



Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Making use of Johan Hjort's "unknown" legacy: reconstruction of a 150-year coastal time-series on northeast Arctic cod (*Gadus morhua*) liver data reveals long-term trends in energy allocation patterns

Olav Sigurd Kjesbu^{1,2*}, Anders Frugård Opdal³, Knut Korsbrekke⁴, Jennifer A. Devine¹, and Jon Egil Skjæraasen¹

¹Institute of Marine Research (IMR) and Hjort Centre for Marine Ecosystem Dynamics, PO Box 1870 Nordnes, Bergen N-5817, Norway

²Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES), PO Box 1066 Blindern, Oslo N-0316, Norway

³Uni Research Computing and Hjort Centre for Marine Ecosystem Dynamics, PO Box 7810, Bergen N-5020, Norway

⁴Institute of Marine Research (IMR), PO Box 1870 Nordnes, Bergen N-5817, Norway

* Corresponding author: tel: +47 93 04 76 11; fax: +47 55 23 85 55; e-mail: olav.kjesbu@imr.no

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Hidden within the seminal 1914 publication by Johan Hjort, we find what is probably one of the first comprehensive teleost time-series ever published. The series is liver size and fat content of northeast Arctic (NEA) cod measured during the traditional winter fishery in Lofoten, Northern Norway, in 1880–1912 and 1883–1913, respectively. The data were collected well before the advent of the great industrialized fisheries in the 1930s. The raw data used by Hjort originate from annual reports of the Lofoten fishery, initiated by Member of Parliament and pioneer fishery inspector of Northern Norway, Ketil Motzfeldt, in 1859. Based on these reports and following various calibration exercises, we present robust estimates of the hepatosomatic index (HSI) from 1859 to 2012 (except 1863), i.e. over 153 years—extending Hjort's analysis both backwards (1859–1879) and forwards (1913–present). This series of bulk HSI contained five major periods: 1859–1880, 1881–1919, 1920–1974, 1975–2003, and 2004–2012; the highest HSI was recorded 1920–1974, whereas the lowest was from the most recent period. Despite variability, total length was a significant predictor of HSI, 1932–2012. A weak but significant relationship existed with both total-stock biomass and ocean temperature, as well as with the North Atlantic Oscillation winter index under a 1-year lag. The present exceptionally long HSI series will give an excellent opportunity for further research on the "quality of the cod" in a historic perspective.

Keywords: Atlantic cod, hepatosomatic index, Johan Hjort, NAO, temperature, time-series.

Introduction

The importance of Johan Hjort's pioneering efforts for the development of marine biology generally and fisheries biology especially can hardly be overstated (Sinclair, 1997; Houde, 2008). Today, his main legacy includes "the critical period hypothesis" for first-feeding larvae, drift (advection) of early life stages including mortality, the formation of strong and weak year classes, spawning migration routes, and

finally, stock variability linked to ecological conditions. His main species of interest were Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*). Above all, his seminal book "Fluctuations in the Great Fisheries of Northern Europe Viewed in the Light of Biological Research" (Hjort, 1914) stimulated research all over the world and remains integral to modern fisheries management, i.e. this ICES volume is still frequently cited 100 years after its release.

Perhaps less known is the fact that Hjort showed one of the first, if not the first, comprehensive time-series on a marine fish with his presentation of data on commercial liver landings of northeast Arctic (NEA) cod from the Lofoten area, the largest coastal fishery in Norway, in the period from 1880 to 1912. The corresponding fat content was also reported for the years 1883–1913. These efforts should not be considered an original approach, since several of his contemporaries were completing similar studies of annual variations in biological traits, e.g. the fat content in Atlantic herring and European sprat (*Sprattus sprattus*; see figures and references in Hjort, 1914). What was novel was the markedly longer length of his established time-series compared with others that existed in this period and that he placed his findings within the context of population dynamics. However, Helland-Hansen and Nansen (1909) were apparently the first to put up an ecological framework by relating “physical conditions” (ocean temperature) with “biological conditions”, here studying a limited subset (1899–1906) of the same liver (and roe) data as used by Hjort (1914). Today, time-series analyses are essential in a broad range of monitoring programmes and analytic assessments, but also to disentangle and show complex causal links, like that of climate (e.g. Ottersen et al., 2010; Petitgas et al., 2013) and fisheries-induced evolution (e.g. Rijnsdorp, 1993; Heino and Godø, 2002) on teleost traits.

Several studies on the monthly resolved Russian NEA cod liver data (1927–present) from the Barents Sea (Sandeman et al., 2008; Yaragina, 1996, 2010), as well as other related studies, including experimental (Skjæraasen et al., 2009), have provided a large amount of knowledge of factors affecting this stock’s investment in liver energy storage. In particular, the close link between relative liver size (hepatosomatic index; HSI) and liver energy content (Lambert and Dutil, 1997; Skjæraasen et al., 2010), but also with the abundance of the main prey, Barents Sea capelin (*Mallotus villosus*), as well as environmental temperature (Sandeman et al., 2008) stand out as important (Marshall et al., 1998). However, as the earlier part of the Barents Sea liver data (1927–1966) is incomplete or grouped by fish weight instead of length, Sandeman et al. (2008) restricted their statistical analyses from 1967 onwards.

Hjort was mainly motivated by the importance of the liver as a commercial product in its own right, but also by the association between liver size and “the quality of the cod”, or more specifically, “its condition in point of nourishment” (*sic*) (Hjort, 1914). Condition is here analogous with “the percentage in volume of the oil”. The main finding was, in his own words, “the remarkable cyclicality of liver landings”, which was accompanied by a similar covariation in liver fat content (Figure 1). In this article, we revisit Hjort’s original time-series and supplement his data with both newer and older data on liver landings (Figure 2). The existence of older, similar data (1859–1879) was somewhat unexpected because there is no specific mention of them in Hjort (1914). The primary source of data was the yearly reports and catch statistical time-series from the Lofoten fisheries (e.g. the Official Fisheries Statistics). Their origin can be traced back to the onset of a government initiated regulation of fisheries in Northern Norway, passed as an amendment to the existing Law of Lofoten (from 1816) in 1858. The intent of the amendment was to shift regulatory power from private proprietors to federal authorities. A significant political advocate for the making and passing of this amendment was Member of Parliament, Ketil Motzfeldt, who, in the following year, became the first Fishery Inspector of Northern Norway and initiated what would become the regular status report series of the Lofoten fisheries, although named differently over time (Anon, 1859–2012). Hence, Hjort could access annual and seasonal information

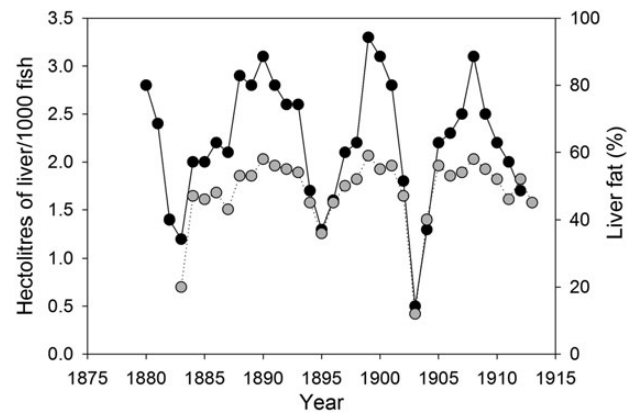


Figure 1. Redrawn plot of Hjort’s Figure 107 (Hjort, 1914) showing hectolitres of liver per thousand fish (dark circles) and the corresponding liver fat content (grey circles) for northeast Arctic cod in the Lofoten fishery, 1880–1912 and 1883–1913, respectively.

from “the Fisheries Inspectors telegraph” on the “average quantity” of “skrei” and the corresponding amount of liver (and occasionally roe; Hjort, 1914). “Skrei” is from old Norse and means to move or to travel, cf. the long spawning migration route of NEA cod from the Barents Sea to the Norwegian coast. The report series, including catch statistics, was primarily intended as a bookkeeping system for social costs and services, as well as, for example, commercially relevant parameters such as weekly turnover, landings, production, and bait prices. In its original form, the reports included no account of biological or ecological aspects. Its biological negligence is exemplified by the common gauge for “quality” being the number of cod required to fill a barrel with the liver. Naturally, Hjort was bound to the same coarse metrics as applied there, i.e. bulk volumetric landings of the liver (initially number of 116 l barrels and later hectolitres), and total number of landed cod (Figure 2). Since Hjort (1914) also contains records of body weights, the “bulk HSI”, a term used by us, could be estimated.

