

Factors contributing to inter- and intra-annual variation in condition of cod *Gadus morhua* in the Barents Sea

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Summary

1. Relative body condition (the quantity of stored energy) is an important tool in understanding demographic variation and the ability of a population to respond to environmental stressors, varying food availability and competition.
2. A high-resolution database was used to examine causes of variation in the condition of north-east Arctic cod (*Gadus morhua* L.) for the period 1967–2004, over annual and monthly timescales. Community dynamics and climate variation were also tested as potential causes.
3. Temperature was shown to have a positive impact on condition at both inter- and intra-annual timescales. Interannually, temperature may affect stock distribution, in particular its overlap with the capelin stock. At shorter timescales it is likely that temperature directly affects the metabolism of the cod.
4. Intra-annually, the quantity of capelin in cod stomachs positively affected cod condition in the current and the preceding month for all lengths of cod. This indicated a time lag between a change in food consumption and a subsequent change in condition, or ‘latency’.
5. Our study has shown that variation in temperature is a vital determinant of changes in condition, both at inter- and intra-annual timescales. Furthermore, the principle of latency has been demonstrated at the population level. Indirect effects of competition for energy-rich resources have been shown to have a negative effect on condition. This study supplements our knowledge of the implications for condition of changes in climate and in potential food resources.

Key-words: condition, climate, generalized least squares, latency, population

Introduction

Condition, a term generally used to refer to the magnitude of stored energy reserves, affects the probability of survival at both individual (Ardia 2006) and population (Jennings *et al.* 2006) levels. Stored fat acts as an energy reserve in both terrestrial and marine animals (Ballantyne 1997; Golet & Irons 1999; Hall, McConnell & Barker 2001). Reserves are utilized in times of physiological stress caused by adverse environment, lack of food, migration, reproductive behaviour or disease. Good condition implies that animals are more likely to endure periods of fasting (Millar & Hickling 1990), therefore the need to forage may be better balanced against predation risk (Murray 2002). Good condition leads to increased reproductive rates (Belant *et al.* 2006) and fecundity (Blanchard, Frank & Simon 2003), more mature individuals in a population (Helle & Kauhala 1995), and earlier maturation (Yoneda *et al.* 2007). Therefore understanding the causes of variation in

condition allows us to understand and predict demographic variation, as well as the ability of a population to respond to environmental stressors.

Many studies have attempted to identify causes of variation in condition (Petren & Case 1996; Casini, Cardinale & Hjelm 2006); however, the majority have used data spanning shorter time periods (Golet & Irons 1999; Hall *et al.* 2001). Factors affecting condition are often complex: some may act indirectly (Petren & Case 1996), whereas others may become apparent only over time (Forchhammer *et al.* 2001). In order to determine the causes of variability in condition accurately, a long-term high-frequency data set is required, with ancillary information on climatic variables, potential competitors and the availability of preferred prey. Commercially harvested fish populations have the potential to provide us with this quality of data.

In fish, lengthy migrations may significantly deplete fat reserves (Redfern *et al.* 2000), so sufficient energy must be acquired beforehand (Comeau, Campana & Chouinard 2002). Maturation processes constitute a major energetic demand

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(Sargent 1996), hence fish may be in poor condition during maturation and spawning. The quantity and quality of available food also has an impact on condition (Rikardsen *et al.* 2006). At timescales of weeks and months, there may be a time lag between a change in food consumption and the subsequent change in condition. Ferron & Leggett (1994) define this lag as 'latency', and discuss studies that found latencies on the scale of days in larval fish. However, it might be expected that juvenile and adult fish would have longer latency times. Black & Love (1986) found that it could take up to ten weeks for energetic reserves to be exhausted in juvenile cod (*Gadus morhua* L.).

Climatic fluctuations cause variations in condition, both inter- and intra-annually. Low temperatures can lead to an increased risk of starvation in endotherms (Gosler 2002; Rogers & Reed 2003), although ectotherms may benefit, as colder temperatures in the tolerance range of a species can decrease metabolic rates and therefore energetic demands (Zenkevich 1963). Inter-annually, temperature variations may affect the available feeding area (Aglen, Drevetnyak & Sokolov 2004) and have an indirect impact on condition. Variation in the North Atlantic Oscillation (NAO) index may be regarded as a reflection of climatic fluctuations in the North Atlantic region (Ottersen & Stenseth 2001): it has been related to female body condition (Lehikoinen, Kilpi & Ost 2006), and indirectly to decreased juvenile survival via a negative impact on maternal condition (Forchhammer *et al.* 2001). The NAO index has been directly linked with temperature fluctuations in some ecosystems (Ottersen & Stenseth 2001), and may have a similar influence on condition.

This paper utilizes a high-resolution database of the liver weights of north-east Arctic (NA) cod (Yaragina & Marshall 2000) collected monthly in the Barents Sea (BaS) from 1927 onwards. The liver is the main energy-storage site in gadoid species (Eliassen & Vahl 1982b). Liver lipids are mobilized rapidly in response to increased energy demands, and are consequently the first reserves to be exhausted (Black & Love 1986; Ferron & Leggett 1994; Grant & Brown 1999). Liver weights are usually reported as the liver condition index (LCI), which expresses the weight of the liver as a percentage of total body weight. The maximum attainable LCI varies with length, with larger cod having a greater capacity for energy storage (Yaragina & Marshall 2000). The LCI is a dynamic and rapidly varying index of condition (Lambert & Dutil 1997; Yaragina & Marshall 2000), providing an accurate description of variation in the relative magnitude of cod energy stores.

