate that the refuse might partly represent leftovers of fish that were cured by the fishing community. At that time, an urban market is not present near the fishermen's site but the processed fish was most probably partly bought by passing tradeships. In any case, whether the cured fish was exported or consumed locally does not influence the analysis of the otoliths from the refuse dumps, since the catch was beheaded before processing (Barrett 1997 pers. comm.).

About 60 gadid otoliths (mainly cod) were found at the site of Akurvik (Iceland), dating between 1200 and 1500 AD (S. Perdikaris, pers. comm.), but this material has not been included in the present project because it is from a region that is very distant from the other sites. In addition, there are two sites from Denmark, located along the Kattegat, of which the otoliths have already been studied for the establishment of the age and season of death. Measurements of the growth increments and calculation of the growth rates have, however, not been carried out (Bødker Enghoff 1994). This material may be of interest in the future, but for the moment it is not included since it belongs to a prehistoric time period (Mesolithic), much older than the dating of the other collections available. Moreover, the Danish material comes from a region rather distant from the find locations of the other samples retained for this study.

Before discussing the material itself, it must be noted that the position of the study sites within the economic chain can have an influence on the composition of the otolith assemblages. Regarding the economy of fish products, the towns of Mechelen, Brugge and, to a certain extent, Oostende differ from Raversijde and Robert's Haven in that they are

consumer sites instead of producer sites. The origin of the fish consumed at Raversijde or Robert's Haven is more or less clear because the majority of the fish was brought in from the sea by the inhabitants themselves and thus represents - for certain species at least - local, coastal catches. The fish consumed at the inland town of Mechelen was certainly not only obtained from the Flemish coast, but also from the southern part of the Dutch coast (Egmond 1997). Another, possibly biasing factor that can be related with the differences between producer and consumer sites, is the selection that can have acted upon the catch before being sold to the towns' markets. Analyses of the Raversijde fish material seem to indicate that the inhabitants of this fishermen's village had a consumer pattern different from the one observed inland. Various species occur in the consumption refuse at Raversijde that have never been found on inland sites (e.g. shark species) and, more importantly in the context of this study, the remains of a commercially important species such as cod are generally smaller at the coastal site than the ones found at contemporaneous inland sites. This clearly indicates that a distinction was made between fish meant for export and those, of lesser commercial value, that were consumed locally (Van Neer and Ervynck 1993; 1994a). This pattern can have influenced the composition of the otolith collections (see below).

The otoliths

More than 2000 otoliths belonging to at least 18 marine species were recovered from the aforementioned sites (Table 1). Otoliths with an un-

certain identification (approximately 5%) or bad preservation were excluded from this list. The identifications were based on the descriptions and images of otoliths in Chaine (1936), Härkönen (1986) and Nolf and Steurbaut (1989), and on comparison with the extensive reference collection of modern otoliths in the Royal Belgian Institute of Natural Sciences (Dr D. Nolf). Due to an overlap in morphology of Pleuronectes platessa and Pleuronectes flesus otoliths, it was sometimes impossible to arrive at a species identification. There are also no reliable characters to distinguish between small specimens of Pollachius virens and P. pollachius (Härkönen 1986). The present study concentrates on the three demersal fish species plaice (Pleuronectes platessa), cod (Gadus morhua), and haddock (Melanogrammus aeglefinus), although sole (Solea solea), flounder (Pleuronectes flesus), dab (Limanda limanda), whiting (Merlangius merlangus), saithe (Pollachius virens) and pollack (Pollachius pollachius) were also represented by sufficiently large numbers. These species will perhaps be analysed in a future study. In Table 2 the otoliths that were successfully thin-sectioned are listed, with indication of the archaeological

In addition to the archaeological material, present-day otolith samples were analysed from research vessel surveys and market sampling programmes. A total of 1210 plaice, 1237 cod, and 596 haddock otoliths were used to analyse the relationship between fish length and otolith width. All of the plaice and haddock otoliths and a subset of the cod otoliths (612) were used to study recent growth patterns in various regions of the North Sea (Fig. 1). The species selected for the present study were (and

	Raversijde	Mechelen	Oostende	Brugge	Robert's Haven
herring (Clupea harengus)	-	=	-	2	=
smelt (Osmerus eperlanus)	155	6	景	1	
conger eel (Conger conger)	1	-		÷	8
cod (Gadus morhua)	32	44	3	1	75
haddock (Melanogrammus aeglefinus)	228	192	42	3	1
whiting (Merlangius merlangus)	450	100	1	15	2
pout (Trisopterus luscus)	1	Η.	2	÷.	ä
saithe (Pollachius virens)	-	<u> </u>	-	÷.	108
pollack (Pollachius pollachius)	-	1 E	Ξ	8	12
horse mackerel (Trachurus trachurus)	5	-	=	=	
greater weaver (Trachinus draco)	1	<u> </u>	Ή.	÷	2
turbot (Psetta maxima)	1	15	+	=	9
brill (Scophthalmus rhombus)	1	-	9	₩.	E
halibut (Hippoglossus hippoglossus)	2	-	9	#	Œ
dab (Limanda limanda)	71	Æ	#	#	6
plaice (Pleuronectes platessa)	627	64	-	45	-
flounder (Pleuronectus flesus)	80	8	2	2	8
sole (Solea solea)	7	2	E	36	無
total	1507	416	48	105	202

Table 1. Overview of the marine fish species represented by otoliths at the different sites. Species retained for study are indicated in bold.

site	context details	period	plaice	haddock	cod
Raversijde	94RAV582	1425-1475	-	2	_
,	94 RAVGR1	1425-1475	58	37	8
	94 RAVGR2	1425-1475	86	53	1
	94 RAVGR3	1425-1475	42	28	3
	94 RAVGR4	1425-1475	53	27	9
	94 RAVGR5	1425-1475	24	13	3
	94 RAVGR6	1425-1475	56	37	4
	94 RAVGR7	1425-1475	26	20	3
	93RAV269 / pit	1425-1475	129	_	_
	94RAV94	1425-1475	-	_	1
	total Raversijde	1425-1475	474	215	32
Mechelen	MVSA OT1-OT11	18th c.	62	189	42
	MVSAMO111Bp141	1875-1925	21	-	-
Oostende		1650-1700	-	30	2
Brugge	WI/55	1650-1750	30	2	_
00	94001/10E'	1350-1450	-	1	-
	GARII/2	1875-1925	14	_	-
Robert's Haven		13th-14th c.	-	1	70
Total			601	440	145

Table 2. Detailed listing of the thin-sectioned archaeological material.

are) all economically important for the North Sea fishery and occur in large numbers in the study area. It is thought that only the distribution area of haddock has significantly changed through time. Data from the 16th century "fish book" of Adriaen Coenen (Egmond 1997) and the relative abundance of haddock at the fishing village of Raversijde suggest that this species must formerly have occurred in large numbers in the southern part of the North Sea. Even during the 20th century, haddock was present in the area (Sahrhage 1964), but now the species is virtually absent.

