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Fish condition: what should we measure in cod (Gadus morhua)?

by

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Abstract. With the closure of major cod fisheries in the Northwest Atlantic, fishery managers need to determine biological criteria on which to rest the process of monitoring the health status of cod stocks and to assist in decision-making about re-opening fisheries. These criteria should rest not only on traditional estimates of stock abundance, but also on measures of stock productivity. This paper proposes such criteria based on fish condition. Fish condition is defined and sources of variability are examined using data for cod in the northern and southern Gulf of St. Lawrence. Sampling recommendations are made. Samples should be taken periodically during the year to identify the extremes in condition. Somatic weight provides a more accurate measure of condition than total weight and should be used whenever possible to assess condition. Small samples are adequate, but samples stratified according to length are required when comparisons are made between size classes or between stocks. For each fish sampled, the minimum information collected must include fork length, total weight, sex, weight of stomach contents, liver and gonads, and water content of liver and muscle. The results from many experiments conducted in the laboratory provide the necessary background for the interpretation of field measures.

Résumé. Suite au moratoire sur la pêche de certains stocks de morue dans l'Atlantique, il est devenu nécessaire d'identifier une série de critères biologiques sur lesquels fonder le programme de monitorage des stocks et les décisions d'une éventuelle réouverture. Ces critères reposeraient non seulement sur les évaluations traditionnelles, mais aussi sur des mesures de la productivité des stocks. Ce document propose de tels critères basés sur l'évaluation de la condition des poissons. La condition est définie et les sources de variabilité sont évaluées à partir de données provenant des stocks du nord et du sud du Golfe Saint-Laurent. Des recommandations précises sont faites. Des échantillons devraient être récoltés périodiquement au cours de l'année pour détecter les niveaux extrêmes. Le poids somatique reflète mieux la condition que le poids total. Par conséquent, il est préférable d'utiliser le poids somatique lorsque celui-ci est disponible. Le nombre d'échantillons requis est faible, mais il est préférable de recourir à l'échantillonnage stratifié selon la longueur pour faciliter la comparaison entre classes de taille ou entre des stocks. Pour chaque poisson échantillonné, il faut mesurer la longueur à la fourche, le poids total, le sexe, le poids du contenu stomacal, du foie et des gonades, et le contenu en eau du foie et du muscle. Des résultats provenant d'expériences effectuées en laboratoire fournissent l'éclairage nécessaire à l'interprétation des mesures de terrain.

Introduction

The recent decline observed in cod stocks in the Northwest Atlantic and in the Gulf of St. Lawrence (Fréchet et al. 1994, Sinclair et al. 1994) has raised questions concerning the methodology used in stock assessments. Typically, research vessels surveys and fisheries statistics provide the basic ingredients for estimating population trends. Estimates of the abundance at age of the population are calculated using an age-length key and the length frequency of the population. Similarly, removals at age by the fishery are calculated from comparable samples taken at landing points. Using this basic information, a sequential population analysis is calibrated using various mathematical procedures (Rivard 1988, ICES 1993). Once the analysis is completed, biomass estimates can be calculated using observed average weights at age. The results provide estimates of the trends in fishing mortality, population abundance and biomass as well as recruitment. While such estimates are essential for management purposes, they do not necessarily provide a complete picture of stock health. The results indicate trends in the aggregate population but do not provide by themselves indications of the condition of the individuals in the population.

Condition can be defined as a state of physical fitness. The state of physical fitness of the animals will determine whether they will be able to meet daily vital requirements and to face a set of seasonal or annual constraints in their environment. Generally, condition refers to energy reserves because energy is required to fuel all metabolic processes. Many species have developped strategies to store energy during periods of food abundance in preparation for long periods of starvation as occurs for instance in northern lakes in salmonids (Dutil 1986) and coregonids (Lambert and Dodson 1990). Energy content is easily measured by direct combustion in a bomb calorimeter (Grodzinski et al. 1975). Condition however can also be derived from body and individual organ or tissue composition (Grodzinski et al. 1975). Proteins and lipids make up the bulk of energy sources in fish (Brett and Groves 1979). Lipids are the main form of storage of usable energy (Shul'man 1974). Food however, does not only provide energy. Vitamins, essential amino acids and essential fatty acids are just as crucial as energy for survival (Carrillo et al. 1993, Kaushik and Luquet 1993). Thus condition may be assessed in terms of quality as much as in terms of quantity and should ideally rest upon a variety of criteria measured simultaneously (Busacker et al. 1990).