This study investigated the impact of environmental factors, food availability and community composition on interannual and monthly variation in the condition of NA cod. The commercial importance of cod (Ottersen, Hjermann & Stenseth 2006), and of cod liver oil (Falch, Rustad & Aursand 2006), has meant that data sets chronicling changes in liver weights are available. This enables us to conduct an in-depth study of condition, potentially an important factor influencing population demography and resilience to stressors. NA cod are found in the BaS, a subarctic ecosystem which is low

in biological diversity but high in productivity (Hamre 1994). Cod, capelin (*Mallotus villosus* Müller) and herring (*C. harengus* L.) are key species in the BaS ecosystem (Hjermann, Stenseth & Ottersen 2004b). Therefore the state of the cod population is important not only commercially, but also as a key species and top predator. Identifying factors that cause condition to vary over different timescales can potentially aid us in improving the management of this species, and therefore of the BaS ecosystem.

Methods

THE NORTH-EAST ARCTIC COD STOCK

NA cod are found mainly in the central and southern BaS or the northern Norwegian Sea, which is close to the extreme north of the species range (Godø 2003). Adult cod return annually to coastal spawning grounds off mid- and northern Norway, with spawning occurring between February and May, peaking at the end of March/beginning of April (Pedersen 1984; Bergstad, Jørgensen & Dragesund 1987; Kjesbu *et al.* 1998). Currents carry eggs and larvae north, with the majority of juveniles reaching the BaS by June or July (Helle & Pennington 1999). After spawning, adult cod migrate to feed along the Polar Front (Nakken 1998), building up energy reserves needed for maturation and growth of gonads.

The main influence on the BaS climate is the inflow of warm Atlantic water from the south-east (Smolyar & Adrov 2003), which varies cyclically (Tretyak *et al.* 1995). Years with greater inflows are characterized by reduced ice coverage with the Polar Front displaced to the north and east (Ådlandsvik & Loeng 1991), and therefore higher primary production. The distribution of NA cod is restricted by the Polar Front and the extent of summer ice, respectively (Aglen *et al.* 2004). Warmer temperatures have been shown to have a positive effect on recruitment (Ottersen, Loeng & Raknes 1994), growth (Michalsen, Ottersen & Nakken 1998) and fecundity (Kjesbu *et al.* 1998) of NA cod; however, the link between temperature and condition is less clear (Yaragina 1996).

Cod in the Barents Sea preferentially consume capelin, a lipid-rich energy source (Copeman & Parrish 2004). The growth rate and average weight of cod decrease when they are forced to switch prey (Jørgensen 1992; Rose & O'Driscoll 2002). Interannually, LCI tends to vary synchronously with the biomass of BaS capelin (Fig. 1a,b), indicating the importance of this species to NA cod. Whereas cod consume adult capelin, herring consume larval capelin (Gjøsæter & Bogstad 1998). High herring stocks may correspond with crashes in capelin stocks (Hjermann, Ottersen & Stenseth 2004a) and therefore have an indirect impact on cod condition.

STUDY DATA

Liver weight data originate from the Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Murmansk, Russia (Table 1). The database contains monthly cod LCI values, calculated as an average per 10-cm-length group. Observations used in this study were gathered by research ship surveys and observers on fishing vessels in the southern BaS, incorporating the majority of International Council for the Exploration of the Sea (ICES) area I and the eastern part of area IIa (Yaragina & Marshall 2000). The LCI data have been collected monthly from 1927, with the exception of World War II. Prior to 1947, LCI was grouped by fish weight

