

# Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves

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**Abstract:** To evaluate interstock differences in condition, it would be advantageous to develop stock-level condition indices from standardized databases on weight and length. This study describes a method for estimating stock-level condition when individual-level observations on length and weight are not easily accessible. For each year in a 56-year time series (1946–2001) for Northeast Arctic cod (*Gadus morhua*), pseudo-observations of weight and length were generated by pairing the Norwegian and Russian values for weight-at-age provided annually to the assessment working group with estimates of length-at-age derived from the same databases. A weight–length relationship fit to each year was then used to predict weight-at-length, i.e., girth, for a range of standard lengths (30–120 cm). This index was uncorrelated with both the liver condition index and the abundance of Barents Sea capelin (*Mallotus villosus*), suggesting that at the stock level, the girth of cod is not necessarily indicative of the magnitude of stored energy reserves. Partitioning body size into length-at-age and girth revealed long-term trends in body size. In particular, large/old cod showed substantially higher values of both length-at-age and girth that could be the result of long-term increases in fishing mortality.

**Résumé :** Afin d'évaluer les différences de condition physique entre les stocks, il serait avantageux de mettre au point des indices de condition à l'échelle des stocks à partir des banques de données standardisées de masses et de longueurs. Notre étude décrit une méthode pour estimer la condition à l'échelle des stocks dans les cas où aucune observation sur la longueur et la masse à l'échelle individuelle n'est facilement disponible. Nous avons généré des pseudo-observations de masses et de longueurs de *Gadus morhua* pour chacune des années d'une série chronologique de 56 années (1946–2001) en associant deux à deux des données norvégiennes et russes de masses en fonction de l'âge à des estimations des longueurs en fonction de l'âge tirées des mêmes banques de données. Une relation masse–longueur ajustée à chaque année a ensuite servi à prédire la masse en fonction de la longueur, c.-à-d., le tour du corps, pour une gamme de longueurs standard (30–120 cm). Cet indice ne montre pas de corrélation, ni avec l'indice de condition hépatique, ni avec l'abondance de capelans (*Mallotus villosus*) de la mer de Barents, ce qui laisse croire qu'à l'échelle du stock, la circonférence du corps n'est pas nécessairement un bon indicateur de l'importance des réserves énergétiques emmagasinées. La division de la taille du corps en longueur en fonction de l'âge et en circonférence montre les tendances à long terme de la taille du corps. En particulier, les morues grandes/âgées ont des valeurs considérablement plus élevées à la fois de longueur en fonction de l'âge et de circonférence qui peuvent être le résultat de l'accroissement à long terme de la mortalité due à la pêche.

[Traduit par la Rédaction]

## Introduction

In fisheries science, condition factors are often used to represent the amount of energy stored within individual fish. However, it is also relevant to estimate condition at the stock level because some fish stocks appear to be especially prone to poor condition (e.g., Dutil and Lambert 2000; Chouinard

and Swain 2002). For example, cod stocks in less productive ecosystems have low and highly variable condition values, whereas cod stocks inhabiting more productive (and usually warmer) ecosystems have high and relatively stable condition values (Dutil et al. 1999). Within stocks, spatial gradients in condition result from variability in habitat quality (Lloret and Rätz 2000; Chouinard and Swain 2002), and

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temporal variation results from fluctuations in prey abundance (Yaragina and Marshall 2000), seasonality in feeding patterns (Schwalme and Chouinard 1999), migration (Comeau et al. 2002), and gonadal maturation (Eliassen and Vahl 1982).

The implications of spatial and temporal variation in condition for population dynamics are manifold. Interannual variation in condition contributes directly to variability in stock biomass and yield. Poor condition can result in increased natural mortality (Dutil and Lambert (2000) and references therein). Fishing mortality could potentially be impacted if fish with lower condition have a lower probability of escapement because of a reduced swimming ability (Martínez et al. 2002, 2003). Condition influences the reproductive potential of a stock via its effects on maturation (Henderson and Morgan 2002), fecundity (Hislop et al. 1978; Kjesbu et al. 1998; Lambert and Dutil 2000), atresia (Ma et al. 1998; Óskarsson et al. 2002; Kurita et al. 2003), egg size (Kjesbu 1989; Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998), egg density (Saborido-Rey et al. 2003), yolk volumes (Morimoto 1996), hatching success (Laine and Rajasilta 1999), and larval survival (Marteinsdottir and Steinarsson 1998). Because of the cumulative impact on reproduction, there have been several suggestions that condition can influence recruitment for both pelagic and demersal species (Kawasaki and Omori 1995; Schülein et al. 1995; Marshall and Frank 1999).

The importance of inter- and intra-stock variation in condition for fisheries management has only recently been examined (e.g., Rätz and Lloret 2003; Dutil et al. 2003). Incorporating such information into routine assessment of stock status requires an index of condition that is based on a sufficient number of observations so as to be representative of the stock as a whole. To facilitate cross-stock comparisons, the index should be computed from data that are available for a large number of stocks. In this respect, the weight and length data routinely collected for many stocks are well suited for estimating morphometric condition indices representing the fatness, or girth, of individuals at a given length. The implicit assumption of this approach to estimating condition is that girth reflects the magnitude of stored energy reserves. Commonly used morphometric indices include the following: (i) Fulton's condition factor ( $K$ ), which is calculated as  $K = 100(W/L^3)$ , where  $W$  represents weight and  $L$  represents length; (ii) relative condition factor ( $K_n$ ), which is calculated as  $K_n = W/\hat{W}$ , where  $W$  and  $\hat{W}$  are, respectively, the observed weight and the weight predicted from an empirical weight-length relationship; and (iii)  $\hat{W}_l$  for a standard length ( $\hat{W}_l$ ) (Bolger and Connolly 1989). The first two indices describe the condition of an individual fish relative to either isometric growth (i.e.,  $K$ ) or the body size characteristics of the group (i.e.,  $K_n$ ). The latter index ( $\hat{W}_l$ ) describes the condition of the group of fish for which the weight-length relationship is established. Thus, it is appropriate for comparing among groups (or stocks) but cannot be used for describing individuals within a group.

Condition indices are straightforward to compute when weight and length observations for individual fish are available. However, the computation of condition indices at the stock level can be problematic if individual-level observations on weight and length are not readily accessible. Such a

situation typically arises when more than one laboratory or country collects length-weight data for the aggregate stock. Stock weight-at-age ( $SW_a$ ) is routinely included in assessment reports because it is used to estimate spawning stock biomass (SSB). In some cases, these estimates of  $SW_a$  are obtained by averaging weight-at-age ( $W_a$ ) values provided by more than one country and (or) laboratory. The individual  $W_a$  time series used to estimate  $SW_a$  may or may not be reported in the assessment. Because the original data used to estimate the  $W_a$  values are archived in different locations and (or) formats, it can be difficult to access and collate the original observations for individual fish. Corresponding values of stock length-at-age ( $SL_a$ ) are not usually included in assessment reports because that information is not used directly in age-based assessments. The net result is that although considerable amounts of weight and length data exist, difficulties in accessing these data, either electronically or via the assessment reports, can impede the estimation of a condition index at the stock level and hinder research into the causes and consequences of variation in condition.

This study illustrates how a condition index for Northeast Arctic cod (*Gadus morhua*) stock can be derived using the  $W_a$  time series provided annually to the International Council for the Exploration of the Sea (ICES) Arctic Fisheries Working Group (AFWG) by Norway and Russia. Briefly, the same primary databases that generated these  $W_a$  time series were used to develop year-specific age-length keys (ALK) for both countries, and the mean length-at-age ( $L_a$ ) values were calculated. These  $L_a$  values were then paired with the corresponding  $W_a$  value to generate a set of pseudo-observations for each year. A fitted weight-length relationship was used to predict stock weight-at-length ( $SW_l$ ) for each year. Isometric growth was tested by comparing the values of exponent of the year-specific weight-length relationships with 3. To determine whether  $SW_l$  accurately reflects the bioenergetic status of the stock, the relationship between the biomass of the preferred prey of Northeast Arctic cod, Barents Sea capelin (*Mallotus villosus*), and  $SW_l$  was evaluated against the positive relationship that has been observed between the liver condition index of cod and capelin stock biomass (Yaragina and Marshall 2000). Because estimating  $SW_l$  and  $L_a$  allowed body size to be partitioned into its two basic constituents (girth and length), the degree of covariance between them was assessed. Several of the factors influencing long-term trends in length and girth were discussed.

## Materials and methods

Both Norway and Russia have extensive long-term databases (1946–2001) describing biological characteristics of Northeast Arctic cod. The two countries sample, via commercial fisheries and during research vessel surveys, different subcomponents of the stock with Russian observations representing cod that are younger and possibly slower growing than cod sampled by Norway. Given that differences in body size characteristics between the two countries are known to exist, it was not an aim of this study to test for significant differences. Instead, the intention was to combine the information from both countries in a manner that is as consistent as possible with the procedures used by the

AFWG to estimate  $SW_a$ . This has the advantage of making the estimates of  $SW_l$  generated in this study directly comparable to  $SW_a$ . Although changes to the estimation procedure were possible, and in some respects desirable, they were not implemented because the resulting estimates would not be comparable to  $SW_a$ .

### Age determinations

Otoliths have been used for age determinations throughout the time period. Similar methodology is used by both countries, and annual exchanges of otoliths have taken place since 1992. To determine whether contemporary ages are in agreement with historical ages, special investigations have recently been undertaken by both countries to re-age otoliths selected at random from Norwegian collection of historical otoliths. Preliminary results for a single year (1967) show that the contemporary ageing by Norwegian readers gave values of mean  $L_a$  that were slightly lower (usually less than 3 cm) than values calculated using the historical ages (see fig. 4.2 in ICES ACFM 2003). A more extensive Norwegian investigation re-aged otoliths from a longer time period (1965–1968) and found that the contemporary age agreed with the historical age in 72% of the cases. Russian re-ageing of the Norwegian otoliths from 1967 gave a larger discrepancy in values of mean  $L_a$  than Norwegian re-ageing (ICES ACFM 2003). On the basis of these few comparisons, it is premature to draw conclusions regarding likely prevalence and direction of ageing bias. No correction was applied here, particularly as applying a correction would have introduced an unwanted discrepancy between values of  $L_a$  estimated here and the values of  $W_a$  used by the AFWG to estimate  $SW_a$ .

### Length-at-age

Norwegian and Russian protocols for measuring length differ slightly in that Norwegian measurements are rounded down (e.g., all fish from 53.1 to 53.9 cm are rounded down to 53 cm), whereas Russian measurements are rounded to the nearest whole centimetre (e.g., all fish from 52.6 to 53.5 cm are rounded to 53 cm). In the most extreme case, a Russian cod of length 52.6 cm and a Norwegian cod of 53.9 cm would have the same length (53 cm) in the database. This systematic difference was not corrected for in the ALK used in this study. However, because the magnitude of the difference is constant, it becomes proportionally smaller with increasing age and length.

Both Norwegian and Russian ALK were constructed using 5-cm length classes. However, there was a 1-cm offset between them such that cod between 50 and 54 cm were grouped in one length class for the Norwegian ALK, whereas cod between 51 and 55 cm were grouped in one length class for the Russian ALK. ALK were constructed for cod ages 3–12. For both Norwegian and Russian ALK,  $L_a$  was estimated for each year as

$$(1) \quad L_a = \sum_l p_{al} z_l$$

where  $p_{al}$  is the proportion of the observations in each length class as given in the ALK ( $a$  and  $l$  index age and length, respectively) and  $z_l$  is the midpoint of the length class. Interannual variation in values of  $L_a$  was examined relative

to the arithmetic average estimated for 1946–2001. The databases used to construct the ALK are described separately for each country in the following sections.

