

Characteristics of early Atlantic cod (*Gadus morhua* L.) catches based on otoliths recovered from archaeological excavations at medieval to early modern sites in northern Norway

Torstein Pedersen^{1,*}, Colin Amundsen² and Stephen Wickler³

¹Department of Arctic and Marine Biology, UiT The Arctic University of Norway, PO Box 6050 Langnes N-9037 Tromsø, Norway

²Museum of Archaeology, University of Stavanger, Peder Klows gate 30 A, 4010 Stavanger, Norway

³The Arctic University Museum of Norway, UiT The Arctic University of Norway, PO Box 6050 Langnes N-9037 Tromsø, Norway

*Corresponding author: Tel: +47 90808210; e-mail: Torstein.Pedersen@uit.no.

We compared stock origin, size- and age-distributions, and length growth rates derived from Atlantic cod otoliths from archaeological excavations at two sites in northern Norway: Vågar in Lofoten (68°12'N, ad 1156–1285) and the Værbukta site (70°57'N, ad 1450–1680). For comparison, modern otoliths were sampled during 1993–2001 from areas situated close to Vågar and Værbukta. Length-at-age from pre-20th century samples was back-calculated from otolith growth increments. The pre-20th century cod from Vågar was dominated by northeast Arctic cod (NEAC) of age 9–16 years and were much older and larger than the pre-20th century cod from Værbukta, which were dominated by coastal cod of age 2–6 years. Cod from Vågar had smaller increments and a shorter back-calculated length-at-age than modern cod from Lofoten. In contrast, the predominantly coastal cod from Værbukta had similar increments width and length-at-age as in modern samples. Age-distributions and mortality rates of the pre-20th century Vågar cod and NEAC from Lofoten in the 1930s were similar, indicating that both age at maturity and longevity were similar for these time periods. This contrasts with truncated and young age-distributions of spawning NEAC in the 1980s and 1990s following the strong increase in fishing and total mortality rate in the period 1955–2000.

Keywords: back-calculation, Barents Sea, cod otoliths, excavations, exploitation baseline, length growth, Lofoten, northeast Arctic cod.

Introduction

Fishery science suffers from the “shifting baseline syndrome”, where a lack of data from lightly exploited ecosystems may hamper the understanding of the effects of human exploitation (Pauly, 1995; Pinnegar and Engelhard, 2008; Barrett, 2019). Exploitation of many fish stocks increased heavily during the 20th century, resulting in declines and collapses of important stocks (Christensen *et al.*, 2003). Concern has been expressed that heavy exploitation of fish stocks may cause evolutionary changes in size, age at maturity, and length growth rate (Law, 2000; Swain *et al.*, 2007). Atlantic cod (*Gadus morhua* L.) has been an ecologically important species in boreal and subarctic ecosystems and a major target species for commercial fisheries (Garrod and Schumacher, 1994; Øiestad, 1994; Godø, 2003). Recent genetic studies on Atlantic cod have given knowledge on how fishery exploitation affects the genome (Martínez-García *et al.*, 2021; Pinsky *et al.*, 2021; Sodeland *et al.*, 2022). The general pattern for Atlantic cod stocks has been an increase in fishing mortality and total mortality rate during the 20th century (Garrod and Schumacher, 1994; Myers *et al.*, 1996). Some cod stocks, i.e. northeast Arctic cod, have experienced decreased exploitation levels in recent decades, followed by responses in stock size and age structure (Rørvik *et al.*, 2022). There is sparse information from cod stocks that are lightly exploited, and since the effects of exploitation and environmental variability are difficult to separate (Godø, 2003; Rørvik *et al.*, 2022), it is challenging to

understand and predict the long-term ecological and evolutionary effects of heavy exploitation. Although it is challenging to reconstruct past environments and populations, there is a long research tradition within palaeoecology, palaeoanthropology, and archaeology that provides useful methodological approaches (Pitcher, 2001; Reitz, 2004; McGovern *et al.*, 2007; Ferrari *et al.*, 2021; Martínez-García *et al.*, 2021; Andrews *et al.*, 2022).

The survival and abundance of cod are very sensitive to fishing pressure. Changes in size and age at sexual maturity and the size and age structure of the catches may reflect changes in the stocks (Jørgensen, 1990; Garrod and Schumacher, 1994). Material such as bones and otoliths from archaeological excavations may be used to reconstruct the size and age structure of the catches (Amorosi *et al.*, 1994; Bolle *et al.*, 2004; Maschner *et al.*, 2008; Ólafsdóttir *et al.*, 2017). Otoliths can also be used to analyse stock origin and to back-calculate the growth trajectories of individual fish (Rollesfsen, 1934; Bolle *et al.*, 2004; Berg *et al.*, 2005) and yield information about changes in the age structure of the catches, growth- and mortality rates, and ambient temperature (Limburg *et al.*, 2008; Geffen *et al.*, 2011; von Leesen *et al.*, 2022). Ageing of cod otoliths was described in the 1930s (Rollesfsen, 1933), and there is sparse knowledge on the population dynamics of cod stocks before 1930, when the exploitation level was relatively low compared to the late 20th century level (Hysten, 2002; Godø, 2003; Bolle *et al.*, 2004; Rørvik *et al.*, 2022). How-

Received: May 10, 2022. Revised: September 16, 2022. Accepted: September 19, 2022

© The Author(s) 2022. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

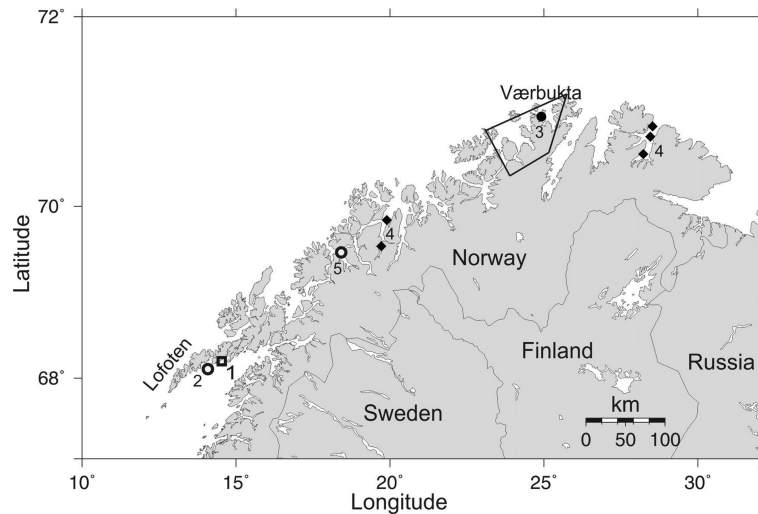


Figure 1. Overview of sampling locations for pre-20th century and modern otoliths (1) pre-20th century Vágur and (2) Lofoten modern; (3) pre-20th century Værbukta, Troms/Finmark modern. (4) Ullsfjord, (4) Tana, and (5) Malangen locations for reconstructed temperature time-series (Hald et al. 2011). The polygon around (3) shows the area for sampling of coastal cod reported in Berg and Albert (2003).

ever, results from studies of cod otoliths from pre-20th century contexts show that otoliths may provide valuable knowledge (Limburg *et al.*, 2008; Hufthammer *et al.*, 2010; Geffen *et al.*, 2011; Ólafsdóttir *et al.*, 2017).

In Norway, cod has been exploited since the Stone Age (Hufthammer *et al.*, 2010) and has historically been a very important species in the fisheries (Rollefsen, 1953; Øiestad, 1994; Nielssen, 2014, 2016). Cod in waters north of 62°N adjacent to Norway are divided into two major groups: the large migratory northeast Arctic cod stock (NEAC) and the more stationary Norwegian coastal cod (NCC), consisting of several sub-units (Rollefsen, 1933, 1934; Jakobsen, 1987; Berg and Albert, 2003; Dahle *et al.*, 2018). Analysis of excavated cod otoliths from non-spawning areas from the medieval period in northern Norway has shown that individual back-calculated length-at-age were variable and dependent on the ambient temperature (Geffen *et al.*, 2011). Historical knowledge is most detailed for the fisheries on the major NEAC spawning grounds in the Lofoten archipelago (Figure 1) (Godø, 2003). During the period from 1932 to 2000, fishing mortality has increased, and age and size composition for the NEAC have changed towards more truncated distributions and age at maturity has decreased (Jørgensen, 1990, 1992; Godø, 2003; Ottersen *et al.*, 2006). After ca. year 2000, fishing mortality of NEAC has decreased with a corresponding increase in age diversity in the stock but with no large change in age at maturity (Rørvik *et al.*, 2022).

Samples of well-preserved cod otoliths from archaeological excavations at two sites in northern Norway dated to the medieval and early modern periods were analysed in this study. These include a medieval submerged cultural deposit radiocarbon dated to cal. AD 1156–1285 from the harbour at the Vágur site in Lofoten and another site dated to ca. AD 1450–1680 from Værbukta in Finnmark County (Figure 1). Lofoten is a major spawning area for the NEAC with long traditions for a winter cod fishery (Sætersdal and Hysten, 1964). We expected that otoliths from pre-20th century catches would show wide age-distributions due to low mortality rates and that fish would grow relatively slowly due to high fish density. The objective of this investigation was to analyse these pre-20th century otoliths and compare stock origin, size, and

age-distributions, and back-calculate growth and mortality rates from these two sites in northern Norway to those of cod catches from the early and late parts of the 20th century.

Material and methods

Sampling areas for medieval to early modern otoliths

The pre-20th century cod otolith samples originated from archaeological excavations at two site locations. The first is Vágur in Vågan Municipality, Nordland County (Figure 1). This site is situated very close to the major spawning grounds for northeast Arctic cod in Lofoten (Pedersen, 1984; Sundby and Nakken, 2008). A total of 38 otoliths from two excavation trenches were analysed. Vágur is the only medieval settlement in northern Norway with urban-like traits and was an important centre for maritime trade (Bertelsen *et al.*, 1987; Bertelsen and Urbańczyk, 1988; Bertelsen, 2008, 2009). The site was transformed from a minor settlement in the 11th century to a major trading location during the following two centuries. This development was directly linked to the commercialization of cod fishing and the trade in dried cod (stockfish), for which Lofoten was the main production centre (Wickler and Narmo, 2014; Nedkvitne, 2016; Wickler, 2021). Several circumstances contributed to the marked decline of Vágur by the close of the 14th century, when it was reduced to an average fishing village. Archaeological excavations at Vágur from 1985 to 1995 documented c. 20000 m² of settlement deposits along the medieval shoreline, which was about 1 m higher than at present, covering a distance of around 500 m (Urbańczyk, 1992). The deposits are up to 2.5 m thick in some locations.

