

# Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*)

N. A. Yaragina, and C. T. Marshall



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Temporal variation in the liver condition index (LCI) of five length classes of Northeast Arctic cod was described and compared to the abundance and availability of capelin and herring in the Barents Sea. On interannual time scales, large and rapid fluctuations in LCI occurred which were synchronous across length classes. For all length classes the annual mean LCI was non-linearly related to capelin stock biomass such that LCI decreased rapidly when capelin stock biomass was below one million tonnes. Liver condition index and the frequency of occurrence of capelin in cod stomachs were positively associated. Neither the abundance of juvenile herring in the Barents Sea nor the frequency of occurrence of herring in cod stomachs were positively correlated with LCI. However, a significant, inverse relationship between the frequency of occurrence of capelin in cod stomachs and total stock biomass of herring was observed suggesting that herring influence cod LCI via predation on capelin. On seasonal time scales, LCI values for February through July were significantly higher in years of high capelin biomass compared to years having low capelin biomass. In years of high capelin biomass the proportion of capelin in the stomach contents of cod showed a peak in March and (or) April.

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N. A. Yaragina: Polar Research Institute of Marine Fisheries and Oceanography, 6, Knipovich St., Murmansk, 183763, Russia. C. T. Marshall: Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway. Correspondence to N. A. Yaragina: tel: +7 8152 4722 31; fax: +7 51295 10518; email: [bottfish@pinro.murmansk.ru](mailto:bottfish@pinro.murmansk.ru)

## Introduction

Capelin (*Mallotus villosus*) is the preferred prey of cod (*Gadus morhua*) in Arcto-boreal ecosystems such as the Barents Sea (Mehl and Sunnanå, 1991; Ushakov *et al.*, 1992), Iceland (Magnússon and Pálsson, 1991), and Newfoundland/Laborador (Lilly, 1991). The availability of capelin to cod is subject to dramatic fluctuations due to variation in capelin abundance (Tjelmeland, 1992) and (or) the degree of spatial overlap between the two species (Ozhigin *et al.*, 1995; Frank *et al.*, 1996). Large reductions in the availability of capelin decrease the growth rates of cod (Steinarsson and Steffánsson, 1991, 1996; Ozhigin *et al.*, 1994; Taggart *et al.*, 1994). A well-documented example of this coupling occurred in 1985 when the capelin stock in the Barents Sea collapsed (Fig. 1). The subsequent decrease in the consumption of capelin by cod (Mehl and Sunnanå, 1991; Ozhigin *et al.*,

1995) was accompanied by significant decreases in the weight-at-age (Jørgensen, 1992; Ozhigin *et al.*, 1994) and fecundity at length of mature cod (Kjesbu *et al.*, 1998). Anomalously low percentages of mature females in length-classes corresponding to repeat-spawners were also observed suggesting that a proportion of female cod skipped spawning (Marshall *et al.*, 1998).

Lipids are an important biochemical link between capelin and cod. Lipids constitute approximately 10–15% of the total wet weight of capelin at the peak of their seasonal cycle in lipid accumulation (Jangaard, 1974). The liver is the primary site of stored lipid reserves in cod (Kjesbu *et al.*, 1991; Hemre *et al.*, 1993); only about 1% of the wet weight of the muscle tissue consists of lipids (Lie *et al.*, 1988). Liver lipid reserves are utilized during periods of food limitation (Takama *et al.*, 1985; Karlsen *et al.*, 1995) and during the annual cycle of gonad maturation (Krivobok and Tokareva

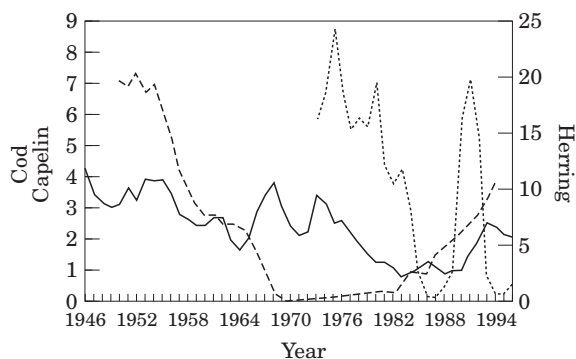


Figure 1. Time series of total stock biomass (million tonnes) of Northeast Arctic cod (solid line; from ICES, 1998), Barents Sea capelin (dotted line; from ICES, 1997), and Norwegian spring-spawning herring (dashed line; from ICES, 1997).

1972; Kjesbu *et al.*, 1991). Lipids normally constitute more than 50% of the liver weight of cod (Makarova, 1968; Eliassen and Vahl, 1982; Lambert and Dutil, 1997a). However, in starved cod the lipid content of the liver can be as low as 2% (Love, 1958). An order of magnitude reduction in the lipid content of the liver is likely to reduce the ability of individual cod to survive periods of food limitation (Lambert and Dutil, 1999). Starving cod can also mobilize muscle proteins for energy (Black and Love, 1986). However, proteins have a lower energy content relative to lipids (Schmidt-Nielsen, 1983) and are likely to be depleted when liver reserves are low. Starved cod can replenish liver reserves rapidly in response to increased food (Karlsen *et al.*, 1995). Thus, liver weight is likely to be a dynamic index of the physiological condition of cod.

Because of the commercial value of cod liver oil there are several sources of long-term data on the liver weights of Northeast Arctic (NA) cod (c.f. Hjort, 1914). Data collected during the annual Lofoten skrei fishery describe the liver condition of mature cod arriving at the spawning grounds in March/April (Øiestad, 1994; Nilssen *et al.*, 1994). The Soviet Union and the Russian Federation, hereafter referred to as Russia, have been measuring the liver weights of NA cod on a monthly basis since 1927, excepting a total of 11 years (Yaragina, 1996). These data are archived as the liver condition index (LCI) which expresses liver weight as a percentage of total body weight. The Russian LCI time series, describing immature and mature cod sampled monthly over a broad geographic range, is comparable in scale to Russian and Norwegian databases on cod feeding.