### Norwegian ALK

The Norwegian data used to construct the ALK used in this study originated in three different databases with individual-level observations being available for all three. The data for 1946–1972 were obtained from a single flatfile (Åge Fotland, Institute of Marine Research, Bergen, Norway) that was previously used for an analysis of long-term trends in maturation (Jørgensen 1990). The observations originated from sampling of the commercial catch. Data for the 1973–1979 time period were also obtained by sampling the commercial catch but were stored in a slightly different format than that of the earlier time period. Since 1980, data have been stored in a relational database that is continuously updated as new data are collected (Fotland et al. 1997). The observations stored in this database originate from the research-vessel surveys, as well as from sampling of the commercial catch (Jakobsen et al. 1997).

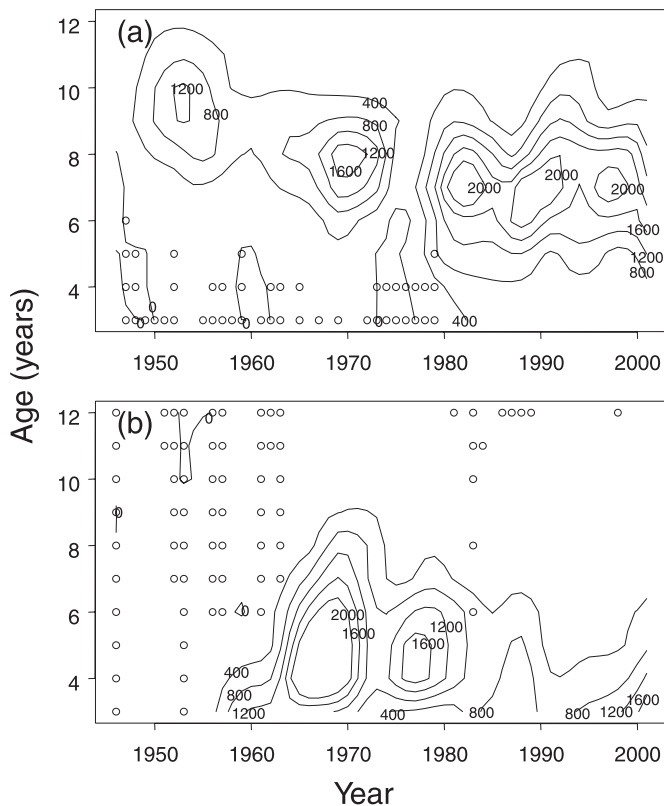
For all three data sources, observations for individual cod were selected so as to exclude Norwegian coastal cod (as identified by otolith type), cod younger than 3 years, and months in the 2nd, 3rd, and 4th quarters. Only observations from the 1st quarter were used because the  $W_a$  time series provided by Norway to the AFWG is based on data from this time period. Biologically, this represents the prespawning period. Because the commercial fishery is dominated by mature fish, the number of young fish sampled is low for the first two time periods and there are frequently years having no observations for cod of ages 3 and 4 (Fig. 1a). Cod in intermediate age classes (ages 5–10) are the best-represented age classes. The number of observations for the younger age classes increased dramatically for the third time period (1980–2001) because of the addition of survey information (Fig. 1a). For this time period, the strong 1975, 1983, and 1989 year classes are evident in the sampling.

### Russian ALK

Russia and the former USSR have conducted annual surveys for young cod and haddock in the southern Barents Sea since 1946. In 1957 the geographical coverage of these surveys was expanded to include the Bear Island – Spitsbergen area (Lepesevich and Shevelev 1997). Observations describing the age, length, and weight of individual cod are not presently archived in an electronic form. However, ALK compiled for the 4th quarter in support of the recent reconstruction of historical weights and maturities undertaken by the AFWG (ICES ACFM 2001) were available to this study. To cover the entire length range, the survey data were occasionally supplemented with observations from sampling the commercial catch in the 1st quarter of the next year.

Early years show a high proportion of missing values and there are frequently years having no observations in the Russian ALK for cod age 10 and older (Fig. 1b). In contrast to the Norwegian ALK, the youngest age classes (cod ages 3 and 4) are well-represented throughout most of the time period and age 5 is most often the predominant age class. This is consistent with the westward shift in the spatial distribution of the stock with increasing age (Ottersen et al. 1998)

**Fig. 1.** Contour plots showing the number of observations used to construct the age-length keys for (a) Norwegian data and (b) Russian data. Open circles indicate years where no observations were recorded.



that results in older fish becoming less available to the Russian sampling programs.

#### Combined ALK

Before they were combined into a single ALK, missing values of  $p_{al}$  in both the Norwegian and Russian ALK were interpolated from adjacent years having data to eliminate gaps. Because the Russian ALK apply to the 4th quarter, they were shifted forward by one year and age class to make them consistent with the Norwegian ALK applying to the 1st quarter. The ALK for the two countries were then combined by arithmetically averaging, with equal weight being given to the ALK from both countries. Both the shifting forward of the Russian data and the equal weighting of data for both countries are consistent with how the AFWG combines the  $W_a$  estimates from both countries to estimate  $SW_a$  (ICES ACFM 2001). The Russian ALK were not adjusted for the growth that would occur between the 4th and 1st quarters because no correction is applied by the AFWG when combining the values of  $W_a$  to estimate  $SW_a$ . Thus, the arithmetic averaging of the Norwegian and Russian data generates estimates that are composite values for the two quarters (roughly time referenced to 1 January). Values of  $SL_a$  were then estimated for each year from the combined ALK using eq. 1. Because the Russian data are shifted forward, only the Norwegian ALK was available for 1946; this precluded estimating  $SL_a$  for that year. The long-term trends for the  $SL_a$  were summarized using a LOESS smoother with confidence

intervals being approximated as twice the standard error of the fitted value.

#### Weight-at-age

The annual assessment reports contain both Norwegian and Russian estimates of  $W_a$  from 1985 onwards only. For this time period, the Norwegian values of  $W_a$  are weighted averages of the estimates obtained from the winter survey of the Barents Sea (table A7 in ICES ACFM 2002) and Lofoten survey (table A9 in ICES ACFM 2002). To represent  $W_a$  for a given year, these two surveys are averaged with weighting according to the acoustic estimate of abundance-at-age. The Russian values of  $W_a$  (table A13 in ICES ACFM 2002) are obtained from the surveys conducted between October and December. The AFWG arithmetically averages the Norwegian and Russian  $W_a$  time series to obtain the  $SW_a$  time series that is then used to estimate SSB for the stock (ICES ACFM 2001).

Before 2001, constant values of  $SW_a$  had been assumed for the period 1946–1984. For the 2001 meeting of the AFWG, both Norway and Russia compiled available historical data to develop year-specific values for  $W_a$  for this period, and these were averaged to obtain revised estimates of  $SW_a$  (ICES ACFM 2001). The databases and procedures used to estimate  $W_a$  for both countries are summarized below.

#### Norwegian $W_a$

For the years preceding the survey time period (1946–1984), historical databases from the Lofoten fishery (described above) and the spring fishery around the Finnmark coast were used. Whereas the Lofoten data describe primarily mature individuals undertaking spawning migrations, the Finnmark data include both immature and mature cod. In the case of the Lofoten database, direct weight observations were missing for 1959–1988; however, length and age information were available. The missing  $W_a$  values were estimated from the  $L_a$  values using the following equation:

$$(2) \quad \log(W_a) = -5.19 + 3.08\log(L_a)$$

where the regression coefficients were estimated as averages of the year-specific values determined for the years in which both length and weight were available (ICES ACFM 2001). In the case of the Finnmark database, the years 1940–1948 were missing. The missing  $W_a$  values were estimated by assuming that the ratio of Lofoten weights to Finnmark weights was constant. To estimate the Norwegian  $W_a$  values, the Lofoten and Finnmark databases were combined. The average  $W_a$  was calculated by weighting the  $W_a$  estimates for the Lofoten and Finnmark areas by the year-specific proportion of mature and immature, respectively. Estimation of these proportions is described in section 10.3.2 of ICES ACFM (2001). Because of missing values for both the Lofoten and Finnmark databases, variation in the Norwegian  $W_a$  values for 1940–1948 is derived solely from the Lofoten data, whereas from 1949 to 1984, interannual variation in the Norwegian  $W_a$  values was introduced by the Finnmark data only.

**Table 1.** Summary statistics for observed liver weights measured during the Norwegian winter surveys of the Barents Sea.

Year	No. of observations	Length range	Liver weight range	<i>a</i> (SE)	<i>b</i> (SE)	PED
1997	1000	9–138	1–2305	–9.37 (0.27)	3.40 (0.063)	0.74
1998	658	24–124	1–1960	–13.70 (0.35)	4.43 (0.084)	0.77
1999	640	14–125	1–2430	–11.21 (0.29)	3.80 (0.070)	0.81
2000	50	40–118	15–1055	–9.34 (1.50)	3.47 (0.35)	0.55
2001	1472	22–131	1–2440	–11.73 (0.22)	3.96 (0.054)	0.73

**Note:** The ranges in length (cm) and liver weights (g) are given for each year. The *a* and *b* values refer to the coefficients in eq. 6, and the standard error (SE) of each coefficient is in parentheses. The proportion of explained deviance (PED) is given as measure of goodness of fit.

### Russian $W_a$

In the early years of the Russian surveys, there was a tendency to exclude fish longer than 36 cm from the sampling. Thus, it is more likely that mean weights for ages 3–4 are underestimated relative to later data. In 1951, 1955, 1956, 1960, and 1962, there were few observations for fish larger than 36 cm. There were no data for 1952. From 1963, the surveys probably covered the entire length range because of changes in the survey design. Visual inspection of the time series suggested that the weights-at-age for ages 5 and 8 in 1959 were anomalously high. These years also had low numbers of observations (8 and 2 specimens, respectively). Consequently, they were deleted. As a result of missing data and excluded data, the resulting time series had some gaps. These missing observations were replaced by the arithmetic average of adjacent values.

### Length–weight regressions

The Norwegian and Russian time series for  $W_a$  were paired with the corresponding values of  $L_a$  estimated from the Russian and Norwegian ALK (eq. 1) to create a set of pseudo-observations for weight and length. Because of missing values for either  $W_a$  or  $L_a$ , or both, the number of observations varied considerably across years. Visual examination of the bivariate plots of weight and length for each year indicated that there were two outlying values reflecting gross errors in the database. This resulted in the Norwegian observation for age 11 in year 1991 and the Russian observation for age 10 in year 1976 being omitted from further analysis.

Length–weight regressions were then constructed for each year using the pseudo-observations for weight (in grams) and length. A generalized linear model (GLM)

$$(3) \quad W = \exp(a + b \log(L))$$

(where *a* and *b* are the fitted coefficients of the model) was fit to the pseudo-observations for each year using a log-link function and assuming a gamma error distribution. This model can be re-expressed as

$$(4) \quad W = \exp(a)L^b$$

making it appropriate for testing the null hypothesis that growth is isometric ( $b = 3$ ). Model fit was evaluated using the proportion of explained deviance (PED) estimated as the difference between the null deviance (the deviance associated with a model having no predictors) and residual deviance for the fitted model expressed as a proportion of the null deviance. These fitted models were then used to gener-

ate estimates of  $SW_l$  for each year for several standard lengths ranging, in 10-cm intervals, from 30 to 120 cm.

### Estimation of liver weight

Russia and the former USSR have monitored the liver weights of cod in the Barents Sea on a monthly basis since 1927 (Yaragina and Marshall 2000). The weights were obtained from the Russian fishing fleet operating in the southern Barents Sea region; although for a few years, observations from the Svalbard area were also used. The database is largely independent of the databases used to generate the Russian  $W_a$  and  $L_a$  values because it is derived primarily from commercial information rather than survey information.