Underwater test excavations conducted by Tromsø University Museum in 1998 revealed a submerged medieval cultural deposit in Austvågen, the eastern harbour at Vágur (Falck *et al.*, 2013; Wickler, 2013) (Figure 2). Radiocarbon dates were obtained from hazelnut shells in two excavation trenches (T-13920, 840 ± 35 BP, and Wk-6700, 810 ± 50 BP). These dates have a pooled calibrated age range of cal AD 1156–1285 (94.4% probability), confirming that the deposit is from the high medieval period. A wide variety of well-preserved organic

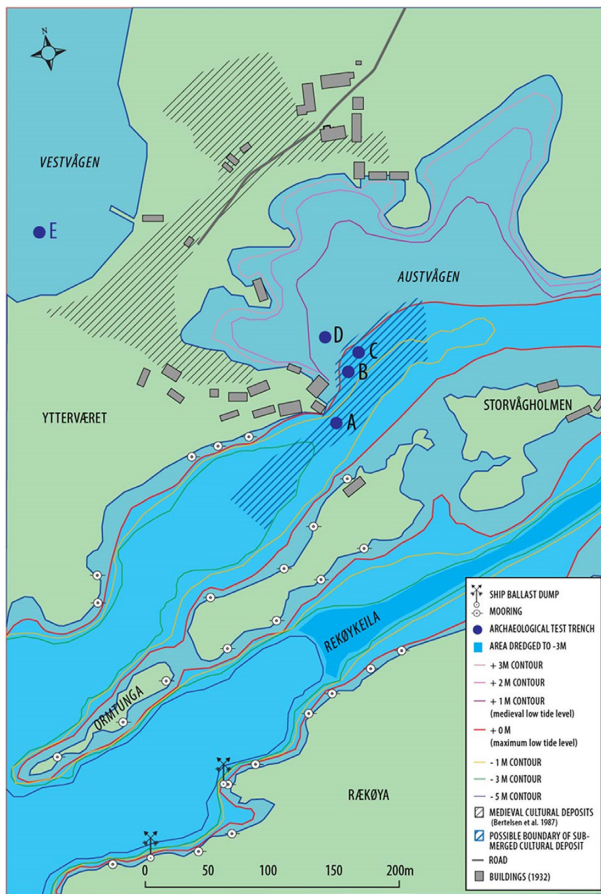


Figure 2. Site map of Vágur showing terrestrial and submerged archaeological deposits and the location of underwater test excavations.



Figure 3. Photo of the submerged medieval cultural deposit at Vágur with a fish bone, a reindeer antler, and other organic remains.

remains were recovered from the submerged cultural deposit, including objects of wood and leather, textiles, and an abundance of animal bone refuse (Figure 3). Of the c. 5700 pieces of bones analysed from the medieval cultural deposit, about 90% are fish and nearly all the remaining bones are domesticated species (cattle, sheep/goat, and pig) (Amundsen and Julsrud, 2007). Cod accounts for 95% of the identified fish bones. Most of the fish bone consists of cranial elements from cod, most likely disposed of during the first stage of stockfish production. The abundance of cod otoliths, with >400 collected,

including 53 from a single ten-liter bulk sample, also supports this conclusion. In contrast, only a handful of otoliths were recovered from the extensive archaeological excavations on land at Vágur due to poor preservation conditions (Perdikaris, 1999). A recent analysis of seven Atlantic cod cranial elements from the deposit successfully retrieved endogenous DNA, thus demonstrating the good preservation conditions of the samples from a submerged marine archaeological context (Ferrari *et al.*, 2021; Martínez-García *et al.*, 2021).

The otolith sample from Vágur used in the current analysis includes specimens from two test trenches where the cultural deposit was largely undisturbed and has been radiocarbon dated. Both trenches contained a highly organic cultural layer with an average thickness of c. 10 cm located 30–40 cm below the seabed surface and overlying a culturally sterile calcareous sand layer excavated to a maximum depth of c. 90 cm.

The second pre-20th century site, Værbukta, is located in Kobbfjord in Måsøy Municipality, Finnmark County (Figure 1). The otoliths were recovered from a large deposit (15 × 15 m) located just outside the entrance of a large multi-room settlement structure (Amundsen, 2008; Olsen *et al.*, 2011). A single radiocarbon date from a piece of mammal bone located at the bottom layer (~1.3 m deep) of the large midden deposit places the site's occupation between AD 1450 and 1680 (Wk 10322, 813 ± 64 BP, cal. AD 1450–1680 94.4% probability). A 1 × 1 m test unit was placed in the midden, but due to an extreme high density of bone material and excellent organic preservation (with a 6.8–7.0 pH level), the test unit was reduced to 0.5 × 0.5 m. All material was excavated stratigraphically and wet sieved through a 3-mm mesh. The test unit reached a maximum depth of 1.3 m, with ~12566 pieces of bone recovered and 10034 identified at the species level. The majority (ca. 99%) of identified bone was cod. A total of 111 otoliths, mostly from cod, were recovered, and 52 of these were used in this study.

All otoliths were inspected to assess their physical integrity. Although some otoliths were damaged, they were still used in this study provided that one end point, either an anterior or posterior, was undamaged and the central portion remained intact.

Modern samples

To obtain material to estimate a relationship between cod length and otolith size, cod were sampled by the R/V *Johan Ruud* using a pelagic trawl from the spawning area in Lofoten close to the Vágur site on 31 March 1993 (Figure 1) (Løken *et al.* 1994). The samples were taken in close proximity (ca. 20 km) to the Vágur site. The sampling year 1993 was chosen because this spawning stock was comprised of relatively large and old individuals, which would ensure comparability to the much earlier and, assumingly, equally large and older individuals of the Vágur material. Out of 70 otoliths recovered from 4 trawl hauls, 65 had sufficiently clear growth increment patterns along the dorsal axis to be measured.

A comparison plot was made of lengths-at-age from pre-20th century Vágur otoliths and cod sampled in Lofoten in 1993 and the mean lengths-at-age of the 1924 year-class of the NEAC from the Lofoten area that were digitized from Rollesfsen (1938). In addition, to test the accuracy of the back-calculation procedure, the mean back-calculated lengths-at-age of cod from the dominating 1983 year-class sampled in 1993 in Lofoten were compared to the mean lengths-at-age

of the strong 1983 year-class from the winter trawl survey in February in the Barents Sea (ICES, 2019).

As a comparison with the pre-20th century Værbukta material, modern cod were sampled at 10 localities with 20 bottom trawl hauls in the coastal areas of Troms and Finnmark County (Figure 1). As a result, a total of 100 otoliths were analysed. Six locations were sampled in 1994 in the Ullsfjord–Sørfjord area in Troms County (Berg and Pedersen, 2001), and four locations were sampled in 2000 in Tanafjord in Finnmark County (Figure 1). These samples were selected because of their relatively close proximity and overall comparability, based on size and age, to the archaeological samples at Værbukta. The data from Troms/Finnmark were length-stratified to ensure that otoliths from fish of all sizes were analysed for estimating a functional relationship between fish length and otolith size. In addition to the material described above, the length-at-age of NCC from the area around Værbukta (Figure 1) was calculated from the results given by Berg and Albert (2003) based on trawl samples taken between 1995 and 2001.

Preparation and measurements on otoliths

Prior to embedding, the otoliths were placed in 100% acetone for 15 min to remove soil and/or foreign material that could possibly contaminate the embedding medium, inhibit an accurate cut, or interfere with the imaging. After cleaning, the otoliths were placed in a shallow plastic embedding mould (0.5 × 2 × 1.5 cm). The rostrum of the otolith was embedded in mounting putty to ensure that the otolith would be firmly anchored during the pouring of the resin. The rostrum was the measuring point to determine the half length of the otolith and to guide the line cut through the block. A two-part marine resin (Top Coat®) with a resin to catalyst ratio of 20–0.3 ml was applied. The resin was cured within three days at room temperature under a ventilated hood.

The hardened block was cut cross-sectionally (transversely) to expose all growth layers and the nucleus. Most specimens were intact enough to cut the otolith at the midpoint (MP) of the total length to expose the nucleus. In cases where the otolith was incomplete, the mid-point was estimated from a relation obtained by linear regression for MP as a function of otolith width (OW): $MP = 2.25 \times OW^{0.645}$ ($r^2 = 0.83, n = 37$). Each resin block was sectioned on a low-speed, petro-thin saw (similar to the Buehler Isomet® low-speed saw) fitted with a 4 inch diamond blade. After the cutting, each sectioned otolith block was placed in an ultrasonicator for 5 min to clean and dislodge any loose particulate. Only in rare cases was polishing with wet/dry sandpaper and/or a diamond wheel necessary.

Modern otoliths from Troms and Finnmark were treated in the same way as the pre-20th-century otoliths. The modern otoliths from Lofoten had already been aged using the conventional technique, where the otolith is broken at their approximate midsection. However, this made them unsuitable for embedding in resin. Total otolith length was measured by putting the fragments together. One otolith fragment was ground using sandpaper to half (+/–0.3 mm) of the total length using a digital calliper for measurements. The otoliths were placed in plasteline and photographed as described for the pre-20th-century otoliths.

A binocular dissecting microscope with a mounted digital camera (Canon Powershot G2®) connected to a PC was used to capture images. Before each imaging session, the micro-

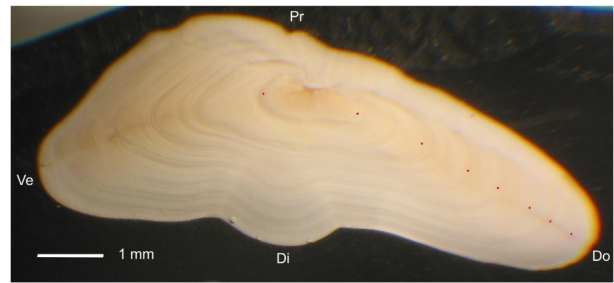


Figure 4. Transversely cut cod otolith from the Værbukta location with marked red points for measurements of growth increments along the dorsal axis. The two leftmost points are placed at the outer margin of the first growth increment around the opaque otolith core, and the other points were placed along the outer margin of opaque zones along the dorsal axis. The dorsal (Do) and ventral (Ve) axes and the proximal (Pr) and distal (Di) margins are labelled. The back-calculated length of the cod was 67.1 cm.

scope was calibrated using a calibrated ruler to ensure consistency and accuracy among all images. Images (format jpeg) were stored at various magnification levels from 6X to 12X to 18X. All otoliths were photographed under reflected light and had glycerol applied to the imaging surface.

The graphical application ImageJ® (Abramhoff *et al.*, 2004) was used for otolith measurements designed to provide data for analysis of individual growth, fish length, and stock origin. Using ImageJ on images with 6X magnification, two points were placed at the opposite margins of the longest axis of the first opaque zone (the core) (Figure 4), and the first growth increment was estimated as half of the distance between the two points. To estimate further growth increment widths, successive points were placed at the outer margins of the opaque zones along the dorsal axis, and one point was placed at the outer margin of the otolith (Figure 4). This procedure was chosen because the outer margin of the translucent zone often had a gradual transition to the next opaque zone and was difficult to measure in many otoliths. Høie *et al.* (2009) showed that the opaque zone in NEAC from the Barents Sea was completed (i.e. the otolith margin was translucent) for ca. 90% of the individuals in December and that ca. 50% of the individuals had completed the translucent zone in April. Thus, the increment we measured ending at the outer margin of the opaque zone corresponded to an age of less than a full year, assuming birth in April (Pedersen, 1984). For pre-20th-century otoliths where the dorsal axis was not intact and one or more growth increments were lacking, the total number of opaque zones was counted along the axis from the core to the distal margin (Figure 4). In the Vågar otoliths, from zero to five (av. 2.1 zones), increments were lacking along the dorsal axis but were clearly visible along the distal part of the otolith. The coordinates in mm (calibrated from pixel values) of the points were transferred to an Excel® spreadsheet, where the growth increment widths were calculated. All measurements along the dorsal axis were performed by a single experienced age reader during 2008–2009.