Methods

Fish otoliths grow by accretion and are therefore characterised by a concentric succession of translucent and opaque zones around a nucleus. At the beginning of each growth season, an opaque zone is deposited which is soon followed by a translucent (or hyaline) zone. There is no sharp boundary between the opaque and translucent zone. Towards the outer margin of the translucent zone, growth slows down and may completely stop. At the onset of a new rapid growth season, a sharp edge is visible between the previous year's translucent zone and the new opaque zone (cf. Rijnsdorp *et al.* 1990). This edge marks the end of the previous 'annulus' and the start of the next one (Fig. 2).

Because of the occurrence of splits, growth checks and false rings, accurate otolith reading requires a long training. According to Williams and Bedford (1974) 6 months should allow readers to deal with the majority of straightforward otoliths,

but they believe readers should be proficient only after 2 years' experience, and having examined at least 5,000 to 10,000 otoliths. Most fishery institutes today have readers specialised in one species only and cross-checking of results between different readers – and by the same reader repeating the reading of a sample at a later date – is necessary to ensure consistency.

All the otoliths used in the present study were processed in the same way (Ayers et al. 2000). They were embedded in black polyester resin and transverse sections of between 0.4 and 0.5mm thick were cut through the center, exposing the nucleus and the annual ring structure. The transverse plane, which bisects the anterio–posterior axis of the otolith, produces the most compressed cross-section with the least surface area and smallest distance between sequential growth structures. However, it is generally the easiest and most accurate method of capturing the full growth history from larval

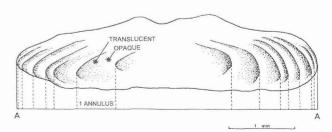


Figure 2. Transversal section of a plaice otolith. Incremental measurements are projected on the main axis of growth A–A.

nucleus to the edge. The otolith images were digitised using a binocular microscope to which a digital camera was attached. The otolith width and incremental measurements were carried out using the digital images of sectioned otoliths and image analysing software. The greatest width of the otolith and the X–Y coordinates of the translucent-opaque transition at the outermost tips of each annulus were recorded. These X-Y measurements were then converted to annulus diameter. The direction of otolith growth changes with age from posterioranterior (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 is 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.

Using the extensive modern samples mentioned earlier, the relationship between total fish length and otolith width has been established for modern plaice, cod and haddock. This relationship typically is linear when total fish length (L) and otolith width (O) are log transformed (Ricker 1973):

$${}^{e}\log (L) = \alpha + \beta^{e}\log (O) \tag{1}$$

with α = the intercept and β = the regression coefficient of the log-log linear relationship.

The parameter estimates of formula (1) can be used to reconstruct fish lengths from the size of otoliths in, for example, stomach contents or archaeological samples. Fishery biologists also use the parameter estimates from the formula to back-calculate the fish growth from year to year for the whole of the animal's life. Doing so, they use the discontinuous, seasonal nature of otolith growth, i.e. the phenomenon of annulus formation, because this enables to define time periods (years) within the otolith's growth (Casselman 1987). The length of a fish at the end of a certain growth season is then expressed as:

$${}^{c}log (L_{i}) = \alpha + \beta^{c}log (O_{i})$$
 or
$$L_{i} = e^{\alpha *} (O_{i})^{\beta}$$
 (2)

in which L_i = fish length at the time of formation of the i^{th} annulus, and O_i = otolith width of the i^{th} annulus.

If the fish length at the time of capture is known then the proportionality method can be used (Rijnsdorp *et al.* 1990):

$${}^{e}log(L_{i}) = {}^{e}log(L_{i}) + \beta({}^{e}log(O_{i}) - {}^{e}log(O_{i}))$$
 or
 $L_{i} = L_{i} * (O_{i} / O_{i})^{\beta}$ (3)

in which L_t = fish length at capture, and O_t = otolith width at capture.

For archaeological otoliths the reconstruction of fish length at the time of annulus formation can only be done using formula (2). The fish length at the time of capture can, of course, never be known from archaeological material, making method (3) impossible to use.

The growth patterns of a fish population can be described by growth curves and growth rate curves. The *growth curves* plot the mean otolith width as a function of age:

$$\sum O_i / n_i = f(i)$$
 (4)

in which i = age, $O_i = otolith$ width of the i^{th} annulus, $n_i = the$ number of measurements for the i^{th} annulus.

The *growth rate curves* plot the mean annual increment as a function of the width class at the beginning of that growing season:

$$\Sigma (O_{i+1} - O_i)_j / n_j = f(j)$$
 (5)

in which j = the width class to which O_i belongs, $(O_{i+1} - O_i)_j = annual$ increment of j^{th} width class and $n_j = the$ number of measurements for the j^{th} width class. If the annual increment is smaller than the range of a width class, then an individual fish can provide more than one measurement for a certain width class. To avoid this, the annual increment per width class was first averaged at the individual level before calculating the sample average (5). So, n_j is actually the number of individuals providing a measurement for the j^{th} width class. It should be noted that, in the context of this study, the age of a fish specimen is defined as the number of years that the animal has completed.

Results

Age distributions

Fig. 3 shows the age distributions recorded from the archaeological otoliths by counting the annuli. However, not all contexts yielded enough material to allow the calculation of distributions for the three species studied. In one instance, the data from two assemblages (the ones dating from around 1900) have been combined. Nevertheless, some patterns appear. The plaice population from Raversijde seems to consist on average of somewhat older animals than the ones from the other archaeological sites. However, the Raversijde material consists of 129 otoliths from the single depositional event and 471 specimens from the general refuse contexts, and the most frequent age class of the distribution of the former assemblage is 5 while that of the latter contexts is 4 (distributions not depicted). The material from the single depositional event could thus slightly bias the interpretation. Still, it must be

concluded that the combined contexts from around 1900 clearly consist of material from younger animals than is the case for late medieval Raversijde. The same could be true for the context from Brugge, dating from around 1700, possibly indicating that older plaice were already becoming less frequent in the southern North Sea during the postmedieval period. The data from 18th century Mechelen show the consumption of animals that are also smaller than the ones from Raversijde. On average, the plaice from Mechelen are somewhat larger than those from the contexts dating around 1900. The overall conclusion could be that there is a diachronic tendency towards an increasing frequency of younger animals, and a simultaneous absence of older specimens, in the youngest samples.

The cod consumed at Raversijde is clearly younger than the ones sold on the market at Mechelen. The age range of cod from Robert's Haven is roughly similar to that from Raversijde. Clearly lacking at both fishermen's villages are the age classes that make up the majority of the cod consumed in the inland town of Mechelen (age groups 8 and older). The age distributions obtained for haddock do not follow the pattern observed for cod. Specimens at the late medieval producer site of Raversijde show similar average ages compared to those at the post-medieval consumer site of Mechelen. The distribution for Oostende, at the same time a fishermen's site and an urban market, proves the presence of animals that are older on average.