Condition reflects the success of an individual fish in the environment as it reflects the ability of an individual or a population in finding and storing energy under prevailing environmental conditions. Fish in good condition are said to have better chances of survival than fish in poor condition. The rationale is that fish in good condition are more efficient and more able to cope with adverse environmental conditions. This theory predicts that individuals in good condition should survive longer to food shortages (Wilkins 1967). Their swimming capacity should be greater which would enhace their ability to catch preys, avoid predators (Booman et al. 1991), move out of marginal habitats and go through seasonal migrations. They should also produce more gametes of higher quality (Cerda et al. 1994, DeMartini 1991, Kjesbu et al. 1991).

Condition will vary among individuals and between stocks, seasons, years and locations (e.g. Craig 1977, DeMartini 1991, Pulliainen and Korhonen 1990). These changes reflect individual fitness as well as spatial and temporal patterns in food availability and environmental conditions. Changes in natural mortality may also occur but will likely be caused by more extreme environmental conditions. Natural mortality will in most cases respond to a prolonged situation while condition will respond to short-term changes. Being in good condition does not necessarily mean higher chances of survival. Some environmental factors will cause natural mortalities indiscriminantly (Bodkin et al. 1987, Maclean 1989, Economidis and Vogiatzis 1992). However, many environmental factors will not impact to the same extent fish in poor and those in good condition. Fishing mortality for instance will affect both fish in poor and good condition, but vulnerability to fishing gears may be increased by condition because fish in poor condition may not have the same ability to swim as fish in good condition. On the other hand, fish in poor condition may be able to escape through the meshes while more rotund (better condition) fish will be retained.

In recent years, there has been a debate in the literature as to how condition indices should be calculated. Bolger and Connolly (1989) concluded that several indices, including the classical Fulton's condition factor (K), can be satisfactory but that the inherent assumptions need to be checked. Some of the various indices that he discussed included Fulton's condition factor, predicted weight at a given length and relative weight. Cone (1989) pointed out that Fulton's condition factor has often been misused insofar as the assumption of isometric growth is not verified. In many cases, condition indices will be length-dependent and the resulting population condition factor may be biased. To avoid bias, in this case, only populations with similar length distributions should be compared or other measures of condition should be examined. In response to Cone (1989), others have presented a case for their favorite condition measurement (see Springer et al. 1990). The debate around the predicted weight estimates focuses around the issue of using either least squares or geometric mean regression. Finally, the difficulty in using the relative weight index lies in the determination of the standard fish. Though the debate still persists as to which measure to use, several condition measurements, including K, are appropriate provided underlying assumptions have been verified (Bolger and Connolly 1989).

This short paper examines condition measurements in Atlantic cod using data for the northern and southern Gulf of St. Lawrence. We review recent information and examine interrelationships between major body constituents in order to propose simple-to-measure meaningful indices of energetic condition that could be used as part of the periodical surveys to provide more insight in stock productivity and to diagnose the health status of individuals in our stocks. Possible sources of bias and their implications on sampling are discussed.

Materials and Methods

Proximate analysis

Proximate composition of cod was analyzed following 2 feeding experiments conducted in 1991 and so as to get a wide range in energy contents. Trunk muscle and liver were examined as they make up the bulk of energy reserves in cod (Love 1970, Holdway and Beamish 1984, Hemre et al. 1993). Duplicate analyses of water, proteins and lipids content were done on homogenates of each tissue. Glycogen was only analyzed in the liver as negligible concentrations are found in cod muscle (Black and Love 1986, Kjesbu et al. 1991). Energy content was calculated using caloric equivalents of 39.5, 23.6 and 17.1 $kJ \cdot g^{-1}$ for lipids, proteins and glycogen, respectively (Kleiber 1975). The analytical procedures are described in Lambert et al. (1994).