To compare with recently published otolith increment values along the distal axis of NEAC from the 20th century (Denechaud *et al.*, 2020), measurements of otolith increments along the distal axis were taken on the Vågar otoliths in 2022. Four otoliths did not have sufficiently clear zones along the distal axis to be measured.

Stock identification, back-calculation of length-at-age, and mortality estimation

The definition of NEAC and NCC was based on the zone pattern of the otoliths (Rollesfsen, 1934, 1953). Individuals characterized as belonging to the NCC-group have a more pronounced oval-shaped nucleus than NEAC, and the distance between the first and second translucent zones is wider in NCC than in NEAC (Berg *et al.*, 2005; Stransky *et al.*, 2008). The otoliths were typed into four categories by experienced personnel at the Institute of Marine Research in Norway according to the procedures described in Mjanger *et al.* (2011). Specifically, these are: (1) NCC, (2) uncertain NCC, (3) uncertain NEAC, and (4) NEAC. The categorizing of otoliths into NEAC (cat. 3 and 4) or NCC (cat. 1 and 2) was based on the examination of photos of otoliths without measuring increment widths. The ratio of first to second otolith growth increment width was calculated, and this measure was expected to reflect the difference in relative size of growth increment widths between NCC (low ratio) and NEAC (high ratio) (Berg *et al.*, 2005; Stransky *et al.*, 2008).

Cumulative increments (CIN_i) for each increment were calculated as the sum of successive growth increments along the dorsal axis, and CIN_c was the total cumulative growth increments at catch for a fish of length FL_c . To back-calculate fish length from otolith growth increments, relationships between fish lengths (FL) and cumulative otolith growth increments (CIN_i) were estimated from modern material using a similar approach as described in Bolle *et al.* (2004). Linear regression with $\ln(FL_c)$ as the dependent variable and $\ln(CIN_c)$ as the independent variable, assuming normally distributed residuals, was estimated as follows:

$$\ln(FL_c) = a1 + b \times \ln(CIN_c), \quad (1)$$

used to estimate the coefficients $a2$ [$a2 = \exp(a1)$] and b of the function:

$$BFL_c = a2 \times CIN_c^b, \quad (2)$$

$$BFL_i = a2 \times CIN_i^b, \quad (3)$$

where BFL_c is the back-calculated length at catch and BFL_i is the length-at-age. It was tested whether the FL–CIN relationship differed between the data from modern cod from Troms/Finnmark and the cod from Lofoten using a linear regression model [$\ln(FL_c = \text{constant} + \text{area} + \ln(CIN_c))$] with area as a factor variable. Equation 1 was used to estimate $a2$ and b , and Equation 3) was used to back-calculate fish lengths-at-age (BFL_i) for the pre-20th century archaeological material CIN_i at each increment. The outermost otolith growth increment, which was a partly completed translucent zone in the Vágur and Lofoten otoliths or a translucent and partly completed opaque zone in the Værbukta and Troms/Finnmark otoliths, was used to calculate CIN_c for the estimation of the FL–CIN relationship but was not used when calculating average annual growth increment widths. To estimate fish lengths at catch from pre-20th century otoliths where the outer part of the dorsal axis was not intact and one or more zones were missing, the incomplete increments were substituted by average increments from fish of the same age and same data set. This substitution practise was not used when estimating average growth increments and when back-calculating fish length-at-age.

The approximate coefficient of determination (R^2) was calculated as the square of the Pearson correlation coefficient for

observed and predicted (back-calculated) fish length. The root mean squared error (RMSE) (Ashworth *et al.*, 2017) was employed as an overall measure of the predictive ability of the regression equation:

$$RMSE = \sqrt{\left(\frac{1}{n}\right) \sum_{i=1}^n (FLobs_i - BFLc_i)^2}. \quad (4)$$

Where $FLobs_i$ and $BFLc_i$ are the observed and back-calculated lengths at catch for fish i , respectively. The n is the total number of fish. As a measure of the bias of the predicted values from the corresponding observed values, the mean error (ME) was calculated:

$$ME = \left(\frac{1}{n}\right) \sum_{i=1}^n (FLobs_i - BFLc_i). \quad (5)$$

Instantaneous total mortality rates (Z , year⁻¹) were calculated from pre-20th century age-distributions using the Chapman–Robson method (Chapman and Robson, 1960), and these mortality values were compared with 20th century values. The method uses the numbers at ages above the age considered fully recruited to the fishery to estimate the total mortality rate:

$$Z = \ln\left(\frac{1 + \bar{a} - 1/n}{\bar{a}}\right), \quad (6)$$

where \bar{a} is the average age of the individuals above recruitment age, and n is the number of fish. The age at recruitment was assessed from a visual examination of the age-frequency distributions of the catches. The mortality estimation was performed using function Chapman–Robson in package “FSA” in R.

For comparison of central tendency for two-groups, a t -test with separate variances (function t -test in R) was applied if the distributions did not deviate significantly from normal distributions (tested using function shapiro.test, package “stats” in R), and the Mann–Whitney test (function wilcox.test in R) was used if the distribution of at least one group deviated from normality. A significance probability of 0.05 was applied. To adjust p -values for multiple comparisons, the Benjamini–Hochberg procedure (function p.adjust, package “stats” in R) was used (Benjamini and Hochberg, 1995). Linear and non-linear regression were performed using the functions lm and nls in R.

Results

Otolith types and growth increment widths

The northeast Arctic (NEAC) and coastal (NCC) otolith types were present in the samples from both Vágur and Værbukta (Table 1 and Supplementary Tables S1–S4). In Vágur, the NEAC dominated (95%), while in Værbukta, the NCC dominated (74%). The ratio of the first to second increment corroborated the otolith typing, with significantly higher average ratios for the pre-20th century otoliths from Vágur (av. = 1.49) than from Værbukta (av. = 0.90, t -test, $df = 90$, $p = 10^{-9}$) (Figure 5). Correspondingly, the modern otoliths from the NEAC dominated Lofoten samples had a higher average ratio of 1.29 compared to 0.95 for the NCC dominated samples from Troms and Finnmark (t -test, $df = 165$, $p = 3 \times 10^{-7}$) (Table 1). Otoliths from Vágur had a slightly higher ratio of first to second increment than modern cod from Lo-

Table 1. An overview of otoliths analysed, aged, and measured and back-calculated fish length (FL) from pre-20th century and modern samples.

Parameter/Measure	Location			
	Vágar	Lofoten	Værbukta	Troms/Finmark
Time period (year)	1156–1285	1993	1450–1680	1994 and 2000
N	38	65	52	100
N (NEAC)	36	62	13	16
N (NCC)	2	3	39	84
Measured fish length (cm)		83.6 (10.4)		52.4 (19.3)
Back-calculated fish length (cm)	87.0 (9.9)	83.8 (9.9)	58.6 (19.3)	51.9 (15.8)
Av. age (years) (SD)	12.0 (1.9)	8.9 (1.6)	5.5 (2.4)	5.3 (2.2)
All cod inc. ratio (av, SD)	1.49 (0.41)	1.29 (0.45)	0.91 (0.42)	0.95 (0.36)
NEAC inc. ratio (av, SD)	1.52 (0.39)	1.30 (0.45)	1.09 (0.57)	1.05 (0.35)
NCC inc. ratio (av, SD)	0.91 (0.15)	1.02 (0.28)	0.85 (0.31)	0.93 (0.36)

Average back-calculated FL and age with standard deviation in brackets are given. The data from Troms/Finmark were sampled using length strata, and thus the average values are not representative for the total samples.

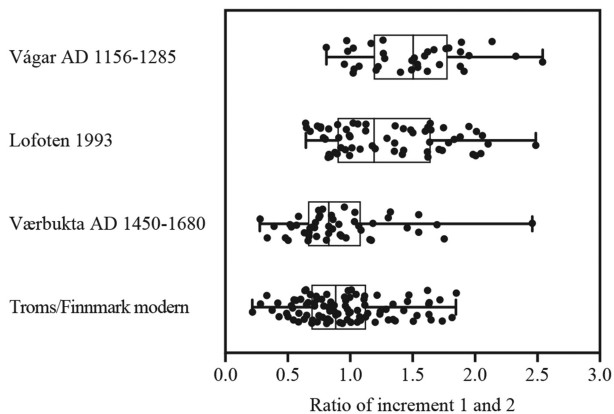


Figure 5. Comparison of distributions of the ratio of first to second otolith growth increment in cod from pre-20th century Vágar, modern Lofoten (1993), pre-20th century Værbukta, and modern Troms and Finnmark. The vertical line in boxes shows the median, and boxes show 25–75% quartiles, and whiskers show minimal and maximal values. Black dots show individual fish.

lofoten (av. = 1.49 versus 1.29, MW, $p = 0.02$), while the ratio was very similar (av. = 0.91 versus 0.95) for otoliths from Værbukta and the modern samples from Troms and Finnmark ($t = 0.5$, $df = 150$, $p = 0.6$) (Figure 5).

The average first otoliths growth increment along the dorsal axis was remarkably similar for the pre-20th century Vágar and the modern Lofoten otoliths on the one hand, and for the pre-20th century Værbukta and modern Troms/Finmark otoliths on the other hand (Figure 6). Pre-20th century otoliths from Vágar had significantly smaller average otolith growth increments than modern Lofoten otoliths for ages 2–3 years and ages 7–9 years (Figure 6; Supplementary Table S5). The pre-20th century Værbukta otoliths had similar growth increments as the modern otoliths from Troms and Finnmark, except for ages 5–6, which were larger for the Værbukta otoliths (Figure 6; Supplementary Table S5). Separating the material into NEAC and NCC by sites showed that excluding the few NCC from the Vágar ($n = 2$) and Lofoten 1993 ($n = 3$) had very little influence on the pattern for otolith increment size versus increment number (Figure 6 and Supplementary Figure S1). There were no clear differences in otolith increment versus number relationships between Værbukta and modern Troms/Finmark for NEAC or NCC (Supplementary Figure S2).

The increment widths along the distal axis for the Vágar otoliths were smaller than the increment values published by Denechaud *et al.* (2020) for the increment numbers 2–9, but were similar for the increment numbers 11–12 (Figure 7, Supplementary Table S6). For three otoliths, the number of increments measured along the distal axis corresponded to an age that was one year older than calculated from the dorsal axis.