Of course, the age distributions of the commercial fish found at the archaeological sites are not sufficient to allow interpretations of the economic value of the species. Much more important is the size of the specimens caught. For archaeological populations it is not possible to do this independently (because the fish length cannot be measured), which implies that the size distributions of the archaeological populations must necessarily be reconstructed. The basis for this is the otolith width which has an allometric relation with the fish length (see earlier). This relationship has been investigated from the recent samples.

Fish length distributions

From the recent samples, the relation between otolith width and fish length has been established, according to the formula described. This has been done separately for male and female specimens (in plaice), per season of capture (first quarter of the year versus third quarter), and per region within the North Sea (Bolle *et al* in prep.). Finally, an overall estimation was made per species for all material combined. Table 3 gives an overview of the parameters obtained. The data in Table 3

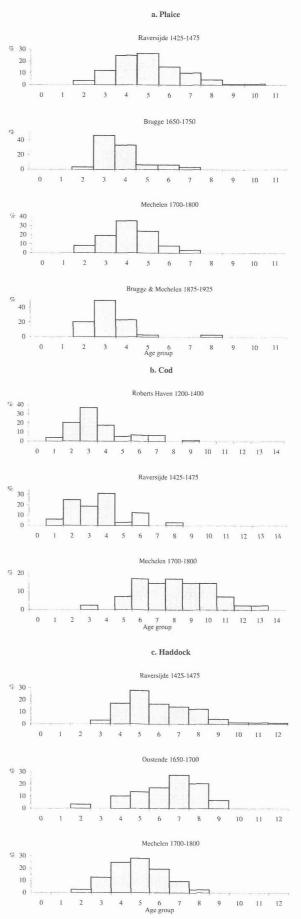


Figure 3. The age distribution of the archaeological otolith samples.

Species	N	\mathbb{R}^2	a	b	OW=2	FL if OW=5	OW=8
Plaice	1207	0.95	1.473	1.399	11.5	41.5	
* males	370	0.94	1.507	1.372	11.7	41.1	
* females	837	0.94	1.462	1.406	11.4	41.5	
first quarter	580	0.94	1.421	1.431	11.2	41.4	
third quarter	627	0.96	1.503	1.381	11.7	41.5	
Region IIIa	118	0.82	1.770	1.236	13.8	42.9	
Region IVa	107	0.83	1.491	1.402	11.7	42.4	
Region IVbe	228	0.97	1.480	1.399	11.6	41.7	
Region IVbw	165	0.91	1.425	1.421	11.1	40.9	
Region IVc	209	0.97	1.506	1.365	11.6	40.6	
Region VIIa	163	0.96	1.382	1.455	10.9	41.4	
Region VIId	177	0.92	1.542	1.354	11.9	41.3	
Region VIa	40	0.88	1.547	1.310	11.6	38.7	
Cod	1232	0.97	1.279	1.456	9.9	37.4	74.2
* first quarter	676	0.97	1.278	1.455	9.8	37.3	74.0
* third quarter	556	0.96	1.279	1.457	9.9	37.5	74.3
* Region IVa	209	0.96	1.326	1.438	10.2	38.1	74.9
* Region IVb	273	0.97	1.231	1.482	9.6	37.2	74.6
Region IVc	233	0.97	1.291	1.451	9.9	37.6	74.3
Region VIIa	177	0.97	1.302	1.451	10.1	38.0	75.1
* Region VIId	219	0.95	1.318	1.418	10.0	36.6	71.3
Region VIa	121	0.93	1.287	1.460	10.0	38.0	75.4
Haddock	592	0.95	1.107	1.521	8.7	35.0	71.5
first quarter	305	0.95	0.975	1.593	8.0	34.4	72.8
third quarter	287	0.94	1.234	1.451	9.4	35.5	70.2
Region IVa	202	0.95	1.205	1.463	9.2	35.1	69.9
Region IVb	222	0.96	1.000	1.585	8.2	34.8	73.4
Region VIa	168	0.92	1.058	1.546	8.4	34.7	71.7
0					0.2	- 417	7 4.17

Table 3. Parameters of the regression model ${}^clog(FL) = \alpha + \beta^* {}^clog(OW)$ estimated separately for sexes, quarters and regions and for all data combined. The asterisk marks the classes which are significantly different in the multiple regression analysis. FL= fish length in cm and OW=otolith width in mm.

clearly illustrate that the differences in the allometric relation between the sexes of plaice are of minor importance. The same is true for the effect of the season of capture. The curves differ more between fish from different geographical zones within the North Sea (especially in the case of cod and haddock). However, for archaeological specimens, these conclusions, although important, are of little practical value because provenance, sex and season of capture are unknown. Moreover, it cannot be excluded that diachronic changes have occurred in the allometric relations within the biometry of the three demersal species, a possibility that can never be proven from the archaeological material. The general conclusion must thus be that only the parameters calculated per species on the basis of the whole of the otolith collections can be used to transform the otolith widths observed on the archaeological material into fish length distributions, thus assuming that the allometric relationship between otolith width and body length did not differ markedly between the archaeological and the recent populations, or between diachronic archaeological samples. Fig. 4 shows the reconstructed fish length distributions that, generally, reveal the same trends as described for the age profiles. Still, the data on fish length are more meaningful in terms of the former economy of the site. For the medieval fisherman or for the fish consumer, size mattered, not age.

It should be realised that the fish length distributions are not simple replicas of the age profiles. Indeed, fish length corresponds with age, but does not follow an identical relationship within all collections studied. The fish length is calculated from the otolith width, which is not necessarily related to age in exactly the same way within each of the archaeological populations. Fortunately, however, the relationship between age and otolith width, described by the growth curves and the growth rate curves, can be investigated from both the archaeological and the recent material (Fig. 5).

Ancient versus modern growth patterns

The biometrical observations on the archaeological otoliths allow comparisons between the otolith width at age between populations, through the

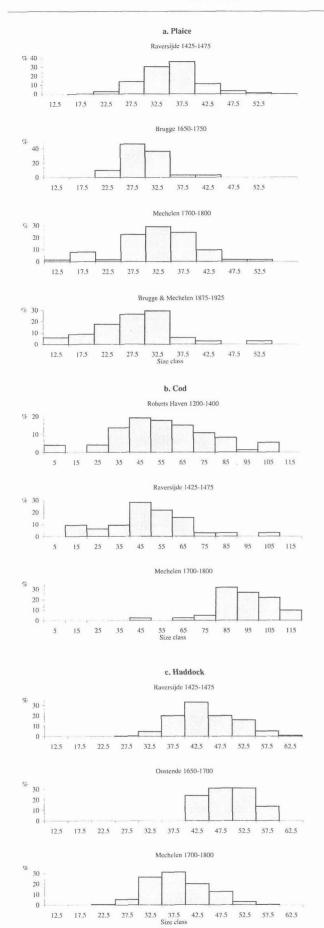


Figure 4. The reconstructed body size in cm total length of the archaeological otolith samples.