The liver weight data have been archived as monthly estimates of the liver condition index (LCI = liver weight/total body weight  $\times$  100) for several length or weight classes. Consequently, it was not possible to compute liver weight directly. However, liver weight (in grams) at a standard length could be derived by multiplying  $SW_l$  (from eq. 4) with the Russian LCI value corresponding to that length class. Thus, the liver weight of a 70-cm cod ( $LW_{70}$ ) in year *t* was estimated as

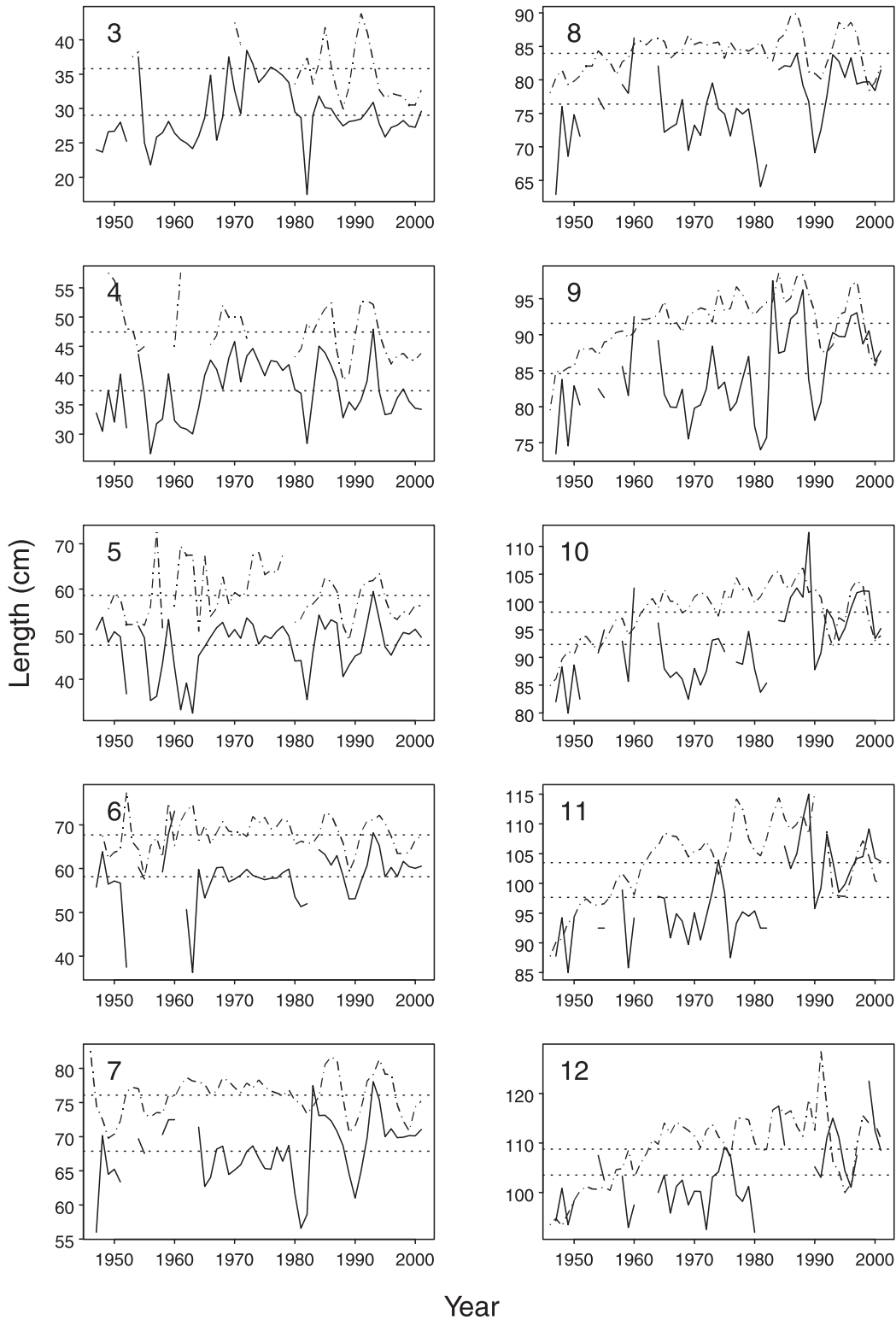
$$(5) \quad LW_{70} = LCI_{61-70} \cdot SW_{70}$$

where  $LCI_{61-70}$  is the annual average LCI for the 61- to 70-cm length class in year *t* – 1. Because  $LCI_{61-70}$  is an annual average for the preceding year and  $SW_{70}$  averages 4th quarter data from year *t* – 1 and 1st quarter data from year *t*, the resulting liver weights will not apply to an exact point in the seasonal cycle but instead integrate information obtained across a fairly broad time window. A standard length of 70 cm was chosen partly because the LCI time series was more complete for the 61- to 70-cm length class than for older age classes (see fig. 3 in Yaragina and Marshall 2000). For the 12 years having missing values,  $LCI_{61-70}$  was either assumed to be equal to values observed that year for a corresponding weight class (1946–1953) or interpolated from the adjacent years (1955, 1983, 1985, and 1992).

Since 1997, liver weights of cod have been measured during Norwegian surveys of the Barents Sea and Lofoten regions conducted in February, March, and April. To evaluate the accuracy of the liver weights derived using eq. 5, liver weight data from the Norwegian surveys were used to develop year-specific relationships as

$$(6) \quad \text{Liver weight} = \exp(a + b \log(L))$$

**Fig. 2.** Time series of mean length-at-age for ages 3–12 estimated from Norwegian (dotted–dashed lines) and Russian (solid lines) age–length keys. The horizontal broken lines indicate the long-term mean values for both time series. The Russian age–length keys for the 4th quarter were shifted forward by one year and one age class.

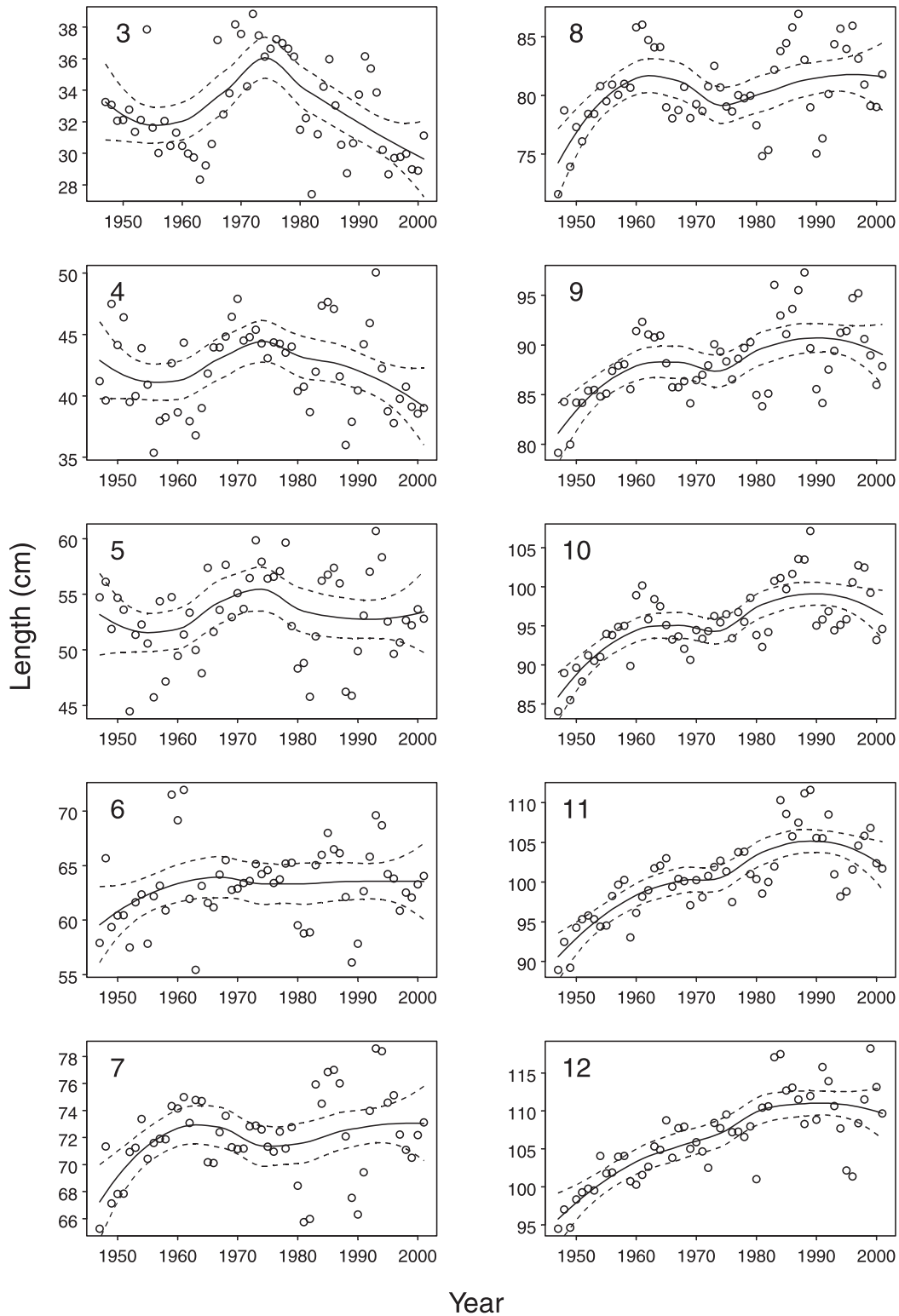


which was fit to data for each year using a log-link function and assuming a gamma error distribution. The resulting models (Table 1) were then used to predict liver weight (in grams) at 70 cm along with the corresponding 95% confidence intervals.

**Capelin stock biomass**

Acoustic surveys of capelin stock biomass have been conducted annually in the autumn since 1973 (Gjørseter 1998). For the time period 1973–1996, acoustic estimates of capelin stock abundance in year *t* were significantly ( $n = 24, p <$

**Fig. 3.** Time series of mean length-at-age for ages 3–12 estimated for the combined age-length keys (open circles). The LOESS smoothers (solid line) with their approximate 95% confidence intervals (broken lines) are also indicated.



0.001,  $r^2 = 0.63$ ) correlated with the percentage of cod stomachs containing capelin the following year ( $P_{cap,t+1}$ ). To hindcast capelin stock biomass for the preceding time period (1946–1972), it was assumed that the intensity of cod feeding on capelin was linearly related to capelin stock biomass.

For the time period 1946–1972, capelin stock biomass in year  $t$  (in tonnes ( $t \times 10^3$ )) was estimated by the following model:

$$(7) \quad \text{Capelin stock biomass} = 159P_{cap,t+1} - 390$$

**Table 2.** Minimum, maximum, and mean values of stock length-at-age (in cm), stock weight-at-length (in kg), and stock-weight-at-age (in kg).