Relationships between proximate composition and condition indices were assessed for a wide range of energy contents. Both field and laboratory samples were examined. Data were obtained from a starvation experiment conducted in 1994 and from samples of wild cod collected periodically in the northern and southern Gulf of St. Lawrence (Lambert and Dutil, in preparation; Schwalme and Chouinard, in preparation). Northern cod were collected in 1993 - 1995 and southern cod in 1991 - 1995.

Fork length (± 1 mm), total weight (± 1g), liver, gonads and stomach contents weights (± 0.1g) were measured. Sex and maturity were determined. Two condition indices were used. Condition factor was expressed as the Fulton's condition factor (K):

$$K = 100 \cdot W / L^3$$

where W is somatic weight (total weight minus gonads and stomach contents weights (g)) and L fork length (cm). Hepato-somatic index (HSI) was calculated as:

$$HSI = (LW / W) \cdot 100$$

where LW and W are liver weight and somatic weight (g), respectively. Head on gutted weight and head off gutted weight were also measured (± 1g) to estimate muscle weight and to allow calculations of somatic weight from gutted weight. Reference values for K and HSI were obtained from an experiment in which cod were either starved or fed to satiation for a prolonged period of time.

Muscle and liver were subsampled to determine water and energy content. Analyses were done in duplicate. Water content was determined by drying tissue samples to constant weight at 65 °C. Energy content was determined using an oxygen bomb calorimeter (Parr, model 1261). Muscle and liver energy content are expressed on both a relative and an absolute basis. Specific energy content was calculated as the quantity of energy (kJ) per gram of fresh tissue and total energy content as the product between specific energy content and tissue mass. Methods are described in detail in Lambert et al. (1994), Lambert and Dutil (in preparation) and Schwalme and Chouinard (in preparation).

Sampling and measurement considerations

Some aspects of sampling fish condition were also examined. In our analyses, somatic weight was used for seasonal data. The impact of using this measure of condition compared to condition factors using total weight was examined with the seasonal data collected in the southern Gulf of St. Lawrence. Both the trends and the magnitude of the coefficient of variation of the samples were examined.

Secondly, a predicted weight index (weight of a fish at 45 cm) was compared with the condition factor. This comparison was done using data from seasonal condition monitoring and the annual groundfish surveys conducted in the southern Gulf of St. Lawrence. For each sample, a weight-length relationship was computed and the predicted weight at 45 cm was computed.

Thirdly, the issue of sample size and sampling efficiency was examined. For this analysis, we used a large sample of 208 cod between 40 and 50 cm collected in June 1992. From this large sample, 30 sub-samples of a sample size of 5 were randomly chosen. After each sub-sample selection, the data were replaced in the original large sample. The mean and coefficient of variation of K were calculated for each of the 30 sub-samples. This procedure was repeated for sample sizes of 10, 15, 20, 25, 30, 35 and 50. The mean of the coefficients of variation with 95% confidence intervals were then computed for each set of a given sample size.