This paper describes trophic influences on interannual and seasonal variation in LCI in the southern Barents Sea (SBS) region which includes most of ICES statistical Area I and the eastern part of statistical Area IIA (Fig. 2). Interannual variation in annual mean LCI values was described for a 70 year time period

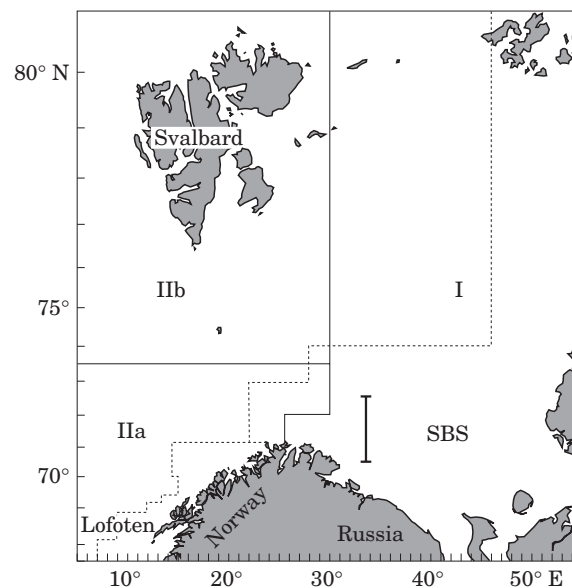


Figure 2. The area of distribution for Northeast Arctic cod. Boundaries of Russian subareas for the southern Barents Sea (SBS), Svalbard area and Norwegian coast are indicated by the dashed lines. Boundaries of ICES statistical Areas I, IIa and IIb are indicated by the solid lines. The thick vertical line in the SBS shows the location of the Kola section.

(1927–1996). The relationship between annual mean LCI and capelin was examined using total stock biomass of capelin and the frequency of occurrence of capelin in cod stomachs as indices of capelin abundance and availability, respectively. Herring (*Clupea harengus*) is another important component of the Barents Sea ecosystem (Hamre, 1994) which could potentially influence LCI either directly as a prey item for cod (Orlova *et al.*, 1995; de Barros *et al.*, 1998) or indirectly as a predator on capelin (Huse and Toresten, 1995). To assess the effect of herring on LCI the relationships between annual mean LCI and both the abundance of juvenile herring in the Barents Sea and the frequency of occurrence of herring in cod stomachs were examined. Seasonal variation in monthly LCI values in years of high capelin biomass was contrasted with that observed in years of low capelin biomass. Seasonal variation in the proportion of capelin in cod stomachs available for a more limited time period (1984–1996) was described with reference to seasonal variation in LCI.

## Data and methods

### Sampling methodology

For the earliest time period (1927–1950) samples were collected on board the Russian fishing fleet which operated mainly within the SBS region, except in 1930–1932 when approximately 10–15% of total Russian

catch was caught in the Svalbard (SV) region and again in 1950 when approximately 35% of the total Russian catch came from the SV region (Maslov, 1960). The LCI values estimated for those 4 years included observations from the SV region, which biased them because LCI values in the SV region are high relative to the SBS region (Yaragina, 1996). The bias was, however, assumed to be negligible because it affected such a small number of years. Since 1967, LCI values for cod in the SV region have been recorded separately (Yaragina, 1996).

During the earliest time period (1927–1950) liver and total body weights were measured of 10–30 individuals in each of three weight classes from a single catch (Sobolev and Bulashevich, 1952). Observations for several (usually less than four) catches were used to estimate the monthly mean LCI values. This basic sampling procedure has been followed throughout the time series. From 1954 to 1996 the total number of liver weight observations in a given year has ranged from a minimum of 456 in 1957 to a maximum of 9514 in 1996.

Throughout the time series the LCI values were estimated for each year, month and size class as follows:

$$LCI = \frac{\sum_n \text{liver wet weight}}{\sum_n \text{total wet weight}} \times 100 (\%) \quad (1)$$

where  $n$  represents the total number of observations in a given year, month, and size class. Data for males and females were pooled although systematic differences between sexes have been noted for cod larger than 60 cm (Yaragina, 1992). Monthly LCI values for 1927–1950 (values for 1931, 1933 and 1941–1945 are not available) were taken from Tables 1–3 in Sobolev and Bulashevich (1952). Their data are aggregated by weight into three size classes: small (0.5–1.5 kg), medium (1.5–3.0 kg), and large (>3.0 kg), and therefore describe LCI values for cod larger than approximately 40 cm. Monthly LCI values for 1954–1966 (values for 1955 and 1964 are not available) are reported in Table 5 of Ponomarenko (1970). These values are for one aggregate length class only (41–70 cm) although the annual mean LCI values for three 10-cm length classes (41–50, 51–60, and 61–70 cm) are given in a separate table. For the most recent time period (1967–1996) monthly LCI values are available for eight 10-cm length classes (21–30 through 91–100 cm). Data for the 21–30, 31–40, and 91–100 cm length classes were not included here because they have a relatively high proportion of missing values which increases the error in the mean LCI values. Only a small proportion (<5%) of cod in the 41–50 cm length class are mature, whereas, the majority (>90%) of cod in the 81–90 cm length class are mature (Ponomarenko and Yaragina, 1994). Thus, the five length classes span a

gradient from predominantly immature to predominantly mature cod.

### Interannual and seasonal trends in LCI

The annual mean LCI ( $LCI_y$ ) for the small- and medium-weight classes was available for the 1927–1950 time period (Sobolev and Bulashevich, 1952). In combination, these two weight classes represent cod approximately 40–70 cm in length (Yaragina, 1996). Estimates of  $LCI_y$  for three 10-cm length classes (41–50, 51–60, and 61–70 cm) were available for the years 1929, 1936, 1937–1938, 1954, 1956–1966 (Ponomarenko, 1970). Interannual variation in LCI for the time period 1967–1996 was described for the five length classes by estimating  $LCI_y$  as the arithmetic mean of the monthly LCI values available for that year. Because of the strong seasonal cycle in LCI, estimates of  $LCI_y$  will be affected by differences among years in the number of missing monthly values of LCI. If four or more of the monthly values for a given year were missing then  $LCI_y$  for that year was recorded as missing. If three or fewer of the monthly values were missing then the missing LCI values were linearly interpolated from adjacent months in the same year and the  $LCI_y$  for the year was estimated using both observed and interpolated monthly values.

Seasonal trends in LCI were examined for the 1967–1996 time period by dividing the time series into two groups: years having a capelin stock biomass less than or greater than 1 million tonnes, respectively. For each group and length class the monthly mean LCI value ( $LCI_m$ ) was estimated as the arithmetic mean of the LCI values available for that month. The interpolation scheme described above for estimating  $LCI_y$  was used to replace missing values. Seasonal variation in LCI was examined by plotting  $LCI_m$  by month for the two groups with the associated 95% confidence intervals.