Body size metric	Abbreviation	Minimum	Maximum	Mean	CV	
Stock length-at-age	SL <sub>3</sub>	27.41	38.83	32.72	0.093	
	SL <sub>4</sub>	35.36	50.04	42.12	0.082	
	SL <sub>5</sub>	44.46	60.67	53.04	0.074	
	SL <sub>6</sub>	55.42	71.95	63.12	0.056	
	SL <sub>7</sub>	65.26	78.58	71.98	0.042	
	SL <sub>8</sub>	71.59	86.93	80.43	0.042	
	SL <sub>9</sub>	79.16	97.28	88.27	0.043	
	SL <sub>10</sub>	84.06	107.10	95.45	0.048	
	SL <sub>11</sub>	88.93	111.62	100.65	0.050	
	SL <sub>12</sub>	94.49	118.23	106.37	0.053	
	Stock weight-at-length	SW <sub>30</sub>	0.10	0.34	0.22	0.18
		SW <sub>40</sub>	0.30	0.77	0.53	0.15
SW <sub>50</sub>		0.68	1.46	1.04	0.12	
SW <sub>60</sub>		1.35	2.47	1.81	0.10	
SW <sub>70</sub>		2.41	3.86	2.88	0.09	
SW <sub>80</sub>		3.62	5.67	4.32	0.09	
SW <sub>90</sub>		5.08	7.95	6.18	0.09	
SW <sub>100</sub>		6.89	10.77	8.51	0.10	
SW <sub>110</sub>		9.04	14.20	11.37	0.11	
SW <sub>120</sub>		11.54	19.64	14.81	0.12	
Stock weight-at-age		SW <sub>3</sub>	0.19	0.52	0.35	0.24
		SW <sub>4</sub>	0.40	1.17	0.70	0.26
	SW <sub>5</sub>	0.79	1.82	1.26	0.19	
	SW <sub>6</sub>	1.48	2.82	2.04	0.16	
	SW <sub>7</sub>	2.14	4.06	3.08	0.15	
	SW <sub>8</sub>	2.92	5.83	4.40	0.15	
	SW <sub>9</sub>	3.65	8.93	5.97	0.17	
	SW <sub>10</sub>	4.56	12.15	7.95	0.21	
	SW <sub>11</sub>	5.84	14.29	9.27	0.20	
	SW <sub>12</sub>	7.08	12.09	10.18	0.13	

**Note:** The coefficient of variation (CV) is also given as an index of the variation in the data. Data for 1981–1984 were excluded from the estimation of minimum, maximum, and mean weights-at-length. The data for stock weight-at-age are taken from ICES ACFM (2002).

which is described in further detail elsewhere (Marshall et al. 2000). Because the capelin stock biomass estimates are time-referenced to 1 October each year, they were shifted forward by 1 year before correlating them with the condition indices. Given that the values of SW<sub>1</sub> are roughly time-referenced to 1 January, the time lag between the capelin index and SW<sub>1</sub> is consistent with the 3- to 4-month time lag that has been observed between the stomach fullness index (i.e., food) and the condition indices (somatic *K* and LCI) for cod in the southern Gulf of St. Lawrence (Comeau et al. 2002).

## Results

### Trends in $L_a$ and $SL_a$

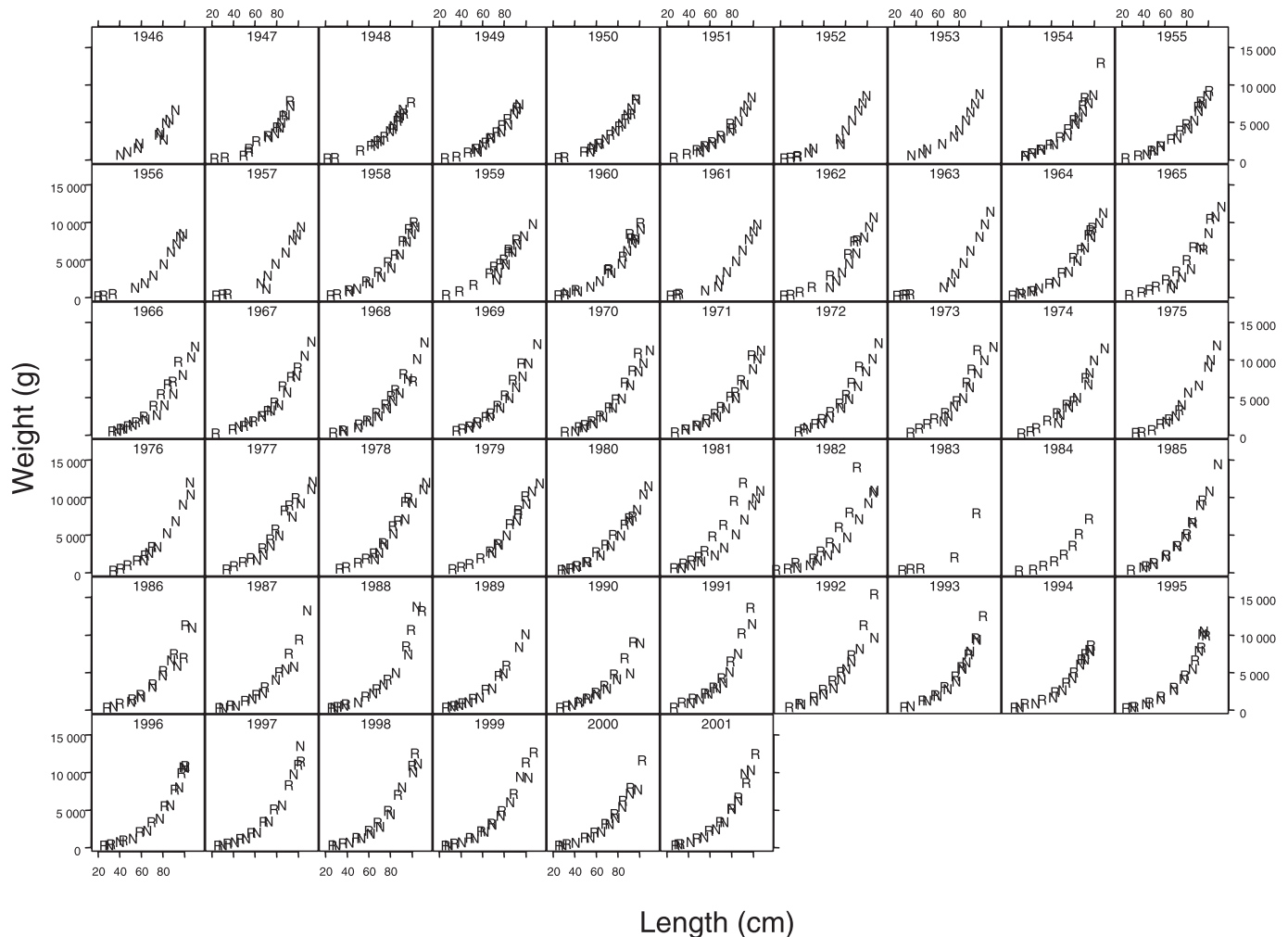
As expected, the time series of  $L_a$  for both countries show the Norwegian values to be consistently higher than the corresponding Russian values (Fig. 2). The difference between Norway and Russia in long-term mean values of  $L_a$  increased from 6.8 cm for age 3 to a maximum of 11.1 cm for age 5. Thereafter, the difference between the long-term means decreased with increasing age to a value of 5.2 cm for age 12. Since the mid-1980s, the difference between Norwegian

and Russian values has been relatively small for cod age 9 and older. For cod ages 3–7, there is no strong evidence of a long-term drift towards smaller or larger values of  $L_a$  over time for either country. However, for cod age 9 and older, there has been an increase in values of  $L_a$  for both countries such that they are currently higher than postwar values. In addition to the long-term trends observed for the older age classes, there was a high degree of short-term variation in both the Norwegian and Russian data. In particular, synchronous reductions in  $L_a$  occurred most notably in the late 1980s and early 1990s as a result of the collapse of the Barents Sea capelin stock in 1986 (Yaragina and Marshall 2000).

The long-term trends in  $SL_a$ , estimated from the combined ALK, show that for cod ages 3–7, the present values of  $SL_a$  are not significantly different from the values at the beginning of the time series (Fig. 3). Since the late 1970s, cod ages 3 and 4 have shown a tendency towards decreasing values of  $SL_a$ . That same time period (1970 to present) showed relatively stable values of  $SL_a$  for cod ages 5–7 and a tendency for increasing values of  $SL_a$  for cod ages 8 to 12 (Fig. 3). This latter trend towards higher  $SL_a$  becomes more pronounced with increasing age such that current values of  $SL_a$  for cod age 12 are almost 15 cm longer than they were



**Fig. 4.** A scatterplot matrix showing the relationship between length and weight (all ages combined) for Norwegian (N) and Russian (R) data for the years 1946–2001.



in 1947. The difference in trends over 1970 to 2001 from decreasing (ages 3 and 4) to stable (ages 5–7) to increasing (ages 9–12) suggests that trends in  $SL_a$  deviate from the lagged correlations that would be expected if cohort effects were primarily responsible for generating temporal trends in  $SL_a$ . When temporal variation is expressed on a relative scale (coefficient of variation), the variation is highest for the youngest age classes (Table 2).

#### Year-specific weight–length relationships

A scatterplot matrix of the weight–length relationships by year (Fig. 4) shows that the data for the two countries usually spanned a similar length range. There were several years having no overlap between the Norwegian and Russian values of  $L_a$  (e.g., 1952, 1956, 1957, 1961, and 1963). For a given length, the Russian weights tend to be slightly higher than the corresponding Norwegian weights with two exceptions (1981 and 1982) when the Russian values were distinctly higher. In combination with differences between Norwegian and Russian  $L_a$  values (Fig. 2), this suggests that the cod sampled by Russia are shorter for their age but heavier for their length relative to the cod being sampled by Norway. The model fit is good, with values of PED higher than 0.9 (Table 3) except for 1981 and 1982 when the

marked discrepancy between Norwegian and Russian values resulted in low values of PED (less than 0.9; Table 3). The cause of this discrepancy is unknown. The two following years were also problematic in having no Norwegian values and relatively few Russian observations (5 and 8 observations for 1983 and 1984, respectively). Because these 4 years generated condition indices that were anomalous in the full time series, they were omitted from subsequent analyses.

Values of the exponent  $b$  from the weight–length relationships (eq. 4) were significantly greater than 3 for 8 years (1948, 1949, 1974–1976, 1985, 1995, and 1998), whereas  $b$  values for the years 1951, 1967, and 1971 were significantly less than 3 (Fig. 5). Thus, 11 of the 52 years (21%) had  $b$  values that were significantly different from the value of 3 that defines isometric growth. Consequently, Fulton's  $K$  cannot be recommended as a measure of stock-level condition for Northeast Arctic cod because the assumption of isometric growth is not valid for a high proportion of years.

#### Time series of $SW_l$

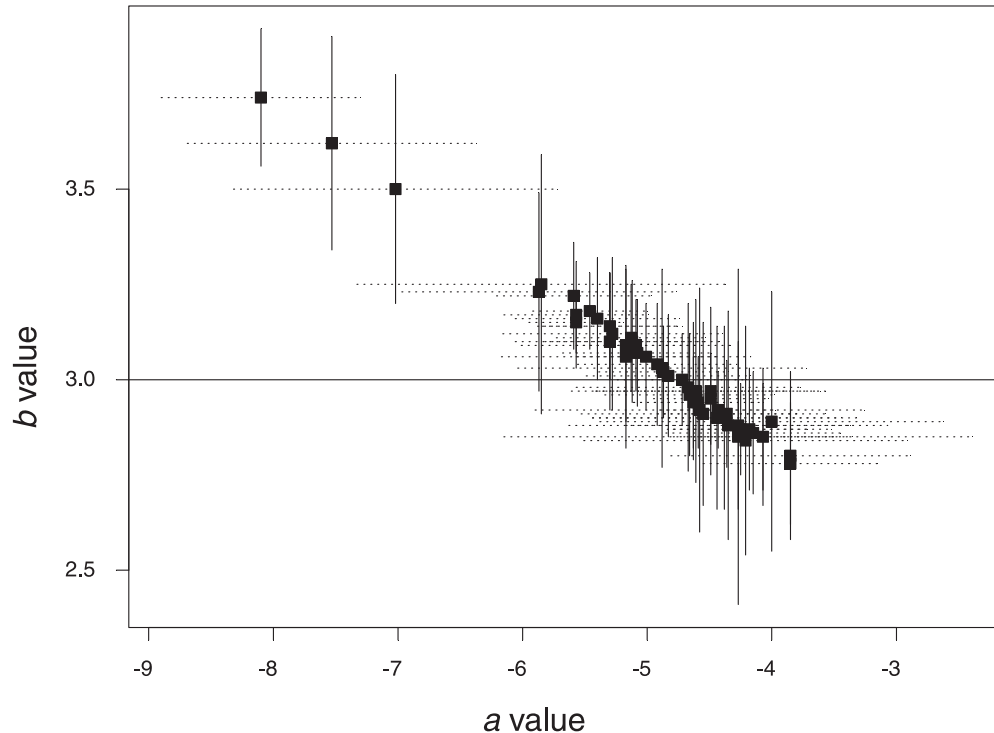
Time series of  $SW_l$  for standard lengths of 30–120 cm (by 10-cm intervals) reveal differences in the long-term trends exhibited by small cod (<60 cm) compared with large cod