Back-calculated length-at-age, size, and age-distributions

It was tested if the relationship between fish length at catch and cumulative growth increments was equal for the modern data from Lofoten and Troms/Finmark for fish longer than 50 cm represented in both areas. We used a linear regression model with $\ln(\text{FL}_c)$ as the dependent variable and sampling area (factor variable) and $\ln(\text{CIN}_c)$ as independent variables [$\ln(\text{FL}_c) = \text{constant} + \text{area} + \ln(\text{CIN}_c)$]. The regression ($df = 2$, 108, $F = 140.5$, $p < 0.001$, $R^2 = 0.71$) showed a significant effect ($p = 0.01$) of sampling area with a lower area value for Troms/Finmark than Lofoten, i.e. a given CIN corresponded to a larger FL for the Lofoten than for the Troms/Finmark data. Then separate functional relationships between FL and CIN were fitted for data from these two areas (Function A and B, Table 2). The exponent b was estimated to 0.82 (95% CI 0.63, 1.04) for the Lofoten data, which was based on fish with a narrow length range from 50 to 100 cm (Table 2, Function B). This function (B) was not considered to be appropriate for the back-calculation of fish lengths for fish with lengths <60 cm due to its concave form ($b < 1.0$). A new function (C) was fitted to the pooled modern data from Troms/Finmark and Lofoten, which resulted in a value for b of 1.29 (95% CI 1.22, 1.37) (function C, Table 2). This function resulted in a mean error (ME) of 1.9 cm, showing an underestimation of back-calculated length for the Vágar fish (Table 2). Thereafter, a new CIN–FL relationship (function D) was estimated for the Lofoten data by fixing the exponent b to 1.29 and estimating a (Function D, Table 2, Figure 8), and this function was used to back-calculate fish lengths from CIN for the Vágar fish. To back-calculate fish length-at-age for the Værbukta data, the function (A) fitted to the modern data from Troms/Finmark was used (Table 2, Figure 8). The functions used for the 20th century Lofoten and the Troms/Finmark data resulted in a root mean square error for back-calculated lengths of 8.1 and 8.9 cm for the Troms/Finmark and the Lofoten samples, respectively (Table 2). The mean errors for back-calculated fish

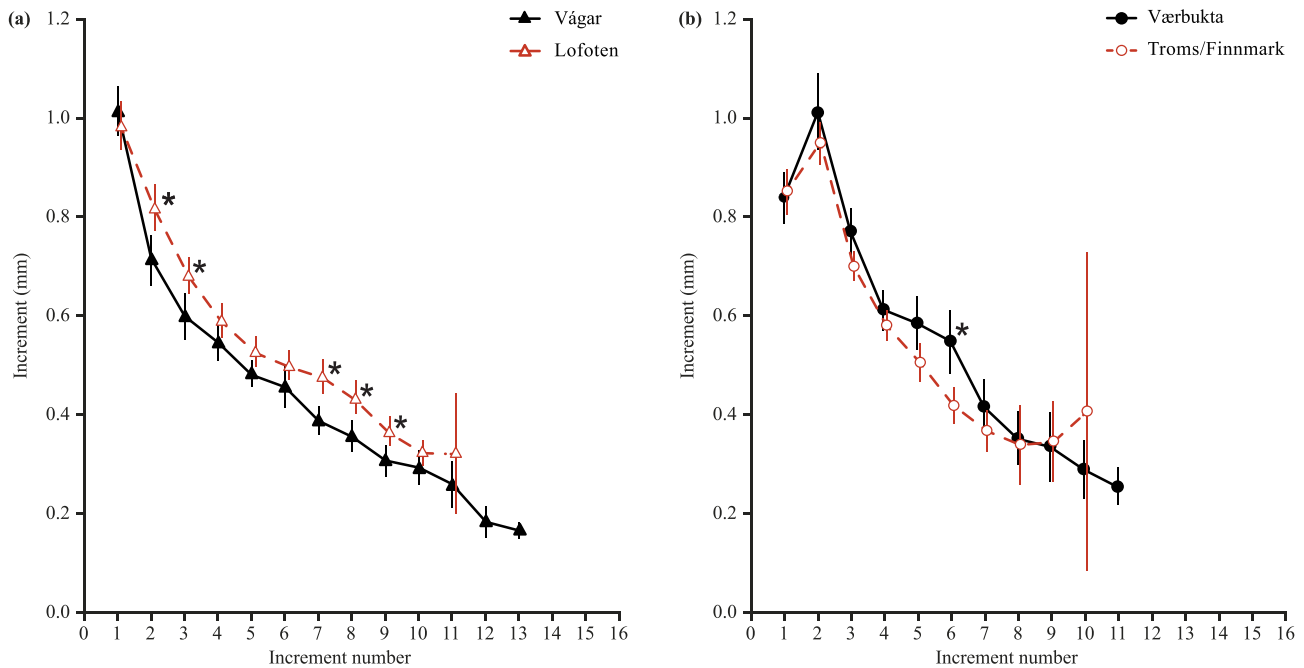


Figure 6. Otolith growth increments along the dorsal axis plotted versus increment number from (a) pre-20th century Vágur and Lofoten 1993 and (b) pre-20th century Værbukta versus modern Troms/Finmark. The asterisk (*) indicates when the distributions (mean or central tendency) of the two data sets deviate significantly from equality. Error bars show 95% confidence intervals.

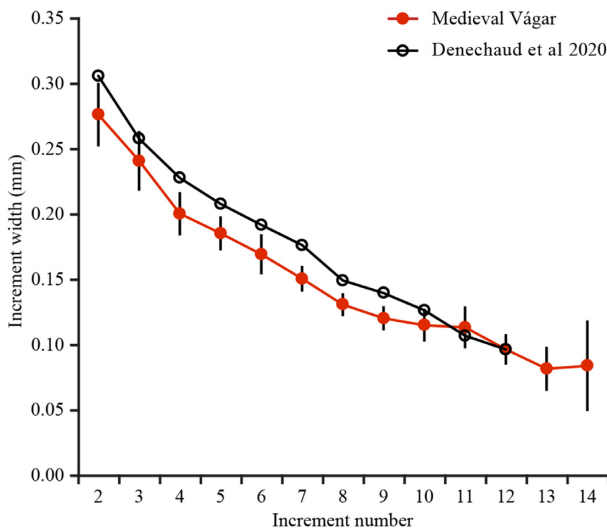


Figure 7. Comparison of average otolith growth increments along the distal axis plotted versus increment number from pre-20th century Vágur and 20th century northeast Arctic cod from Denechaud *et al.* (2020). Error bars show 95% CI.

lengths were 0.5 and -0.1 cm for the Troms/Finmark and the Lofoten samples, respectively (Table 2).

Pre-20th century cod from Vágur had shorter back-calculated length-at-age than 20th century cod from Lofoten (Figure 9a). The average back-calculated lengths-at-age from otoliths for the 1983 year-class that dominated the samples in Lofoten in 1993 were very similar to the winter trawl survey estimates of lengths-at-age (Figure 10). Fish from Værbukta had similar length-at-age for ages 4–8 that were about 1–5 cm longer than for NCC sampled during the period 1995–2001 for the area near to Værbukta (Figures 1 and 9b) (Berg and Al-

bert, 2003). The Værbukta lengths-at-age were generally similar to values for the cod sampled from Troms and Finnmark (Figure 1), but were slightly longer than the modern Troms and Finnmark cod for ages 3–7 years (Figures 1 and 9b).

The pre-20th century cod from Vágur were dominated by cod aged 9–16 years (av. age = 12.0 years, $SD = 1.9$ years, av. BFL = 87.0 cm, $SD = 9.9$ cm), were on average much older and longer than cod from Værbukta, which were dominated by fish of age 3–7 years (av. age = 5.5 years, $SD = 2.4$ years, av. BFL = 58.6 cm, $SD = 19.3$ cm) (Table 1, Figure 11). The Vágur cod also on average had large size and were older than the modern cod sampled in Lofoten in 1993 (av. FL = 83.6 cm, $SD = 10.4$ cm, av. age = 8.9 years, $SD = 1.6$ years) (Table 1). For the Værbukta data, NCC individuals were generally younger (MW, $p < 0.001$) and had lower back-calculated lengths (MW, $p < 0.001$) than NEAC individuals (Table 1, Figure 11).

Total mortality rates were estimated to $Z = 0.36 \text{ year}^{-1}$ (CI 0.20, 0.55 year^{-1}) for the Vágur cod using ages 10–16 years and at $Z = 0.43 \text{ year}^{-1}$ (CI 0.19, 0.68 year^{-1}) for cod using ages 11–16 years.

Discussion

Type of fisheries and cod stock origin

The characteristics of the otoliths providing age- and length distributions from the two pre-20th century samples show that they had originated from two different fisheries. The fish caught in Lofoten and excavated in Vágur were from a fishery of pre- and post-spawning, i.e. older and larger cod, dominated by NEAC, while the Finnmark fishery at Værbukta was based on both NCC and NEAC and had with a much larger range in size and age of fish. The dominance of larger and older fish caught in Vágur was similar to catches from other northern cod stocks during the medieval period (Amorosi *et*

Table 2. Overview of estimated functions relating fish length (FL) and cumulative otolith growth increments (CIN); $FL = a \times CIN^b$.

Function	A	B	C	D
Measure	Troms/Finmark*	Lofoten	Troms/Finmark and Lofoten	Lofoten**
<i>n</i>	100	65	165	65
<i>a</i>	9.82 (8.45, 11.40)	20.4 (14.4, 27.8)	9.10 (8.14, 10.17)	9.47 (9.22, 9.72)
<i>b</i>	1.22 (1.06, 1.33)	0.84 (0.63, 1.04)	1.29 (1.22, 1.37)	1.29
R^2	0.83	0.50	0.88	0.45
RMSE (cm)	8.1	7.6	8.7	8.9
ME (cm)	0.5	-0.5	1.9	-0.1

Functions A, B, and C were estimated using linear regression on log-transformed FL and CIN, and function D was estimated using linear regression with *b* fixed to 1.29 taken from function C [function; $\ln(FL) = \ln(a) + 1.29 \times \ln(CIN)$]. R^2 is the approximate coefficient of determination, RMSE is the root mean square error [Equation (4)], and ME is the mean error [Equation (5)]. The 95% CI is given in brackets. (*) function used to back-calculate length for Værbukta otoliths (**) function used to back-calculate fish length for the Vágar material; *b* fixed to 1.29.

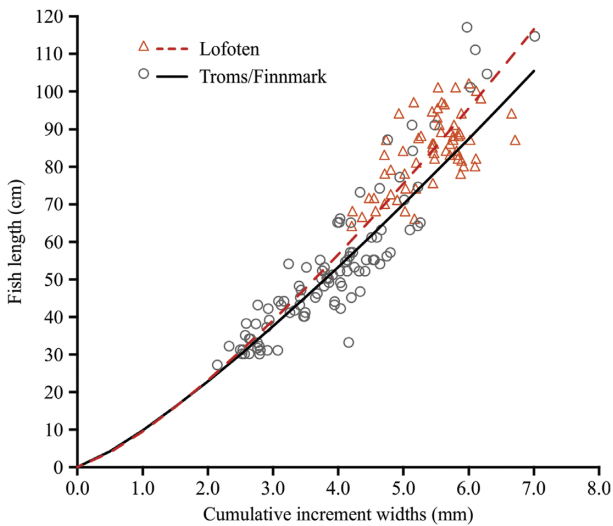


Figure 8. Relationship between fish length and cumulative otolith growth increment for modern cod. Lines show functions for the back-calculation of fish length (BFL) from cumulative growth increments (CIN); $BFL = a \times CIN^b$. Points show data from Lofoten in 1993 (red triangles) and Troms/Finmark (black circles). Functions used to back-calculate fish length from growth increments in otoliths are shown by the red dashed line for the pre-20th century Lofoten and the black continuous line for the pre-20th century Værbukta.

al., 1994). In contrast, the cod fished at Værbukta lacked the characteristics of a spawning fishery and were likely caught during the summer and autumn when NCC and some immature NEAC are present at the coast (Bergstad *et al.*, 1987; Løken *et al.*, 1994; Nøstvik and Pedersen, 1999). Most other records based on archaeological material are similar to the Vágar material, with large fish presumably fished from spawning grounds, but a sample from a location in Iceland (Miðbær) and a location at Másøy near Værbukta had similar small-sized cod as the Værbukta material (Amorosi *et al.*, 1994; Amundsen *et al.*, 2005; Geffen *et al.*, 2011).