The primary task of our work was to expand as far as possible Hjort’s liver data both backwards and forwards in time in a coherent way to obtain (i) a better insight into the “condition” of NEA cod at the time of his seminal research, and (ii) a long-term proxy of the dynamics of liver size and thereby energy allocation patterns in this stock. In the analysis, we opted for HSI as the universal expression of investment in liver size vs. body size. We consulted recent publications on the relationship between fat content and HSI, as well as fisheries-independent annual values on the mean HSI, to ground-truth as much as possible the present series on bulk HSI. Finally, we examined the whole time-series in terms of general trends and shorter oscillations, concentrating on investigations into broad mechanisms that might be responsible for the observed patterns in HSI.

Material and methods

General overview

Commercial landings

Commercial landings of NEA cod were restricted to be from within the same geographical area during the spawning season, i.e. the Lofoten area. This defines the main spawning time and ground of this major gadoid stock. Immature fish and fish that skip spawning were unaccounted for because they rarely undertake such migrations to the Norwegian coast and therefore remain in the Barents Sea feeding area (Trout, 1957; Jørgensen et al., 2006; Yaragina, 2010; Skjæraasen

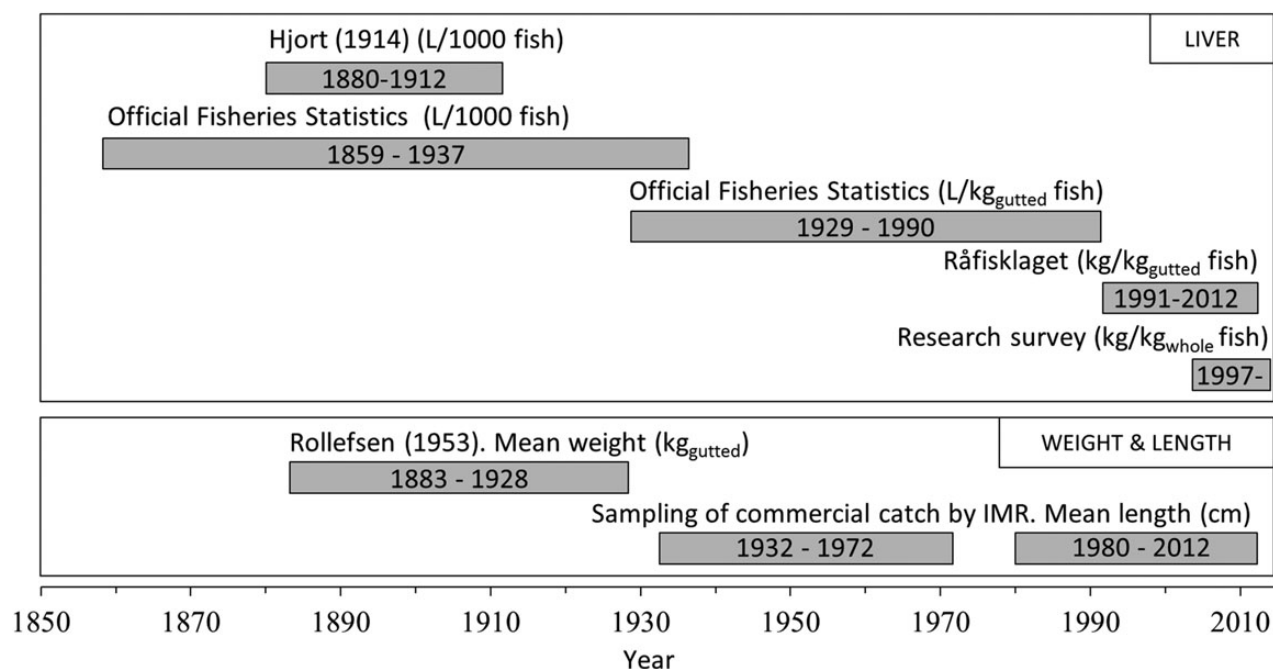


Figure 2. Overview of data sources from the annual Lofoten cod fishery and research monitoring programme. Upper panel shows Fisheries Statistics data of the relative amount of liver, including the data consulted by Hjort (1914), presented either in litre of liver per thousand fish or litre of liver per kilo gutted weight, the recent Råfisklaget series, reporting kilo of liver per kilo gutted weight, and the research survey data, reporting kilo per kilo whole weight. Lower panel shows supplementary data sources on gutted weight and total length.

et al., 2012). Some large immature specimens might, however, show extended winter migrations to the coast, i.e. so-called “dummy runs”, and thereby appear close to the spawning ground (Trout, 1957; Woodhead and Woodhead, 1965). The main part of the data were from the long-running report series established by the Norwegian authorities in 1859, initially named “Om Lofotfiskeriet”, but renamed “Lofotfiskeriet” in 1879, “Lofotfisket” in 1922, and then “Melding fra utvalgsformannen for Lofotfisket” in 2000. However, this report series discontinued their account of landed quantities of the liver in 1990 and data for the latter period (1991–2012) was therefore obtained through Norges Råfisklag (<http://www.rafisklaget.no/>), commonly called “Råfisklaget” (Figure 2). Råfisklaget is the largest fishers’ sales organization in Norway, administrating, among other tasks, all catches and catch statistics of cod from local landing ports under strict governmental laws and regulations.

Research survey data

A fisheries-independent liver series of NEA cod, established as part of the Institute of Marine Research (IMR) statutory acoustic spawning migration survey in the Lofoten area in March–April 1997–2013, was included to be contrasted with the corresponding commercial series in overlapping years (Figure 2). Whole body weight and liver weight were measured onboard to the nearest gramme using a motion compensated balance.

Bulk measures from the Lofoten fishery

Data presented in the yearly Official Fisheries Statistics (Anon, 1859–2012), hereafter referred to as the Fisheries Statistics, including those of Hjort (1914), were collated from bulk measures of landed cod and liver during the Lofoten fishery. To establish a coherent extension of Hjort’s original time-series, the same source was consulted for 1859–1990, whereas after 1990, analogous data had

to be obtained from landings data recorded by Råfisklaget (Figure 2). For the earlier period, the Lofoten area was defined by the principal communities used in the Fisheries Statistics. These included Flakstad, Moskenes, Vestvågøy, Værøy, Vågan, Røst, and Lødingen. Only NEA cod caught in the period of the Lofoten fishery, i.e. January to April, were considered.

For total landings of NEA cod, the Fisheries Statistics denote numbers of landed individuals (thousands) from 1859 to 1937 (Figure 2). In an overlapping period from 1929 to 1937, total landings were recorded both in numbers and in tonnes gutted weight, whereas after 1937, total landings were only available in tonnes gutted weight (Figure 2). Here, gutted weight excludes the head, guts, roe, and liver. Liver quantities before 1881 were logged as the number of barrels (å 116 l), whereas from 1881 to 1990, total quantities were expressed in hectolitres (100 l). The statistics from Råfisklaget used for the remaining period (1991–2012) were given in tonnes, both for the amount of cod liver and gutted weight.

Standardization of commercial Lofoten data

Hjort’s (1914) original time-series on the amount of landed liver of NEA cod (1880–1912) used hectolitres/1000 fish (Figures 1 and 2). This was a convenient measure at the time because catch statistics of liver landings were recorded in volumetric units and fish in numbers. However, when extending the time-series forward in time, we found that the Fisheries Statistics switched to cod landings in gutted weight, not numbers, and this practice continued with Råfisklaget. We believe that it is more biologically meaningful to divide liver size by total body weight, i.e. to adopt the common HSI (see formal definition below).