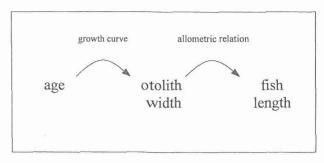


Figure 5. Scheme of the interaction between the parameters studied.

construction of so-called growth curves (see earlier, formula 4). These growth curves only deal with otolith width and not with fish length, in order to circumvent the possibility of different allometric relationships between these two parameters within different populations. Additional information can be gained from growth rate curves (formula 5) which describe, per population, the growth that can be expected for an otolith of a certain width. The growth patterns recorded in the archaeological otoliths are shown in Fig. 6, and are compared with data from recent populations (Bolle et al. 2000; in prep). Amongst the latter, when possible, data are always selected from the southern part of the study area and from the northernmost region. Naturally, not all archaeological sites studied have yielded curves for all three fish species investigated, and in the case of haddock recent data are lacking for the southern North Sea.

The growth curve (Fig. 6a top) seems to be more or less similar for all plaice caught before AD 1875 but appears to be slightly higher in the period AD 1875–1925. Present-day growth again seems to be higher than in the archaeological populations. Concerning the archaeological data, the observations on the otoliths of the oldest individuals must be disregarded because they are few in number. Observing the growth rate curves (Fig. 6a bottom), it is clear that present-day populations of plaice have higher growth rates in the smaller size classes, but that no change is seen in the adult growth. Within the archaeological material, the difference between the finds dating from the period AD 1875-1925 and the older collections is less clear in the growth rate curve than in the growth curve. Of course, the latter shows a cumulative effect and is therefore more gradual in nature. The growth rate curve for the period AD 1875-1925 is more irregular, although the values obtained are almost always the highest amongst the archaeological collections. The conclusion can be that there is a diachronic trend towards faster growing plaice and that this is merely the result of increased growth in the younger animals.

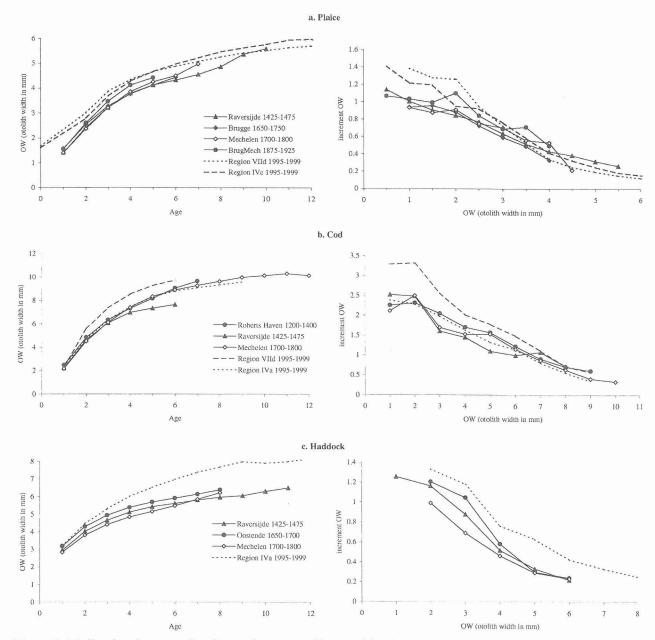


Figure 6. Medieval and post medieval growth patterns illustrated by the mean otolith size-at-age (left), and the mean annual otolith increment per size class (right). Data from modern otoliths have also been included in the graphs.

The recent growth curves clearly illustrate that, within the North Sea, cod is growing faster in southern than in northern waters. The archaeological data show that the specimens consumed at 15th-century Raversijde belonged to a significantly slower growing population compared to the ones occurring now in the North Sea. Cod consumed at 18th-century Mechelen was growing faster, reaching the growth pattern that can now be observed in the northern North Sea. Remarkably, the growth curve for the late medieval Scottish site of Robert's Haven indicates a much faster growth of cod compared to the more southern site of Raversijde. The curves for Mechelen and Robert's Haven are more or less

similar. Also taking into account the growth rate curves, it must be concluded that the archaeological populations show a slower growth in the smaller size classes compared to the recent fast growing animals of the southern North Sea. Generally, the growth of archaeological cod is comparable to that of the present-day population of northern waters, except in the case of Raversijde, where slower growth is visible in the older age classes (4+ and older).

In haddock, the present-day growth is higher in all size classes, in comparison to the archaeological samples. There are no dramatic differences between the diachronic archaeological populations, although the growth seems to have been somewhat faster in the haddock consumed at 17th century Oostende than in the specimens from 15th century Raversijde. The 18th century population from Mechelen shows a somewhat slower growth compared to the two earlier archaeological sites.

Interpretation and Discussion

Market strategies and consumption behaviour

From the data on age, size and growth, obtained from the otoliths, some interpretations can be put forward regarding the fish trade and consumption in late and post-medieval Flanders. The Scottish site can only be used as a comparison for the Flemish sites (and this only in the case of cod). Because it is the only site available from the northern part of the British Isles (for otolith analysis), it does certainly not yet provide sufficient insight in the medieval fish economy in that part of the world.

The majority of the plaice consumed at the late medieval fishermen's village of Raversijde falls between the lengths of 30 and 40 cm. (Fig. 4a). A graphical appreciation of the size distribution, suggests that it is skewed due to an under-representation of the larger size classes (>40 cm). Several explanations for this pattern can be proposed: choice of fishing grounds, fishery techniques or overfishing. Alternatively, large specimens may have been sold away while smaller plaice were eaten in the village, a pattern that must have been part of a market strategy. Possibly, the inland, urban markets demanded large flatfish. Remarkably, the average plaice from late 17th to early 18th century Brugge and 18th century Mechelen are not larger than the ones eaten at Raversijde but these contexts are at least two centuries younger than the material from the fishermen's village. It is therefore possible that larger plaice had become rarer off the Flemish coast, perhaps related to an increasing fishing pressure. Moreover, the late 17th to early 18th century finds from Brugge show a skewed size distribution, perhaps pointing towards a deliberate avoidance of the smallest specimens. The material from around 1900, coming from inland markets, supports the interpretation of larger plaice becoming rarer in the North Sea. The distribution proves the consumption of very small plaice and a near absence of large specimens on the urban markets, again producing a skewed distribution. However, an alternative explanation could be that the financial possibilities of the households that yielded these finds from around 1900, were rather low, suggesting that they could not afford to buy the larger animals from amongst the market's supply. In conclusion, it is possible that the otolith size data illustrate the market strategy within a producer place, and a decreasing supply through time (both in general and especially for the larger specimens), but more comparative data are needed to test these hypotheses. In any case, the age distributions could support the interpretations put forward on the basis of the size distributions. The age distribution for Raversijde has virtually no skewness (Fig. 3a), indicating that the absence of larger plaice (Fig. 4a) is not related to the age structure of the population, but can be linked to a deliberate selection of the catch. The age distribution of the finds from around 1900 is again not skewed (regardless of one outlier), in contrast to the size distribution. This indicates a fish population with a heavy fishing pressure starting from a certain size class (regardless of the age of the animals since there are fast and slow growers within the population), or a selection for small plaice (deliberate or imposed) by the households that were responsible for the deposition of the material studied.