The similarity in ratio of first and second growth increment for the pre-20th century and modern NEAC-dominated samples from Vágar and Lofoten on the one hand, and the NCC-dominated otoliths from Værbukta and Troms/Finmark on the other hand, indicate a similar stock structure within the sampling areas for the pre-20th century and modern samples. The growth patterns of the otolith during the first two years of life are strongly influenced by environmental conditions in the nursery habitats, which differ for NEAC and NCC (Rollefsen,

1953; Godø and Moksnes, 1987; Løken *et al.*, 1994). Young NCC inhabit shallow (<60 m depth) water at the coast, while young NEAC mainly inhabit deeper waters in the cold northern and eastern parts of the Barents Sea (Bergstad *et al.*, 1987; Løken *et al.*, 1994; Fevolden *et al.*, 2012). Tagging studies show that most of the NCC that spawn in Lofoten the rest of the year are mainly inhabiting the coastal banks from Lofoten and north to ca. 70°N (Hysten, 1964). In contrast, NCC further north in Troms and Finnmark mainly spawn in the fjords and have shorter migrations than the NCC spawning in Lofoten (Jakobsen, 1987; Nøstvik and Pedersen, 1999; Pedersen *et al.*, 2008; Michalsen *et al.*, 2014).

Methods and limitations of the study

In general, the relatively good quality and high readability of the archaeological otoliths suggest that measurements are as reliable as for modern otoliths. Fishing gear is both size and hence age-selective; however, it is not known with certainty which type of gear was used to catch the cod in the medieval to early modern period. It is likely that hand lines with baited hooks were the dominant gear (Bratrein, 1990; Helberg, 1993; Pulsiano *et al.*, 1993; Helle, 2003; Hansen, 2006). Fishing at substantial depth was already well established during the Iron Age (Jones, 1988; Barrett, 2012), and the catches at Vágar and Værbukta are unlikely to be restricted to shallow waters (i.e. <30 m depth).

Baited hooks are generally not as size-selective as gill-nets, but hooks tend to have a modal size-selectivity curve with low selectivity for very small and large fish (Hysten, 1962; Saetersdal, 1963; Løkkeborg and Bjordal, 1992). Since individual growth is variable within year-classes, lengths-at-age of different year-classes will show large overlap, especially if length growth rates are as low as those observed in the Vágar cod. Thus, it is unlikely that a moderately size-selective gear like a handline will bias the age-distribution of pre-20th century cod substantially. For archaeological material, there is also uncertainty with regard to whether all sizes of heads, and thus, otoliths, had an equal probability of being deposited and preserved for subsequent excavation. For the Værbukta otoliths, it is uncertain at what time of the year the fish with excavated otoliths had been caught, and this added uncertainty to the interpretation of the otolith zone pattern and hence age estimation.

The functional relationship between CIN and FL used to back-calculate length-at-age for the Vágar and Værbukta otoliths differed for large fish but was similar for small fish. The lack of small NEAC for back-calculation is unlikely to

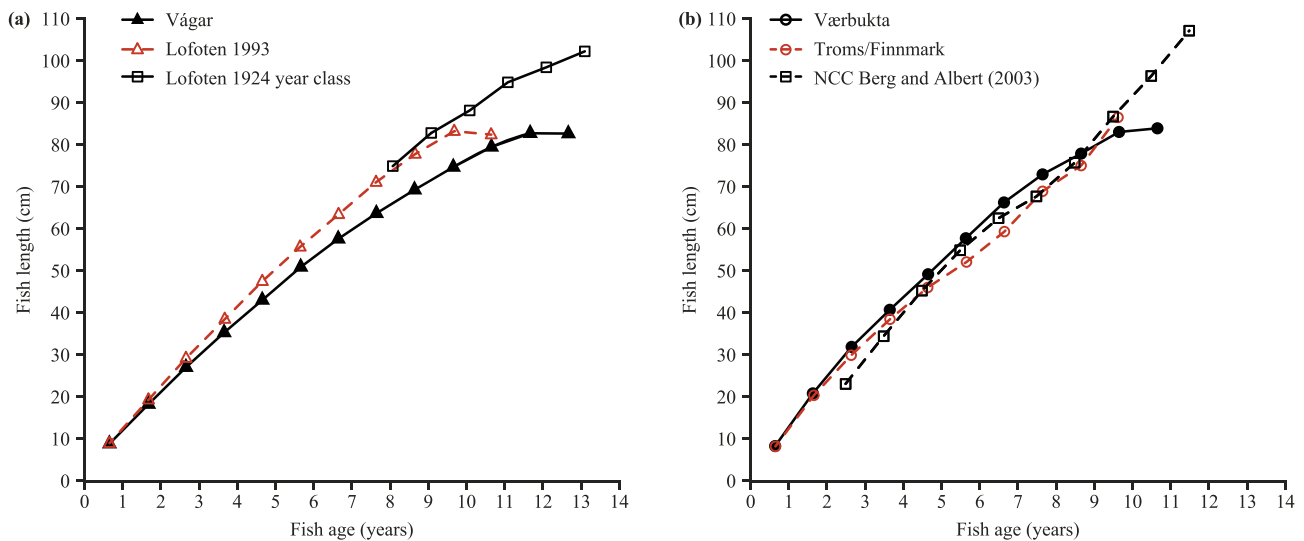


Figure 9. Comparison of back-calculated length-at-age of cod from pre-20th century and modern time periods and various areas: (a) pre-20th century cod from Vágur compared with modern fish from Lofoten 1993 and with mean measured length-at-age of the 1924 year-class sampled in Lofoten (Rollefsen, 1938), (b) back-calculated length-at-age of pre-20th century cod from Værbukta compared with back-calculated length at age of cod from Troms and Finnmark sampled in 1994–2000, and with measured length-at-age of coastal cod from the Måsøy area sampled in 1995–2001 (Berg and Albert, 2003).

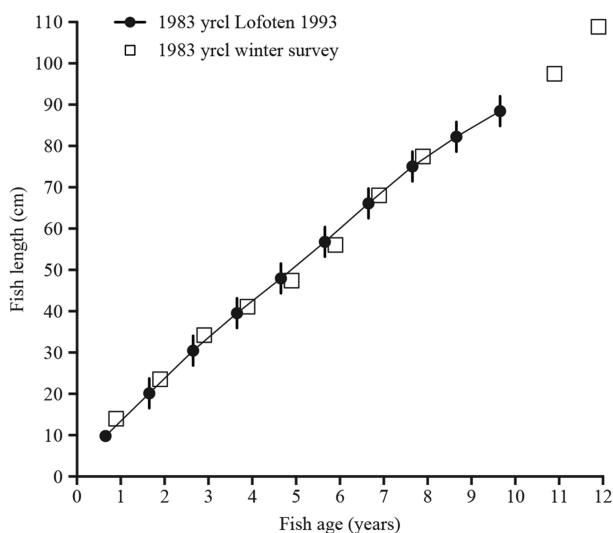


Figure 10. Comparison of back-calculated average length-at-age of the 1983 year-class sampled in Lofoten in 1993 and measured average fish length-at-age values from the Norwegian winter trawl survey in February in the Barents Sea (ICES, 2019). Error bars show 95% CI. The ages of back-calculated lengths of Lofoten cod correspond to the time of year for completion of the opaque otolith zone. Age at survey length-at-age assumes birth date of 1st April.

bias length-at-age much, and the same relationship was used for the comparison of pre-20th century and modern otoliths within each sampling area. The difference in CIN–FL relationship between the Lofoten and the Troms/Finnmark material is likely a consequence of differences in otolith morphology between NEAC and NCC (Rollefsen, 1933, 1953; Stransky *et al.*, 2008).

The fact that the back-calculated lengths-at-age and the survey measured lengths for the 1983 NEAC year-class were very similar suggests that the back-calculation may produce accurate values for length-at-age. The 1983 year-class experienced bad feeding conditions when the capelin stock collapsed

during 1985–1989, resulting in relatively low length growth rates and poor body condition (Jørgensen, 1992; Nilssen *et al.*, 1994; Denechaud *et al.*, 2020), but still, the cod sampled in 1993 had higher average lengths-at-age than the pre-20th century Vágur cod.

Growth rates and length-at-age

That the first dorsal axis growth increment widths were similar for the pre-20th century cod from Vágur and modern cod from Lofoten, as well as for Værbukta and Troms/Finnmark, indicates similar ambient environmental conditions for the cod juveniles during the pelagic phase in the upper water column. Early stages of cod are pelagic for ~6 months (Bergstad *et al.*, 1987). That the second and older growth dorsal axis increments were generally smaller for the pre-20th century than for the modern NEAC suggests a difference in ambient environmental conditions between the time periods. The comparison of increments measured along the distal axis between the Vágur otoliths and those of the 20th century otoliths published by Denechaud *et al.* 2020, showed a similar pattern with smaller pre-20th century increments for the youngest ages as for the comparison of Vágur and 20th century Lofoten otolith increments measured along the dorsal axis.

Temperature affect growth rates of cod strongly and temperature variability affects the length growth rate of small young cod more than older cod (Björnsson *et al.*, 2007). Reconstructed temperatures of Atlantic bottom water during the last 2000 years are available from a location in Malangen (69°29.66'N, 18°22.92'E, 218 m depth, Figure 1) between Lofoten and Værbukta. For the 20th century, the temperature of the Malangen time series is well correlated to the Kola temperature indicator for the Barents Sea (Dalpadado *et al.*, 2020). The Malangen reconstructed bottom temperature during the period AD 1156–1285, when the otoliths from Vágur were deposited, and during the period AD 1450–1680, when the Værbukta otoliths were deposited, were on average ~0.8 and