From fish numbers to weight

For the period when gutted weight was available together with the amount of liver collected (1929–2012; Figure 2), gutted weights

were multiplied by 1.5, which is the common conversion factor used to calculate total (“round” or whole) weight from gutted weight in the Norwegian cod fisheries (<http://www.fiskeridir.no/fiske-og-fangst/omregningsfaktorer>). For the earlier period (1859–1928), only numbers of landed cod were available in combination with the liver data. However, for the larger part of this period, matching information on fish size was found in Rollefson (1953), who presents official catch statistics of mean gutted weight of commercially landed NEA cod in Lofoten from 1883 to 1953. Hence, numbers of cod could be converted to total weight in the period 1883–1928 using the corresponding data in Rollefson (1953; Figure 2). However, for the years 1859–1882, data on cod size were unavailable and a proxy of bulk HSI was estimated from a linear regression (see Section “Turning hectolitres of liver into HSI”) based on the period where data for both the number of fish and mean gutted weight were available (1883–1937).

From liver volume to weight

While data on liver landings from Råfisklaget (1991–2012) were presented in weight, the Fisheries Statistics (1859–1990) used volumetric measurements (Figure 2). To calculate HSI, liver volume had to be converted to liver weight. The specific density of a liver will vary due to variations in its content of fat, water, and protein, with the latter constituent exhibiting less variation (Lambert and Dutil, 1997; Skjæraasen et al., 2010). A liver containing no fat is expected to have a specific density of $\approx 1 \text{ g ml}^{-1}$, i.e. only water and minor amounts of protein, whereas a liver containing only fat would have a specific density of $\approx 0.9 \text{ g ml}^{-1}$, i.e. only fat and minor amounts of protein. In reality, neither extreme is likely (e.g. a fat liver will also contain some water) and the range of possible density values is therefore limited. We used a specific density of 0.96 g ml^{-1} for all years in question based on the available liver proximate composition data on captive spawning individuals of cod in moderate to good condition (Kjesbu et al., 1991). Hence, liver weight was estimated as $0.96 \times$ liver volume.

Turning hectolitres of liver into HSI

For the period 1883–2012, the standard formula used to estimate the bulk hepatosomatic index (HSI_{Bulk}) was:

$$\text{HSI}_{\text{Bulk}} = 100 \times \frac{\text{total amount of liver}}{\text{total amount of fish}}, \quad (1)$$

where both the denominator and the numerator are the measures of mass presented in kg. For the earliest part of the Fisheries Statistics time-series (1859–1882), where systematic information on NEA cod body size was lacking, we applied a somewhat different procedure to get HSI_{Bulk} . Because there exists an overlapping period in the Fisheries Statistics (1883–1937) where liver quantities are available in both l/1000 fish (denoted as Hectolitres_{1000 fish}) and l/kg gutted fish (Figure 2), we utilized the linear relationship between these two measures (Figure 3) to estimate HSI_{Bulk} for the earliest period without fish weight (1859–1882):

$$\text{HSI}_{\text{Bulk}} = 2.40 + 1.236 \times \text{Hectolitres}_{1000 \text{ fish}}, \quad (2)$$

where $r^2_{\text{adjusted}} = 0.89$ (d.f. = 54 and $p < 0.0001$). Within this particular period, observed values of Hectolitres_{1000 fish} ranged from 2.00 to 4.22 (Figure 3). For the sake of readability, HSI_{Bulk} will from here on be referred to only as HSI, or bulk HSI if necessary to avoid confusion with individual HSI.

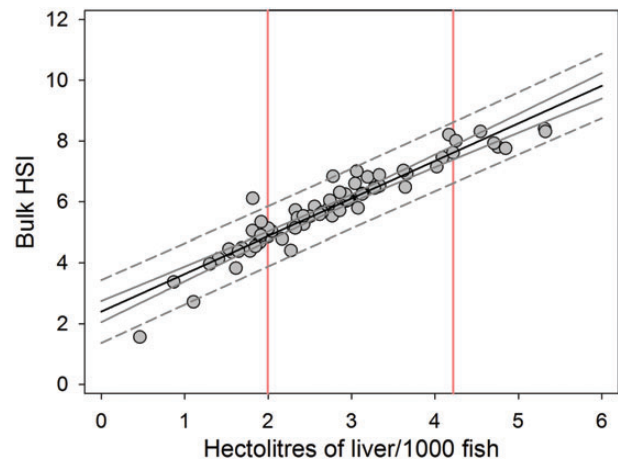


Figure 3. Linear regression between the measured amount of hectolitres of liver per thousand fish vs. the correspondingly estimated bulk HSI from the Lofoten northeast Arctic cod fishery, 1883–1937. Black solid line, regression line; grey solid lines, 95% confidence band; grey broken lines, 95% prediction band. Vertical lines show the range of values used in the prediction for the period 1859–1882.

Exploratory analyses

Fat content vs. HSI

As the fat content data in Hjort (1914) were limited, similar data from the Barents Sea and Lofoten area in 2007/2008 were consulted in Skjæraasen et al. (2010) to statistically relate HSI to liver “condition”. In Hjort (1914), no clear statements on which methods were used to extract the fat were given, only that the content of “medicinal oil” was reliably estimated by a person named Mr P. M. Heyerdahl, personally observing “the course of the fishery”. Skjæraasen et al. (2010) used a standard laboratory techniques of today, including extraction by ethyl acetate and spectrophotometric determination of triplicates. In our analysis, four outliers (out of 91 observations) were deleted; see applied statistical tests in Skjæraasen et al. (2010). Note that in Skjæraasen et al. (2010), data were presented as somatic HSI values, i.e. $\text{HSI} = 100 \times \text{liver weight} \times (\text{total fish weight} - \text{gonad weight})^{-1}$, whereas in the present study the same data are presented as percentages of total weight, i.e. $\text{HSI} = 100 \times \text{liver weight} \times \text{total fish weight}^{-1}$ [Equation (1)], to allow for direct comparisons with data from Hjort (1914). To investigate whether a change-point existed in liver fat percentage for a given HSI value, piecewise linear regression was used, where the inflection point was presumed unknown (estimated). The regression and 95% bootstrap confidence intervals (CIs) were fit using the SiZer package (Sonderegger, 2012) in R (R Development Core Team, 2013). Piecewise linear regression estimates one, abrupt change in the slope, but the data suggested that the change might be better fit by a curve. Therefore, a bent-cable regression for independent data was also fit, using the bentcableAR package (Chiu, 2012).

Trends in HSI

Basic statistics on HSI from the Lofoten fishery were reported in three different ways: (i) the HSI for each year based on the total amount of landings of cod and liver in that year (see above), (ii) the smoothed 9-year average of bulk measures (the level of smoothing was based on trials to properly account for interannual variability), and (iii) the grand mean of HSI measures for a specific time segment (change-point analysis). Change-point analysis was used to identify the location of multiple change-points, or abrupt

changes in the mean level, within the HSI series. For the change-point analysis, a Segment Neighbourhood algorithm (Auger and Lawrence, 1989) was chosen because it does not sacrifice accuracy (Killick and Eckley, 2013). Thereafter, the Akaike Information Criterion (AIC) was consulted (change-point package in R; Killick and Eckley, 2013) to assess a penalty for the number of segments used to describe the data and thus prevent overfitting. Trends in bulk HSI were tested with the earlier mentioned piecewise linear regression package using the complete dataset from 1864 onwards; no data existed for 1863. The annual mean HSI from the fisheries-independent survey data were compared with the commercial bulk HSI.