The cod consumed at late medieval Raversijde is clearly younger and smaller than the ones sold on the market at 18th century Mechelen. That this difference is linked to market strategies (fishermen eating the lowest priced items from their catch) is likely but difficult to evaluate since both assemblages do not come from contemporaneous sites. The original idea that cod consumed at the coastal fishermen's villages was smaller than the one eaten in inland towns was developed through the comparison of late medieval fish bones from Raversijde with those from the contemporaneous Flemish towns of Gent and Antwerpen (Van Neer and Ervynck 1993; 1994a). The latter urban sites, however, did not yield sufficient fish otoliths to be incorporated in this study. Still, the interpretation that there was a selection against small cod at Mechelen's market is not only based on the size difference with the Raversijde material, but is also corroborated by the skewness of the size distribution from Mechelen. The age and size range of cod from Robert's Haven is roughly similar to that from Raversijde, but this similarity is unlikely to be linked to market strategies, because of the absence of an urban consumer group within that part of medieval Scotland. The small size distribution reflected by the otoliths could result from a catch in coastal waters. Indeed, for all sites discussed, it should be noted that the location of the fishing grounds where the cod came from, must have had an influence on the fish sizes within the catch. It should be noted, however, that there are slight differences between the size distribution obtained from the cod otoliths from Robert's Haven and the one based on premaxillae previously published by Barrett et al. (1999). The latter distribution shows two peaks, one around 40 cm and one around 90 cm, while the graph based on the otoliths displays a more continuous distribution. It is unclear how this difference should be explained. Variation in the regression curves can be involved, but also the taphonomy of the contexts and preservation conditions for the material studied.

Haddock consumed at Raversijde were on average younger and somewhat smaller than the ones eaten at Oostende. Possibly, the same market mechanism as attested for cod reveals itself. However, the context from Oostende being at least two centuries younger than the one from the fishermen's village, it is conceivable that the difference would have been more pronounced when comparing contemporaneous sites. Possibly, early post-medieval haddock coming in from the southern North Sea were on average already smaller than the late medieval catch, but the selection of the specimens to be sold on the urban market could have obscured this pattern. An alternative explanation could be that the post-medieval fishermen of Oostende visited fishing grounds where larger haddock were present than in the waters exploited by the late medieval fishermen of Raversijde (open sea versus coastal waters). In any case, the data from 18th century Mechelen seem to support the idea of a diachronic size decline in the available haddock. The size of the animals sold at this post-medieval urban consumer site is significantly smaller than that of the haddock eaten at the late medieval producer site (and according to the market strategy it should be much larger). Finally, a critical approach could be to minimize the differences observed, because the market strategy for cod would not have been valid for haddock. The explanation could lie in the fact that haddock was less expensive than cod (see the arguments in Ervynck and Van Neer 1994), and that therefore price calculations were less influential for the haddock. However, when market strategies were taken into account for plaice (also a less expensive commodity than cod), they must also be considered for haddock.

Temporal variations in fish populations possibly related to fishery practice

The data on growth clearly indicated differences amongst the archaeological and the recent populations of the three demersal species studied. These results are of prime importance for fishery sciences as the time series held at fisheries institutes are restricted to the Industrial Era. Both temperature rise and increasing nutrient availability can have influenced fish growth in the North Sea through time, and especially during the last century (Rijnsdorp and van Beek 1991; Fonds *et al.* 1992; Brander 1995). Apart from these variables, it is also assumed that diachronic changes have occurred in the growth of demersal North Sea fish, from the Middle Ages

to recent times, related to fishing pressure. This change can have been phenotypic or can have had a genetic cause. Over time, fish stocks have been reduced considerably as a result of the increased fishing effort, starting from the Middle Ages but especially apparent since the mid-19th century. It is indeed conceivable that in the time periods prior to the era of industrialised fishing, demersal fish populations were at a much higher level of abundance and that under those conditions growth rate was reduced through density-dependent competition for food. For all species, a density-dependent reduction in adult growth is then expected, but for the juveniles a species-specific response must be hypothesized because species differ in their life history (overlap in distribution between juveniles and adults). In species where juveniles and adults are spatially separated (plaice) no change in juvenile growth was expected. Lower growth rates were expected for juveniles of species where adults and juveniles utilise the same food sources and spatially overlap (haddock, and to some extent, cod). In species where the juvenile abundance may be negatively affected by a large cannibalistic adult stock (cod), juvenile growth was expected to be higher in historic time periods, because the larger adult stock was expected to have reduced the juvenile stock due to cannibalism. During and shortly after the Second World War, growth rate reductions were observed in North Sea fish, that were believed to be linked to an increase of the population density, and thus of the intra-species competition (Beverton and Holt 1957; Rijnsdorp and van Leeuwen 1992). Concerning genetic changes, it can be envisaged that the recent, high fishing pressure induces a selection towards animals that grow faster and therefore become sexually mature at an earlier age (in fish, sexual maturity depends on body size). The slow growers indeed run a higher risk than the fast growers of being caught before spawning the first time. It should be noted that this argument only holds when the size at which the fish become sexually active equals or exceeds the size above which the fish are caught. When the size of sexual maturity is significantly lower than the size of capture, the slow growers have an advantage (because they stay longer under the capture threshold while already being reproductive). However, in the species considered the observed minimum capture sizes are always lower than the known sizes of sexual maturity (data from Muus and Nielsen 1999).

In the case of plaice, a possible diachronic trend towards faster growth was observed. This pattern was found to be especially related to increased juvenile growth, and is possibly the result of selective pressure linked with increasing fishing intensity. The increasing fishing pressure also revealed itself

when the age and size distributions were discussed but it remains strange that the effect of this selective factor is not visible as increased growth in the large size classes. A decrease in intra-species competition due to a reduction of the population numbers by increasing fishing intensity can also not explain the growth changes observed because in that case the change should be most apparent in the adult animals. Another possibility is that the somewhat faster growth of the juveniles of the plaice consumed around 1900 at Mechelen and Brugge was the result of gradual eutrophication of the estuarine and coastal waters. This influence will have been less important in the deeper waters, resulting in the absence of change in the adult growth. Alternatively (or simultaneously), the rise in temperature during the 19th and 20th century (Fig 7) can be held responsible for the changes in juvenile growth. Here again, the coastal and estuarine waters will have been more affected than the open sea in which the adult plaice are living. However, in contradiction with the latter explanation, Rijnsdorp and van Leeuwen (1996) were not able to detect a temperature signal in the variations in the growth of plaice over a period of 35 years (1950 – 1985). An increase in growth rate of the smaller size classes has been observed in the 1960s and 1970s but was believed to be related to the increased productivity of the benthic system in coastal waters of the southeastern North Sea due to the enhanced levels of nutrients and the impact of beam trawling (Rijnsdorp and van Beek 1991; Rijnsdorp and van Leeuwen 1992; 1996). This

apparent increase in growth rates of the smaller size classes during the second half of the 20th century points towards eutrophication but could at the same time indicate that the change in growth is only a recent phenomenon. However, this interpretation ignores the possible difference between the growth curve of the material from around 1900 and these from the older sites.