Results and discussion

Tissue composition and energy content

Muscle and liver show marked differences in composition. Cod muscle is a lean tissue with proteins accounting for 10 to 15% of fresh weight, roughly 75% of dry weight (figure 1). Similar values were found by Dambergs (1963, 1964), Fraser et al. (1961) and Eliassen and Vahl (1982). Values ranging up to 18-19% were reported by Love (1970), Jobling et al. (1991) and Holdway and Beamish (1984). Lipids make up 1% of muscle fresh weight (figure 1)(Dambergs 1963, 1964; Fraser et al. 1961; Love 1970; Holdway and Beamish 1984). The bulk of muscle energy content is made up of proteins and changes in muscle energy content are associated with changes in protein content, rather than with changes in lipid content, the concentration of lipids being remarquably constant over the whole range of muscle energy contents. Lipids are on the other hand largely responsible for changes in liver composition (figure 2). Specific lipid content varied widely from 5 to 70% of fresh weight. Similar ranges have been reported by Black and Love (1986), Holdway and Beamish (1984), Hemre et al. (1993) and Jobling et al. (1991). Lipids make up the bulk of energy reserves in the liver. Muscle glycogen content was not measured, but it has been estimated to be less than 0.3% of muscle fresh weight (Black and Love 1986, Kjesbu et al. 1991). This is equivalent to 5% of muscle energy reserves.

Liver glycogen varied between 1 and 5% of fresh weight) or 1 to 9% of liver energy reserves. The relationships between muscle protein or liver lipid and energy content are highly significant ($P < 0.0001$, $R^2 > 0.92$; figures 1 and 2).

Muscle energy (protein) and liver energy (lipid) contents can be estimated very precisely from measurements of water content. Minimal values for muscle and liver energy contents (1.5 $kJ \cdot g^{-1}$ and 5.0 $kJ \cdot g^{-1}$) coincided with maximum water contents, 90% water in muscle and 80% water in liver. Inversely, maximum energy contents (5 $kJ \cdot g^{-1}$ in muscle and 30 $kJ \cdot g^{-1}$ in liver) coincided with minimum water contents (78% and 20% for muscle and liver, respectively). Correlations between energy and water contents are strong ($P < 0.0001$, $R^2 > 0.96$; figure 3). Clearly however, muscle and liver do not yield the same information. Because lipids are stored in the liver (figure 2), higher liver water contents indicate a depletion of lipid reserves in a fish whereas higher muscle water contents indicate that an individual fish is getting exhausted (figure 4). When no food is available for instance, muscle water contents >84% mean that energy is being obtained from muscle proteins and not from lipids stored in the liver. Thus low water contents in the liver will not yield the same interpretation depending on the muscle water content.

Condition indices and energy content

Both K and HSI are reliable indicators of the energy content of cod. Changes in total energy content reflect both changes in specific energy content and changes in mass. Changes in specific energy content are not linear (figure 5). Muscle energy content and liver energy content per gram wet weight increase steeply as K and HSI increase, but they soon reach a plateau at intermediate values of K and HSI. Nevertheless total muscle and total liver energy content are linearly related to K and HSI so that these indicators would provide an accurate assessment of energetic condition (figure 6).

Potential values for various indicators

While condition indices such as K, HSI, muscle and liver water content reflect the energetic condition of cod and thus may give rise to comparisons or inferences, it may be easier and more enlightening to compare actual values against a scale of potential values as obtained under controlled conditions. From our own experiments, in which cod were either starved or fed to satiation for prolonged periods of time, and from the literature we determined minimal and maximal values for each of these variates. K and HSI values are based on somatic weight. Feeding experiments showed that cod fed capelin to satiation 3 times a week reached a condition factor value of 1.03 (range 0.83 - 1.25) and an HSI value of 7.1% (range 4.2 - 9.9), but HSI values higher than 10% have been observed in cod fed fatty diets (Jobling 1988, Lie et al. 1986). Water content was very low in the liver and muscle of well-fed cod, 22% (15-32) in the liver and 78% (77-80) in the muscle. Critical values were reached in cod that died from exhaustion following prolonged starvation. They had on average 87 and 88% water in muscle (range in the first experiment, 83-92; range in the second experiment, 84-92), 75 and 78% water in liver (range 61-81 and 68-83), and showed extremely low values for K (0.54 and 0.47, range 0.44-0.68 and 0.36-0.63) and of course HSI (1.0 and 0.6%, range 0.7-1.4 and 0.3-1.1). Black and Love (1986) starved cod over a shorter period of time as compared to our study. They observed K values ranging from 0.59 to 0.66 and a mean HSI value of 0.8%. Muscle water content reached 88% and liver water content 75%.