Predictors of HSI

Our inclusion of biometric predictors was limited to total length (TL), which is believed to have the main effect on the HSI (Yaragina, 1996, 2010; Sandeman *et al.*, 2008). Reports on TL were taken from the IMR commercial catch sampling programme, conducted between January and May in the Lofoten area from 1932 (Figure 2). To reflect the protocol of the corresponding bulk liver sampling programme, we combined TL information from all types of gears, but only used specimens classified by otolith expert readers as "certain skrei", i.e. NEA cod from the main Barents Sea area (Rollefson, 1933, 1934). TL information was lacking for 7 years in the 1970s. The 1989 estimated length (67 cm) was omitted from the analysis as it appeared to be an outlier. Change-point analysis was performed to identify the location of changes in mean TL. The maximum number of change-points used was four based on the inspection of segment length.

Other factors that might explain the dynamics in the HSI were also investigated. The influence of ocean temperature (Sandeman *et al.*, 2008), represented by the Kola transect temperature series (hereafter Kola temperature) from the Barents Sea (0–200 m depth, 70°30'–72°30'N 33°30'E) (Boitsov *et al.*, 2012), was chosen because of its influence on prey abundance and individual growth and condition. Temperature, categorized as high (warm) or low (cold) within a year, was defined in relation to the average Kola temperature for 1900–2012, i.e. Δ_{temp} = annual temperature - mean Kola temperature. Also consulted was Godø's (2003) definition of warm and cold periods, largely based on Kola temperature, especially before 1900 when only anecdotal information on temperature was available. The North Atlantic Oscillation (NAO) winter index, established from 1899 (Hurrell *et al.*, 2003), was also included. When the NAO is in a positive phase, oceanic responses in the Barents Sea are reinforced; this typically results in increased Atlantic Water inflow, which increases both the temperature and the influx of zooplankton prey into the Barents Sea. The principal component-derived index was used instead of the station-based index because it is considered a more optimal representation of the full NAO (Hurrell *et al.*, 2013). Total spawning-stock biomass (TSB, i.e. mass of specimens aged 3 years and older) and spawning-stock biomass (SSB, i.e. mass of maturing, spawning, or spent specimens) were selected to investigate the effect of density-dependence on HSI; series for both indices were available from 1900 (Hysten, 2002; ICES, 2012). However, because of collinearity, only a few of these factors were included in the final model; TL and TSB were significantly correlated ($r = 0.39$, $p = 0.0005$), as were TSB and SSB ($r = 0.53$, $p < 0.0001$), and Kola temperature and NAO ($r = 0.36$, $p < 0.0001$). Only TL and SSB were uncorrelated ($r = 0.05$, $p = 0.689$).

Due to the collinearity of possible explanatory factors (noted above), only those that were not correlated but believed to have a relationship with the HSI were included in the same model. The effects of TSB and Kola temperature (including a lagged effect, investigated *a posteriori*) on the HSI were investigated using a GAM (Generalized Additive Model) with a Gaussian error structure and identity link. Kola temperature was included in the final multivariate model, not the NAO index because regional or local environmental effects were expected to have a greater direct effect on cod than large-scale atmospheric factors. The effect of the NAO on the HSI was investigated separately, using again a GAM with Gaussian error structure and identity link. Both the HSI and NAO data were standardized to a mean of zero and a standard deviation of one before the analysis to put the indices on a common scale. A plot of the HSI and NAO indicated a slight non-linear effect. Because this could be the result of a lagged effect in the predictor variable, the effect of a 1-year lag was also investigated *a posteriori*. GAMs were run in R (R Development Core Team, 2013) using the mgcv package (Wood, 2011). All remaining data explorations were done either with Microsoft Office Excel 2007, Systat[®] 13 or SigmaPlot[®] 12.

Results

Fat content vs. HSI

The combination of recent and historical liver fat data indicated a markedly lower HSI-specific liver fat content in Hjort (1914) than today (Figure 4). No statistical test was performed because the raw data were different in nature, i.e. bulked and individual data, respectively. Hjort's HSI data were also very restricted in range ($1.6 \leq \text{HSI} \leq 7.0$) compared with the present-day HSI values ($1.5 \leq \text{HSI} \leq 16.0$). Although both Hjort (1914) and Skjæraasen *et al.* (2010) reported the same minimum HSI, in terms of liver fat, the minimum content observed in the two studies was very

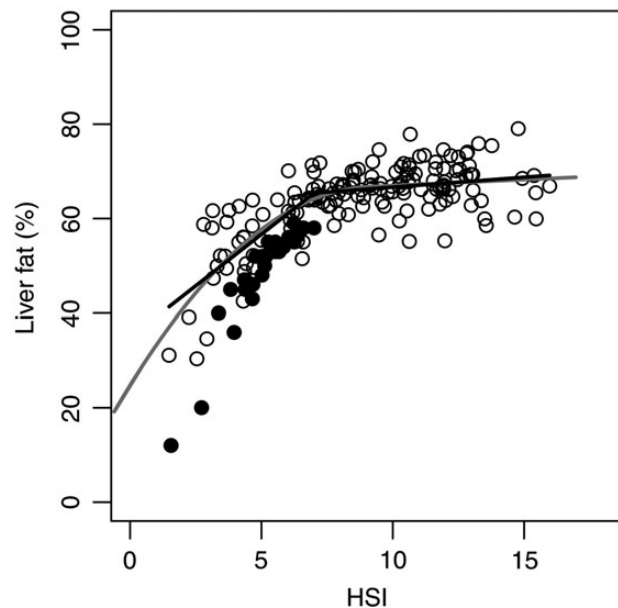


Figure 4. Relationship between historical (filled circles) and recent (open circles) HSI and liver fat content of northeast Arctic cod. Grey line is the bent-cable regression fit, while the black line is the piecewise linear regression.

different; 12 and 30%, respectively. The maximum liver content was also dissimilar; 59 and 79%, respectively.

Use of the individual data from Skjæraasen *et al.* (2010) showed an inflection point, where the growth in the percentage of liver fat reached an asymptote at $\sim 70\%$ (Figure 4). Both the piecewise linear regression and the bent-cable regression model indicated a change in slope (inflection point) at HSI = 7.0 (liver index = 65.4% at this point). However, the bootstrapped 95% CIs of the inflection point were wide for both models; 3.8–9.0 for the piecewise linear regression and 4.2–9.6 for the bent-cable regression model.

Trends in the HSI

The collation of information from the Lofoten fishery (Figure 2) made it possible to establish a 153-year long HSI time-series for NEA cod from 1859 to 2012 except for 1863, where no record on liver landings was found (Figure 5). These reports on the bulk HSI were centred on ≈ 6 (grand mean: 5.89; 95% CI: 5.70–6.09), but annual fluctuations were evident; the CV (coefficient of variation; s.d./mean) was estimated at 0.20. The most recent HSI values were comparable with the low values seen at the end of the 19th/beginning of the 20th century (Figure 5). Fisheries-independent data from the period 1997–2012 (Figure 2) were similar to the commercially based HSI and showed no evidence of contrasting values ($p = 0.063$, Wilcoxon signed-rank test), except in 2011 and 2012, when the research survey series had markedly higher values (≈ 1.5 per cent points; Figure 5). Excluding these 2 last years from the test, the p -value changed to 0.198. Furthermore, the mean HSI from the 2013 research survey was as high as 5.64 (Figure 5). This marked contrast with the commercial HSI series might indicate that there are differences in how livers are currently processed.

Minimum and maximum HSI values spanned a broad range of ocean temperatures. Using mean Kola temperature as reference

point (1900–2012: 3.99°C), the lowest value, found within “Hjort’s time-series”, i.e. 1.6 in 1903, occurred when ocean temperatures were below average ($\Delta_{\text{temp}} = -0.91^\circ\text{C}$). The second lowest HSI value of 2.7 in 1883 occurred before the Kola series began, but was most likely during a period of ocean cooling (Godø, 2003). The next three lowest HSI values appeared both during warm and cold ocean periods: 2012 (HSI = 3.3, $\Delta_{\text{temp}} = 1.37^\circ\text{C}$), 1904 (HSI = 3.4, $\Delta_{\text{temp}} = -0.43^\circ\text{C}$), and 2011 (HSI = 3.5, $\Delta_{\text{temp}} = 0.38^\circ\text{C}$). The maximum HSI appeared in 1953 with a record of 9.1, but this was during a cool ocean phase ($\Delta_{\text{temp}} = -0.20^\circ\text{C}$).