### Abundance of capelin

Total stock biomass of Barents Sea capelin and the frequency of occurrence of capelin in cod stomachs ( $F_{cap}$ ) were used as measures of capelin abundance and availability, respectively, on interannual time scales. Total stock biomass of Barents Sea capelin has been estimated for the time period 1973–1996 from acoustic surveys conducted jointly by Norway and Russia in the autumn (Gjøsæter, 1998). Capelin abundance was also expressed as the ratio of capelin stock biomass to cod stock biomass, the latter having been estimated by virtual population analysis (VPA; ICES 1998).  $F_{cap}$  was estimated using cod feeding observations which have been collected year-round on commercial and research vessels as part of a sampling programme initiated by Russia in 1947 (Ponomarenko and Yaragina, 1978; Ponomarenko *et al.*, 1978). For non-empty cod

stomachs it was recorded which of the following categories of prey items were observed: capelin, juvenile cod, redfish, herring, shrimp, euphausiids, and other.  $F_{\text{cap}}$  is simply the percentage of non-empty cod stomachs which contain capelin (Ponomarenko and Yaragina, 1984). Values of  $F_{\text{cap}}$  are not resolved with respect to length class. Therefore, the analysis assumes that there are no significant differences among length classes in  $F_{\text{cap}}$  over time.  $F_{\text{cap}}$  values are disaggregated by geographic region and only values for SBS are reported here. The total number of cod stomachs examined for the SBS region ranges from a minimum of 5129 in 1948 to a maximum of 42 085 in 1994.

Regression relationships between  $\text{LCI}_y$  and two indices of capelin abundance (ln-transformed capelin stock biomass and the capelin:cod biomass ratio) were established for each of the five length classes. Because time series data violate the standard assumption of uncorrelated errors, the number of observations in the time series was corrected for autocorrelation by:

$$n^* = \frac{n}{1 + 2r_1r'_1 + 2r_2r'_2} \quad (2)$$

where  $n$  is the number of observations in each of the two time series,  $r_1$  and  $r'_1$  are the lag-one autocorrelations of the two series and  $r_2$  and  $r'_2$  are the lag-two autocorrelations of the two series (Quenouille, 1952). The statistical significance of the univariate models ( $p^*$ ) was estimated using  $n^*$ . For multivariate models both the Durbin-Watson statistic and the first-order autocorrelation of the residuals are reported. When the Durbin-Watson statistic is well below 2 the significance levels computed using ordinary regression should not be considered exact.

Data from a joint Russian/Norwegian cod stomach sampling programme (Mehl and Yaragina, 1992) were used to describe the variation in capelin consumption by month (unpub. data courtesy of A. Dolgov, Polar Research Institute of Marine Fisheries and Oceanography, Murmansk). The proportion of capelin in cod stomachs ( $P_{\text{cap}}$ ) for a given month was estimated as:

$$P_{\text{cap}} = \frac{\sum_n \text{wet weight of capelin in stomach bolus}}{\sum_n \text{total wet weight of food in stomach bolus}} \times 100 (\%) \quad (3)$$

where  $n$  represents the total number of observations of non-empty cod stomachs in a given month and year. The values of  $P_{\text{cap}}$  are not disaggregated by geographic region or by length class. Therefore, the analysis assumes that there are no significant differences among length classes or among geographic regions in  $P_{\text{cap}}$  over time. The time period having estimates of  $P_{\text{cap}}$  (1984–1996) includes the dramatic decrease in capelin abundance in 1987 (Fig. 1).

## Herring abundance indices

Total abundance of juvenile herring in the Barents Sea and the frequency of occurrence of herring in cod stomachs ( $F_{\text{her}}$ ) were used as indices of the abundance and availability, respectively, of herring. Virtual population analysis estimates of abundance at age of Norwegian spring-spawning herring on 1 January are available for 1950–1994 (ICES, 1997). Herring aged 0 and 1 were assumed to constitute the age classes which could be utilized by cod as prey. However, the VPA estimates of the number at age 0 and 1 ( $N_{\text{vpa},0,y}$  and  $N_{\text{vpa},1,y}$ , respectively) do not correspond to the number of herring available to Barents Sea cod because a variable fraction of these age classes reside in coastal areas (Dragesund *et al.*, 1980). For the years 1950–1988 the total abundance of juvenile herring in the Barents Sea in the year  $y$  ( $N_{\text{bar},\text{juv},y}$ ) was estimated as:

$$N_{\text{bar},\text{juv},y} = (N_{\text{vpa},0,y} + N_{\text{vpa},1,y}) \times K_y \quad (4)$$

where  $K_y$  is the smoothed proportion of juvenile herring resident in the Barents Sea in year  $y$  (Holst and Slotte, 1998). Values of  $K_y$  ranged from 0.1 to 0.95. For 1989 onwards,  $N_{\text{bar},\text{juv},y}$  was estimated as:

$$N_{\text{bar},\text{juv},y} = N_{\text{vpa},0,y} + N_{\text{vpa},0,y} - N'_{\text{sur},\text{juv},y} \quad (5)$$

where  $N'_{\text{sur},\text{juv},y}$  is the corrected abundance of juvenile herring along the coast estimated by acoustic surveys. Because the acoustic surveys are conducted in November/December the value for the preceding year ( $N_{\text{sur},\text{juv},y-1}$ ; Table 3.3.6 in ICES, 1997) was adjusted to 1 January of year  $y$  ( $N'_{\text{sur},\text{juv},y}$ ) by:

$$N'_{\text{sur},\text{juv},y} = N_{\text{sur},\text{juv},y-1} e^{-zt} \quad (6)$$

where  $z$  for immature herring was assumed to be 0.9 (ICES, 1997) and  $t$  was equal to 0.17 (i.e. 2 months of mortality). The percentage of non-empty cod stomachs which contained herring ( $F_{\text{her}}$ ) was used as an index of herring availability to cod. This value was estimated in the same way as  $F_{\text{cap}}$ . The effect of interannual variation in herring abundance on the availability of capelin to cod was assessed by examining the relationship between  $F_{\text{cap}}$  and total stock biomass of herring (ICES, 1997).

## Temperature effects

The Kola section time series (Tereshchenko, 1996) describes variation in monthly mean water temperatures along a transect located in the central part of the Barents Sea (33°30'E between 70°30' and 72°30'N; Fig. 2). In this study monthly mean temperatures for the 0–200 m layer were used as an index of the annual mean temperature.

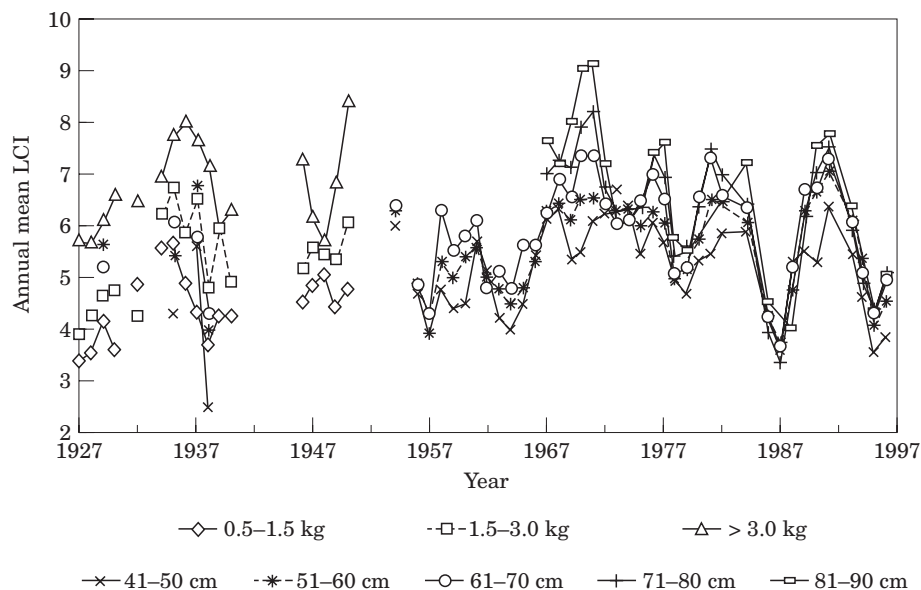


Figure 3. Time series of annual mean LCI (%) of Northeast Arctic cod.