Based on the above results, the following criteria can be used to interpret condition in cod. The survival of cod with condition factor values below 0.70 is jeopardized. This situation is alarming particularly if HSI values are close to 1%, with water contents over 60% in the liver and over 88% in the muscle. Cod having a low condition factor, but having a HSI value above 2% may have fed recently. Water content in the liver should be below 60% and muscle water content should tend to decrease towards 84%. HSI values in the range 2 to 6% with condition factor values in the range 0.80 - 1.00 indicate a good condition. Water content in the liver should be lower than 40% and muscle water content should not be higher than 84%. Cod in excellent condition will have condition factor values over 1.00, HSI values over 6%, and will exhibit low water content in the liver (22%) and muscle (80%). Values for K, HSI and water content should however be considered in a seasonal perspective. Condition factor values around 0.80 for instance do not have the same meaning in late fall at the onset of maturation and following a period when feeding should have been intensive as in spring at the end of the spawning period.

Potential biases associated with sampling and with condition factors

A - Seasonal variation

Fish condition varies seasonnally and an assessment of condition should take such variability into consideration. From 1991 to early 1995, both the northern and southern Gulf of St. Lawrence cod stocks exhibited a marked seasonal variation in condition (figures 7 and 8). Cod reached peak K and HSI values at the end of summer. The peak condition did not persist in time as frequent samplings have shown for instance in fall 1993 for the northern stock. Lowest condition occurred in spring and early summer at the end of the spawning season. The value of a unique sample collected at a fixed time during the year (as in groundfish surveys) to monitor fish condition may be limited if fish are experiencing a marked change in condition during that period or if the cycle is coupled to specific environmental conditions. In this case, values of condition may be aliased. Consequently, given this pronounced annual cycle in condition, regular sampling during the year is necessary to accurately depict inter-annual changes in condition.

B) Spatial variation

Differences in fish condition are also likely to occur between locations. Potential differences were minimized by collecting samples for a given stock from its main seasonal area of distribution, for both the southern and northern Gulf of St. Lawrence. Samples for the southern Gulf originated from 4Vn in January, western Cape Breton in early spring, western southern Gulf (4Tk and 4Tl) in summer and western Cape Breton again in late fall. Samples for the northern Gulf originated from 3Pn in January and from the southern part of 4R in early spring. During summer and fall, samples were taken in 4R and 4S. The issue of within-stock variability in condition factor between locations should be examined.

C) Biases in K and comparisons of condition factors

Condition factor for the southern Gulf of St. Lawrence was calculated only for fish in the 40 to 50 cm range to minimize a potential problem of correlation between condition index and length. Within that size range, we found no relationship ($P>0.05$) between condition factor and length in all but three of the twenty-seven seasonal samples. The slope was marginally significant in these three cases. Condition factor was however observed to be independent of size for cod ranging in size between 30 and 55 cm in the northern Gulf of St. Lawrence (Lambert and Dutil, in preparation). The assumption of isometric growth inherent to condition factors should be verified when assessing condition, particularly when examining populations with a broad range in length or comparing stocks or local populations which differ in size distribution.

Condition factor values based on somatic and total weight were compared to each other and to predicted weight for cod at 45 cm. Condition factor values based on somatic weight or total weight and predicted weight at 45 cm followed similar seasonal patterns (figures 9 and 10). Predicted weight at 45 cm was highly correlated to condition factor based on total weight (r^2=0.98)(figure 11). Somatic weight however yielded lower values of the coefficient of variation for the condition factor than total weight (figure 12). This resulted from large differences between somatic and total weight which occured in spring, due to maturation of the gonads, and in late summer, due to intense feeding and heavy stomach contents. Because feeding intensity and gonad maturation can vary significantly within and between stocks, and because somatic weight is a more precise reflection of condition than total weight, somatic weight and not total weight should be used whenever possible to assess condition.