Although the HSI oscillated considerably over the time-series, some broader patterns were discernible after smoothing (Figure 6), the HSI declined from the start of the time-series in 1859 until the 1880s, when it remained low. Then, the HSI increased noticeably from the 1920s up to the 1950s, after which it remained relatively high until the mid-1970s before decreasing. The change-point analysis on the complete HSI series identified five different periods (Figure 6), the respective grand means being: (i) 1859–1880: 6.1; (ii) 1881–1919: 5.0; (iii) 1920–1974: 6.8; (iv) 1975–2003: 5.5; (v) 2004–2012: 4.4. Exclusion of predicted values (1859–1882) from the analysis did not affect the location of the four later segments.

Kola temperature and the HSI, both smoothed over 9 years, varied in close synchrony until the 1970s, but then the Kola temperature increased with no comparable response in the HSI (Figure 6). From the mid-1980s, the two series have trended in opposite directions. The piecewise linear regression analysis (1864–) showed a change in the annual trend in the HSI in 1954 (97.5% CI: 1951–1966), which occurred shortly after a decline in the Kola temperature (1950–pre-1990).

Predictors of the HSI

The body size of NEA cod fluctuated markedly (Figure 7a), and this dynamic had a significant effect on the HSI (Figure 7b;

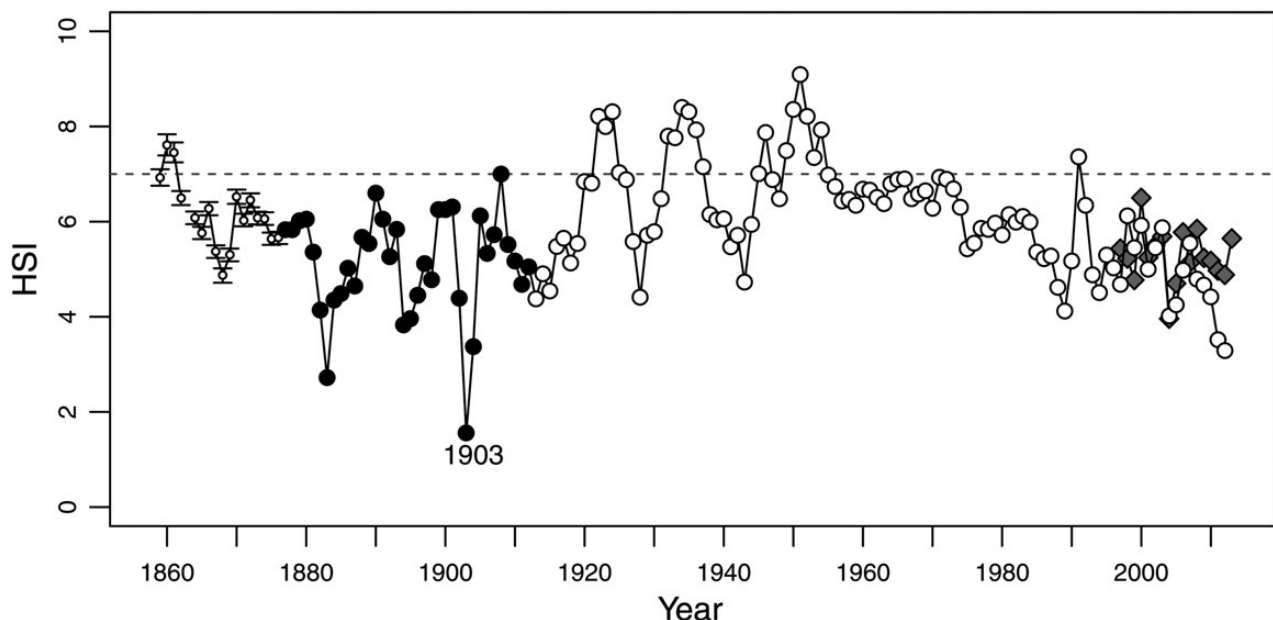


Figure 5. Annual variation in the northeast Arctic cod bulk HSI from the Lofoten fishery (1859–2012; circles) and the mean HSI (diamonds) from the Institute of Marine Research (IMR) Lofoten research survey (1997–2013). Values for 1859–1876 were estimated and include the 95% CI of the estimates. Black circles indicate the period of Johan Hjort’s investigations. The dotted line (HSI = 7.0) is the inflection point from the piecewise and bent-cable regressions (see Figure 4).

$r^2_{\text{adjusted}} = 0.25$, $p < 0.0001$, linear regression). Change-point analysis indicated four periods in TL size [grand mean (cm): (i) 1932–1946: 86.1; (ii) 1947–1965: 90.2; (iii) 1966–1986: 81.8; (iv) 1987–2012: 79.0 (Figure 7a)]. Generally, the HSI increased with the mean TL, but the last 2 years (2011 and 2012) had the lowest recorded HSI, although the mean TL in these years was not atypical (grand mean entire period = 83.7 cm).

From 2010, TSB has been high but within the normal range seen within the time-series, whereas SSB has been at a historical high (above 1.2 million tonnes; Figure 8a). No evidence of a relationship between HSI and SSB was present. Both TSB and Kola temperature

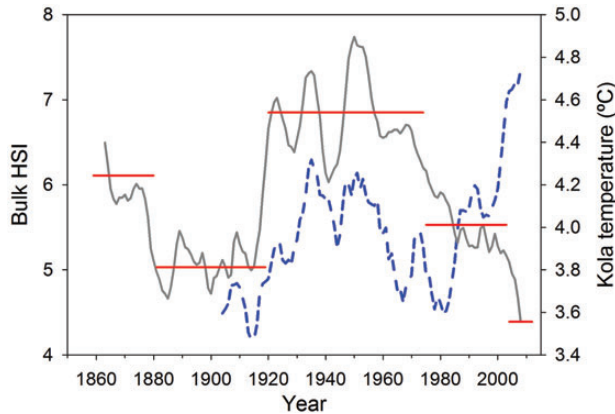


Figure 6. Temporal trends in 9-year smoothed HSI (solid line) and Kola temperature (broken line). Horizontal lines are the grand mean HSI for a specific period (segment) located by change-point analysis.

were positively related to the HSI, but each factor explained less than the mean TL, and their contribution was insignificant ($p > 0.05$) if combined with TL. TSB regressed on the HSI showed an $r^2_{\text{adjusted}} = 0.13$ ($p < 0.0001$, linear regression; Figure 8b), whereas the % deviance explained for HSI vs. Kola temperature was 10.3 [GCV (Generalized Cross-Validation) score = 1.44, $p = 0.03$, GAM; Figure 8c]. Kola temperature appeared to be positively related to the HSI at temperatures below 4°C, but negatively above 4°C, i.e. there were weak indications of a convex response curve (Figure 8c). Time-lags were investigated, but lagged temperature was not found to be significantly related to changes in the HSI. In the multivariate model, the HSI was positively related to both TSB ($p < 0.0001$) and Kola temperature ($p = 0.009$) but a large amount of variability was left unexplained by the GAM (% deviance explained = 24.2, GCV score = 1.29), indicating that other factors may be important. The winter NAO index did not predict changes in the HSI ($p = 0.10$) but there was a marginally significant linear relationship ($p = 0.045$) at a lag of 1 year (Figure 8d).