Table 1. Summary data describing the relationship between LCI and two indices of capelin abundance (1973–1996). Capelin stock biomass was transformed to natural logarithms then simple linear regression was used. Values of  $a$  and  $b$  given below correspond to model:  $LCI_y = a + b$  (Indep. Var.).

Indep. Var.	Length class (cm)	n	$r^2$	$p^*$	a	b
ln Capelin stock biomass	41–50	21	0.61	<0.01	-1.58	0.47
	51–60	21	0.60	<0.01	-1.19	0.47
	61–70	21	0.65	<0.01	-2.25	0.57
	71–80	21	0.76	<0.01	-4.12	0.70
	81–90	16	0.60	<0.01	-3.19	0.64
Capelin:cod biomass ratio	41–50	21	0.51	<0.01	8.16	0.43
	51–60	21	0.59	<0.01	8.88	0.47
	61–70	21	0.66	<0.01	9.79	0.57
	71–80	21	0.73	<0.01	10.60	0.69
	81–90	16	0.58	<0.01	10.34	0.63

The effect of temperature on  $LCI_y$  was examined by including the annual mean temperature as an independent variable in a multivariate regression model which also contained ln-transformed capelin stock biomass.

## Results

### Interannual variation in LCI

The full LCI time series (1927–1996) shows rapid fluctuations which are more or less synchronous across size classes (Fig. 3). Values of  $LCI_y$  varied between approximately 3 and 9% through time and across all five of the length classes. In the first 4 years of the time

period  $LCI_y$  values were usually less than 6%. Both the weight-based and length-based  $LCI_y$  suddenly decreased in 1938. Values of  $LCI_y$  were relatively stable from 1946–1963, but one to two percentage points lower than the 1967–1976 time period, which was a sustained period of high (>5%) values. During the 1967–1976 period  $LCI_y$  increased with increasing length class within a given year. Decreases in  $LCI_y$  occurred during 1977–1979 and 1984–1987. The strongest variation in  $LCI_y$  was observed in the most recent years (1987–1996) when minima in 1987 and 1995 coincided with or followed minima in capelin stock biomass (Fig. 1). In 1986–1988 values of  $LCI_y$  for the two largest length classes were equal to or lower than those of the smallest

length classes suggesting that the decline in  $LCI_y$  was disproportionately great for large cod.

#### Trophic influences on interannual variation in LCI

Significant ( $p^* < 0.01$ ), positive relationships were observed between  $LCI_y$  and ln-transformed values of capelin stock biomass (Table 1). Below a capelin stock biomass of 1 million tonnes values of  $LCI_y$  decreased rapidly, whereas only slight increases in  $LCI_y$  occurred above a capelin stock biomass of 2 million tonnes (Fig. 4). High capelin stock biomass results in higher values of  $LCI_y$  in large cod (Fig. 4c–e) compared to small cod (Fig. 4a,b). There were significant ( $p^* < 0.01$ ), positive relationships between  $LCI_y$  and the ratio of capelin stock biomass to cod stock biomass although the biomass ratio usually explained a slightly smaller amount of variability in the relationship (Table 1). Values of  $LCI_y$  decreased rapidly below a capelin:cod biomass ratio of approximately one.

The relationship between  $LCI_y$  and  $F_{cap}$  was positive for all five length classes (Fig. 5). This pattern of variation in the smallest length classes was distinctive: both low and high values of  $LCI_y$  were observed at low values of  $F_{cap}$  but only high values of  $LCI_y$  were observed when the  $F_{cap}$  was high (Fig. 5a–c). These length classes had an upper boundary of  $LCI_y$  between 6 and 7% (Fig. 5a–c). The relationships between  $LCI_y$  and  $F_{cap}$  for the two largest length classes were approximately linear (Fig. 5d,e) and there was less evidence of an upper boundary in  $LCI_y$ .

A positive relationship between  $LCI_y$  and  $N_{bar,juv,y}$  would be expected if herring were an important prey item for cod. However, none of the five length classes showed a statistically significant, positive relationship between  $LCI_y$  values and  $N_{bar,juv,y}$  or ln-transformed  $N_{bar,juv,y}$  (Table 2). Likewise, there was no significant, positive relationship between  $LCI_y$  and  $F_{her}$  (Table 2). The only statistically significant ( $p^* < 0.05$ ) relationships between  $LCI_y$  and  $F_{her}$  (for the 41–50, 51–60, and 61–70 cm length classes) were negative. There was a significant, negative relationship ( $r^2 = 0.27$ ,  $p^* < 0.01$ ) between  $F_{cap}$  and the log-transformed total stock biomass of Norwegian spring-spawning herring (Fig. 6).

#### Temperature effects on interannual variation in LCI

In the multivariate model which included ln-transformed capelin biomass and annual mean temperature as independent variables, the capelin biomass term was consistently significant (Table 3). Annual mean temperature had a significant ( $p = 0.02$ ) effect on  $LCI_y$  for only one of the length classes and a marginally