**Table 3.** Coefficients for the model  $W$  (in grams) =  $\exp(a + b \log(L))$  for each year.

Year	$a$	$b$	SE $a$	SE $b$	Residual	Null	df	PED
1946	-4.27	2.85	0.94	0.22	0.29	4.70	8	0.94
1947	-5.87	3.23	0.55	0.13	0.67	15.39	14	0.96
1948	-5.57	3.15	0.19	0.04	0.08	13.92	15	1.00
1949	-5.57	3.17	0.29	0.07	0.19	14.14	17	0.99
1950	-4.63	2.94	0.24	0.06	0.15	14.56	17	0.99
1951	-3.85	2.78	0.35	0.08	0.20	10.98	15	0.98
1952	-5.17	3.06	0.50	0.12	0.51	18.92	11	0.97
1953	-4.44	2.90	0.50	0.12	0.12	7.02	8	0.98
1954	-5.01	3.06	0.28	0.07	0.17	16.27	18	0.99
1955	-4.43	2.92	0.23	0.05	0.14	16.06	17	0.99
1956	-4.59	2.94	0.26	0.06	0.11	16.41	9	0.99
1957	-4.58	2.92	0.66	0.16	0.85	15.13	9	0.94
1958	-4.36	2.91	0.28	0.07	0.23	17.84	17	0.99
1959	-3.85	2.80	0.48	0.11	0.42	9.63	15	0.96
1960	-4.18	2.87	0.33	0.08	0.36	19.46	18	0.98
1961	-4.21	2.84	0.65	0.15	0.81	16.29	10	0.95
1962	-4.38	2.90	0.53	0.12	0.80	16.74	14	0.95
1963	-4.55	2.91	0.49	0.12	0.57	20.22	10	0.97
1964	-4.15	2.86	0.35	0.08	0.41	21.43	18	0.98
1965	-4.35	2.88	0.64	0.15	1.08	16.02	16	0.93
1966	-4.67	2.98	0.45	0.11	0.50	17.67	18	0.97
1967	-4.25	2.87	0.27	0.06	0.18	15.97	17	0.99
1968	-4.66	2.96	0.34	0.08	0.32	17.58	18	0.98
1969	-4.83	3.01	0.33	0.08	0.18	13.95	17	0.99
1970	-5.17	3.09	0.42	0.10	0.41	17.33	18	0.98
1971	-4.07	2.85	0.28	0.07	0.22	16.71	18	0.99
1972	-5.28	3.12	0.44	0.10	0.29	13.65	16	0.98
1973	-5.85	3.25	0.74	0.17	0.72	12.82	15	0.94
1974	-7.02	3.50	0.65	0.15	0.55	14.57	14	0.96
1975	-8.10	3.74	0.40	0.09	0.16	16.27	12	0.99
1976	-7.53	3.62	0.58	0.14	0.35	14.98	12	0.98
1977	-4.88	3.03	0.58	0.13	0.56	13.19	16	0.96
1978	-4.61	2.97	0.50	0.12	0.44	13.02	16	0.97
1979	-4.87	3.02	0.26	0.06	0.10	12.49	15	0.99
1980	-4.72	3.00	0.26	0.06	0.19	20.57	18	0.99
1981	-2.28	2.49	0.78	0.19	1.71	16.15	17	0.89
1982	-1.51	2.30	0.71	0.17	2.08	19.86	17	0.90
1983	-4.66	2.91	1.37	0.35	0.40	9.10	3	0.96
1984	-7.44	3.55	0.77	0.19	0.22	9.67	6	0.98
1985	-5.46	3.18	0.23	0.05	0.09	16.53	15	1.00
1986	-4.63	2.97	0.39	0.09	0.30	15.86	15	0.98
1987	-5.30	3.10	0.38	0.09	0.32	19.43	14	0.98
1988	-4.92	3.04	0.32	0.08	0.32	25.02	15	0.99
1989	-4.49	2.95	0.23	0.06	0.10	17.22	13	0.99
1990	-4.07	2.85	0.36	0.09	0.27	15.20	15	0.98
1991	-4.00	2.89	0.69	0.17	0.77	15.07	15	0.95
1992	-4.49	2.97	0.46	0.11	0.45	16.00	16	0.97
1993	-5.12	3.10	0.35	0.08	0.22	14.45	16	0.99
1994	-4.27	2.88	0.45	0.11	0.47	16.24	16	0.97
1995	-5.30	3.14	0.27	0.07	0.22	21.66	16	0.99
1996	-5.30	3.14	0.29	0.07	0.27	22.98	16	0.99
1997	-5.59	3.22	0.31	0.07	0.24	23.04	15	0.99
1998	-5.40	3.16	0.33	0.08	0.31	22.34	16	0.99
1999	-5.09	3.09	0.24	0.06	0.17	21.76	16	0.99
2000	-5.08	3.07	0.30	0.07	0.25	19.80	16	0.99
2001	-5.13	3.11	0.30	0.07	0.23	19.89	16	0.99

**Note:** The standard errors (SE) for the model coefficients, the residual and null deviances, residual degrees of freedom (df), and proportion of explained deviance (PED) are indicated.  $W$ , weight;  $L$ , length.

**Fig. 5.** The bivariate relationship between coefficients  $a$  and  $b$  for the model  $W = \exp(a + b \log(L))$  fit to each year in the time period 1946–2001 excluding 1981–1984. The 95% confidence intervals for the estimates of  $a$  (horizontal dotted lines) and  $b$  (vertical solid lines) are indicated. The horizontal solid line indicates  $b = 3$ , which is assumed for isometric growth.



(>70 cm) (Fig. 6). For the smaller length classes (30, 40, and 50 cm), current values of  $SW_l$  are not significantly different from the postwar values, suggesting that there has been no long-term change (Fig. 6). However, for cod 70 cm and larger, the current values of  $SW_l$  are significantly higher than the postwar values (Fig. 6). The temporal trends differ among these age classes. For example, the  $SW_l$  for 80- and 90-cm cod show a near-linear increase over the entire time period, whereas the increase in  $SW_l$  of the largest length classes leveled off in the mid- to late 1970s. The magnitude of the increases is substantial. For example, the weight of 120-cm cod in recent years is approximately 2.5 kg higher than it was in the postwar period. Temporal variation expressed on a relative scale (coefficient of variation) in  $SW_l$  shows a decrease with increasing length (Table 2).

#### Comparing trends in $SL_a$ and $SW_l$

For Northeast Arctic cod, comparisons between age- and length-based body size metrics are facilitated by growth being fairly linear up to approximately age 9. As a simple rule of thumb, the length of a Northeast Arctic cod can be approximated as 10 times their age (Fig. 3). To evaluate whether the long-term trends in the two different body size metrics covary, the LOESS trends in  $SL_a$  for ages 3, 5, 7, and 9 (Fig. 3) were contrasted with the LOESS trends in  $SW_l$  for lengths of 30, 50, 70, and 90 cm (Fig. 6). To remove scale differences, the LOESS trends were standardized by dividing by the long-term mean of the LOESS values. Cod of lengths 30 cm and 50 cm exhibited an oscillatory pattern in  $SW_l$  that was the inverse of the trends in  $SL_a$  for ages 3 and 5, respectively (Fig. 7), indicating that cod in this length–age range alternate between a long, lean form and a

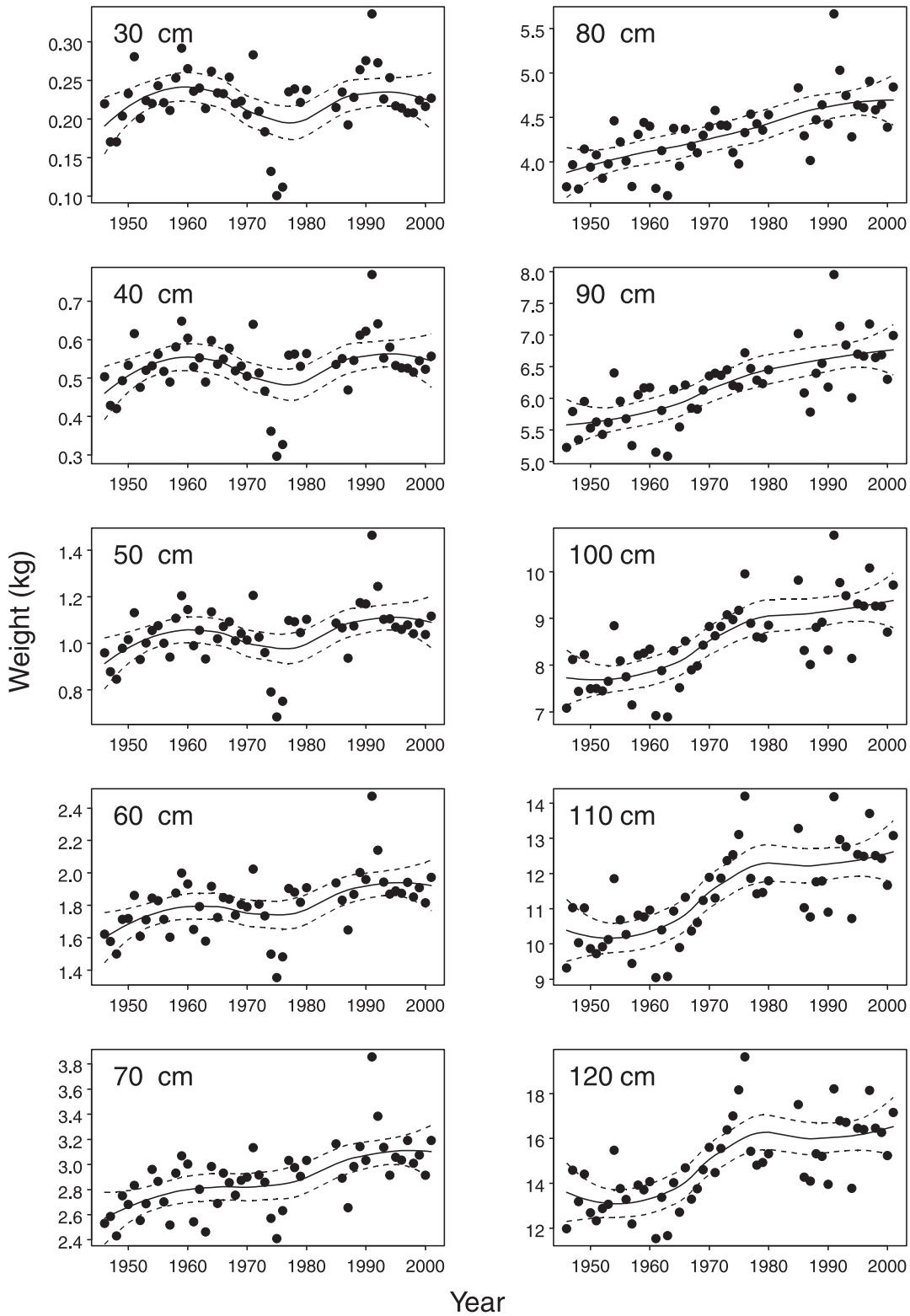
short, heavy form. Over the entire time period, older, larger cod (age 7, 70 cm, and age 9, 90 cm) exhibit a strong directional trend towards larger values of both  $SL_a$  and  $SW_l$  (Fig. 7). Thus, large cod have become both longer and heavier over the entire time period.