Discussion

One might wonder if Johan Hjort, when collating and interpreting his liver time-series (1880–1912) on NEA cod from the Lofoten area, was aware that Ketil Motzfeldt's initiative of Fisheries Statistics records (1859–1879) existed. If Hjort had elongated his time-series to cover 54, instead of 33, years, he might have been in a better position to fully judge the "condition" of NEA cod within his period of interest. Condition was generally on the poor side over the longer period, i.e. not only in 1903 as stated in his book, and included much larger interannual variability. The year 1903 is worth special attention for both biological and social reasons; the

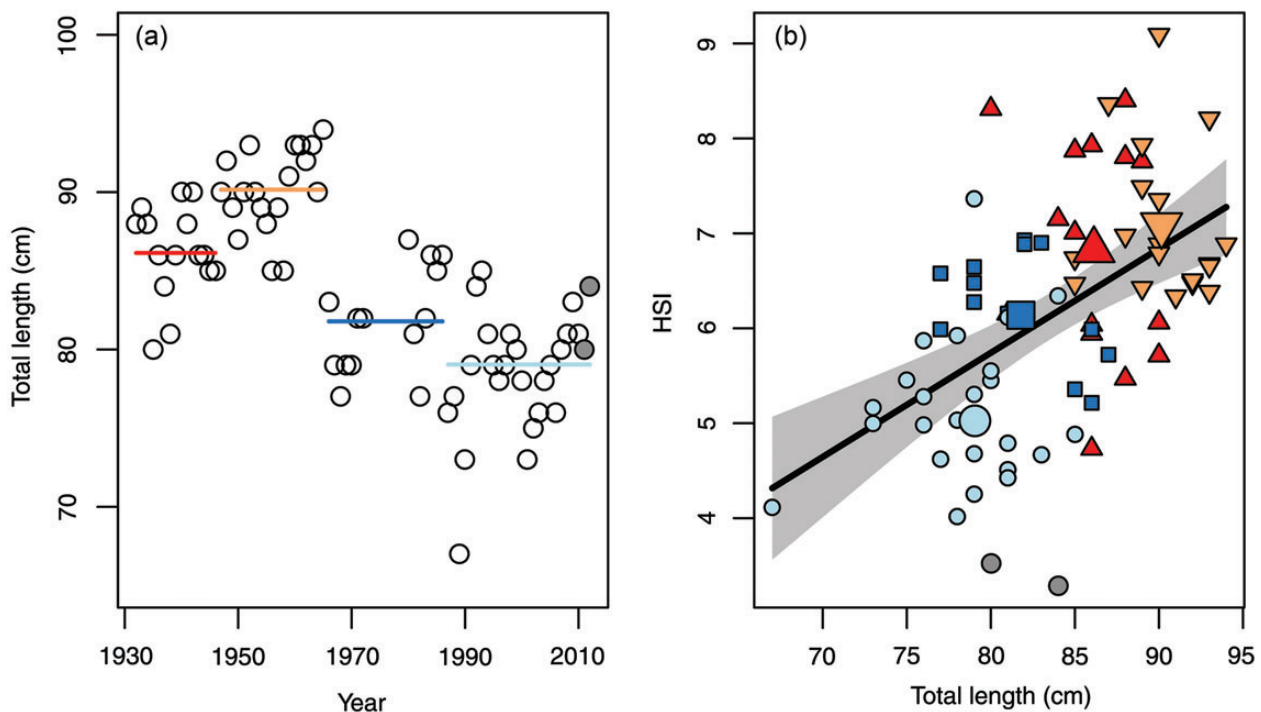


Figure 7. Variation in northeast Arctic cod (a) mean TL, 1932–2012 and (b) the resulting relationship with the HSI. Horizontal coloured lines are the average TL per period identified by change-point analysis, whereas the solid black line is the linear relationship with the 95% confidence band (shaded area). Grey circles in both panels are the years 2011 and 2012. Symbol colour in (b) corresponds to segment line colour in (a). Large symbols in (b) are the mean HSI for each period as defined in (a).

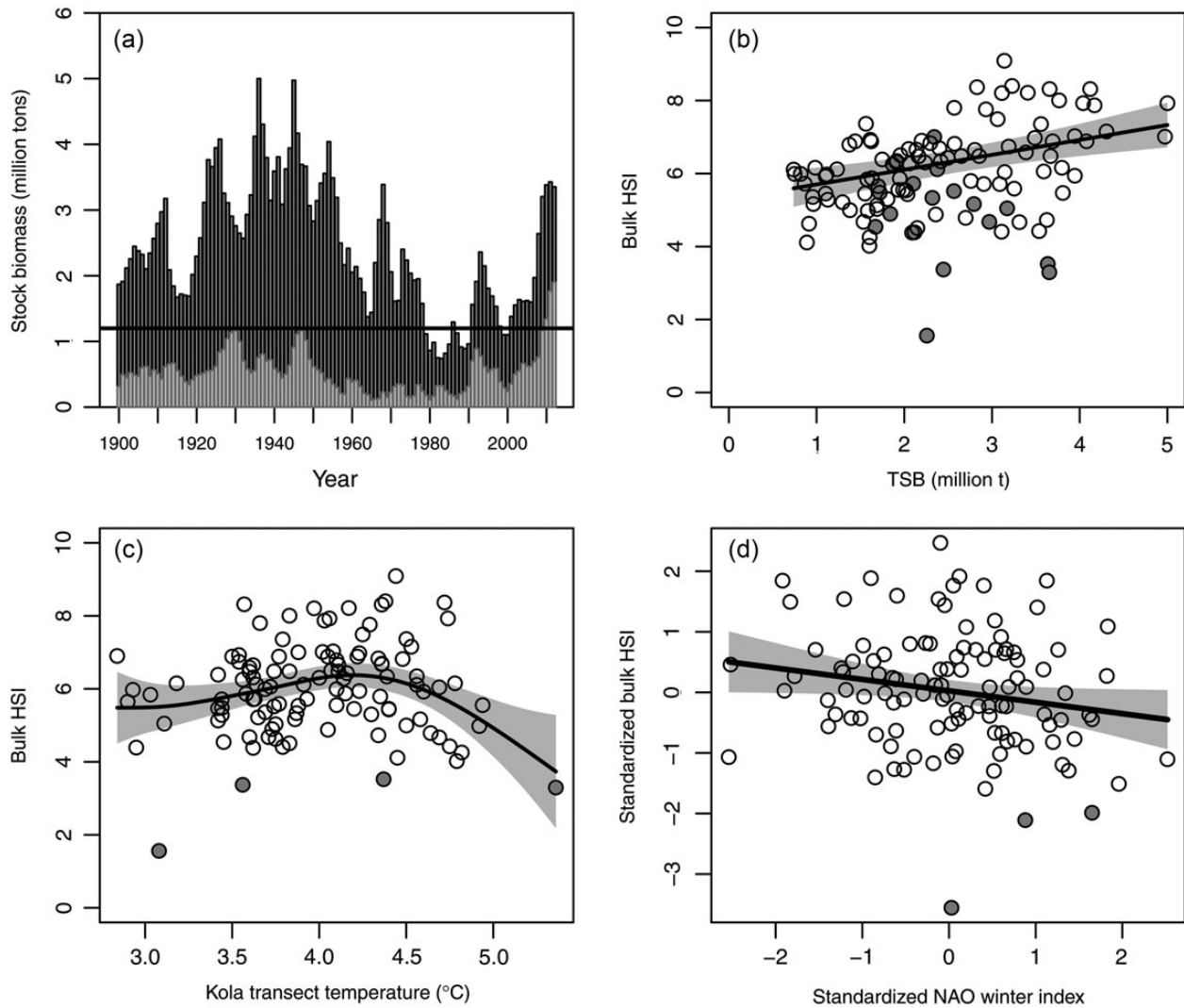


Figure 8. Trends in (a) total-stock (black columns) and spawning-stock biomass (grey columns) of northeast Arctic cod, (b) HSI vs. total-stock biomass (TSB), (c) HSI and Kola temperature, and (d) standardized HSI vs. standardized NAO winter index (lagged by 1 year). Line in (a) refers to the maximum spawning-stock biomass through 2009, i.e. 1.2 million tonnes. Lines in (b)–(d) are the fitted regression or GAM models, whereas the shaded areas are the 95% confidence band. Grey circles in (b)–(d) indicate the low HSI from years 1903, 1904, 2011, and 2012.