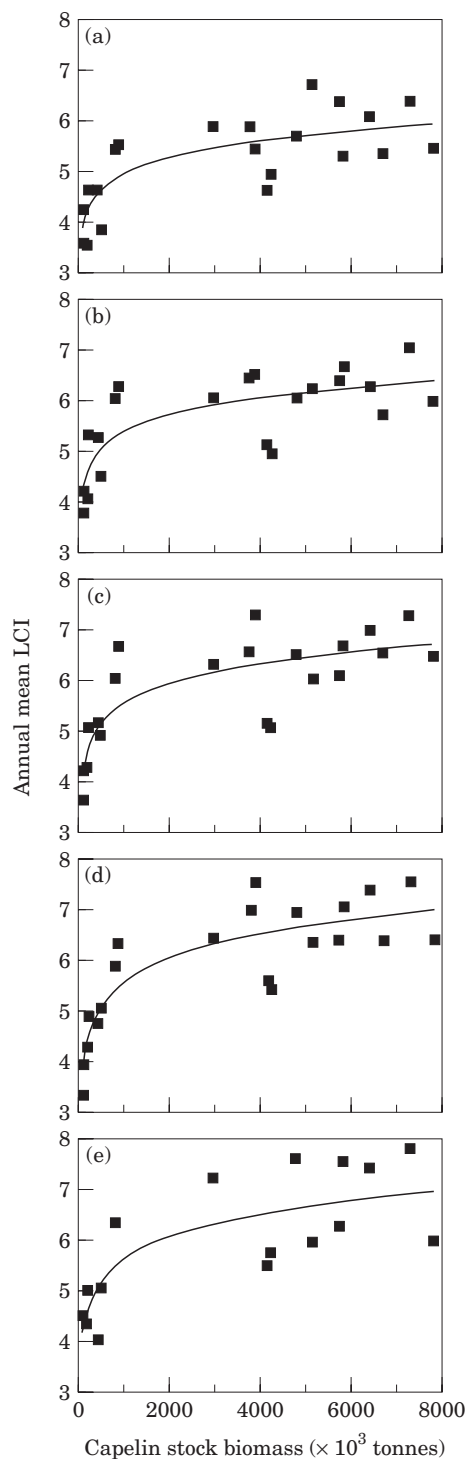
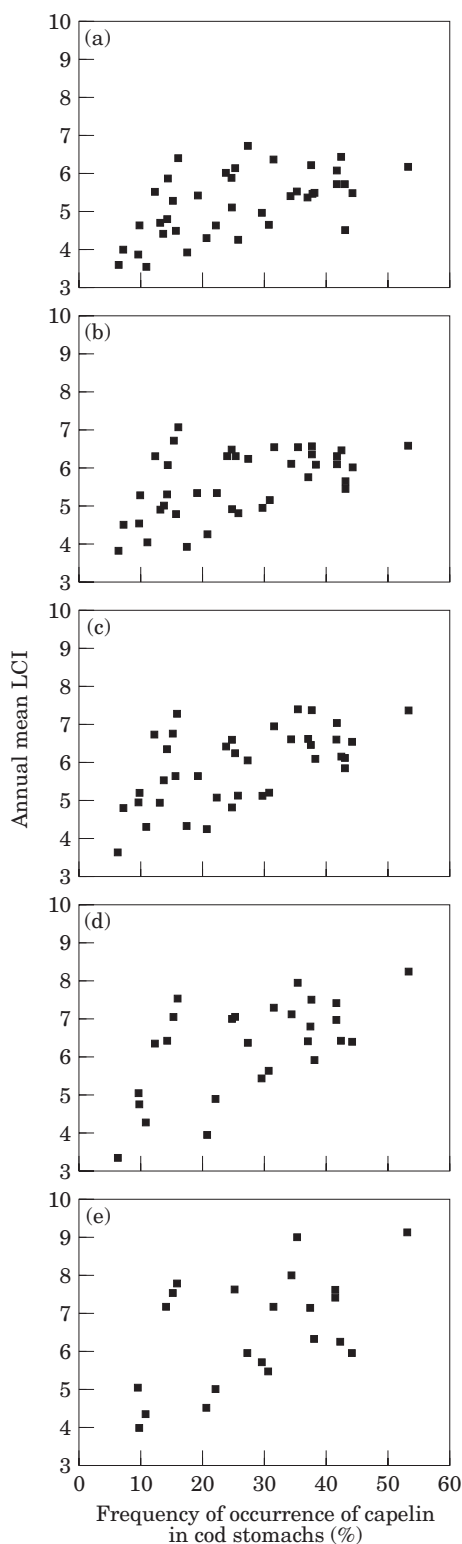


Figure 4. Relationship between annual mean LCI (%) and capelin stock biomass (1973–1996). Solid lines indicate the regression relationships between the annual mean LCI and ln-transformed capelin stock biomass given in Table 1. (a) 41–50 cm cod, (b) 51–60 cm cod, (c) 61–70 cm cod (d) 71–80 cm cod, and (e) 81–90 cm cod.



significant effect ( $p=0.05$ ) for two others (Table 3). Neither the Durbin-Watson statistic  $d$  and first-order autocorrelation of residuals suggested that the time series nature of the data unduly biased estimates of statistical significance.

### Seasonal variation in LCI

Significant differences between high and low capelin biomass years in  $LCI_m$  were observed for the months of February through July in all five length classes (Fig. 7). From September through January, LCI values for the high and low capelin biomass years were not significantly different from each other. For the three smallest length classes peak values of  $LCI_m$  were observed from March through May in high capelin years, whereas, peak values occurred in October or November in poor capelin years (Fig. 7a–c). In the two largest length classes seasonal peaks were less evident in high capelin biomass years, whereas peak values occurred in November or December in low capelin biomass years (Fig. 7d,e). In both high and low capelin biomass years the  $LCI_m$  values for smaller length classes in February through July are similar in magnitude to the corresponding values for the larger length classes (Fig. 7). Therefore, differences between small and large length classes in maximum values of  $LCI_y$  noted for both Figures 4 and 5 result from the LCI values for smaller length classes being lower from September to January relative to the larger length classes.

### Seasonal variation in capelin consumption

Differences in the magnitude of  $P_{cap}$  among months and years are striking (Fig. 8). Poor capelin feeding years, defined here as years having values of  $P_{cap}$  consistently less than 50%, include 1987, 1988, 1995, and 1996. Good capelin feeding years, defined here as years having more than three observations of  $P_{cap}$  which are greater than 50%, include 1990, 1991, 1993, and 1994. Capelin stock biomass was at a maximum (7.3 million tonnes) in 1991 (Fig. 1). In this year, six of the nine observed values of  $P_{cap}$  were higher than 50% and the maximum value of  $P_{cap}$  was 98%. Within a given year, maximum values of  $P_{cap}$  occurred most often in March and April. In several years (1989, 1991–1994), a secondary peak was observed in the second half of the year. Thus, fall peaks as well as spring peaks in  $P_{cap}$  appear to characterize good capelin feeding years.

Figure 5. Relationship between annual mean LCI (%) and the frequency of occurrence of capelin in cod stomachs. (a) 41–50 cm cod (1954–1996), (b) 51–60 cm cod (1954–1996), (c) 61–70 cm cod (1954–1996), (d) 71–80 cm cod (1967–1996), and (e) 81–90 cm cod (1967–1996).

Table 2. Summary data describing the relationship between LCI and indices of herring abundance or availability. Values of a and b given below correspond to model:  $LCI_y = a + b$  (Indep. Var.).