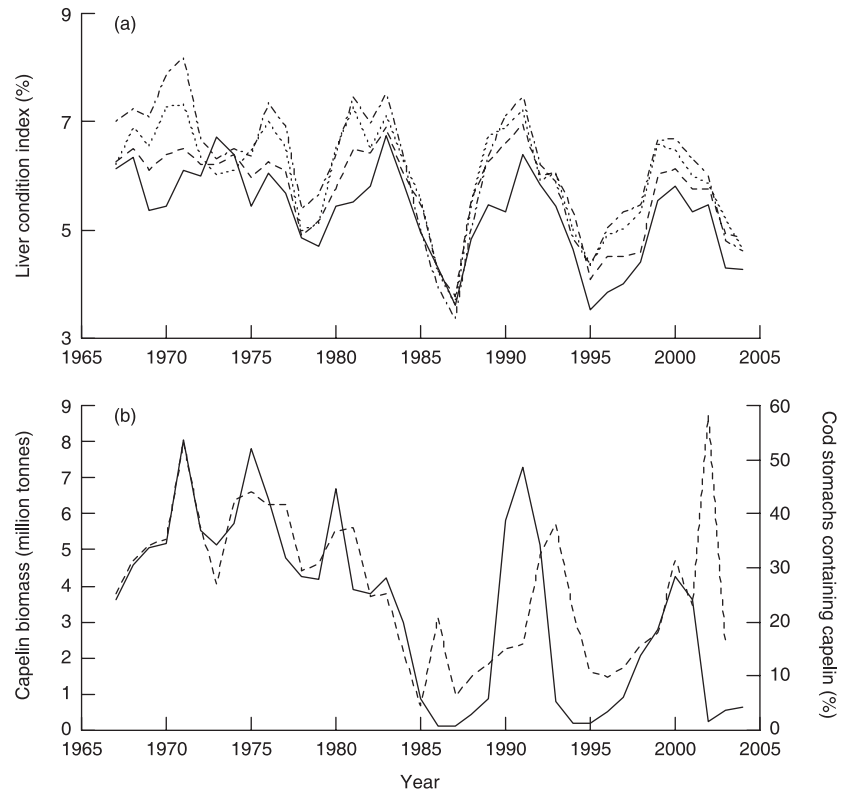


Fig. 1. (a) Annual average of cod liver condition index from 1967 to 2004, plotted for each length class separately. Solid line = 41–50; dashed line = 51–60; dotted line = 61–70; dashed and dotted line = 71–80-cm cod. (b) Time series of capelin biomass (Cap_{bio} , solid line) and cod stomachs containing capelin (Sto_{cap} , dotted line). From 1973 onwards, capelin biomass predicted via acoustic estimates. Previous data points are predicted via an assumption of linearity between capelin biomass and cod consumption (Marshall *et al.* 2000).

Table 1. Summary of biological and environmental variables input into generalized least squares models

Abbreviation	Variable	Resolution and timescale	Source	Area*
LCI	Liver condition index	Monthly (1927–2004)	Polar Institute of Marine Fisheries & Oceanography (PINRO), Murmansk, Russia (Yaragina 1996)	ICES Area I
Num_{obs}	Number of observations for LCI	Monthly (1927–2004)	PINRO (Yaragina 1996)	ICES Area I
K_{temp}	Kola section temperature	Monthly (1921–2004)	PINRO (Tereshchenko 1996)	33°30' E and 70°30'–72°30' N
$Prop_{cap}$	Proportion of capelin in cod stomachs	Monthly (1984–2004)	PINRO (Dolgov 2002)	ICES Area I+IIa+IIb
NAO	NAO index	Monthly (1821–2007)	Climatic Research Unit of the University of East Anglia†	–
Cap_{bio}	Capelin biomass	Annual (1973–2005)	ICES Arctic Fisheries Working Group (Anonymous 2006)	ICES Area I+II‡
Sto_{cap}	Percentage of cod stomachs containing capelin	Annual (1947–2004)	PINRO – mean value over year (Ponomarenko & Yaragina 1978)	ICES Area I
Sto_{empty}	Percentage of empty cod stomachs	Annual (1947–2004)	PINRO – mean value over year (Ponomarenko & Yaragina 1978)	ICES Area I
$NSSH_{bio}$	Norwegian spring-spawning herring	Annual (1950–2005)	ICES Working Group on Northern biomass Pelagics & Blue Whiting (ICES 2005)	ICES Area IIa2

*Definitions of the ICES areas and access to the working group reports cited here can be found at <http://www.ices.dk>

†http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm

‡Excluding division IIa west of 5° W.

rather than length, and data gathered before 1967 have a higher frequency of missing values. Therefore only data from 1967 onwards are used in the present analysis.

The number of fish sampled to calculate an average LCI for each 10 cm length class (Num_{obs}) was also available. The smallest and largest fish are caught less often, therefore there is a higher frequency

of missing values at these lengths. Usually, fewer samples are taken in winter, when weather conditions are less favourable. In the mid-1970s and mid-1980s, increased sampling efforts occurred when capelin stocks were low. Only four length classes contained sufficient data to construct models for the chosen time period: 41–50, 51–60, 61–70 and 71–80 cm. The LCI varies with fish length as the relative

weight of the liver is greater in larger fish (Yaragina 1996). The fact that some of the larger cod in this study may be mature, and therefore potentially expending energy in maturation and spawning processes, must also be considered. It is therefore of interest to maintain the length separations in the data in order to test for potential differences in the causes of variability in LCI in the various length classes.

To investigate the relationship between food consumption and changes in LCI, a database of cod stomach contents was used. Stomachs were collected from fish different from those utilized for the LCI database. Stomach data before 1984 are from a Russian database (collated by PINRO). However, in 1984 a joint sampling programme was initiated by PINRO and the Institute of Marine Research (IMR), Bergen, Norway (Mehl & Yaragina 1992). Stomach data are not divided by length, but cod between 20 and 79 cm had good coverage (Mehl & Yaragina 1992), encompassing the LCI length classes used in this study. The percentage of cod stomachs that contain capelin (Sto_{cap}) and the percentage of empty stomachs (Sto_{empty}) are available annually from 1947 onwards. Evidence of regurgitation resulted in a specimen being discarded (Mehl & Yaragina 1992) when Sto_{empty} data were collected. $Prop_{cap}$, the weight of capelin in cod stomachs divided by the total weight of the stomach bolus, was collected monthly from 1984 onwards. The resolution of the $Prop_{cap}$ data enabled the study of latency.