To evaluate whether the year-specific values of  $SL_a$  and  $SW_l$  showed significant covariation, the correlations between  $SL_a$  (ages 3–9) and  $SW_l$  for three of the standard lengths ( $(10 \times \text{age}) - 10$  cm,  $(10 \times \text{age})$  cm, and  $(10 \times \text{age}) + 10$  cm) were examined. None of the correlations between the  $SL_a$  and  $SW_l$  time series was statistically significant (Table 4), indicating that the long-term trends in length-at-age and girth are essentially decoupled. For the younger/smaller cod, the correlation coefficients are negative, indicating that the  $SL_a$  and  $SW_l$  time series are negatively related, albeit not significantly (Table 4).

#### Variation in liver weights

A bivariate plot of the  $SW_{70}$  versus capelin stock biomass shows that there is no significant correlation ( $n = 50$ ,  $p = 0.66$ ,  $r^2 < 0.01$ ) between the two variables (Fig. 8a). Given that the magnitude of variation in  $SW_{70}$  during this time period was substantial (Table 2), the lack of a significant relationship is not due to insufficient contrast in the data. For the same time period, there is a significant, positive correlation between  $LCI_{61-70}$  and capelin stock biomass ( $n = 54$ ,  $p < 0.001$ ,  $r^2 = 0.44$ ; Fig. 8b). Because of this latter correlation, there is also a significant, positive correlation between  $LW_{70}$  and capelin stock biomass ( $n = 50$ ,  $p < 0.001$ ,  $r^2 = 0.24$ ; Fig. 8c). Thus, at the stock level, condition indices based on liver weights are more sensitive to variation in prey availability compared with condition indices based solely on total body

**Fig. 6.** Predicted weight-at-length values for a cod (*Gadus morhua*) of standard lengths ranging (10-cm intervals) from 30 to 120 cm. The LOESS smoothers (solid line) with their approximate 95% confidence intervals (broken lines) are also indicated.



weight. Furthermore,  $SW_{70}$  and  $LCI_{61-70}$  are uncorrelated ( $n = 51$ ,  $p = 0.095$ ,  $r^2 = 0.06$ ), indicating that there is no significant relationship between indices representing girth and liver weight of the stock.

When plotted as a time series, the  $LW_{70}$  varies by a factor of approximately 2.5 over the entire time period (Fig. 9). There is no evidence of a long-term trend in values; however, there is marked short-term variability in liver weight

**Table 4.** Correlation coefficients and levels of significance (in parentheses) for correlations between the length-at-age and weight-at-length time series.

	SL <sub>3</sub>	SL <sub>4</sub>	SL <sub>5</sub>	SL <sub>6</sub>	SL <sub>7</sub>	SL <sub>8</sub>	SL <sub>9</sub>
SW <sub>30</sub>	-0.21 (0.13)	-0.03 (0.85)					
SW <sub>40</sub>	-0.17 (0.23)	0.00 (0.99)	-0.23 (0.11)				
SW <sub>50</sub>		0.04 (0.79)	-0.19 (0.19)	0.07 (0.65)			
SW <sub>60</sub>			-0.13 (0.38)	0.09 (0.53)	0.06 (0.69)		
SW <sub>70</sub>				0.11 (0.42)	0.08 (0.59)	0.04 (0.76)	
SW <sub>80</sub>					0.09 (0.42)	0.04 (0.75)	0.14 (0.32)
SW <sub>90</sub>						0.04 (0.78)	0.16 (0.26)

**Note:** In all cases, the number of observations was 49 as there were no SL<sub>a</sub> values for 1946 and the SW<sub>l</sub> values for 1980–1983 were excluded.

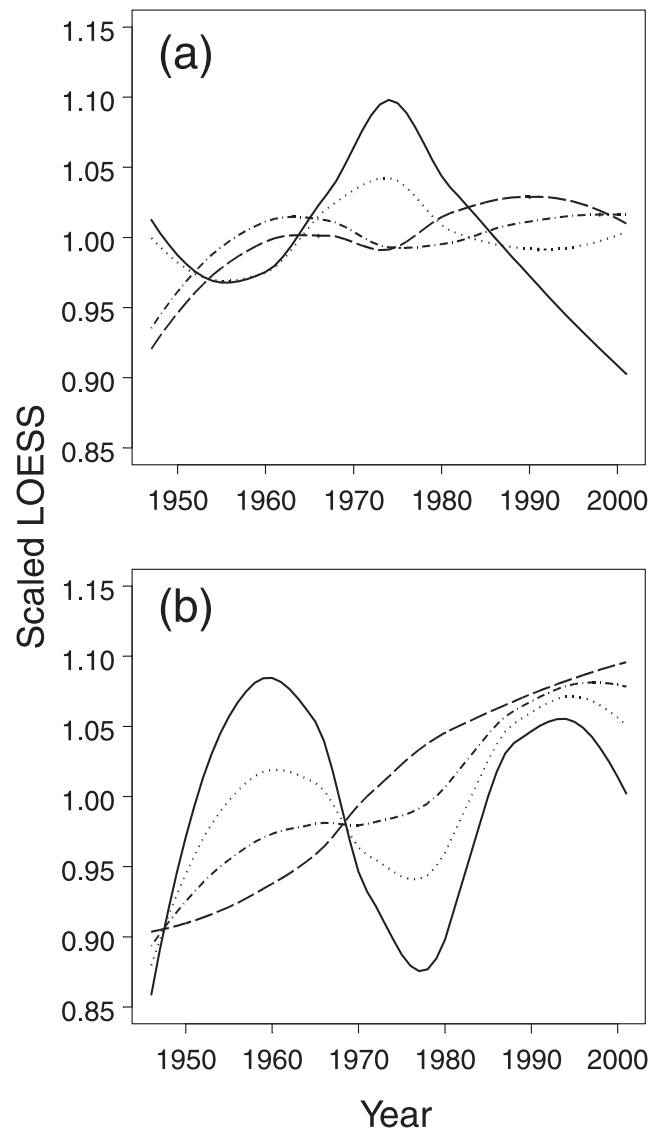
that seems to have increased in recent years. For example, the LW<sub>70</sub> varies from a historical low in 1988 (108 g) to a historical high in 1991 (260 g). The Norwegian survey values for 1997–2001 are both higher and lower than the derived liver weights (Fig. 9), which suggests that the derived liver weights are on a similar scale to the values that were measured during surveys conducted in the first quarter.

## Discussion

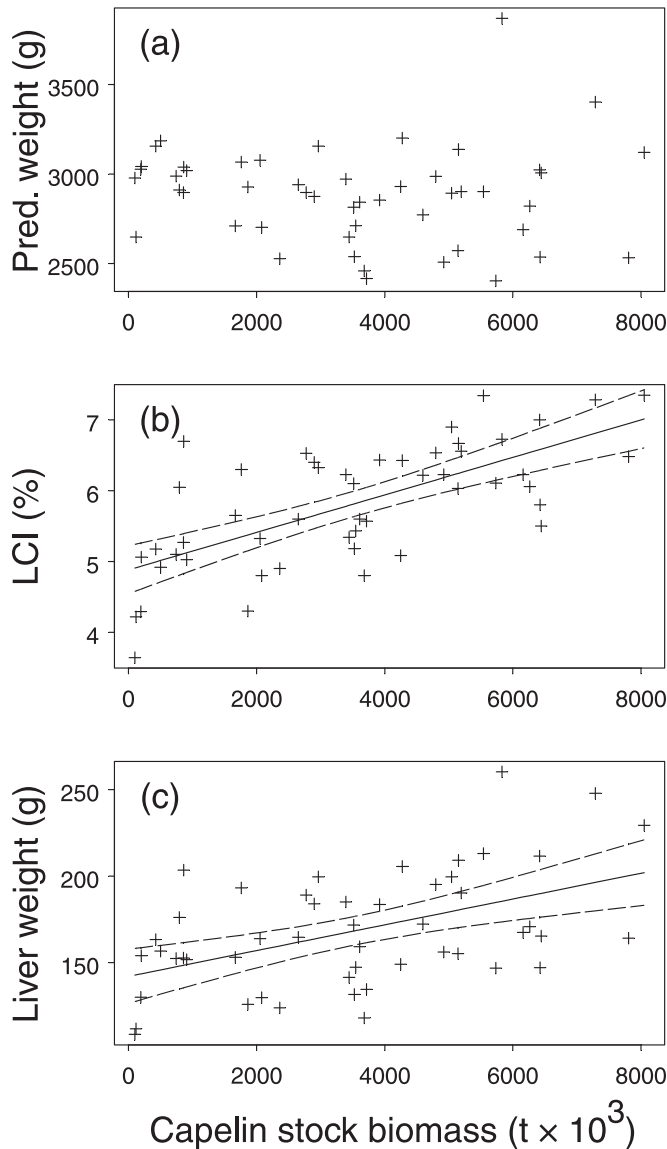
The goals of this study were, firstly, to develop a morphometric condition index for the Northeast Arctic cod stock from stock-level data and, secondly, to evaluate whether this index was an accurate measure of the bioenergetic status of the stock using the liver condition index (Yaragina and Marshall 2000) as a benchmark. The first goal was achieved by generating pseudo-observations of weight and length using the databases underlying the SSB estimates and then calculating a morphometric condition index from these pseudo-observations. Although this approach is undeniably circuitous compared with estimating condition directly from observations made on individual cod, it was necessitated by the practical difficulties in accessing raw data for the entire time period from both Norwegian and Russian sources. Similar difficulties exist for many stocks and particularly those that are sampled by more than one country or institute. Fortunately, ALK were available for both Norway and Russia, enabling a reconstruction of historical trends in  $L_a$  for Northeast Arctic cod that could then be matched with the  $W_a$  time series used by the AFWG to estimate  $SW_a$ . Despite their routine use in the assessment, the accessibility of historical ALK is often as limiting as the accessibility of individual-level observations. The problems encountered in accessing historical fisheries data illustrate the need to evaluate current reporting practices, as well as the archiving of standard fisheries data. One relatively simple change would be to ensure that both  $L_a$  and  $W_a$  are routinely reported for all of the primary data sources used to estimate  $SW_a$ .

The second question that was addressed here was whether the morphometric condition index developed from stock-level data constituted an accurate measure of the energy reserves of the stock. The significant, positive relationship that was observed between the LCI and capelin stock biomass provides strong evidence of the prey effect on the energy reserves of Northeast Arctic cod. However, the lack of sig-

**Fig. 7.** LOESS curves scaled to the long-term mean LOESS value (1946–2001) for selected ages and lengths: (a) stock length-at-age (SL<sub>a</sub>) from Fig. 3 for age 3 (solid line), age 5 (dotted line), age 7 (dotted-dashed line), and age 9 (broken line); and (b) stock weight-at-length (SW<sub>l</sub>) from Fig. 6 for 30 cm (solid line), 50 cm (dotted line), 70 cm (dotted-dashed line), and 90 cm (broken line).

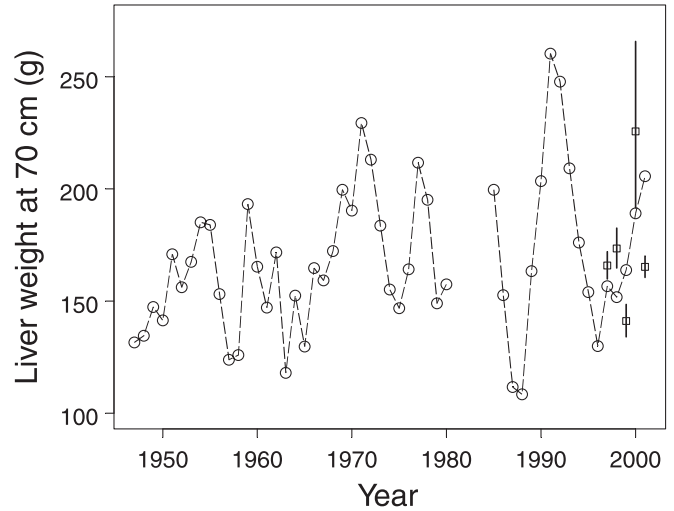


**Fig. 8.** The bivariate relationships between capelin (*Mallotus villosus*) stock biomass ( $t \times 10^3$ ) and (a) predicted (Pred.) weight at 70 cm, (b) liver condition index (LCI) of the 61- to 70-cm length class, and (c) estimated liver weight at 70 cm. Observations are denoted by year. Solid line indicates the least squares model fit, and broken lines indicate approximate 95% confidence intervals for the estimate. The model fit is not shown in (a) because the correlation was not significant.