The differences between the growth patterns of cod from the three archaeological populations studied are not easily interpreted. The fact that the animals eaten at late medieval Robert's Haven were growing faster than the ones from the more southern late medieval site of Raversijde is remarkable (the difference between recent northern and southern cod would suggest the reverse) and remains unexplained at first sight. Whether the faster growth at post-medieval Mechelen, compared to late medieval Raversijde, is influenced by fishing pressure, is also difficult to prove. It must not be overlooked that the selection against large specimens at Raversijde promoted the proportion of slow growing animals within the remaining population, while the selection for large specimens at Mechelen favoured the presence of fast growers. Whether such a 'sampling bias' can also explain the differences between Robert's Haven and Raversijde, is difficult to attest. Perhaps the cod at the Scottish site, although being small, was not selected, but only the result of fishing near the coast, yielding only young specimens? In that case, fast growers would also be equally represented in the captured population.

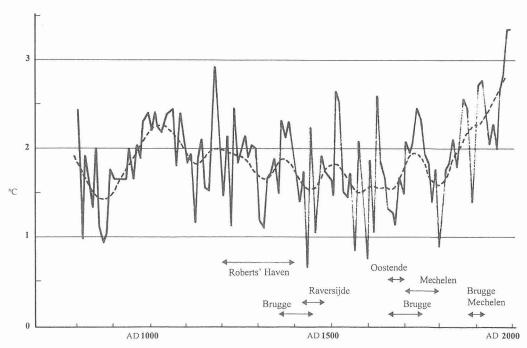


Figure 7. Ten year average winter temperature (solid line) and running mean over 150 years (broken line) from AD 800 to the present (after KNMI 1999).

Additionally, it is possible that the cod eaten at Raversijde was captured in northern waters, which would also help to explain the slow growth of the cod from that site. Historical sources indeed indicate that during the 15th century cod fishing was practiced by Flemish fishermen on the Dogger-Bank (Hovart 1985). Finally, the results indicate that recent cod grow faster than the archaeological populations, especially during the younger ages. Whether this is related to an increased fishing pressure, reducing the presence of adults exercising cannibalistic predation on the juvenile stock, or whether this shift is related to other factors (e.g. temperature), remains unclear.

Hypothetically, the (slight) growth difference between the haddock from Raversijde and those from Oostende could be explained by the selection for the larger animals within the catch at the latter site. Most probably, the haddock from these two sites represents local catch. The rather high number of otoliths collected at the Belgian sites and historical data (Egmond 1997) indeed suggest that haddock must have been quite numerous in the southern North Sea in the late medieval and early postmedieval period. The slower growth within the younger population from Mechelen could have been caused by the fact that these specimens were caught in more northern waters, perhaps because haddock were already becoming rarer off the Flemish coast. In this context, the fact that the animals sold on the urban market of Mechelen are generally smaller than the ones eaten at the fishermen's village is also meaningful. That the present-day growth of haddock is higher in all size classes, compared to the archaeological samples may be related to the increase in growth that has been observed for this species between the late 1920s and the 1960s (Jones and Hislop 1978). The underlying cause for this recent growth increase can be multiple.

Identification of fishing grounds

The commercially important North Sea species analysed in this study have a wide distribution and it was hoped that the growth increment data would allow a more precise identification of the explored fishing grounds through time. The diachronic study of fish remains from Belgium has shown that there was a shift in the exploited and commercialised fish species through time (Van Neer and Ervynck 1993; 1994a; 1994b). Generally, in mid and late medieval times, there was a shift from a fishery concentrated in coastal waters, going mainly for flatfish by nets, to a fishery in which at least three strategies were followed: flatfish fishing in coastal waters, capturing of gadids with lines, mainly in more open sea, and herring fishery using floating nets (Bødker Enghoff 2000). Concerning the Flemish

archaeological material, establishing the fishing grounds is especially crucial in the case of the gadids, since they could be fished off the Flemish coast or in more northern waters. Historical sources mention the so-called 'doggevaerdt', a cod fishing season that started around Whitsuntide and was practiced on the Dogger-Bank (Hovart 1985), and demonstrate the presence of Flemish fishermen in the harbours of northern England from the 13th century onwards (Asaert 1980). Whether these fishing trips also went for haddock, is not clear but at least for cod it would be interesting to learn from the archaeological finds when precisely this fishing in northern waters started and what the importance was for the inland markets of northern cod versus cod captured off the Flemish coast.

The modern otolith samples show that, within the North Sea, there is an increase in the growth rate of cod from north to south. In theory, these differences in modern growth rate could thus be used as a basis for the establishment of the former fishing grounds when studying archaeological material (Van Neer et al. 1999). However, the approach needs to be abandoned because the growth rate is influenced by many other factors, in addition to water temperature. The present study has demonstrated that the growth rates are possibly also influenced by species distribution and density, food availability (present-day eutrophication) and fishing pressure, that have all changed over time. Moreover, the archaeological otolith collections are presumably biased due to selection of the catch. Before any identification of former fishing grounds can be performed systematically, a dataset will be needed of growth data for several periods and regions. This can only be obtained from well-dated sites for which, in addition, good historical sources indicating the fishing grounds are available. Otolith elemental analysis (Secor et al. 1995) and stable isotope analysis (C and O) (Joukhadar et al. 2002) may also provide more information in the future. By following the individual life histories of fish, as reflected by the microchemistry and isotope ratios in their otoliths, information on the water temperatures and salinities might be obtained that indicate the visited waters, including the ones where the fish was captured.