Gutted weight and not somatic weight are generally available in commercial sampling information. Somatic weight can be estimated precisely from gutted weight. Figure 13 shows regressions of gutted vs somatic weight for cod used in our studies using both head-on and head-off gutted weights for a range of sizes and levels of condition. Fulton's condition factor values based on somatic weight differ markedly from values based on head-on and head-off gutted weights. This difference increases as K increases. Condition factor drops from 0.50 (somatic weight) to 0.48 and 0.31, for head-on and head-off gutted weights, respectively, for fish in poor condition, and from 1.25 to 1.07 and 0.86, for fish in excellent condition.

D) Sample size

The results of efficiency calculations indicate that relatively small samples are adequate for the calculation of seasonal condition factors. Coefficients of variation were reduced by roughly 33% by increasing the sample size from 5 to 10 fish and by another 24% by increasing sample size from 10 to 15 (figure 14). Subsequent additions of 5 fish to the sample size reduced the coefficient of variations by approximately 10%. From these calculations, sample sizes of 20 to 30 produced coefficients of variation for the mean K of about 2%. From a sampling efficiency point of view, samples of 30 fish appear to be adequate to monitor fish condition.

Sampling recommendations

Since the closure of the cod fishery in 1993, the Fisheries Resource Conservation Council asked for a set of biological criteria on which to rest the process of monitoring the health status of the stocks and to assist in decision-making about re-opening fisheries. This paper provides the background for the interpretation of measures of condition. The following recommendations will insure that condition is measured accurately and can be interpreted meaningfully. Measuring condition should be viewed as an original and informative simple-to-measure stock characteristic describing the physiological status of the population. This important characteristic has, in our opinion, been overlooked in the past.

1- Samples should be taken periodically during the year. Monthly samples are required in the spring and 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.

2- 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. Stratified samples (3 fish / cm - 30 fish / 10 cm) would allow for comparisons between size groups and may facilitate comparison of condition between stocks.

3- Fulton's condition factor and hepato-somatic index should be calculated using somatic and 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.

4- For each fish sampled, the minimum information collected must include fork length (±1 mm), total weight (±1 g), weight of stomach contents (±1 g), sex, gonads weight (±0.1 g), liver weight (±0.1 g), water content of liver and muscle (%).

5- The above-mentionned variates are simple to measure and do not require extensive training or complex laboratory procedures. These measurements could be done by the industry. The cost is negligible.

References

Black, D. and R. M. Love. 1986. The sequential mobilization and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. J. Comp. Physiol. B 156: 469-479.

Bodkin, J. L., G. R. Van Blaricom and R. J. Jameson. 1987. Mortalities of kelp-forest fishes associated with large oceanic waves off central California, 1982-1983. Environ. Biol. Fish 18: 73-76.

Bolger, T. and P. L. Connolly 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. 34: 171-182.

Booman, C., A. Folkvord and J. R. Hunter. 1991. Responsiveness of starved northern anchovy *Engraulis mordax* larvae to predatory attacks by adult anchovy. Fish. Bull. 89: 707-711.

Brett, J. R. and T. D. D. Groves. 1979. Physiological energetics, p. 279-352. *In* W. S. Hoar, D. J. Randall and J. R. Brett (eds) Fish physiology. Vol. VIII. Bioenergetics and growth. Academic Press, New York, 786 p.

Busacker, G. P., I. R. Adelman and E. M. Goolish. 1990. Growth, p. 363-387. *In* C. B. Schreck and P. B. Moyle (eds) Methods for fish biology. American Fisheries Society, Bethesda, Maryland, 684 p.

Carrillo, M., L. Dahle, J. Morales, P. Sorgeloos, N. Svennevig and J. Wyban (eds). 1994. From discovery to commercialization. European Aquaculture Society, Special Publication No 19, European Aquaculture Society, Oostende, Belgium, 632 p.

Cerda, J., M. Carrillo, S. Zanuy, J. Ramos and M. de la Higuera. 1994. Influence of nutritional composition of diet on sea bass, *Dicentrarchus labrax*, reproductive performance and egg and larval quality. Aquaculture 128: 345-361.

Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. 118: 510-514.

Craig, J. F. 1977. The body composition of adult perch, *Perca fluviatilis*, in Windermere, with reference to seasonal changes and reproduction. J. Anim. Ecol. 46: 617-632.

Dambergs, N. 1963. Extractives of fish muscle. 3. Amounts, sectional distribution, and variations of fat, water-solubles, protein and moisture in cod (*Gadus morhua*) fillets. J. Fish. Res. Bd Can. 20: 909-918.

Dambergs, N. 1964. Extractives of fish muscle. 4. Seasonal variations of fat, water-solubles, protein and water in cod (*Gadus morhua*) fillets. J. Fish. Res. Bd Can. 21: 703-709.

DeMartini, E. E. 1991. Annual variations in fecundity, egg size and the gonadal and somatic conditions of queenfish *Seriphus politus* (Sciaenidae). Fish. Bull. 89: 9-18.

Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*) of the Nauyuk Lake system. Copeia 1986: 945-955.

Economidis, P. S. and V. P. Vogiatzis. 1992. Mass mortality of *Sardinella aurita* (Pisces, Clupeidae) in Thessaloniki Bay (Macedonia, Greece). J. Fish Biol. 41: 147-149.

Eliassen, J.-E. and O. Vahl. 1982. Seasonal variations in the gonad size and the protein and water content of cod, Gadus morhua, muscle from Northern Norway. J. Fish Biol. 20: 527-533.

Fraser, D. I., A. Mannan and W. J. Dyer. 1961. Proximate composition of Canadian Atlantic fish. III. Sectional differences in the flesh of a species of Chondrostei, one of Chimerae, and of some miscellaneous teleosts. J. Fish. Res. Bd Can. 18: 893-905.

Fréchet, A., Y. Gagnon, P. Schwab, D. D'Amours, J.-D. Dutil, Y. Lambert, L. Bourassa and C. Rollet. 1994. Revue de l'état du stock de morue du nord du Golfe Saint-Laurent (3Pn, 4RS) en 1993. Ministère des Pêches et des Océans (Canada), Pêches de l'Atlantique, Doc. Rech. 94/29: 50 p.

Grodzinski, W., R. Z. Klekowski, and A. Duncan (eds). 1975. Methods for ecological bioenergetics. International Biological Program, Handbook No 24, Blackwell, Oxford. 367 p.

Hemre, G. -I., Ø. Karlsen, G. Lehmann, J. C. Holm and Ø. Lie. 1993. Utilization of protein, fat and glycogen in cod (*Gadus morhua*) during starvation. Fisk. Dir. Skr. Ser. Ernæring 6: 1-9.

Holdway, D. A. and F. W. H. Beamish. 1984. Specific growth rate and proximate body composition of Atlantic cod (*Gadus morhua*). J. Exp. Mar. Biol. Ecol. 81: 147- 170.

ICES. 1993. Reports of the Working Group on methods of fish stock assessments. International Council for the Exploration of the Seas, Cooperative Research Report No 191: 249 p.

Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua*, with particular reference to growth under farmed conditions. Aquaculture 70: 1-19.

Jobling, M., R. Knudsen, P. S. Pedersen and J. Dos Santos. 1991. Effects of dietary composition and energy content on the nutritional energetics of cod, *Gadus morhua*. Aquaculture 92: 243-257.

Kaushik, S. J. and P. Luquet (eds). 1993. Fish nutrition in practice: International Symposium on Fish Nutrition and Feeding (IV). Institut National de la Recherche Agronomique (France), Colloques de l'INRA No 61, 972 p.

Kjesbu, O. S., J. Klungsøyr, H. Kryvi, P. R. Witthames and M. Greer Walker. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48: 2333-2343.

Kleiber, M. 1975. The fire of life: an introduction to animal energetics. Krieger Publishing, New York, 453 p.