“revolt in Finnmark” (Northern Norway) took place that year, when angry fisher attacked the local whale oil factory and blamed this industry for the poor cod fishery (Hanssen, 1963). The more likely reasons for the failure in the cod fishery were a collapse in the capelin stock and invasion of seals to the coast (Hanssen, 1963). In other words, a situation resembling “the ecological crisis in the Barents Sea” seen in the late 1980s (Hamre, 1994). The extremely low HSI of 1.6 in 1903 could be argued to be unrealistically low (Figure 5), but such values are also detected in more recent articles, for both individuals (Skjæraasen *et al.*, 2010) and length classes of smaller cod ($TL \leq 80$ cm; Sandeman *et al.*, 2008; Skjæraasen *et al.*, 2012). Likewise, the fat content of 12% in 1903 is probably not a reporting mistake (Kjesbu *et al.*, 1991), especially after accounting for the inefficient fat extraction procedure at Hjort’s time, where it was several per cent points less effective than in today’s laboratory (Figure 4). Extreme low HSI values appear when spawners are both small in size and in poor condition (Hjort, 1914), and high HSI values result when the opposite is the case (Marshall *et al.*, 1998).

Note also that the 1903 HSI value was linked to an extremely cold year, which may have influenced individual size and condition in that year. A useful cut-off between relatively poor and good condition for NEA cod might be the threshold $HSI = 7$, i.e. the inflection point in the liver fat content curve (Figure 4). However, this point value should not be taken too literally as the statistical analyses showed that variance in liver fat content at this threshold was moderately large. Furthermore, the average HSI is typically around 6; higher average values are rare and were found mainly in the 1920–1950s in some of the years (Figure 5). Taken together, one’s perspective regarding trends and magnitude of change is very much dependent upon the length of the time-series, but extreme values are important to address and clarify main causal factors.

The liver data in the 1914 publication of Johan Hjort inspired us to establish the current series; his data formed a natural “bridge” between the earliest and the latest Fisheries Statistics data. The presented biological series, 1859–2012; 153 years (no data in 1863), is probably one of the longest in the world, although there are

examples of others, e.g. White Sea herring (*Clupea pallasii marisalbi*) catch statistics that go back to the 1780s (Lajus *et al.*, 2007). This statement ignores species of no commercial interest, as well as proximate (e.g. Øiestad 1994), anecdotal information (Kurlansky, 1997) and limited or non-sequential data. To create this long series, we had to assume that the manner and frequency of how liver was extracted from and landed together with cod were similar throughout the time-series. This latter view was challenged by the introduction of the fisheries-independent HSI series; relatively less liver is probably landed when the fishing ground is densely packed with spawners, as seen in recent years (see below). This issue should be looked into more closely in future studies.

Although we focused on a characteristic life-history metric, i.e. its liver size, of a capital spawner (Alonso-Fernandez and Saborido-Rey, 2012), the Fisheries Statistics have also been used to document the loss of spawning fields in southern Norway, i.e. a northerly shift, over time (1866–1969; Jørgensen *et al.*, 2008; Opdal, 2010). The Fisheries Statistics also form a central input in the unique series of NEA cod population dynamics (1900–present; Hylen, 2002), which shows large fluctuations in stock size and recruitment. Furthermore, series from stock assessments (ICES, 2012) clarify that both the SSB and TSB of today are among the highest in history, particularly for SSB, which is the highest recorded. This high biomass (Figure 8a) appeared in exceptionally warm waters (Figure 6), although the causal mechanisms are obviously complex. The temperature series used in our analyses was chosen because of its high quality (length and completeness) and relevance (reflecting both temperature *per se* and advection of Atlantic water masses; Boitsov *et al.*, 2012). The same argument applies to the NAO index, although reflecting instead westerly wind in the North Atlantic, which is known to influence multiple factors that might affect fish population dynamics (Hurrell *et al.*, 2003).

The lack of any potentially suitable explanatory time-series before 1900 makes any advanced exploratory analysis for the whole length of the present NEA cod liver index series highly challenging or speculative. However, for the sake of clarity metrological data as such can be traced several hundreds of years back in time (Parker *et al.*, 1992), but is difficult to compile such series for the area near Northern Norway. We therefore restricted the analysis to a limited number of series, all commencing around 1900, i.e. Kola temperature, SSB, TSB, and the NAO index, which starts before our series and continuing up today. A long list of other less data-rich covariates, not considered here, may also be expected to influence the HSI, such as sex ratio (Marshall *et al.*, 1998; Yaragina, 2010), length and age at maturity (Jørgensen, 1990; Nash *et al.*, 2010), capelin abundance (Marshall *et al.*, 1998; Sandeman *et al.*, 2008), migration distance (Jørgensen *et al.*, 2008; Opdal, 2010), and, possibly, fisheries-induced evolution (Heino *et al.*, 2002; Olsen *et al.*, 2004; Jørgensen *et al.*, 2007, 2009).

The HSI vs. Kola temperature analysis (Figure 8c) resembles a "dose–response curve", as seen in physiology; however, only a small amount of the deviance was explained, which indicates that other factors might be responsible for the observed changes. Because individual HSI can change rapidly with food consumption and is heavily influenced by fish size, care must be taken not to over-interpret these results. Nevertheless, Kola temperature has been shown to not always have a positive effect on the HSI (Sandeman *et al.*, 2008), whereas we have shown that large-scale atmospheric factors (that influence many other factors) do not appear to play a strong role in determining HSI. Godø (2003) grouped temperature

into likely warm and cold periods, beginning in 1866 (see also Opdal, 2010). The last cold period ended in the mid- to late 1980s and the Barents Sea is currently in a warm period. The higher HSI was typically associated with warm periods, and cold periods with a lower HSI, but the recent HSI values are surprisingly low, contradicting this pattern.

TSB, but not SSB, appeared to have a weak relationship with the HSI. This result may be an artefact of the strong correlation between TSB and TL, which has a strong relationship with the HSI. TL clearly began to decline after 1965 (Figure 7a), but the HSI began its downwards trend in 1954, although still being reasonably high up to the mid-1970s (Figure 6). Several things were happening in this period that might be responsible for the trends. The temperature in the Barents Sea was declining and cold periods appear to indicate the lower HSI. But perhaps more importantly, the effects of industrialized fishing began to change the demographic structure of the cod population (Jørgensen, 1990). With declining fish size, the HSI continued to decline. Hence, the remarkably close association seen between HSI and Kola temperature, provided smoothing both dataserries (currently over 9 years), from 1900 and up to this time vanished. Because the relationship between size and HSI is much stronger than that with temperature, the HSI continued to decline with size even after temperature shifted to a warm phase. The effects of temperature on the HSI are weak and the conclusions drawn regarding its effects are, at best, speculative, therefore we argue that the link between size and HSI appears currently to be the key to HSI dynamics. What causation that is behind this association is an interesting topic for future work.

In summary, we have successfully established an extremely long time-series but firm conclusions regarding potential environmental stressors, demographic factors, or evolutionary effects influencing HSI must be postponed until more in-depth analyses. The use of commercial catch statistics obviously has great merits because of their uninterrupted annual resolution and massive collection programme within a rather restricted season and geographical area.

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References

- Alonso-Fernandez, A., and Saborido-Rey, F. 2012. Relationship between energy allocation and reproductive strategy in *Trisopterus luscus*. *Journal of Experimental Marine Biology and Ecology*, 416: 8–16.