Estimates of total fish population biomass were obtained from ICES assessment reports (<http://www.ices.dk>). Norwegian spring-spawning herring biomass (NSSHbio) was available annually from 1950 onwards. NSSH are a major predator on capelin (Hjermann *et al.* 2004a), and therefore a potential competitor with NA cod. Yearly estimates of BaS capelin biomass (Cap_{bio}) from acoustic surveys were also used (Anon 2006), the majority of which are carried out in autumn. Capelin are the preferred prey of cod in the length range used here (Dolgov 2002). Survey data are available from 1973

onwards; however, the time series has been backdated to 1946 by assuming the intensity of cod feeding on capelin is linearly related to capelin stock biomass (Marshall *et al.* 2000).

Monthly sea temperature and the NAO index were used as measures of climate variability. Temperature for 1921–2004 was taken from the Kola hydrographic section (offshore of the Kola peninsula, Russia; Tereshchenko 1996), averaged over 0–200 m depth (K_{temp}). The Kola section is widely used to represent the temperature of the southern BaS (Ottersen & Loeng 2000; Hjermann *et al.* 2004b). Fluctuations in the NAO have been closely associated with temperature in the BaS over the previous few decades (Ottersen *et al.* 2001). Monthly NAO data are available from 1821 onwards from the Climatic Research Unit of the University of East Anglia (http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm).

STATISTICAL ANALYSIS

All analyses were carried out using R (R Development Core Team 2006). To examine interannual variation in the monthly LCI, a lattice plot of LCI was constructed (Fig. 2). Data were plotted for the full time series, from 1967 to 2004, with each month graphed separately. Interannual trends for each month were illustrated by fitting Tukey's smoother; a running median smoother, with a window of length three repeated until convergence (Tukey 1977). Only the smallest and largest length classes are represented in Fig. 2, as the two smaller (41–50 and 51–60 cm) and two larger (61–70 and 71–80 cm) classes exhibited similar variability.

To investigate annual and monthly variation in LCI, models of relevant biological and environmental variables were constructed over both timescales. Initial data exploration indicated autocorrelation in the dependant variable (LCI) as well as violation of homogeneity. Therefore generalized least squares (GLS) models were selected.

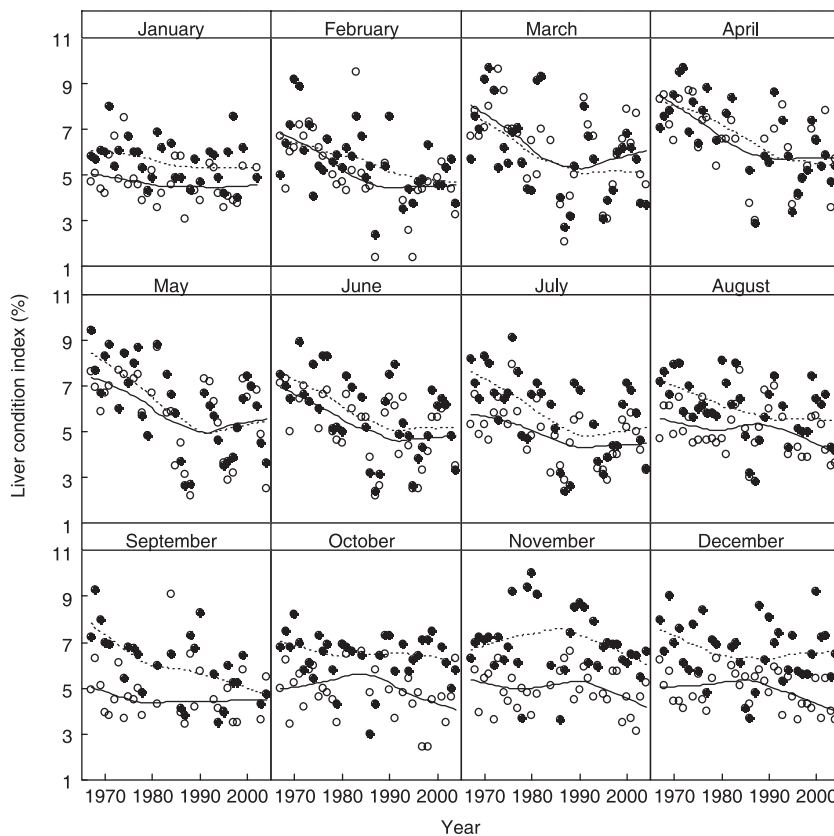


Fig. 2. Variations in liver condition index by month. White circles and solid lines, 41–50-cm cod; black circles and dotted lines, 71–80-cm cod. Smoothing lines were created using Tukey's running median smoother.

GLS models are fitted in a manner similar to ordinary least squares regression models. However, they have the added advantage that models of data with unequal variance and correlation of within-group errors (Pinheiro & Bates 2000) may be constructed. Weightings in GLS models are applied in a manner different from ordinary least squares models. In GLS, these may be used to describe non-constant error variance in the data set (heteroscedasticity); where the variance is the square of the standard deviation divided by the specified weightings (σ^2/w_i) (Carroll & Ruppert 1988; Davidian & Giltinan 1995). GLS models do not allow missing values in raw data. Therefore linear interpolation was used to estimate missing values where necessary (Mann *et al.* 2005).