For the moment, only the basic data on age and body size reconstructed on the basis of otolith measurements (Figs. 3 and 4) allow statements about the fishing zones formerly exploited. The majority of the plaice found at the Brugge and Mechelen sites dated AD 1875–1925, and the Brugge site dated AD 1650–1750 are 3 years old and 25–30 cm long. Plaice from Raversijde and 18th century Mechelen are slightly older and larger, the majority are 4–5 years and 30–35 cm. The underrepresentation or total absence of older specimens which are regularly

found in the modern, more northern samples (Wimpenny 1953) indicate that the plaice must have come from the southern North Sea. These findings are in agreement with the historical data (Egmond 1997). Considering the gadids, the data for Robert's Haven suggest a catch in local, coastal waters. For the Flemish sites, the size and age data are less trustworthy because of the market strategies (selection for large or small fish) that have biased the samples. It is therefore not clear, for example, whether the small cod consumed at Raversijde represent a catch of smaller specimens, characteristic for coastal waters, or the leftovers from a catch in open sea (merely consisting of larger animals that have been traded away). The former possibility does not contradict the market strategy hypothesized earlier, only, in that case, the selection acted between catches from different fishing grounds instead of within a catch from one area only. In the case of haddock, interpretations are additionally hampered by the possible temporal differences in distribution of this fish.

Conclusion

The foregoing analysis demonstrates that otoliths have a high potential for archaeological interpretations but that at the same time the search for a causal explanation of changes and trends observed is very complicated. Especially in the case of growth patterns, multiple factors can have produced the changes observed (equifinality). In the case of the size and age distributions, the main problem is the fact that archaeological samples are almost always biased, making it for example difficult to compare producer and consumer sites. In general, the interpretations about the onset and impact of gradual overfishing would benefit from the analysis of a sample that pre-dates the epoch in which marine fish from open sea became an important commodity. Such a sample, however, is per definition impossible to find at an archaeological site.

Acknowledgements

The authors wish to thank Dr. James Barrett (University of York), Bieke Hillewaert (Stedelijke Archeologische Dienst Brugge), the 'Mechelse Vereniging voor Stadsarcheologie', and Marnix Pieters (Institute for the Archaeological Heritage of the Flemish Community, IAP) for providing the otoliths, Luc Muylaert (IAP) for helping in the retrievement of the otoliths from the sieved residues, Dr. Dirk Nolf (Royal Belgian Institute of Natural Sciences) for assisting with the identification of the otoliths, and Richard Ayers (CEFAS), Piet van Leeuwen (Nether-

lands Institute for Fisheries Research), Daphne Stalpaert (Royal Museum for Central Africa, KMMA) and Peter De Smedt (KMMA) for their help with otolith reading and measuring. The research was made possible thanks to the support of the European Commission (through a grant under the FAIR Programme) and of Dutch national research programmes (Netherlands Institute for Fisheries Research RIVO DLO-Programme 324: Aquatic Ecosystems and Fisheries, Centre for Estuarine Fisheries and Aquaculture Research CEFAS Programme, Department of Sea Fisheries Programme). The contribution of Wim Van Neer to this paper also presents research results of the Interuniversity Poles of Attraction Programme - Belgian State, Prime Minister's Office -Federal Office for Scientific, Technical and Cultural Affairs.

References

- Asaert, G. 1980. Scheepvaart en visserij, pp. 128–34, in *Algemene Geschiedenis der Nederlanden 4*. Haarlem: Fibula-Van Dischoeck.
- Ayers, R., Bolle, L., Van Neer, W., van Leeuwen, P., Ongenae, E., De Smedt, P., Stalpaert, D., Boon, M. and Rink, G. 2000. Methods, pp. 19–21 in Bolle, L. and Rijnsdorp, A. D. (eds.), Changes in Growth of Demersal Fish in the North Sea in Medieval and Recent Time Periods, with Particular Reference to the Effect of the Industrialisation of the Fisheries. Unpublished Final Report EU-Contract FAIR CT97–3462.
- Barrett, J. H. 1997. Fish trade in Norse Orkney and Caithness: a zooarchaeological approach. *Antiquity* 71, 616–38.
- Barrett, J. H., Nicholson, R. A. and Ceron-Carrasco, R. 1999. Archaeo-ichthyological evidence for long-term socioeconomic trends in Northern Scotland: 3500 BC to AD 1500. *Journal of Archaeological Science* 26, 353–88.
- Beverton, R. J. H. and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations (Fisheries Investigations 2, 19). London: Her Majesty's Stationery Office.
- Bødker Enghoff, I. 1994. Fishing in Denmark during the Ertebølle period. *International Journal of Osteoarchaeology* 4, 65–96.
- Bødker Enghoff, I. 2000. Fishing in the southern North Sea region from the 1st to the 16th century AD: evidence from the fish bones. *Archaeofauna* 9, 59–132.
- Boelmans Kranenburg, H. A. H. 1979. Visserij in de Zuidelijke Nederlanden 1650–1795, pp. 261–4 in *Algemene Geschiedenis* der Nederlanden 8. Haarlem: Fibula-Van Dischoeck.
- Boelmans Kranenburg, H. A. H. 1980. Visserij in de Zuidelijke Nederlanden 1580–1650, pp. 170–1 in *Algemene Geschiedenis* der Nederlanden 7. Haarlem: Fibula-Van Dischoeck.
- Bolle, L., Rijnsdorp, A. D., van Leeuwen, P., Ayers, R., Ongenae, E. and Stalpaert, D. 2000. Spatial and temporal variations in growth rates of plaice, cod, haddock and saithe, pp. 36–41 in Bolle, L. and Rijnsdorp, A. D. (eds.), Changes in Growth of Demersal Fish in the North Sea in Medieval and Recent Time Periods, with Particular Reference to the Effect of the Industrialisation of the Fisheries. Unpublished Final Report EU-Contract FAIR CT97–3462.
- Brander, K. M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua L.*). ICES Journal of Marine Science 52, 1-10.
- Carlson, C. 1988. An evaluation of fish growth annuli for the determination of seasonality in archaeological sites, pp. 67–