- Anon. 1859–2012. Official fisheries statistics from Lofoten [in Norwegian]. Om Lofotfiskeriet (-1879), Lofotfiskeriet (-1922), Lofotfisket (-1979), Melding fra utvalgsformannen for Lofotfisket (2002-). <http://biblioteket.imr.no/e-tidsskrifter/omlofotfiskeriet/> (last accessed 19 September 2013).
- Auger, I. E., and Lawrence, C. E. 1989. Algorithms for the optimal identification of segment neighborhoods. *Bulletin of Mathematical Biology*, 51: 39–54.
- Boitsov, V. D., Karsakov, A. L., and Trofimov, A. G. 2012. Atlantic water temperature and climate in the Barents Sea, 2000–2009. *ICES Journal of Marine Science*, 69: 833–840.
- Chiu, G. 2012. CSIRO Mathematics, Informatics, Statistics. *bentcableAR*: Bent-Cable Regression for Independent Data or Autoregressive Time Series. R package version 0.2.3. <http://CRAN.R-project.org/package=bentcableAR>
- 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.
- Hamre, J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodiversity and Conservation*, 3: 473–492.
- Hanssen, A. 1963. “Opprøret” i Finnmark 1903. Sven Foyns kvaloljefabrikkevnet med jorden av rasende fiskere. Lofotenposten 27 April 1963. OCR-Lenvik Museum 2009 (in Norwegian).
- Heino, M., Dieckmann, U., and Godø, O. R. 2002. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to northeast Arctic cod. *ICES Journal of Marine Science*, 59: 562–575.
- Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, 70: 639–656.
- Helland-Hansen, B., and Nansen, F. 1909. The Norwegian Sea. Its Physical Oceanography based upon the Norwegian Researches 1900–1904. Report on Norwegian Fishery and Marine-Investigations, 2 (2). Det mallingske bogtrykkeri, Kristiania. 390 pp. + 25 supplementary plates.
- Hjort, J. 1914. Fluctuations in the great fisheries of the northern Europe viewed in the light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 20: 1–228.
- Houde, E. D. 2008. Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41: 53–70.
- Hurrell, J. W., Kushnir, Y., Ottersen, G., and Visbeck, M. 2003. An overview of the North Atlantic Oscillation. *In* The North Atlantic Oscillation: Climatic Significance and Environmental Impact, pp. 1–36. Ed. by J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. American Geophysical Union, Washington, DC.
- Hurrell, J., and National Center for Atmospheric Research Staff (Eds.). 2013. The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (PC-based). <http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-pc-based> (last accessed 27 June 2013).
- Hysten, A. 2002. Fluctuations in abundance of northeast Arctic cod during the 20th century. *ICES Marine Science Symposia*, 215: 543–550.
- ICES. 2012. Report of the Arctic Fisheries Working Group 2012 (AFWG), 20–26 April 2012. ICES Headquarters, Copenhagen. ICES Document CM 2012/ACOM: 05. 633 pp.
- Jørgensen, C., Dunlop, E. S., Opdal, A. F., and Fiksen, Ø. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology*, 89: 3436–3448.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2007. Ecology - managing evolving fish stocks. *Science*, 318: 1247–1248.
- Jørgensen, C., Ernande, B., Fiksen, Ø., and Dieckmann, U. 2006. The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 200–211.
- Jørgensen, C., Ernande, B., and Fiksen, Ø. 2009. Size-selective fishing gear and life history evolution in the northeast Arctic cod. *Evolutionary Applications*, 2: 356–370.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil, Conseil International pour l'Exploration de la Mer*, 46: 235–248.
- Killick, R., and Eckley, I. 2013. *changepoint*: an R package for change-point analysis. R package version 1.1. <http://CRAN.R-project.org/package=changepoint>.
- Kjesbu, O. S., Klungsoyr, J., Kryvi, H., Witthames, P. R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2333–2343.
- Kurlansky, M. 1997. *Cod: A Biography of the Fish that Changed the World*. Walker, New York. 304 pp.
- Lajus, D. L., Alekseeva, Y. I., and Lajus, J. A. 2007. Herring fisheries in the White Sea in the 18th-beginning of the 20th centuries: spatial and temporal patterns and factors affecting the catch fluctuations. *Fisheries Research*, 87: 255–259.
- Lambert, Y., and Dutil, J. D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 104–112.
- Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1766–1783.
- Nash, R. D. M., Pilling, G. M., Kell, L. T., Schön, P. -J., and Kjesbu, O. S. 2010. Investment in maturity-at-age and -length in northeast Atlantic cod stocks. *Fisheries Research*, 104: 89–99.
- Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: northeast Arctic cod. *ICES Marine Science Symposia*, 198: 17–30.
- Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932–935.
- Opdal, A. F. 2010. Fisheries change spawning ground distribution of northeast Arctic cod. *Biology Letters*, 6: 261–264.
- Ottersen, G., Kim, S., Huse, G., Polovina, J. J., and Stenseth, N. C. 2010. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems*, 79: 343–360.
- Parker, D. E., Legg, T. P., and Folland, C. K. 1992. A new daily Central England temperature series 1772–1991. *International Journal of Climatology*, 12: 317–342.
- Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., Drinkwater, K., et al. 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22: 121–139.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rijnsdorp, A. D. 1993. Fisheries as a large-scale experiment on life-history evolution - disentangling phenotypic and genetic-effects in changes in maturation and reproduction of North-Sea plaice, *Pleuronectes platessa* L. *Oecologia*, 96: 391–401.
- Rollefsen, G. 1933. The otoliths of cod. *Fiskeridirektoratets Skrifter Serie Havundersøkelser*, 4: 6 plates 14.
- Rollefsen, G. 1934. The cod otolith as a guide to race, sexual development and mortality. *Rapports et Procès-Verbaux des Réunions*, 88: 1–5.
- Rollefsen, G. 1953. Observations on the cod and cod fisheries of Lofoten. *Rapports et Procès-Verbaux des Réunions du Conseil International Pour l'Exploration de la Mer*, 136: 40–47.
- Sandeman, L. R., Yaragina, N. A., and Marshall, C. T. 2008. Factors contributing to inter- and intra-annual variation in condition of cod

- Gadus morhua* in the Barents Sea. *Journal of Animal Ecology*, 77: 725–734.
- Sinclair, M. 1997. Prologue. Recruitment in fish populations: the paradigm shift generated by ICES Committee A. *In* *Early Life History and Recruitment in Fish Populations*, pp. 1–27. Ed. by R. A. Chambers, and E. A. Trippel. Chapman & Hall, London.
- Skjæraasen, J. E., Kennedy, J., Thorsen, A., Fonn, M., Strand, B. N., Mayer, I., and Kjesbu, O. S. 2009. Mechanisms regulating oocyte recruitment and skipped spawning in northeast Arctic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 1582–1596.
- Skjæraasen, J. E., Nash, R. D. M., Kennedy, J., Thorsen, A., Nilsen, T., and Kjesbu, O. S. 2010. Liver energy, atresia and oocyte stage influence fecundity regulation in northeast Arctic cod. *Marine Ecology Progress Series*, 404: 173–183.
- Skjæraasen, J. E., Nash, R. D. M., Korsbrette, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K. H., *et al.* 2012. Frequent skipped spawning in the world's largest cod population. *Proceedings of the National Academy of Sciences of the USA*, 109: 8995–8999.
- Sonderegger, D. 2012. SiZer: SiZer: Significant Zero Crossings. R package version 0.1-4. <http://CRAN.R-project.org/package=SiZer>.
- Trout, G. C. 1957. The Bear Island cod: migration and movements. *Fishery Investigations, London, Series II*, 21: 1–51.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73: 3–36.
- Woodhead, A. D., and Woodhead, P. M. J. 1965. Seasonal changes in the physiology of the Barents Sea cod, *Gadus morhua* L., in relation to its environment. I. Endocrine changes particularly affecting migration and maturation. *ICNAF Special Publication*, 6: 691–715.
- Yaragina, N. 1996. Change of liver condition index of North-east Arctic cod in the 1970–90's. *ICES Document CM/G*: 41.
- Yaragina, N. A. 2010. Biological parameters of immature, ripening, and non-reproductive, mature northeast Arctic cod in 1984–2006. *ICES Journal of Marine Science*, 67: 2033–2041.

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