ANNUAL MODELS

The dependant variable in all models was the annual average of LCI from 1967 to 2003. Separate models were fitted for each length class. The independent variables were the annual mean of all monthly variables along with annually resolved variables (Table 1), with the exception of Prop_{cap} and Sto_{cap}. No interactions were specified, as interaction plots did not indicate any. The Prop_{cap} time series began in 1984 and was therefore excluded due to insufficient length of time series. Sto_{cap} was highly correlated with Cap_{bio}, and therefore removed from the model to avoid collinearity. Cap_{bio} was preferentially retained as it was more closely correlated to LCI, particularly for larger fish, than Sto_{cap}. Prior to its inclusion in the model, Cap_{bio} was transformed using Log_e to give a linear relationship between Cap_{bio} and LCI. The monthly Num_{obs} data for LCI were averaged over year and applied as a weighting in the form 1/Num_{obs}. Therefore variance was minimized for LCI data points which represented a greater number of samples. Backward selection was used, and models were compared using a likelihood-ratio test, which tests the hypothesis that the probability of obtaining the expected result is equal to the probability of observing the sampled result (Sokal & Rohlf 2003). Autocorrelation plots showed that, in each case, the selected model minimized autocorrelation.

MONTHLY MODELS

Predicted annual means (from annual models) were subtracted from the monthly LCI data for each of the four length classes. This was used to 'detrend' the monthly data through removal of the annual signal. It must be considered that the exact annual trend is not obtained from the model, but is merely an estimate of this value. Spurious autocorrelation is therefore likely to be introduced into the detrended time series (Diggle 2004). Monthly models of LCI in the period 1984–2003 were then constructed for each of the four length classes using the detrended data. In order to test for latency, it was necessary to use a monthly measurement of capelin consumption. As Prop_{cap} was available only from 1984 onwards, it was therefore necessary to restrict the time period to 1984–2004 to test for latency.

All monthly variables (Table 1) were input into the model. Annual variables were excluded as they are unlikely to represent monthly variability in the detrended data. Interactions between Prop_{cap} and NSSH_{bio}, Prop_{cap} and K_{temp}, and NSSH_{bio} and K_{temp} were included in the initial model. Black & Love (1986) found that liver lipids in 50–60 cm cod were mobilized almost instantaneously on the onset of starvation, and completely exhausted after ten weeks. Therefore Prop_{cap} was also included as a lagged variable at both one and two months, when testing for evidence of latency. Model weights were applied as 1/Num_{obs}, backward selection of model terms was

used, and new models were compared with existing ones using a likelihood-ratio test. For all models, autocorrelation was present in the residuals. An autoregressive (AR) model was therefore fitted to the errors for each of the four models. Examination of autocorrelation and partial-autocorrelation function plots indicated that an AR(1) model would provide the best fit. The distribution of the residuals for models with the AR(1) fit were closer to a normal distribution with reduced residual autocorrelation.

Results

EXPLORATORY ANALYSIS

When interannual trends in monthly LCI are plotted, differences are evident both between months and between length classes. The two smallest (41–50 and 51–60 cm) and two largest (61–70 and 71–80 cm) length classes exhibit similar variability in LCI. Hence, for clarity, only the smallest (41–50 cm) and largest (71–80 cm) length classes are represented in Fig. 2. For all length classes from October to January, LCI values remained relatively constant from 1967 to 2004. Larger cod were generally in better condition than smaller cod throughout the study. For February to July, a period encompassing both spawning and feeding migrations, LCI declined in all length classes over the first half of the time series (1967–83). The greatest decrease of approximately 3–4% occurred in May. However, in the latter half of the time period, LCI stabilized at a lower level. In August and September, clear differences between length classes were evident. As cod length increased, the rate of decrease in LCI over the two months, particularly in September, became more pronounced.

ANNUAL MODELS

In the annual GLS models, K_{temp} was shown to have a significant positive effect on LCI for all length classes ($P < 0.001$ for 41–50; $P = 0.005$ for 51–60; $P = 0.016$ for 61–70; $P = 0.037$ for 71–80-cm cod) (Table 2). As cod length increased, the effect of K_{temp} became less significant. NAO was not retained in the models for any length class. A significant positive relationship with Log_e(Cap_{bio}) was found for all length classes ($P < 0.001$ for all models; Table 2). A negative relationship between NSSH_{bio} and LCI was found for three of the four length classes ($P = 0.002$ for 41–50; $P = 0.053$ for 51–60; $P = 0.022$ for 71–80 cm). No interaction terms were retained as significant (at $P = 0.05$). Residuals from the annual models were examined to ensure that no trends were present in the errors and that remaining autocorrelation was minimized. The residuals indicated that the model fitted less accurately in the first half of the time period (1967–83). The improved fit in the second half of the study period (1984–2002) coincides with a change in the manner in which condition fluctuated, with a higher-amplitude cyclic pattern emerging (Fig. 1a).