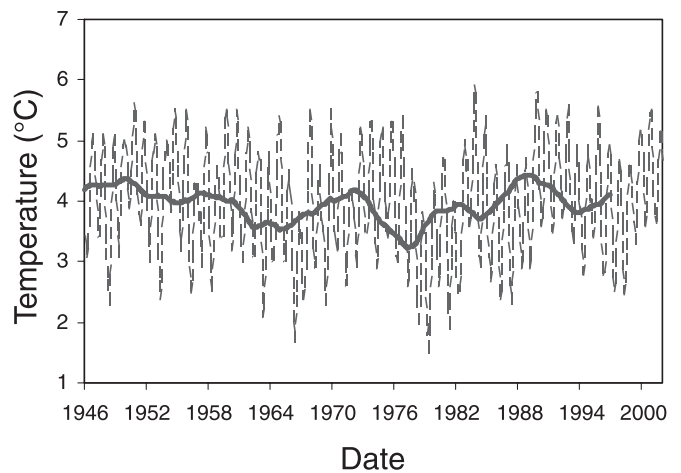


nificant correlations between either  $SW_l$  and capelin stock biomass or  $SW_l$  and LCI suggests that stock-level condition indices describing girth do not reflect the true magnitude of stored energy reserves. This conclusion is consistent with a study at the individual level, suggesting that total lipid reserves of Arctic char cannot be predicted using a morphometric condition index (Fulton's  $K$ ) alone (Adams et al. 1995). Similarly, weight- and lipid-based condition indices estimated for spawning females differ in their ability to resolve linkages between energy reserves and fecundity. For Icelandic cod, the LCI was more strongly correlated with relative fecundity (potential fecundity / total weight) than

**Fig. 9.** Time series of estimated liver weight (g) for a 70-cm cod, *Gadus morhua* (broken line, open circles). Values estimated from liver weight observations made during the Norwegian surveys of the Barents Sea and Lofoten regions are indicated by open squares with approximate 95% confidence intervals being represented by the vertical lines.



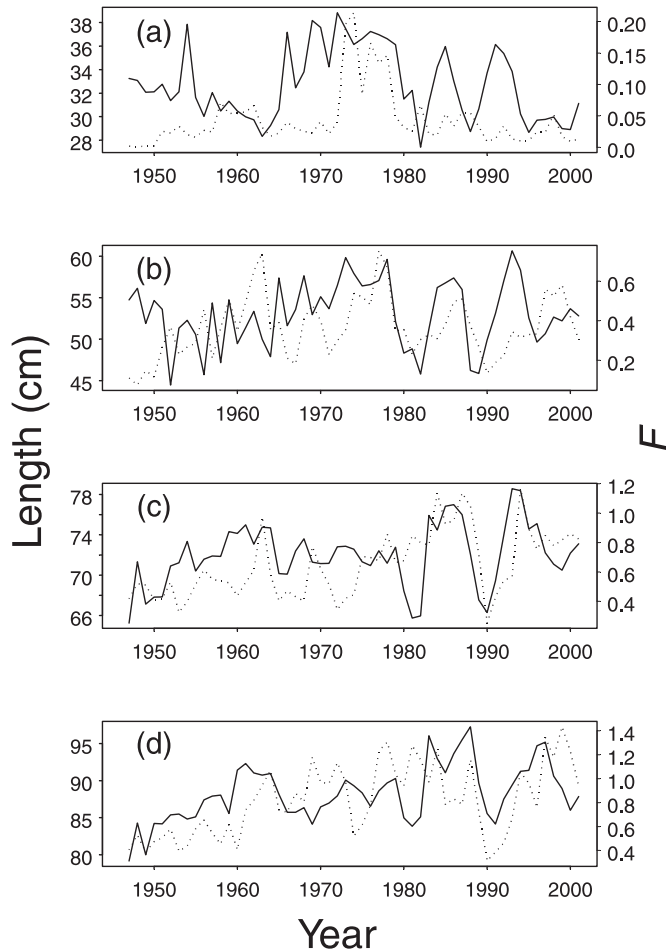
**Fig. 10.** Monthly temperature values measured at the Kola hydrographic section in the Barents Sea (broken line) and the 5-year running mean temperature for the time series (solid line) representing the long-term trend.



Fulton's  $K$  in each of the 6 study years and, in two of those years, explained more of the variation in relative fecundity than did total length (Marteinsdottir and Begg 2002). For haddock on the eastern Scotian Shelf, the LCI explained a higher proportion of variability in fecundity than did  $Kn$  in a model that also included length when data for the 3 years were pooled (Blanchard et al. 2003). Clearly, it is unwise to assume a priori that morphometric condition indices are sensitive indices of condition without independent and preferably bioenergetic evidence supporting this assumption.

Irrespective of whether or not  $SW_l$  constitutes a sensitive measure of condition, it can be considered a basic descriptor of fish girth. The lack of temporal correlation between  $SL_a$  and  $SW_l$  for Northeast Arctic cod suggests that temporal trends in length and girth are decoupled to a greater extent

**Fig. 11.** Time series (1946–2001) of stock length-at-age ( $SL_a$ ; solid line) and fishing mortality ( $F$ ; dotted line) estimated for that age class: (a) age 3; (b) age 5; (c) age 7; and (d) age 9.



than has been realized. For example, the temporal trends in length and girth described here indicate that young cod alternate between a long, lean form and a short, heavy form. More highly resolved growth models should be developed treating length and girth as separate terms, particularly as the environmental factors affecting length may differ from those affecting girth. For example, variability in condition factor and growth rates for northern cod were explained by food and temperature, respectively (Krohn et al. 1997).

Although the degree to which cod growth is genetically determined is uncertain (Imslund and Jónsdóttir 2002), there have nevertheless been repeated calls for genetic considerations to be included in fisheries management (Heino 1998; Conover and Munch 2002; Kenchington et al. 2003). It has previously been suggested that size- and stage-specific exploitation has resulted in selection for a fast-growing, early-maturing genotype in Northeast Arctic cod (Law and Grey 1989). If true, then a fast-growing genotype should manifest itself at early life history stages. In this context, it was noted that neither the  $SL_a$  for cod ages 3 and 4 or  $SW_l$  for cod 30 and 40 cm has shown any trend towards either increased or decreased values over the entire 56-year time period. Thus, the observed trends in body size for the youngest/smallest age/size classes are not consistent with the hypothesis that

**Table 5.** Correlation coefficients and levels of significance for correlations between the length-at-age and fishing mortality ( $F$ ) for that age class (from ICES ACFM 2002).

Age class	$r^2$	$p$
3	0.15	0.0042
4	0.003	0.667
5	0.018	0.32
6	0.0055	0.59
7	0.14	0.0043
8	0.17	0.0017
9	0.17	0.0021
10	0.29	<0.001
11	0.014	0.37
12	0.025	0.24

**Note:** In all cases, the number of observations was 54 because the  $SL_a$  value for 1946 was not available.

the high levels of fishing mortality experienced by this stock has selected for a fast-growing genotype. In fact, the strongest evidence of a trend towards larger body size was observed for older age classes in which the phenotype had been substantially modified by the cumulative effects of size-selective mortality from fishing.

The considerable increase in  $SL_a$  values that has occurred for the oldest/largest cod is one of the most striking features of the data. This is unlikely to be the result of ageing bias given that the limited data available suggest that discrepancies between contemporary and historical ages result in minor differences in mean length. Furthermore, if historical ages give higher mean lengths than would be calculated for contemporary ages, then correcting the full time series for this possible source of bias would only strengthen the trend towards a long-term increase in  $SL_a$ . Temperature in the Barents Sea has not exhibited any directional tendency over the entire time period (Fig. 10), making it unlikely that the long-term increase in  $SL_a$  was due to temperature-dependent changes in growth rates of older fish. The long-term trends in  $SL_a$  for older age classes occurred at the same time as a substantial long-term increase in fishing mortality ( $F$ ) estimated for the older age classes (Fig. 11). The older age classes show reasonably simultaneous increases and decreases in both  $SL_a$  and  $F$  (Figs. 11c, 11d), with the correlations between the two time series being statistically significant ( $p < 0.05$ ) for cod ages 7–10 (Table 5). Among these four age classes, the degree of correlation increases with increasing age and is strongest for cod age 10. These observations suggest that the temporal trends in  $F$  are modifying the size structure of age classes that are fully recruited to the fishery such that larger individuals dominate the age class when  $F$  is high. Within an age class, high  $F$  could favour the differential survival of large cod that swim faster and have a higher probability of escapement. The cumulative nature of survival probabilities could cause the phenotype to become more prevalent with increasing age, thus explaining why the correlation between  $SL_a$  and  $F$  increased with increasing age up to age 10 (Table 5). If this interpretation is correct, then the selection gradient being applied to fully recruited age classes by high  $F$  (favouring survival of large cod) is opposite to the

**Table 6.** General recommendations for adapting sampling programs for measuring individual condition, as adapted from Dutil et al. (1995).

Topic	Recommendation
Frequency	Samples should be taken periodically during the year. Monthly samples are required in the spring and the fall to identify the extremes in condition. Given the pronounced seasonal cycle in condition and possible variability in this cycle, one sample taken annually is not sufficient to monitor condition adequately.
Sampling protocol	Samples should contain a minimum of 30 fish. This number should be increased when assessing condition in stocks characterized by a wide range in size, particularly if condition factor and length are correlated. Length-stratified samples would allow for comparisons between size groups and may facilitate comparison of condition between stocks.
Formulation of index	Fulton's condition factor and hepatosomatic index should be calculated using somatic weight, not total weight. Somatic weight provides a more accurate measure of condition and will facilitate both within- and between-stocks comparisons because it is not affected by potential differences in feeding intensity and timing of maturation as will occur when comparing different sites or time periods.
Variables measured	For each fish sampled, the minimum information collected must include total length, total weight, weight of stomach contents, sex, gonad weight, liver weight, and water content of liver and muscle.

selection gradient that is often assumed to apply to partially recruited age classes favouring the survival of smaller, slow-growing cod at high  $F$  (Kristiansen and Svåsand 1998). The direction of selection gradients is not constant through time (Hanson and Chouinard 1992; Sinclair et al. 2002a); therefore, it is possible for the direction of the selection gradient to vary across age/size classes. There could also be a density-dependent basis for the positive correlations between  $SL_a$  and  $F$  given that high  $F$  reduces the abundance of these age classes, thereby enhancing per capita food availability. The two mechanisms (size-selective mortality favouring the differential survival of large cod and density-dependent growth) are not mutually exclusive. For example, a negative effect of population density on the growth of cod in the southern Gulf of St. Lawrence was detected in addition to the significant effects of size-selective mortality (Sinclair et al. 2002b).

The substantial increase in both  $SL_a$  and  $SW_l$  that has been observed in older/larger age classes in combination with the overall decline in numerical abundance are likely to have had repercussions for the reproductive potential of the Northeast Arctic cod stock. To evaluate the impacts of changes in growth and demography on stock reproductive potential, alternative indices are required given that SSB is likely to be an inaccurate index of total egg production for this stock (Marshall et al. 1998, 2003). Because reproductive traits of Northeast Arctic cod vary according to length rather than age, a length-based approach to quantifying reproductive potential of the stock is warranted. The ALK and year-specific weight-length relationships developed here facilitate this in several important ways. The combined ALK can be used to convert the values of number-at-age given in the annual assessment to number-at-length. These estimates can then be coupled with length-based databases and models, e.g., the year-specific weight-length relationships, the length-based Russian liver condition database (Yaragina and Marshall 2000), or length-based fecundity models (e.g., Kjesbu et al. 1998; Marteinsdottir and Begg 2002), to develop alternative estimates of reproductive potential (e.g., Blanchard et al. 2003). The age-based SSB and the length-based alternative index of reproductive potential would be directly comparable given that the ALK and year-specific weight-length relationships used for estimating the alternative are derived from

the same primary databases. A high degree of comparability between SSB and the alternative index is an important attribute when evaluating whether there are substantial differences between them (Marshall et al. 2003).