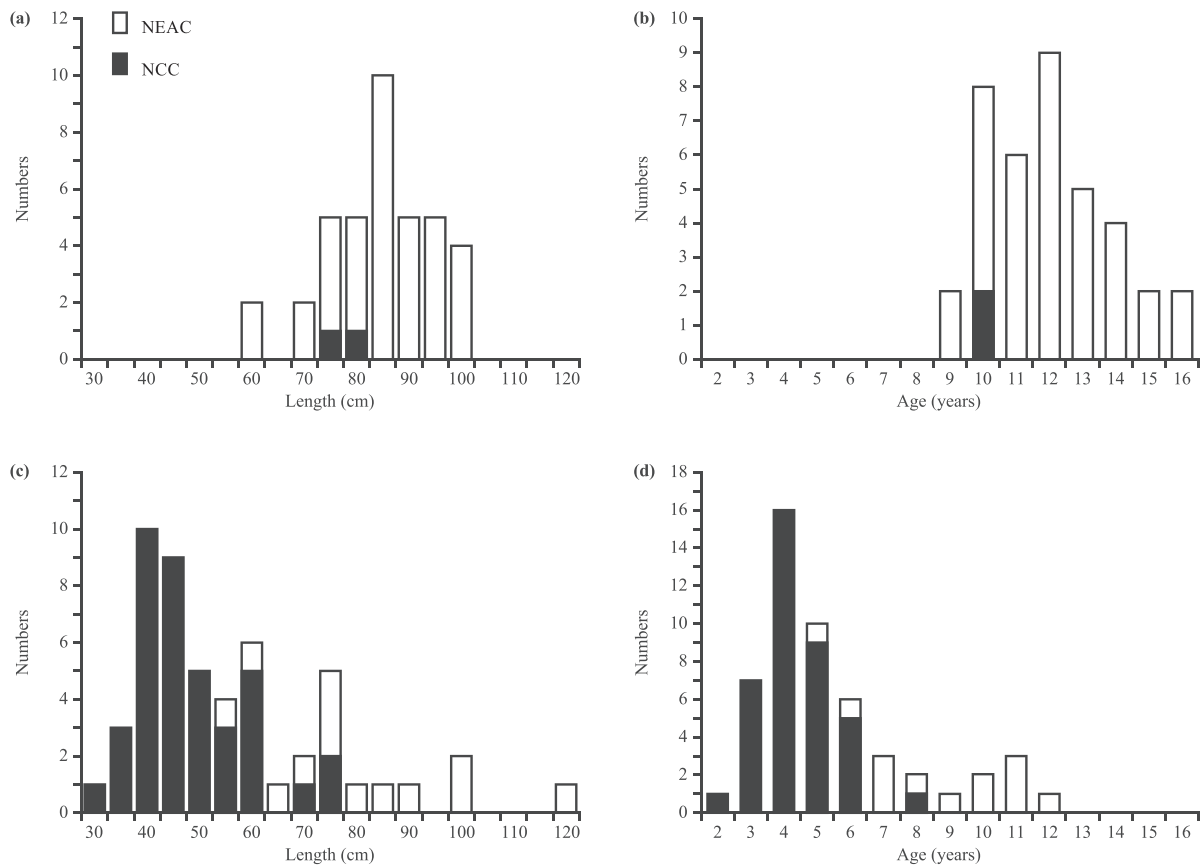


Figure 11. Comparison of back-calculated fish length- and age-frequency distributions from pre-20th century cod otoliths from Vágur and Værbukta, northern Norway: (a) back-calculated length- and (b) age-distribution from Vágur; (c) back-calculated length- and (d) age-distribution from Værbukta. Lower limits of each 5 cm length class are given on the axis label. NCC is coastal cod, and NEAC is northeast Arctic cod.

0.9°C colder than during the 20th century, respectively (Hald *et al.*, 2011). The time period when the otoliths from Vágur may have been deposited was at the end of the Medieval Climate Anomaly from 950 to 1250, which was a relatively warm period (Mann *et al.*, 2009), and cooling was observed from ca. AD 1250 onwards in the Malangen time-series (Hald *et al.*, 2011). During the Little Ice Age, considered to last from about 1400–1700 (Mann *et al.*, 2009), the fishery for and presumably also stock abundance of NEAC were variable and low (Øiestad, 1994). In line with this, the Malangen time-series showed relatively low temperatures during the period from 1400 to 1700 (Hald *et al.*, 2011).

Considerable short-term variability in lengths-at-age and otolith growth increment widths for NEAC within the 20th century was observed both in the 1930s and between 1953 and 1990 (Rollesfsen, 1938; Jørgensen, 1992; Denechaud *et al.*, 2020). Rollesfsen (1938) observed that NEAC of the same age were 6–9 cm longer in 1936 than in 1932–1933, and during 1953–1990, length-at-age varied within an amplitude of 10–15 cm depending on the abundance of the main prey capelin (*Mallotus villosus*) and water temperature (Jørgensen, 1992). However, no long-term change in length-at-age of NEAC was observed during the period 1953–1990, and the growth pattern was approximately linear with a growth rate of ca. 10 cm year⁻¹ (Jørgensen, 1992). In a study using large amounts of material from the period 1924–2014, otolith growth increments in NEAC from the Barents Sea were affected negatively by cod density and fishing mortality and positively by temper-

ature and capelin abundance (Denechaud *et al.*, 2020). Cod density had the strongest effect.

In the NEAC, the age at 50% maturity changed from ca. 10 years before the late 1940s to ca. 7 years after the year 2000 (Rørvik *et al.*, 2022). This change has been linked to the increase in fishing mortality for the NEAC during the 20th century and a fisheries adaptive change towards earlier maturation during the period (Rørvik *et al.*, 2022). This change in age of maturation is likely to be reversible with demographic recovery (Rørvik *et al.*, 2022), but it is uncertain how length-at-age is related to changes in age at maturity.

The otolith growth increment widths and back-calculated lengths-at-age of the pre-20th century Vágur cod in this study were relatively low compared to the corresponding values for the 20th century. A study of stable oxygen isotopes from micro milled NEAC otoliths (annual averages) from 1933 to 2015 indicated that the ambient temperature of immature (age 3) and mature (age 8) cod decreased with increasing cod density (von Leesen *et al.*, 2022). Thus, it is likely that high cod density combined with lower ambient temperatures when the Vágur cod lived may explain their low otolith growth rates compared to NEAC in the 20th century. Water temperature in the Barents Sea has a direct effect on each cod individual, affecting food consumption and metabolism (Jobling, 1988). Temperature also has an indirect effect in the Barents Sea through increasing open water area, primary production, and ecosystem production, promoting cod production in warm periods (Dalpadado *et al.*, 2020; Pedersen *et al.*, 2021). Thus, the effects

of temperature and cod density may be inter-twined and their effects on cod length growth rates may be difficult to separate.

The Værbukta otoliths that were deposited during AD 1450–1680, which is considered to be within the Little Ice Age (Hald *et al.*, 2011), had otolith and fish length growth rates that were similar to 20th century NCC from the same and similar areas. That the modern Troms/Finnmark back-calculated length-at-age values were lower than the values from Berg and Albert (2003) is probably because the Troms/Finnmark samples were from more inner fjord areas where the NCC tend to have slower length growth rates than in outer fjord and open coastal areas such as the Værbukta location (Berg and Pedersen, 2001; Berg and Albert, 2003). Due to the low migratory tendency of the NCC and the variable environmental conditions within the coastal zone, the spatial variability in length growth rates of the NCC may be large (Berg and Pedersen, 2001; Berg and Albert, 2003). Geffen *et al.* (2011) used stable oxygen isotope analysis of material from cod otoliths from two sites, Vanna (70°14'N) and Måsøy (71°0'N), in northern Norway, from the period AD 1390–1770 to determine ambient temperatures. They found that NCC from the period before 1600 had lower ambient temperatures and lower length growth rates than after 1600, and this suggests that ambient temperature for NCC likely varied within the Little Ice Age. Knowledge on the exploitation and population dynamics of coastal cod in the coastal zone is sparse for the period before the 16th century. We cannot rule out the possibility that a shift towards higher length growth rates of NCC due to changes in cod density and/or temperature may have occurred before the 16th century, and to investigate this further, we would require sufficient coastal cod otolith material from before the 16th century.

Our results point towards different patterns of change in length growth rates over time between the NEAC and NCC groups in northern Norway. The similarity in back-calculated length-at-age for the cod from Værbukta and the modern NCC from 1995 to 2001 (Berg and Albert, 2003) suggests relatively good length growth of the pre-20th century NCC-dominated Værbukta cod and may indicate similar environmental conditions and density of larger cod as in the 1990s. Stomach samples from coastal cod reveal relatively high occurrences of cannibalism (Pedersen and Pope, 2003). NCC may have an efficient density-dependent regulation of abundance of recruits due to the limited nursery areas in shallow water, and the large spatial overlap of small cod with large cod may facilitate high cannibalism rates at high abundances of large cod (Pedersen and Pope, 2003).

Other studies suggest that patterns for changes in length growth rates between the pre-20th century and the 20th century seem to differ between fish species within ecosystems. In a study of historical (AD 1200–1925) and modern (AD 1984–1999) fish otoliths from the North Sea, modern haddock (*Melanogrammus aeglefinus*) had higher length growth rates than historical fish, but for cod, the changes in length growth rates had occurred within the 20th century (Bolle *et al.*, 2004). The results for NEAC from Vágar and modern Lofoten parallel the results for haddock in the North Sea and Atlantic croaker (*Micropogonias undulatus*) from Florida, USA, which had a large increase in growth rates from the pre-20th century to modern times, indicating food and/or density-dependent growth regulation (Stanton Hales and Reitz, 1992; Bolle *et al.*, 2004). According to the “concentration hypothesis”, fish stocks that concentrate spatially into nursery grounds

may saturate the carrying capacity of the juvenile habitat, whereas adult fish may not be limited by the adult habitat and show limited density-dependent growth as adults (Beverton, 1995; Iles and Beverton, 2000; Bolle *et al.*, 2004). Cod, plaice, and saithe in the North Sea may be in this category (Bolle *et al.*, 2004), and we suggest that NCC may also be in this category.

Possible changes in interspecies competition for food from the pre-20th century to modern times should also be considered (Bogstad *et al.*, 2015). The dominating mammal consumers of prey in the Barents Sea, harp seals (*Pagophilus groenlandicus*) and minke whales (*Balaenoptera acutorostrata*) (Bogstad *et al.*, 2000), probably had much higher abundance during pre-20th century times than during the mid-to late part of the 20th century due to heavy human exploitation in the first part of the 20th century (Roman and Palumbi, 2003; Skaug *et al.*, 2007; Pedersen *et al.*, 2021). Thus, competition with mammals for food may have affected prey stocks and NEAC growth more in the pre-20th century than in the 20th century.

Size- and age-distributions, mortality rate, and change in fishing pressure

The fact that the lowest age of cod from the pre-20th century Vágar samples was 9 years indicates that sexual maturation may have started at about an age of 9 years. In the 1930s, average age at maturation of NEAC was 10.5 years, and the age-distributions from Lofoten comprised very low proportions of cod with ages 7–8 and with modal ages ranging from 11 to 13 years (Rollefsen, 1934). The average back-calculated fish length (87 cm) of the Vágar cod is similar to the average fish length of 85 cm of the NEAC sampled in Lofoten during the period 1913–1932 and was within the range of 87–93 cm for the annual average fish lengths of the NEAC sampled during 1932–1937 (Supplementary Table S7). The average age of Vágar cod of 12 years was similar to the average age of NEAC sampled from catches in Lofoten that decreased from 12.2 to 10.8 years from 1932 to 1935 (Supplementary Table S7). This similarity may suggest that both age at maturity and mortality patterns for the NEAC were similar for these time periods.

The pre-20th century mortality estimates of the Vágar cod were based on a few age-determined otoliths, but despite the wide CI, the mortality values were informative. The mortality rate estimate based on the Vágar otoliths ($Z = 0.4 \text{ year}^{-1}$) was slightly lower than the Z of ca. 0.5 year^{-1} for mature NEAC in the period 1913–1929 (Hysten, 2002), but much lower than the average Z of ca. 0.7 year^{-1} for age 5–10 years in the period 1955–2000 (Table 3) (Nakken *et al.*, 1996; Godø, 2003). After 1955, there was a dramatic increase in the fishing mortality rate for the NEAC, and the total mortality rate peaked at ca. 1.0 year^{-1} . This increase in total mortality rate during the 20th century caused a dramatic change in age structure in the spawning stock towards younger fish and fewer year classes (Jørgensen, 1990). The lack of NCC-individuals older than 7 years in the Værbukta sample may be due to the high mortality rate or the fact that older and larger NCC-individuals were inhabiting deeper waters that were out of reach for the fishery, and therefore, we did not estimate mortality rates for this location. Few other cod stocks have estimates on pre-20th-century mortality rates, but Baltic cod had a total mortality estimate ($Z = 0.75 \text{ year}^{-1}$) based on Neolithic otoliths (4500 BP) (Limburg *et al.*, 2008), which is much higher than our

Table 3. Overview of total mortality rate (Z , year⁻¹) estimates for cod stocks in pre-20th century and 20th century time. BP is “before present”

Area/Main stock	Time period	Z (year ⁻¹) (95% CI)	Source
Vágar, mainly northeast Arctic cod	1156–1285	0.36 (0.20, 0.55) 0.43 (0.19, 0.68)	This study, ages 10–16 years and 11–16 years
Northeast Arctic cod	1913–1929	0.5	Hylen (2002)
	1955–2000	0.7*	Godø (2003)
Baltic cod	4500 BP	0.75 (0.56, 0.94)	Limburg <i>et al.</i> (2008), regression based catch-curve
	1995	0.99 (0.87, 1.19)	
	2003	1.28 (0.99, 1.31)	

(*) average for 5–10 years old cod.

mortality estimates for Vágar, and the mortality-values for the Baltic cod rose to even higher values during the 20th century (Table 3).