- 78 in Webb, E. (ed.), Recent Developments in Environmental Analysis in Old and New World Archaeology (BAR International Series 416). Oxford: British Archaeological Reports.
- Casselman, J. M. 1987. Determination of age and growth, pp. 209–42 in Weatherly, A. H. and Gill, H. S. (eds.), The Biology of Fish Growth. London: Academic Press.
- Chaine, J. 1936. Recherches sur les otolithes des poissons. Etude descriptive et comparative de la sagitta des Téléostéens (suite). Actes de la Société Linnéenne de Bordeaux 88, 5–246.
- Degryse, R. 1944. Vlaanderens Haringbedrijf in de Middeleeuwen. Antwerpen: De Nederlandse Boekhandel.
- Desse, J. and Desse-Berset, N. 1992. Age et saison de mort des poissons: applications à l'archéologie, pp. 341–53 in Baglinière, J.-L., Castanet, J., Conand, F. and Meunier, F. J. (eds.), *Tissus Durs et Age Individuel des Vertébrés* (Collection Colloques et Séminaires). Paris: ORSTOM.
- De Witte, H., Hillewaert, B. and Maertens, J.-P. 1995. Archeologisch jaarrapport 1993–1994, pp. 72–95 in Vermeersch, V. (ed.), Jaarboek 1993–94. Brugge Stedelijke Musea. Brugge: Vrienden van de Stedelijke Musea.
- Egmond, F. 1997. Een Bekende Scheveninger. Adriaen Coenen en zijn Visboeck van 1578. Den Haag: Centrum voor Familiegeschiedenis van Scheveningen.
- Ervynck, A. and Van Neer, W. 1994. A preliminary survey of fish remains in medieval castles, abbeys and towns of Flanders (Belgium), pp. 303–8 in Heinrich, D. (ed.), Archaeo-Ichthyological Studies. Papers presented at the 6th Meeting of the I.C.A.Z. Fish Remains Working Group (Offa 51). Neumünster: Wachholtz Verlag.
- Fonds, M., Cronie R., Vethaak, A. D. and van der Puyl, P. 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Netherlands Journal of Sea Research 29, 127–43.
- Hales, L.S. and Reitz, E.J. 1992. Historical changes in age and growth of Atlantic croaker; Micropogonias undulatus (Perciformes: Sciaenidae). Journal of Archaeological Science 19, 73–99.
- Härkönen, T. 1986. Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic. Hellerup, Denmark: Danbui ApS.
- Higham, T. F. G. and Horn, P. L. 2000. Seasonal dating using fish otoliths: results from the Shag River Mouth Site, New Zealand. Journal of Archaeological Science 27, 439–48.
- Hovart, P. 1985. Zeevisserijbeheer in vroegere eeuwen. Een analyse van normatieve bronnen. Mededelingen van het Rijksstation voor Zeevisserij 206, 1–188.
- Jones, R. and Hislop, J. R. G. 1978. Changes in North Sea haddock and whiting. Rapports et Proces-verbaux des Réunions/ Conseil International pour l'Exploration de la Mer 172, 58–71.
- Joukhadar, Z., Patterson, W. P., Todd, T. N. and Smith, G. R. 2002. Oxygen isotopic studies of the life history of Coregonus artedii in the St. Mary's River, Laurentian Great Lakes. Proceedings of the Symposium for Coregonid Research (in press).
- KNMI (Royal Dutch Meteorological Institute) 1999. http://www.knmi.nl/voorl/nader/klim/omslag.gif
- Muus, B. J. and Nielsen, J. G. 1999. Zeevissen van Noord- en West-Europa. Haarlem: Schuyt.
- Nolf, D. and Steurbaut, E. 1989. Evidence from otoliths for establishing relationships within gadiformes, pp. 89–111 in Cohen, D. M. (ed.), Papers on the Systematics of Gadiform Fishes (Science series 32). Los Angeles: Natural History Museum of Los Angeles County.
- Pieters, M. 1997. Raversijde: a late medieval fishermen's village along the Flemish coast (Belgium, province of West-Flanders, municipality of Ostend), pp. 169–77 in De Boe, G. and Verhaeghe, F. (eds), Rural Settlements in Medieval Europe. Papers of the 'Medieval Europe Brugge 1997' Conference 6 (IAP)

- Rapporten 6). Zellik: Institute for the Archaeological Heritage of the Flemish Community.
- Pieters, M., Bouchet, F., Cooremans, B., Desender, K., Ervynck, A. and Van Neer, W. 1996. Granaatappels, een zeeëngel en rugstreeppadden. Een greep uit de inhoud van een bakstenen beerput uit het 15de-eeuwse Raversijde (stad Oostende, prov. West-Vlaanderen). Archeologie in Vlaanderen 5, 193–224.
- Pieters, M., Dewilde, M., Impens, Y. and Tratsaert, B. 1994a.
 Zes eeuwen bewoningsgeschiedenis op het Mijnplein te Oostende (prov. West-Vlaanderen). Interimverslag. Archeologie in Vlaanderen 4, 187–203.
- Pieters, M., Ervynck, A., Van Neer, W. and Verhaeghe, F. 1994b. Raversijde: een 15de eeuwse kuil, een lens met platvisresten, en de betekenis voor de studie van de site en haar bewoners. *Archeologie in Vlaanderen* 4, 253–77.
- Ricker, W. 1973. Linear regressions in fishery research. *Journal of Fisheries Research Board of Canada* 30, 409–34.
- Rijnsdorp, A. D. and van Beek, F. A. 1991. Changes in growth of plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the North Sea. *Netherlands Journal of Sea Research* 27, 441–47.
- Rijnsdorp, A. D. and van Leeuwen, P. I. 1992. Density dependent and independent changes in somatic growth of female North Sea plaice, *Pleuronectes platessa*, between 1930 and 1985 as revealed by back-calculation of otoliths. *Marine Ecology Progress Series* 88, 19–32.
- Rijnsdorp, A. D. and van Leeuwen, P. I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES Journal of Marine Science* 53, 1119–213.
- Rijnsdorp, A. D., van Leeuwen, P. I. and Visser, T. A. M. 1990. On the validity and precision of back-calculation of growth from otoliths of the plaice *Pleuronectes platessa* L. *Fisheries Research* 9: 97–117.
- Sahrhage, D. 1964. Über die Verbreitung der Fischarten in der Nordsee. I. Juni-Juli 1959 und Juli 1960. Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung 17, 165– 278
- Secor, D. H., Henderson-Arzapalo, A. and Piccoli, P.-M. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *Journal of Experi*mental Marine Biology and Ecology 192, 15–33.
- Van Neer, W. and Ervynck, A. 1993. Archeologie en Vis. Zellik: Instituut voor het Archeologisch Patrimonium.
- Van Neer, W. and Ervynck, A. 1994a. L'Archéologie et le Poisson. Ath: ASBL Promotion du Tourisme et des Musées Athois.
- Van Neer, W. and Ervynck, A. 1994b. New data on fish remains from Belgian archaeological sites, pp. 217–29 in Van Neer, W. (ed.), Fish Exploitation in the Past. Proceedings of the 7th Meeting of the ICAZ Fish Remains Working Group (Sciences Zoologiques 274). Tervuren: Annales du Musée Royal de l'Afrique Centrale.
- Van Neer, W. and Pieters, M. 1997. Evidence for processing of flatfish at Raversijde, a late medieval coastal site in Belgium. *Anthropozoologica* **25/26**, 571–8.
- Van Neer, W., Lougas, L. and Rijnsdorp, A. D. 1999. Reconstructing age distribution, season of capture and growth rate of fish from archaeological sites based on otoliths and vertebrae. *International Journal of Osteoarcheology* 9, 116–30.
- Van Uytven, R. 1979. Visserij in de Zuidelijke Nederlanden, pp. 138–44 in Algemene Geschiedenis der Nederlanden 6. Haarlem: Fibula-Van Dischoeck.
- Williams, T. and Bedford, B. C. 1974. The use of otoliths for age determination, pp. 114–23 in Bagenal, T. B. (ed.), Ageing of Fish. Unwin, Surrey: The Gresham Press.
- Wimpenny, R. S. 1953. The Plaice. London: Arnold.