Although the importance of bioenergetic condition indices for understanding the growth and reproduction of fish is clear (Shulman and Love 1999), relatively few long-term databases exist at the stock level. Adapting existing sampling programs to collect more detailed information on condition has previously been advocated (Dutil et al. 1995). That study provided a series of recommendations for the routine monitoring of condition that are summarized here (Table 6). These recommendations, which were developed in the wake of the collapse of several Canadian cod stocks, have yet to be widely adopted. We concur with their view that the measurement of condition "should be viewed as an original and informative simple-to-measure stock characteristic" that has been largely overlooked. There are signs that sampling programs are being modified so as to collect more detailed measurements. For example, the Norwegian surveys of the Barents Sea began measuring liver weights in 1997, and liver weights of cod in the southern and northern Gulf of St. Lawrence are now monitored regularly through a combination of sentinel and research-vessel surveys (J.-D. Dutil, Institut Maurice-Lamontagne, 850 route de la Mer, Mont-Joli, QC G5H 3Z4, Canada, personal communication). Samples taken annually at a fixed point in time will probably be inadequate given the pronounced seasonal cycle in condition and the possible variability in this seasonal cycle (Dutil et al. 1995, 2003; Yaragina and Marshall 2000). Measurements that are highly resolved in space and time pose a considerable logistical challenge; however, many of the existing high-resolution condition databases were developed in support of or by commercial fisheries. For example, industrial sources of information have been used to derive monthly condition indices for pelagic stocks in the Southern California region (Parrish and Mallicoate 1995) and Benguela system (Schülein et al. 1995).

This study has shown that although it is possible to generate a morphometric index representing the girth of Northeast Arctic cod at the stock level using standardized fisheries databases, the resulting index does not accurately reflect the magnitude of stored energy reserves. It is important to rec-



ognize that this conclusion was developed from stock-level data collected over broad spatiotemporal scales and may not necessarily apply to short-term studies conducted at the individual level. Its applicability to other stocks is difficult to gauge given the relatively small number of stocks having long-term data on fish growth (length and girth), lipid reserves, and food availability. The importance of developing time series of condition that accurately track fluctuations in the energy reserves of the stock is increasingly clear given the impact of condition on all major elements of population dynamics, including natural mortality, fishing mortality, growth, and recruitment. For commercially exploited stocks that experience variable environmental conditions, the technical and logistical impediments to monitoring condition should be considered as minor relative to the costs of not monitoring this key variable.

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## References

- Adams, C.E., Huntingford, F.A., and Jobling, M. 1995. A non-destructive morphometric technique for estimation of body and mesenteric lipid in Arctic charr: a case study of its application. *J. Fish Biol.* **47**: 82–90.
- Blanchard, J.L., Frank, K.T., and Simon, J.E. 2003. Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock. *Can. J. Fish. Aquat. Sci.* **60**: 321–332.
- Bolger, T., and Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* **34**: 171–182.
- Chambers, R.C., and Waiwood, K.G. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. *Can. J. Fish. Aquat. Sci.* **53**: 1986–2003.
- Chouinard, G.A., and Swain, D.P. 2002. Depth-dependent variation in condition and length-at-age of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **59**: 1451–1459.
- Comeau, L., Campana, S.E., and Chouinard, G.A. 2002. Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern Gulf of St. Lawrence: interannual variability and proximate control. *ICES J. Mar. Sci.* **59**: 333–351.
- Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science (Wash., D.C.)*, **297**: 94–96.
- Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **57**: 826–836.
- Dutil, J.-D., Lambert, Y., Chouinard, G.A., and Fréchet, A. 1995. Fish condition: what should we measure in cod (*Gadus morhua*)? DFO Atlantic Fisheries Research Document No. 95/11.
- Dutil, J.-D., Castonguay, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **56**: 1818–1831.
- Dutil, J.-D., Gauthier, Y., Lambert, Y., Fréchet, A., and Chabot, D. 2003. Cod stocks rebuilding and fish bioenergetics: low productivity hypothesis. Canadian Science Advisory Secretariat Res. Doc. No. 2003/060.
- Eliassen, J.-E., and Vahl, O. 1982. Seasonal variation in biochemical composition and energy content of liver, gonad and muscle of mature and immature cod, *Gadus morhua* (L.), from Balsfjorden, northern Norway. *J. Fish Biol.* **20**: 707–716.
- Fotland, Å., Borge, A., Gjøsæter, H., and Mjanger, H. 1997. Håndbok for prøvetaking av fisk og krepsdyr. Internal document published by the Department of Marine Resources, Institute of Marine Research, Bergen, Norway. [In Norwegian.]
- Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia*, **83**: 453–513.
- Hanson, J.M., and Chouinard, G.A. 1992. Evidence that size-selective mortality affects growth of Atlantic cod (*Gadus morhua* L.) in the southern Gulf of St. Lawrence. *J. Fish Biol.* **41**: 31–41.
- Heino, M. 1998. Management of evolving fish stocks. *Can. J. Fish. Aquat. Sci.* **55**: 1971–1982.
- Henderson, B.A., and Morgan, G.E. 2002. Maturation of walleye by age, size and surplus energy. *J. Fish Biol.* **61**: 999–1011.
- Hislop, J.R.G., Robb, A.P., and Gauld, J.A. 1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.), in captivity. *J. Fish Biol.* **13**: 85–98.
- International Council for the Exploration of the Sea Advisory Council on Fisheries Management (ICES ACFM). 2001. Report of the Arctic Fisheries Working Group. ICES CM 2001/ACFM:19.
- ICES ACFM. 2002. Report of the Arctic Fisheries Working Group. ICES CM 2002/ACFM:18.
- ICES ACFM. 2003. Report of the Study Group on biological reference points for Northeast Arctic cod. ICES CM 2003/ACFM:11.
- Imslund, A.K., and Jónsdóttir, O.D.B. 2002. Is there a genetic basis to growth in Atlantic cod? *Fish Fish.* **3**: 36–52.
- Jakobsen, T., Korsbrette, K., Mehl, S., and Nakken, O. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents Sea during winter. ICES CM 1997/Y:17.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *J. Cons. Int. Explor. Mer.* **46**: 235–248.
- Kawasaki, T., and Omori, M. 1995. Possible mechanisms underlying fluctuations in the Far Eastern sardine population inferred from time series of two biological traits. *Fish. Oceanogr.* **4**: 238–242.
- Kenchington, E., Heino, M., and Nielsen, E.E. 2003. Managing marine genetic diversity: time for action? *ICES J. Mar. Sci.* **60**: 1172–1176.
- Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. *J. Fish Biol.* **34**: 195–206.
- Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Greer Walker, M. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J. Sea Res.* **40**: 303–321.
- Kristiansen, T.S., and Svåsand, T. 1998. Effect of size-selective mortality on growth of coastal cod illustrated by tagging data and an individual-based growth and mortality model. *J. Fish Biol.* **52**: 688–705.

- Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **54**(Suppl. 1): 113–121.
- Kurita, Y., Meier, S., and Kjesbu, O.S. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *J. Sea Res.* **323**: 1–17.
- Laine, P., and Rajasilta, M. 1999. The hatching success of Baltic herring eggs and its relation to female condition. *J. Exp. Mar. Biol. Ecol.* **237**: 61–73.
- Lambert, Y., and Dutil, J.-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Can. J. Fish. Aquat. Sci.* **57**: 815–825.
- Law, R., and Grey, D.R. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* **3**: 343–359.
- Lepesevich, Yu.M., and Shevelev, M. 1997. Evolution of the Russian survey for demersal fish: from ideal to reality. *ICES CM 1997/Y:09*.
- Lloret, J., and Rätz, H.-J. 2000. Condition of cod (*Gadus morhua*) off Greenland during 1982–1998. *Fish. Res.* **48**: 79–86.
- Ma, Y., Kjesbu, O.S., and Jørgensen, T. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.* **55**: 900–908.
- Marshall, C.T., and Frank, K.T. 1999. The effect of interannual variation in growth and condition on haddock recruitment. *Can. J. Fish. Aquat. Sci.* **56**: 347–355.
- 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? *Can. J. Fish. Aquat. Sci.* **55**: 1766–1783.
- Marshall, C.T., Yaragina, N.A., Ådlandsvik, B., and Dolgov, A.V. 2000. Reconstructing the stock–recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. *Can. J. Fish. Aquat. Sci.* **57**: 2433–2442.
- Marshall, C.T., O'Brien, L., Tomkiewicz, J., Marteinsdóttir, G., Morgan, M.J., Saborido-Rey, F., Köster, F.W., Blanchard, J.L., Secor, D.H., Kraus, F., Wright, P., Mukhina, N.V., and Björnsson, H. 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *J. Northwest Atl. Fish. Sci.* **33**: 161–190.
- Marteinsdóttir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod, *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **235**: 235–256.
- Marteinsdóttir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod (*Gadus morhua* L.) eggs and larvae. *J. Fish Biol.* **52**: 1241–1258.
- Martínez, M., Gunderley, H., Nelson, J.A., Webber, D., and Dutil, J.-D. 2002. Once a fast cod, always a fast cod: maintenance of performance hierarchies despite changing food availability in cod (*Gadus morhua*). *Physiol. Biochem. Zool.* **75**: 90–100.
- Martínez, M., Gunderley, H., Dutil, J.-D., Winger, P.D., He, P., and Walsh, S.J. 2003. Condition, prolonged swimming performance and muscle metabolic capacities of cod (*Gadus morhua*). *J. Exp. Biol.* **206**: 503–511.
- Morimoto, H. 1996. Effects of maternal nutritional conditions on number, size and lipid content of hydrated eggs in the Japanese sardine from Tosa Bay, southwestern Japan. *In* *Survival strategies in early life stages of marine resources. Edited by Y. Watanabe, Y. Yamashita, and Y. Oozeki.* A.A. Balkema, Rotterdam. pp. 3–12.
- Óskarsson, G.J., Kjesbu, O.S., and Slotte, A. 2002. Predictions of realized fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *J. Sea Res.* **48**: 59–79.
- Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of north-east Arctic cod. *ICES J. Mar. Sci.* **55**: 67–85.
- Parrish, R.H., and Mallicoate, D.L. 1995. Variation in the condition factors of California pelagic fishes and associated environmental factors. *Fish. Oceanogr.* **4**: 171–190.
- Rätz, H.-J., and Lloret, J. 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fish. Res.* **60**: 369–380.
- Sabarido-Rey, F., Kjesbu, O.S., and Thorsen, A. 2003. Buoyancy of Atlantic cod larvae in relation to developmental stage and maternal influences. *J. Plankton Res.* **25**: 291–307.
- Schülein, F.H., Boyd, A.J., and Underhill, L.G. 1995. Oil-to-meal ratios of pelagic fish taken from the Northern and the Southern Benguela systems: seasonal patterns and temporal trends, 1951–1993. *S. Afr. J. Mar. Sci.* **15**: 61–82.
- Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *ICES J. Mar. Sci.* **56**: 303–319.
- Shulman, G.E., and Love, R.M. 1999. Biochemical ecology of marine fishes. *Adv. Mar. Biol.* **36**.
- Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002a. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Can. J. Fish. Aquat. Sci.* **59**: 361–371.
- Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002b. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Can. J. Fish. Aquat. Sci.* **59**: 372–382.
- Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod. *ICES J. Mar. Sci.* **57**: 42–55.