MONTHLY MODELS

Variation in annual mean LCI indicates that it may be divided into two time periods. From the late 1960s until the mid-1980s,

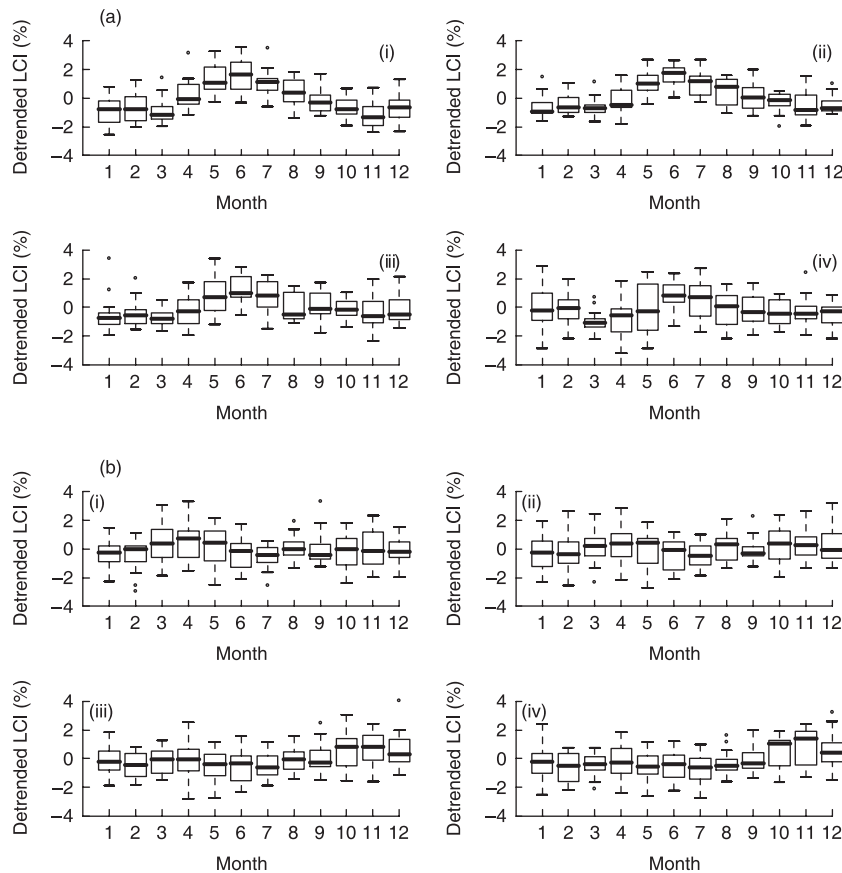


Fig. 3. Monthly liver condition index (LCI) data, annual trend removed: (i) 41–50; (ii) 51–60; (iii) 61–70; (iv) 71–80-cm cod. The top and bottom of each box represent 25 and 75% quantiles; dotted lines 1.5 times the interquartile range. Boxplot A denotes the first half of the time series (1967–83); plot B denotes the second half (1984–2002). Time series were split into two because there was a change in the BaS ecosystem in the mid-1980s, and previous changes in the seasonality of LCI have been linked with concurrent changes in the BaS ecosystem (see Discussion).

Table 2. Generalized least squares models fitted to annual data

Size class (cm)	Fixed effect	Coefficient	<i>t</i>	<i>P</i>
41–50	Log _e (Cap _{bio})	0.334	4.273	<0.001
	NSSH _{bio}	–0.001E-04	–3.320	0.002
	K _{temp}	0.847	4.223	<0.001
51–60	Log _e (Cap _{bio})	0.353	4.552	<0.001
	NSSH _{bio}	–0.001E-04	–2.009	0.053
	K _{temp}	0.654	2.996	0.005
61–70	Log _e (Cap _{bio})	0.495	2.602	<0.001
	K _{temp}	0.549	2.535	0.016
71–80	Log _e (Cap _{bio})	0.594	5.661	<0.001
	NSSH _{bio}	0.000	–2.396	0.022
	K _{temp}	0.546	2.170	0.037

Liver condition index modelled as a function of capelin consumption, herring biomass, sea temperature and percentage of empty cod stomachs for north-east Arctic cod. Initially all terms were entered into a saturated model, then a likelihood ratio test was used for backward selection.

LCI was generally good (5% or higher; Marshall *et al.* 2000), with relatively small fluctuations. After this period, variability in LCI increased (Fig. 1a) in response to changes in capelin biomass (Fig. 1b). Following the construction of annual

models, subsequent analysis proceeded using monthly data with annual trends removed. Detrended monthly LCI was found to vary differently in the first (Fig. 3a) and second (Fig. 3b) halves of the time series. In the earlier part of the time series (Fig. 3a), LCI peaked around June. Additionally, in the largest length class (71–80-cm cod; Fig. 3a, iv) there is potentially a secondary peak in January and February. Monthly variation is less clear in the latter part of the detrended time series (Fig. 3b). However, condition appears to peak in spring for the two smaller length classes (Fig. 3b, i and ii) and in late autumn/early winter for larger cod (Fig. 3b, iii and iv).