Indep. Var.	Length class (cm)	n	r <sup>2</sup>	p*	a	b
N <sub>bar,juv,y</sub>	41–50	37	0.01	0.51	5.33	$-7.82 \times 10^{-13}$
	51–60	37	<0.01	0.75	5.62	$4.01 \times 10^{-13}$
	61–70	37	<0.01	0.85	5.93	$2.74 \times 10^{-13}$
	71–80	25	<0.01	0.79	6.35	$6.23 \times 10^{-13}$
	81–90	20	<0.01	0.71	6.69	$1.08 \times 10^{-12}$
ln N <sub>bar,juv,y</sub>	41–50	37	0.10	0.07	7.92	-0.11
	51–60	37	0.04	0.23	7.42	-0.08
	61–70	37	0.05	0.18	8.16	-0.09
	71–80	25	0.03	0.46	8.30	-0.09
	81–90	20	0.02	0.57	8.61	-0.08
F <sub>her</sub>	41–50	39	0.10	0.05	5.38	-0.07
	51–60	39	0.15	0.02	5.82	-0.09
	61–70	39	0.11	0.04	6.11	-0.08
	71–80	27	0.06	0.23	6.48	-0.32
	81–90	22	0.05	0.31	6.85	-0.34

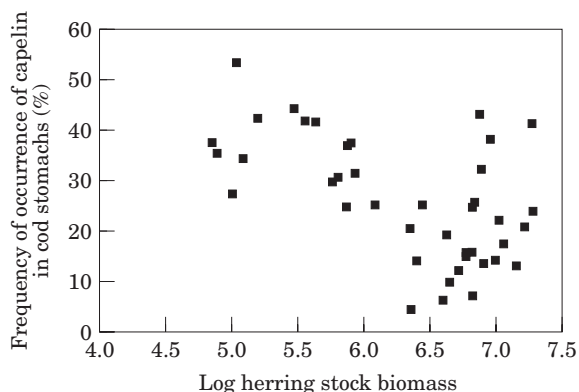


Figure 6. Relationship between the frequency of occurrence of capelin in cod stomachs and log-transformed total stock biomass of Norwegian spring-spawning herring (1953–1994).

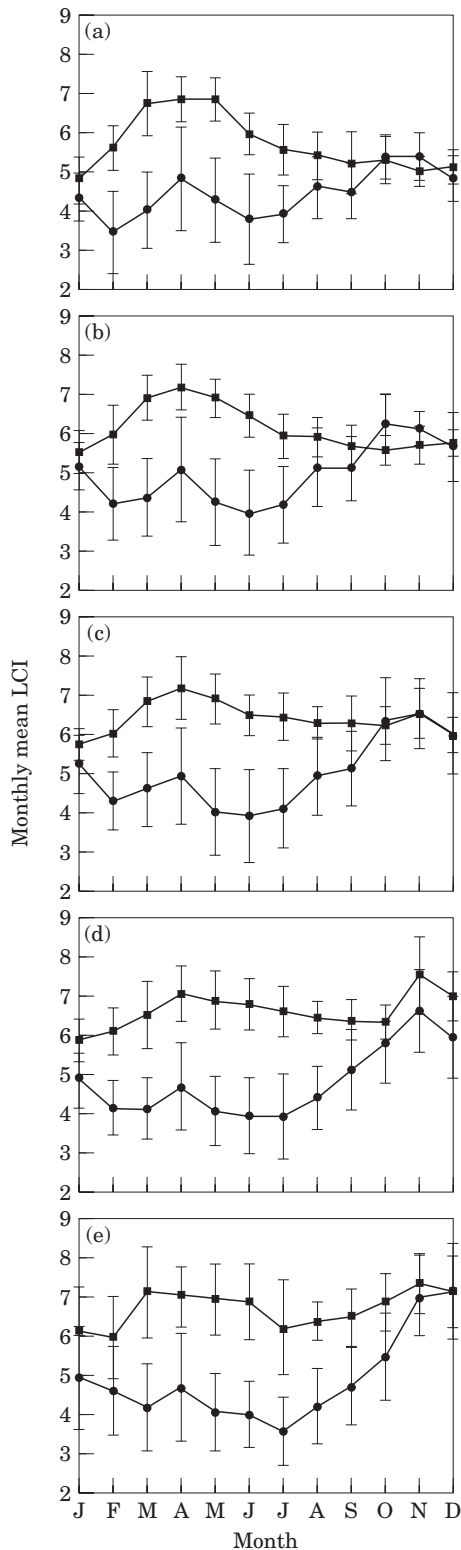
To examine further the relationship between LCI and capelin feeding, values of P<sub>cap</sub> were plotted against LCI for the same month. Positive trends were observed for all

five length classes (Fig. 9), however, the observed pattern of variation was not a simple linear relationship with constant variance. Instead, LCI was both high and low when P<sub>cap</sub> was low but only high when P<sub>cap</sub> was high. In other words, the combination of high P<sub>cap</sub> and low LCI was not observed. The pattern of variation is similar to that observed in the relationship between LCI<sub>y</sub> and F<sub>cap</sub> (Fig. 5). The degree of scatter in these relationships remained approximately the same if LCI lagged P<sub>cap</sub> by 1 or 2 months. The possibility that a portion of the variability in these relationships resulted from pooling data across months having different relationships between LCI and P<sub>cap</sub> was examined using analysis of covariance with month as the treatment variable and P<sub>cap</sub> as the covariate. There were statistically significant (p<0.05) differences in the intercepts of the relationships between LCI and P<sub>cap</sub> among the different months (Table 4) indicating that the relationship between LCI and P<sub>cap</sub> exhibits a significant degree of seasonality. Slopes were significantly different for the 41–50 cm length class only (Table 4).

Table 3. Summary data describing the relationship between LCI and ln-transformed capelin stock biomass (ln Cap. Bio.) and annual mean temperature (Mean Temp.). Multivariate regression was used to fit the model:  $LCI_y = a + b_1 \ln \text{Cap. Bio.} + b_2 \text{Mean Temp.}$ . The values for a, b<sub>1</sub>, and b<sub>2</sub> are given below. The p values for b<sub>1</sub> and b<sub>2</sub> are in parentheses. The Durbin–Watson statistic (d) and the first order autocorrelation of the residuals are also given.