We conclude that the pre-20th century cod otoliths from excavations in northern Norway provide good baseline data for lightly exploited stocks, and the otolith-derived values showing increases in length growth rates and mortality rates of NEAC in Lofoten following increased exploitation during the 20th century were according to expectation. In contrast, the NCC-dominated sample did not show a clear increase in length growth rates by the 20th century, suggesting that length growth rate and stock dynamics may differ between the NEAC and NCC.

Acknowledgements

Per Ågotnes and Hildegunn Mjanger from the Institute of Marine Research are acknowledged for stock typing of the cod otoliths. The crew on the RV *Johan Ruud* is thanked for help during the sampling of the modern cod. Côme Denechaud is acknowledged for providing the summary statistics for the distal axis in 20th century increments for the comparison with the Vágar measurements.

Supplementary data

The following [Supplementary material](#) is available at *ICESJMS* online version of the manuscript. Seven supplementary tables S1–S7 and two figures S1 and S2 are provided in the Supplementary Material. Five of the tables (S1–S4 and S6) give the measurement data for the otolith increment widths.

Author contributions

All authors contributed to the conceptualization, data curation, writing, and revision of the manuscript.

Data availability statement

The data underlying this article are available in the article and in its online supplementary material.

References

Abramhoff, M. D., Magelhaes, P. J., and Ram, S. J. 2004. Image processing with ImageJ. *Biophotonics International*, 11: 36–42.

Amorosi, T., McGovern, T. H., and Perdikaris, S. 1994. Bioarchaeology and cod fisheries: a new source of evidence. *ICES Marine Science Symposia*, 198: 31–48.

Amundsen, C. P. 2008. Culture Contact, Ethnicity and Food Practices of Coastal Finnmark, Norway (1200 to 1600 AD). PhD dissertation, Department of Anthropology, The Graduate Center, City University of New York, New York, NY.

Amundsen, C., and Julsrud, L. 2007. Faunal analysis of remains from a submerged medieval cultural deposit at Storvågan, Lofoten Islands. Unpublished report prepared for Tromsø University Museum.

Amundsen, C., Perdikaris, S., McGovern, T. H., Krivogorskaya, Y., Brown, M., Smiarowski, K., Storm, S. *et al.* 2005. Fishing booths and fishing strategies in medieval Iceland: an archaeofauna from the of Akurvík, north-west Iceland. *Environmental Archaeology*, 10: 127–142.

Andrews, A. J., Di Natale, A., Bernal-Casasola, D., Aniceti, V., Onar, V., Oueslati, T., Theodropoulou, T. *et al.* 2022. Exploitation history of Atlantic bluefin tuna in the eastern Atlantic and Mediterranean—insights from ancient bones. *ICES Journal of Marine Science*, 79: 247–262.

Ashworth, E. C., Hesp, S. A., and Hall, N. G. 2017. A new proportionality-based back-calculation approach, which employs traditional forms of growth equations, improves estimates of length at age. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 1088–1099.

Barrett, J. H. 2012. *Being an Islander: Production and Identity at Quoygrew, Orkney, AD900–1600*. McDonald Institute for Archaeological Research, Cambridge. pp. 275–293.

Barrett, J. H. 2019. An environmental (pre) history of European fishing: past and future archaeological contributions to sustainable fisheries. *Journal of Fish Biology*, 94: 1033–1044.

Benjamini, Y., and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57: 289–300.

Berg, E., and Albert, O. T. 2003. Cod in fjords and coastal waters of North Norway: distribution and variation in length and maturity at age. *ICES Journal of Marine Science*, 60: 787–797.

Berg, E., and Pedersen, T. 2001. Variability in recruitment, growth and sexual maturity of coastal cod (*Gadus morhua* L.) in a fjord system in northern Norway. *Fisheries Research*, 52: 179–189.

Berg, E., Sarvas, T. H., Harbitz, A., Fevolden, S. E., and Salberg, A. B. 2005. Accuracy and precision in stock separation of north-east Arctic and Norwegian coastal cod by otoliths—comparing readings, image analyses and a genetic method. *Marine and Freshwater Research*, 56: 753–762.

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

Bertelsen, R. 2008. Vágar i de første to hundreårene—en annerledes bydannelse. In *UBAS Nordisk 5. De første 200 årene—nytt blikk på 27 skandinaviske middelalderbyer*, pp. 125–134. Ed. by Andersson H., Hansen G., and Øye I. University of Bergen, Bergen.

Bertelsen, R. 2009. Vágar, en kortlevd by eller et urbant fiskevær? In *Den urbane underskog, Strandsteder, utvekslingssteder og småbyer i vikingtid, middelalder og tidlig nytid*, pp. 199–212. Ed. by Brendalmo J., Eliassen F.-E., and Gansum T. Novus Forlag, Oslo.

- Bertelsen, R., Buko, A., Fossnes, A., Hood, J., Kobylinski, Z., Lind, K., and Urbańczyk, P. 1987. The storvågan project 1985–86. *Norwegian Archaeological Review*, 20: 51–55.
- Bertelsen, R., and Urbańczyk, P. 1988. Two perspectives on Vågan in Lofoten. *Acta Borealia*, 1/2: 98–110.
- Beverton, R. J. H. 1995. Spatial limitation of population size; the concentration hypothesis. *Netherlands Journal of Sea Research*, 34: 1–6.
- Björnsson, B., Steinarsson, A., and Árnason, T. 2007. Growth model for Atlantic cod (*Gadus morhua*): effects of temperature and body weight on growth rate. *Aquaculture*, 271: 216–226.
- Bogstad, B., Haug, T., and Mehl, S. 2000. Who eats whom in the Barents Sea. *North Atlantic Marine Mammals Commission Scientific Publications*, 2: 98–119.
- Bogstad, B., Gjosæter, H., Haug, T., and Lindstrøm, U. 2015. A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Frontiers in Ecology and Evolution*, 3: 1–17.
- Bolle, L. J., Rijnsdorp, A. D., Van Neer, W., Millner, R. S., van Leeuwen, P. I., Ervynck, A., Ayers, R. *et al.*. 2004. 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. *Journal of Sea Research*, 51: 313–328.
- Bratrein, H. D. 1990. Magerøy i middelalderen. *Tromsø Kulturhistorie*, 17: 19–25.
- Chapman, D. G., and Robson, D. S. 1960. The analysis of a catch curve. *Biometrics*, 16: 354–368.
- Christensen, V., Guenette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D., and Pauly, D. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries*, 4: 1–24.
- Dahle, G., Quintela, M., Johansen, T., Westgaard, J. - I., Besnier, F., Aglen, A., Jørstad, K. E. *et al.*. 2018. Analysis of coastal cod (*Gadus morhua* L.) sampled on spawning sites reveals a genetic gradient throughout Norway's coastline. *BMC genetics*, 19: 42.
- Dalpadado, P., Arrigo, K. R., van Dijken, G. L., Skjoldal, H. R., Bagøien, E., Dolgov, A., Prokopchuk, I. *et al.*. 2020. Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea. *Progress in Oceanography*, 185: 102320.
- Denechaud, C., Smoliński, S., Geffen, A. J., Godiksen, J. A., and Campana, S. E. 2020. A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biology*, 26: 5661–5678.
- Falck, T., Nymoen, P., and Wickler, S. 2013. Betragtninger om middelalderens Vågar basert på undervannsarkeologiske kilder. In *Nord-Norge i Europa—Arkeologi, historie og kulturvern: Venneskrift til Reidar Bertelsen*, pp. 59–76. Ed. by Blankholm H. P. and Bratrein H. D.. Tromsø Museums Skrifter, Tromsø.
- Ferrari, G., Cuevas, A., Gondok-Wyrozemska, A. T., Ballantyne, R., Kersten, O., Pálsdóttir, A. H., van der Jagt, I. *et al.*. 2021. The preservation of ancient DNA in archaeological fish bone. *Journal of Archaeological Science*, 126: 105317.
- Fevolden, S. E., Westgaard, J. I., Pedersen, T., and Praebel, K. 2012. Settling-depth vs. genotype and size vs. genotype correlations at the Pan I locus in 0-group Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, 468: 267–278.
- Garrod, D. J., and Schumacher, A. 1994. North Atlantic cod: the broad canvas. *ICES Marine Science Symposia*, 198: 59–76.
- Geffen, A. J., Hoie, H., Folkvord, A., Hufthammer, A. K., Andersson, C., Ninnemann, U., Pedersen, R. B. *et al.*. 2011. High-latitude climate variability and its effect on fisheries resources as revealed by fossil cod otoliths. *ICES Journal of Marine Science*, 68: 1081–1089.
- Godø, O. R. 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. *Fish and Fisheries*, 4: 121–137.
- Godø, O. R., and Moksness, E. 1987. Growth and maturation of Norwegian coastal cod and Arcto—Norwegian cod under different conditions. *Fisheries Research*, 5: 235–242.
- Hald, M., Salomonsen, G., Husum, K., and Wilson, L. 2011. A 2000 year record of Atlantic water temperature variability from the Malangen fjord, northeastern North Atlantic. *The Holocene*, 21: 1049–1059.
- Hansen, L. I. 2006. Sami fisheries in the pre-modern era: household sustenance and market relations. *Acta Borealia*, 23: 56–80.
- Helberg, B. H. 1993. Fiskeriteknologi som uttrykk for sosial tilhørighet: en studie av nordnorsk fiske i perioden 400-1700 e. Kr. Master thesis, University of Tromsø, Tromsø.
- Helle, K. 2003. *The Cambridge History of Scandinavia*. Cambridge University Press, Cambridge.
- Høie, H., Millner, R. S., McCully, S., Nedreaas, K. H., Pilling, G. M., and Skadal, J. 2009. Latitudinal differences in the timing of otolith growth: a comparison between the Barents Sea and southern North Sea. *Fisheries Research*, 96: 319–322.
- Hufthammer, A. K., Hoie, H., Folkvord, A., Geffen, A. J., Andersson, C., and Ninnemann, U. S. 2010. Seasonality of human site occupation based on stable oxygen isotope ratios of cod otoliths. *Journal of Archaeological Science*, 37: 78–83.
- Hysten, A. 2002. Fluctuations in abundance of northeast Arctic cod during the 20th century. *ICES Marine Science Symposia*, 215: 543–550.
- Hysten, A. 1962. Notfisket i Lofoten. *Fiskets Gang*, 43: 581–587.
- Hysten, A. 1964. Coastal cod and skrei in Lofoten. *Fiskeridirektoratets Skrifter Serie Havundersøkelser*, 13: 27–42.
- ICES. 2019. Arctic fisheries working group (AFWG). *ICES Scientific Reports*, 1: 30.
- Iles, T. C., and Beverton, R. 2000. The concentration hypothesis: the statistical evidence. *ICES Journal of Marine Science*, 57: 216–227.
- Jakobsen, T. 1987. Coastal cod in northern Norway. *Fisheries Research*, 5: 223–234.
- Jobling, M. 1988. A review of the physiological and nutritional energetics of the cod with particular reference to growth under farmed conditions. *Aquaculture*, 70: 1–19.
- Jones, A. K. G. 1988. Provisional remarks on fish remains from archaeological deposits at York. (ed. P. Murphy & C. French). *The exploitation of wetlands. Archaeological Reports British Series*, 186: 113–127.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of northeast Arctic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 46: 235–248.
- Jørgensen, T. 1992. Long-term changes in growth of north-east Arctic cod (*Gadus morhua*) and some environmental influences. *ICES Journal of Marine Science*, 49: 263–277.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659–668.
- Limburg, K. E., Walther, Y., Hong, B., Olson, C., and Stora, J. 2008. Pre-historic versus modern Baltic Sea cod fisheries: selectivity across the millennia. *Proceedings of the Royal Society B-Biological Sciences*, 275: 2659–2665.
- Løken, S., Pedersen, T., and Berg, E. 1994. Vertebrae numbers as an indicator for the recruitment mechanism of coastal cod of northern Norway. *ICES Marine Science Symposia*, 198: 510–519.
- Løkkeborg, S., and Bjordal, Å. 1992. Species and size selectivity in long-line fishing: a review. *Fisheries Research*, 13: 311–322.
- Mann, M. E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., Ammann, C. *et al.*. 2009. Global signatures and dynamical origins of the little ice age and medieval climate anomaly. *Science*, 326: 1256–1260.
- Martínez-García, L., Ferrari, G., Oosting, T., Ballantyne, R., Van der Jagt, I., Ystgaard, I., Harland, J. *et al.*. 2021. Historical demographic processes dominate genetic variation in ancient Atlantic cod mitogenomes. *Frontiers in Ecology and Evolution*, 342.
- Maschner, H. D. G., Betts, M. W., Reedy-Maschner, K. L., and Trites, A. W. 2008. A 4500-year time series of Pacific cod (*Gadus macrocephalus*) size and abundance: archaeology, oceanic regime shifts, and sustainable fisheries. *Fishery Bulletin of the U.S.*, 106: 386–394.
- McGovern, T. H., Vésteinsson, O., Fridriksson, A., Church, M., Lawson, I., Simpson, I. A., Einarsson, A. *et al.*. 2007. Landscapes of settlement in northern Iceland: historical ecology of human impact and climate fluctuation on the millennial scale. *American Anthropologist*, 109: 27–51.