For the monthly models, the necessity of including a monthly measurement of capelin consumption meant that data were available only from 1984 onwards. In the fitted models, K_{temp} had a significant positive effect on LCI for all length classes ($P = 0.005$, $P = 0.034$, $P < 0.001$, $P < 0.001$). Prop_{cap} was significant for three length classes ($P < 0.001$ for 41–50; $P < 0.001$ for 51–60; $P = 0.001$ for 61–70 cm). However, Prop_{cap} lagged one month was highly significant ($P < 0.001$) for all length classes as confirmed by cross-correlation plots. A negative interaction was found between Prop_{cap} and K_{temp} ($P < 0.001$) for 41–50-cm cod. No other interaction terms were retained as significant (at $P = 0.05$).

Discussion

In this study, we utilized a uniquely long-term database to determine the causes of intra- and interannual variation in

cod condition. Our results suggest that causes of variation in condition do not differ among length classes for cod in the length range studied here. We also find evidence of a one-month latency between a change in capelin consumption and the following change in cod condition. We elucidated a positive effect of temperature on condition for all length classes at both inter- and intra-annual timescales.

CAUSES OF VARIATION IN CONDITION

This study provides evidence of the significant influence of temperature on condition at both annual and monthly timescales. Temperature had a positive effect at a monthly timescale, potentially via the metabolism of the fish. Finstad *et al.* (2004) found a 30% decrease in the resting metabolic rate of juvenile Atlantic salmon (*Salmo salar* L.) in colder temperatures. Warmer waters should increase metabolic rate and therefore the rate of energy turnover. Michalsen *et al.* (1998) found faster growth in NA cod year classes exposed to higher temperatures in winter. North-east Arctic cod are at the northern limit of the species' range (Planque & Frédou 1999; Godø 2003) and therefore particularly sensitive to environmental fluctuations. Thus higher temperatures within the tolerance range of cod may prove beneficial in times of sufficient food availability. A larger NA cod stock is related to a more easterly distribution (Michalsen *et al.* 1998), which occurs in warmer winters with reduced ice cover. The positive interannual effect on condition of warmer sea temperatures, found here, has been demonstrated for other cod stocks at the northern limit of the species' range (Krohn, Reidy & Kerr 1997), and there is a strong body of evidence that annual variation in temperature is vital in determining condition for both marine and terrestrial species (Yaragina & Marshall 2001; Gosler 2002).

The monthly resolution LCI data used here enabled investigation of possible latency between food consumption and a subsequent change in condition. A latency of one month was found to be highly significant for all lengths of cod studied here, which is within the timescale found by Black & Love (1986). Our work provides evidence that latency can be detected at the population scale, and demonstrates the principle in older juvenile and mature fish, whereas previous studies have concentrated on larval and 0-group fish (Ferron & Leggett 1994; Grant & Brown 1999). Black & Love (1986) found a lag of up to ten weeks between the almost instantaneous mobilization of energetic reserves and their complete exhaustion in juvenile cod in laboratory studies. The shorter period of one month found in this study, in comparison with that of ten weeks found by Black & Love (1986), may be connected to differences between laboratory and natural conditions. Wild cod are likely to switch prey or migrate from an area, rather than allowing their energetic reserves to decline to complete exhaustion.

A significant negative effect of increased herring biomass on cod condition was found for three length classes. Immature cod (Bogstad & Gjøsaeter 1994) and herring (Hjermann *et al.* 2004a) are distributed in similar areas in the southern BaS in

winter. However, while cod in the length range studied here preferentially consume capelin (Dolgov 2002), *Calanus finmarchicus* (Gunnerus) dominates the diet of immature herring (Prokopchuk & Sentyabov 2006). Adult herring consume larval capelin, negatively affecting capelin recruitment (Gjøsaeter & Bogstad 1998). It is therefore likely that the effect of herring is indirect, removing larval capelin before cod are able to consume adults. Similarly, Petren & Case (1996) found an indirect influence on condition via food competition in two species of gecko.

There was no relationship found between variation in the NAO and variation in condition for NA cod. This contrasts with other studies (e.g. Forchhammer *et al.* 2001 on Soay sheep, *Ovies aries* L.; Lehikoinen *et al.* 2006 on the common eider, *Somateria mollissima* L.) where condition and NAO were clearly linked. However, our results are supported by Kaňuščák *et al.* (2004), who found that air temperature, not NAO, affected condition in River Warblers (*Locustella fluviatilis* Wolf). In the BaS, temperature and NAO have followed similar trends over the past few decades (Ottersen & Stenseth 2001). The two climatic variables may therefore explain similar variation. Another consideration is that the NAO is potentially a less precise indicator of the BaS climate than the localized Kola section temperature.

For all the monthly models, autocorrelation and partial autocorrelation were still present in the residuals. The autocorrelation pattern indicated weak monthly cycles, and partial autocorrelation was significant at a lag of one month. Fitting an AR(1) model to the residuals greatly improved the fit for all length classes; however, it did not completely remove the residual autocorrelation. Autocorrelation may inflate the variance of the fitted model, especially if the correlation is strongly significant (Diggle 2004). The minimal amount of autocorrelation, in addition to strongly significant *P* values (Table 3), suggests that confidence may still be placed in the models. In a highly seasonal environment, such as that of the BaS, which has various multiannual climate cycles (Yndestad 2003), a model is unlikely to account for all of this variance. In addition, detrending of temporally autocorrelated data, such as those used here, is likely to create spurious autocorrelation (Diggle 2004).