Length class (cm)	n	r <sup>2</sup>	a	b <sub>1</sub>	b <sub>2</sub>	d	Autocorrelation
41–50	21	0.69	-3.30	0.45 (<0.01)	0.53 (0.05)	1.53	0.12
51–60	21	0.71	-3.29	0.45 (<0.01)	0.63 (0.02)	1.56	0.19
61–70	21	0.72	-4.22	0.55 (<0.01)	0.58 (0.05)	1.44	0.24
71–80	21	0.79	-5.63	0.68 (<0.01)	0.47 (0.10)	1.59	0.18
81–90	16	0.65	-5.14	0.61 (<0.01)	0.61 (0.18)	1.68	0.11





## Discussion

Rapid fluctuations in the abundance of pelagic stocks in the Barents Sea (Fig. 1) affect the LCI and, hence, the stored energy reserves of the NA cod stock. The annual mean LCI decreases rapidly when the biomass of Barents Sea capelin stock falls below approximately one million tonnes or a capelin:cod biomass ratio of 1:1. No positive effect of herring abundance or availability on the annual mean LCI was detected. This suggests that herring are not of major importance as a prey item for cod, a conclusion consistent with the observation that herring comprised approximately 6% of the total consumption of NA cod (Bogstad and Mehl, 1997). By comparison, capelin accounted for 36 and 34% of the diet of cod age 4 and 7, respectively (Bogstad and Mehl, 1997). The inverse relationship between the frequency of occurrence of capelin in cod stomachs and the abundance of the Norwegian spring-spawning herring stock (Fig. 6) suggests that herring affect LCI by influencing the availability of capelin to cod. High abundance of Norwegian spring-spawning herring has been previously associated with reduced abundance of Barents Sea capelin (Hamre, 1988, 1994; Gjøsaeter and Bogstad, 1998). This inverse relationship might result from herring feeding on 0-group capelin as the capelin migrate from coastal spawning areas to the Barents Sea (Huse and Toresen, 1995). The resurgence of the herring stock in the Barents Sea beginning in the early 1980s (Fig. 1) may have triggered the capelin collapses which began in the early 1980s and early 1990s and the subsequent declines in LCI. Likewise, the strong 1959 herring year class has been implicated in the collapse of the Barents Sea capelin stock in 1962–1964 (H. Gjøsaeter, Institute for Marine Research, Bergen, pers. comm.). This could explain the decrease in the annual mean LCI which was observed from 1961 to 1964 (Fig. 3).

In our analysis, temperature, as represented by the Kola section temperature, was not consistently correlated with the annual mean LCI (Table 3). However, temperatures measured at fixed hydrographic stations may not be representative of the ambient temperature experienced by cod on either seasonal (Godø and Michalsen, 1997) or interannual scales (Michalsen *et al.*, 1998). Significant effects of per capita food abundance and Kola section temperature on a weight-based measure of growth of NA cod have been noted previously (Nilssen *et al.*, 1994). Similarly, both capelin

Figure 7. Monthly mean LCI (%) of NA cod for the years when capelin stock biomass was less than 1 million tonnes (diamonds) and years when capelin stock biomass was greater than 1 million tonnes (squares). The 95% confidence limits are shown. (a) 41–50 cm cod, (b) 51–60 cm cod, (c) 61–70 cm cod, (d) 71–80 cm cod, and (e) 81–90 cm cod.

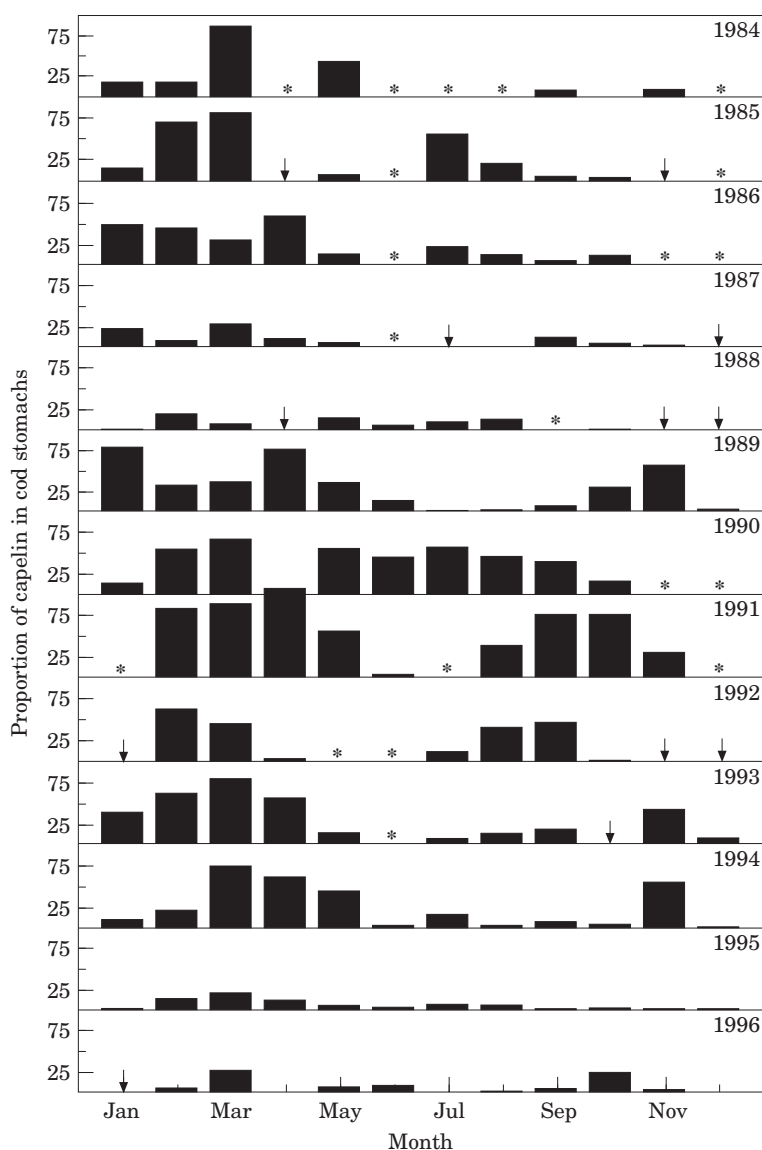


Figure 8. The proportion of capelin in the stomach contents (% wet weight) of Northeast Arctic cod by month and year (1984–1996). Arrows denote null values and asterisks denote missing values.

stock biomass and temperature have significant effects on weight (expressed as Fulton's  $K$ ) of northern cod (Krohn *et al.*, 1997) and the mean weight-at-age of Icelandic cod (Steinarsson and Steffánsson, 1996). The lack of a strong temperature effect on LCI could be due to the fact that LCI is a ratio value which standardizes for variation in total body weight. Liver weights could also be more strongly affected by food availability than by temperature.

Links between LCI and capelin are also detectable on seasonal time scales. In years when capelin were abundant peak values in monthly mean LCI occurred in the spring for three smallest length classes (Fig. 7a–c).