- Michalsen, K., Johansen, T., Subbey, S., and Beck, A. 2014. Linking tagging technology and molecular genetics to gain insight in the spatial dynamics of two stocks of cod in northeast Atlantic waters. *ICES Journal of Marine Science*, 71: 1417–1432.
- Mjanger, H., Hestenes, K., Svendsen, B., and de Lange Wenneck, T. 2011. *Håndbok for prøvetaking av fisk og krepsdyr*, 195. Versjon 3.16. Institute of Marine Research, Bergen.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology-Progress Series*, 138: 293–308.
- Nakken, O., Sandberg, P., and Steinshamn, S. I. 1996. Reference points for optimal fish stock management. A lesson to be learned from the northeast Arctic cod stock. *Marine Policy*, 20: 447–462.
- Nedkvitne, A. 2016. The development of the Norwegian long-distance stockfish trade. *Cod and Herring: The Archaeology and History of Medieval Sea Fishing*, 50–59. Ed by Barrett J. H. and Orton D. C., Oxford Publisher: Oxford Books.
- Nielsen, A. R. 2014. Del 4. Seinmiddelalderen, ca 1350–1600. Fangstmenn, fiskerbønder og værfolk. *In Norges fiskeri- og kysthistorie*, pp. 301–400. Ed. by Nielsen A. Fagbokforlaget, Bergen.
- Nielsen, A. R. 2016. Early commercial fisheries and the interplay among farm, fishing station and fishing village in North Norway. Pages *In Cod and Herring: The Archaeology and History of Medieval Sea Fishing*, pp. 42–49. Ed. by Barrett J. H. and Orton D. C.. Oxbow Books, Oxford.
- Nilssen, E. M., Pedersen, T., Hopkins, C. C. E., Thyholdt, K., and Pope, J. G. 1994. Recruitment variability and growth of northeast Arctic cod: influence of physical environment, demography, and predator-prey energetics. *ICES Marine Science Symposia*, 198: 449–470.
- Nøstvik, F., and Pedersen, T. 1999. Movement patterns and growth of wild cod (*Gadus morhua* L.) and hatchery-reared cod released as 1-group. *In Stock Enhancement and Sea Ranching*, pp. 315–333. Ed. by Howell B., Moksness E., and Svåsand T. S.. Fishing News Books, Oxford.
- Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: northeast Arctic cod. *ICES Marine Science Symposia*, 198: 17–30.
- Ólafsdóttir, G. Á., Pétursdóttir, G., Bárðarson, H., and Edvardsson, R. 2017. A millennium of north-east Atlantic cod juvenile growth trajectories inferred from archaeological otoliths. *PLoS One*, 12: e0187134.
- Olsen, B., Urbańczyk, P., and Amundsen, C. 2011. Hybrid Spaces: Medieval Finnmark and the Archaeology of Multi-Room Houses. Novus Press, Oslo.
- Ottersen, G., Hjermann, D. O., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15: 230–243.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, 10: 430.
- Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. *Flødevigen Rapportser*, 1984: 301–316.
- Pedersen, T., Cuveliers, E., and Berg, E. 2008. Spatial scales of movement in northeast Atlantic coastal cod. *Reviews in Fisheries Science*, 16: 371–379.
- Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P. E., Nascimento, M. C., Blanchet, M. - A., Ellingsen, I. *et al.*. 2021. Overexploitation, recovery and warming of the Barents Sea ecosystem during 1950–2013. *Frontiers in Marine Science*, 8: 732637.
- Pedersen, T., and Pope, J. G. 2003. How may feeding data be integrated into a model for a Norwegian fjord population of cod (*Gadus morhua* L.). *Scientia Marina*, 67: 155–169.
- Perdikaris, S. 1999. From chiefly provisioning to commercial fishery: long-term economic change in Arctic Norway. *World Archaeology*, 30: 388–402.
- Pinnegar, J. K., and Engelhard, G. H. 2008. The ‘shifting baseline’ phenomenon: a global perspective. *Reviews in Fish Biology and Fisheries*, 18: 1–16.
- Pinsky, M. L., Eikeset, A. M., Helmersen, C., Bradbury, I. R., Bentzen, P., Morris, C., Gondek-Wyrozemska, A. T. *et al.*. 2021. Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. *Proceedings of the National Academy of Sciences*, 118: e2025453118.
- Pitcher, T. J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecological Applications*, 11: 601–617.
- Pulsiano, P., Wolf, K., Acker, P., and Fry, D. 1993. *Medieval Scandinavia: An Encyclopaedia*. Garland Publishing Inc, Hamden, CT.
- Reitz, E. J. 2004. “Fishing down the food web”: a case study from St. Augustine, Florida, USA. *American Antiquity*, 69: 63–83.
- Rollefsen, G. 1933. The otoliths of the cod. *Fiskeridirektoratets Skrifter Serie Havundersøkelser*, 4: 1–14.
- Rollefsen, G. 1934. The cod-otolith as a guide to race, sexual development and mortality. *Rapports et Proces-Verbaux des Reunions, Conseil International, pour l’Exploration scientifique de la Mer*, 88: 1–6.
- Rollefsen, G. 1938. Changes in mean age and growth-rate of the year-classes in the Arcto-Norwegian stock of cod. *Rapports et Proces-Verbaux des Reunions, Conseil International, pour l’Exploration scientifique de la Mer*, 158: 58–64.
- Rollefsen, G. 1953. Observations on the cod and cod fisheries of Lofoten. *Rapports et Proces-Verbaux des Reunions, Conseil International pour l’Exploration de la Mer*, 136: 40–47.
- Roman, J., and Palumbi, S. R. 2003. Whales before whaling in the North Atlantic. *Science*, 301: 508–510.
- Rørvik, C. J., Bogstad, B., Ottersen, G., and Kjesbu, O. S. 2022. Long-term interplay between harvest regimes and biophysical conditions may lead to persistent changes in age at sexual maturity of northeast Arctic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 79: 576–586.
- Saetersdal, G. 1963. Selectivity of long lines. The selectivity of fishing gear. *International Commission for the Northwest Atlantic Fisheries, Special Publication*, 5: 189–192.
- Saetersdal, G., and Høyen, A. 1964. The decline of the skrei fisheries: a review of the landing statistics 1866–1957 and an evaluation of the effects of the postwar increase in the total exploitation of the Arctic cod. *Fiskeridirektoratets Skrifter Serie Havundersøkelser*, 13: 56–69.
- Skaug, H. J., Frimannslund, L., and Øien, N. I. 2007. Historical population assessment of Barents Sea harp seals (*Pagophilus groenlandicus*). *ICES Journal of Marine Science*, 64: 1356–1365.
- Sodeland, M., Jentoft, S., Jorde, P. E., Mattingsdal, M., Albretsen, J., Kleiven, A. R., Synnes, A.-E. W. *et al.*. 2022. Stabilizing selection on Atlantic cod supergenes through a millennium of extensive exploitation. *Proceedings of the National Academy of Sciences*, 119: e2114904119.
- Stanton 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.
- Stransky, C., Baumann, H., Evolden, S. E., Harbitz, A., Hoie, H., Nedreaas, K. H., Salberg, A. B. *et al.*. 2008. Separation of Norwegian coastal cod and northeast Arctic cod by outer otolith shape analysis. *Fisheries Research*, 90: 26–35.
- Sundby, S. and Nakken, O. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, 65: 953–962.
- Swain, D. P., Sinclair, A. F., and Hanson, J. M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B-Biological Sciences*, 274: 1015–1022.
- Urbańczyk, P. 1992. *Medieval Arctic Norway*. Institute of the History of Material Culture, Polish Academy of Sciences, Warsaw.
- van Leesen, G., Bogstad, B., Hjørleifsson, E., Ninnemann, U. S., and Campana, S. E. 2022. Temperature exposure in cod driven by changes in abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 79: 587–600.
- Wickler, S. 2013. The potential of shoreline and shallow submerged iron age and medieval archaeological sites in the Lofoten Islands, North-

- ern Norway. *In* Ancient Maritime Communities and the Relationship between People and Environment along the European Atlantic Coasts, pp. 63–73. Ed. by Daire M.-Y., Dupont C., Baudry A., Billard C., Large J. M., Lespez L., Normand E. , *et al.*. Archaeopress, Oxford.
- Wickler, S. 2021. The medieval stockfish trade: a maritime perspective from northern Norway. ARGOS—Journal of the Maritime Museum of Ílhavo, 9: 100–107.
- Wickler, S., and Narmo, L. E. 2014. Tracing the development of fishing settlement from the iron age to the modern period in northern Norway: a case study from Borgvær in the Lofoten Islands. *The Journal of Island and Coastal Archaeology*, 9: 72–87.

Handling Editor: Allen Hia Andrews