INTERANNUAL AND MONTHLY VARIATION IN LCI

Intra-annual trends in LCI varied depending on the time of year and length of cod. In August and September, condition declined for both smaller (41–50 and 51–60 cm) and larger (61–70 and 71–80 cm) cod, but the decrease was greater for larger fish. There were greater numbers of mature cod in larger length classes after the rapid decline in length at maturity in the early 1980s (Marshall *et al.* 2006). Spawning and maturation are energetically expensive processes (Eliassen & Vahl 1982a) likely to have a significant impact on condition. From October to January, a period that Skjæraasen, Nilsen & Kjesbu (2006) found to be important in determining fecundity for Norwegian coastal cod, there was no evidence for a decline in condition for any length class of BaS cod. Therefore these

Table 3. Generalized least squares models fitted to monthly data

Size class (cm)	Fixed effect	Coefficient	<i>t</i>	<i>P</i>
41–50	Prop _{cap}	0.070	4.357	<0.001
	Prop _{cap} (lagged 1 month)	0.018	5.314	<0.001
	K _{temp}	0.411	2.817	0.005
	Prop _{cap} : K _{temp}	−0.014	−3.570	<0.001
51–60	Prop _{cap}	0.012	3.708	<0.001
	Prop _{cap} (lagged 1 month)	0.015	5.103	<0.001
	K _{temp}	0.254	2.131	0.034
61–70	Prop _{cap}	0.010	3.279	0.001
	Prop _{cap} (lagged 1 month)	0.011	3.643	<0.001
	K _{temp}	0.586	5.198	<0.001
71–80	Prop _{cap} (lagged 1 month)	0.010	3.396	<0.001
	K _{temp}	0.552	4.995	<0.001

Liver condition index modelled as a function of capelin consumption, past capelin consumption (latency) and sea temperature for north-east Arctic cod. Initially all terms were entered into a saturated model, then a likelihood ratio test was used for backward selection.

two factors may not be linked, although variation in female LCI may be masked by that of the males, as this study lacks data separated by sex.

All length classes exhibited a similar declining trend in LCI in the months of February to July, over the first half of the study period. The decrease of greatest magnitude occurred in May. For the second half of the study period, however, the decline appeared to halt. Spawning takes place between February and May, peaking at the end of March/beginning of April (Pedersen 1984; Bergstad *et al.* 1987; Kjesbu *et al.* 1998). This study has found evidence of a one-month latency in all length classes considered here. The greatest decline in condition (in May) occurred one month after the peak in spawning, suggesting that, over time, the negative impact of spawning on condition may have increased. In the second half of the time period there is no longer a trend in LCI, which then fluctuates around 5%. This is the value below which NA cod may be considered to be in poor condition (Marshall *et al.* 2000). Therefore, in the latter part of the study period, cod were able only to maintain sufficient condition rather than good condition.

When monthly data with the annual trend removed were examined, differences were found between the first and second halves of the time series. These differences are not, however, unprecedented. Yaragina (1996) discussed Russian work from the 1930s and 1940s that found LCI increasing from spring to autumn, reaching a maximum in winter. However, in the 1950s the dynamics of LCI changed, with two 'waves' of increase and decrease in fatness during a year. This change was connected with alterations in feeding regimes and monthly migrations (Maslov 1960 cited by Yaragina 1996), all of which co-occurred with a major change in the climate

(Drinkwater 2006). Similarly, during the period of this study, there was a major change in the BaS ecosystem. A long cold period ended and the mid-1980s saw low zooplankton abundance leading to a sharp decline in capelin biomass (Skjoldal, Gjøsæter & Loeng 1992). This may have been the trigger for the more cyclic 'boom-and-bust' pattern that was present in the capelin stock after this point in time. The crash in the capelin stock allowed zooplankton levels to rise rapidly, thus aiding the subsequent recovery of the capelin stock (Skjoldal *et al.* 1992). As the preferred prey of cod and an energy-rich species, it is probable that the variation in cod condition would follow the changed pattern in capelin biomass.

This study utilizes the uniquely comprehensive databases available from the monitoring of commercially fished species to enhance knowledge of the causes of variation in condition. Results from our study point to the importance of the impact of varying temperature on condition. The effects of climate are likely to be particularly important where the species is at the range margin, climatically speaking, or where the animal is an ectotherm. The BaS is currently showing a warming trend (Anon 2006), which suggests that this is likely to benefit NA cod. However, this cold-adapted population may not prosper if temperatures continue to rise. Additionally, capelin are an arcto-boreal species, therefore the effects of climate warming may affect them more dramatically, with an indirect negative impact on cod condition. The idea of latency demonstrated here indicates that changes in food supply should be considered not just as a direct effect, but also over a time lag. The fact that there is clear evidence of latency at the population scale suggests that similar effects may be detectable in other species.

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