This could reflect intense feeding on capelin by cod during the annual spring migration of mature capelin to coastal spawning areas (Dragesund *et al.*, 1973). Spring peaks in the proportion of capelin in the stomach contents of cod are indicated in Figure 8. In years of high and low capelin stock biomass, a peak in monthly mean LCI was observed in November or December in large cod (Fig. 7d,e). This fall peak could be related to the annual cycle of gonad maturation. However, seasonality of LCI in mature and immature cod are often synchronous which suggests that it is dependent on the availability of shared food resources rather than maturation dynamics. For example, immature and mature

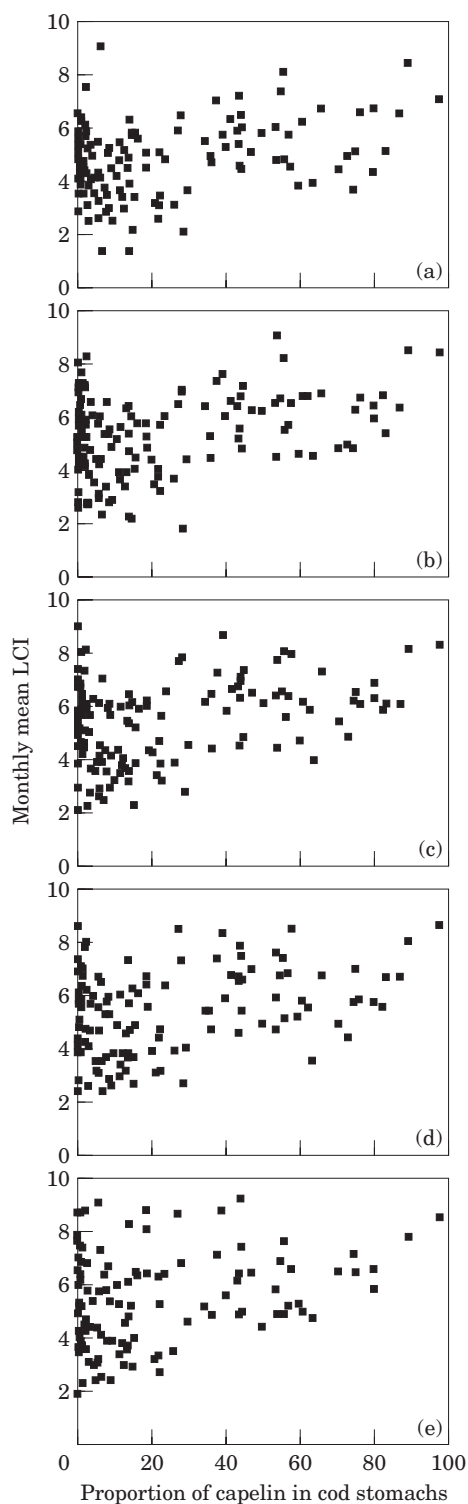


Figure 9. Relationship between monthly mean LCI (%) and the proportion of capelin in the stomach contents (% wet weight) of Northeast Arctic cod (1984–1996). (a) 41–50 cm cod, (b) 51–60 cm cod, (c) 61–70 cm cod, (d) 71–80 cm cod, and (e) 81–90 cm cod.

Table 4. Summary data for analysis of covariance where LCI for a given month and length class is the dependent variable, the proportion of capelin in stomach contents ( $P_{\text{cap}}$ ) in that same month is the covariate and month is the treatment variable. The ANCOVA model was fit with an interaction term ( $P_{\text{cap}} \cdot \text{month}$ ). Significance of the covariate, treatment variable, and interaction term are given below along with the number of observations (n) and coefficient of determination ( $r^2$ ).

Length class (cm)	n	$r^2$	$P_{\text{cap}}$	Month	$P_{\text{cap}} \cdot \text{month}$
41–50	131	0.37	<0.01	0.01	0.04
51–60	135	0.38	<0.01	<0.01	0.29
61–70	134	0.40	<0.01	<0.01	0.66
71–80	134	0.42	<0.01	<0.01	0.42
81–90	114	0.37	<0.01	<0.01	0.78

coastal cod showed similar seasonal variation in liver weight, increasing from October until January (Eliassen and Vahl, 1982). Immature and mature cod in the SV region of the Barents Sea show a distinct fall peak in LCI which has been attributed to higher feeding rates in the July through October period (Yaragina, 1996). Furthermore, seasonal peaks in LCI do not necessarily precede spawning. For example, cod in the northern Gulf of St Lawrence have peak LCI values in August but spawn in May to early July (Lambert *et al.*, 1997b).

In the months September through January (Fig. 7) values of monthly mean LCI converge towards common values such that LCI in years when capelin are abundant are indistinguishable from LCI in years when capelin are scarce. This suggests that the LCI in the months immediately prior to spawning would be a poor index of interannual differences in energetic reserves of spawners. The differences between high and low capelin biomass years are greatest in May and June (Fig. 7) which are the months immediately following the feeding peaks in March and April (Fig. 8). LCI values at this time of the year are therefore more likely to indicate interannual variation in the physiological condition of spawners.

Being able to resolve variation in LCI with respect to body size is an important attribute of the Russian LCI database. Both low and high annual mean LCI were observed for cod in the 41–60 cm size range when the frequency of occurrence of capelin in cod stomachs was low (Fig. 5a,b). High LCI when capelin are scarce suggests that these cod can utilize alternative prey to achieve values comparable to those attained when capelin are abundant. For these length classes there was an upper boundary in annual mean LCI between 6 and 7% (Figs 4a,b and 5a,b), indicating that there is an upper limit to the amount of energy they allocate to stored reserves. For larger length classes higher values of annual mean LCI were observed when capelin abundance/availability was high (Figs 4d,e and 5d,e). This suggests that large cod may have a greater capacity

to store energy in the liver year round. They are, however, more dependent than small cod on capelin to achieve these high LCI values. A greater capacity for storing energy would be a sensible strategy given that large cod utilize a disproportionately large amount of energy during spawning (Kjesbu *et al.*, 1991). Large cod consume a higher proportion of lipid-rich piscivorous prey such as capelin than do small cod (Bogstad and Mehl, 1997) which might contribute to the higher LCI values in the former size classes.

The strong links between Barents Sea capelin and LCI of NA cod indicate that the two cannot be considered in isolation. This coupling influences the reproductive potential of the cod stock. For example, cod will have a lower fecundity at length in years when capelin (LCI) is low compared to years when capelin (LCI) is high (Kjesbu *et al.*, 1998). Low capelin (LCI) may also increase mortality in spawning females whose energy reserves are exhausted as has been suggested for cod in the northern Gulf of St Lawrence (Lambert and Dutil, 1999). Declines in capelin (LCI) have accompanied the collapse of cod stocks off Newfoundland/Labrador (Lilly, 1997). There is a need to evaluate the degree to which depleted food resources reduce the energy reserves of the spawning stock and constrain recruitment in fish stocks (Cochrane and Hutchings, 1995; Kawasaki and Omori, 1995; Lambert and Dutil, 1997b). Long-term databases describing prey abundance and physiological condition of spawners are critical to testing this hypothesis.

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