Lambert, Y. and J. J. Dodson. 1990. Freswater migration as a determinant factor in the somatic cost of reproduction of two anadromous coregonines of James Bay. Can. J. Fish. Aquat. Sci. 47: 335-345.

Lambert, Y., J.-D. Dutil and J. Munro. 1994. Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 51:1569-1576.

Lie, O., E. Lied and G. Lambertsen. 1986. Liver retention of fat and fatty acids in cod (*Gadus morhua*) fed different oils. Aquaculture 59: 187-196.

Love, R. M. 1970. The chemical biology of fishes. Academic Press, New York, 547 p.

Maclean, J. L. 1989. Indo-Pacific red tides, 1985-1988. Mar. Poll. Bull. 20: 304-310.

Pulliainen, E. and K. Korhonen. 1990. Seasonal changes in condition indices in adult mature and non-maturing burbot, *Lota lota*, in the north-eastern Bothnian Bay, northern Finland. J. Fish Biol. 36: 251-259.

Rivard, D. 1988 (ed). Collected papers on stock assessment methods. Department of Fisheries and Oceans (Canada), Canadian Atlantic Fisheries Scientific Advisory Committee, Res. Doc. 88/61: 167 p.

Shul'man, G. E. 1974. Life cycles of fish: physiology and biochemistry. Wiley, New York, 257 p.

Sinclair, A., G. Chouinard, D. Swain, R. Hébert, G. Nielsen, M. Hanson, L. Currie and T. Hurlbut. 1994. Assessment of the fishery for southern Gulf of St. Lawrence cod: may, 1994. Department of Fisheries and Oceans (Canada), Atlantic Fisheries, Res. Doc. 94/77: 116 p.

Springer, T. A., B. R. Murphy, S. Gutreuter, R. O. Anderson, L. E. Miranda, D. C.Jackson and R. S. Cone 1990. Comments - Properties of relative weight and other

condition indices. Trans. Am. Fish. Soc. 119: 1048-1058.
Wilkins, N. P. 1967. Starvation of the herring, Clupea harengus: survival and some gross biochemical changes. Comp. Biochem. Physiol. 23: 503-518.

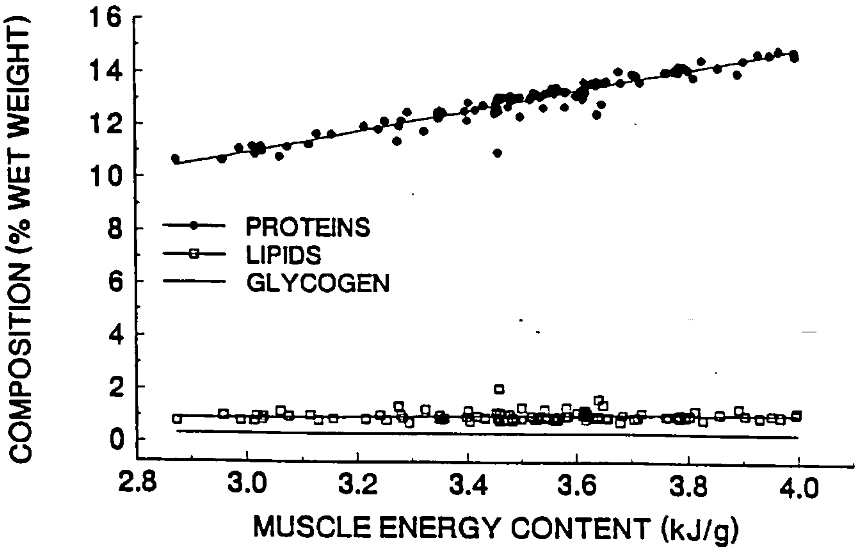

Figure 1. Variations in the protein, lipid and glycogen composition of muscle in relation to changes in muscle energy content in cod. Muscle proteins, lipids and glycogen are expressed as percentages of wet weight. Glycogen composition was taken from Black and Love (1986) and from Kjesbu et al. (1991).

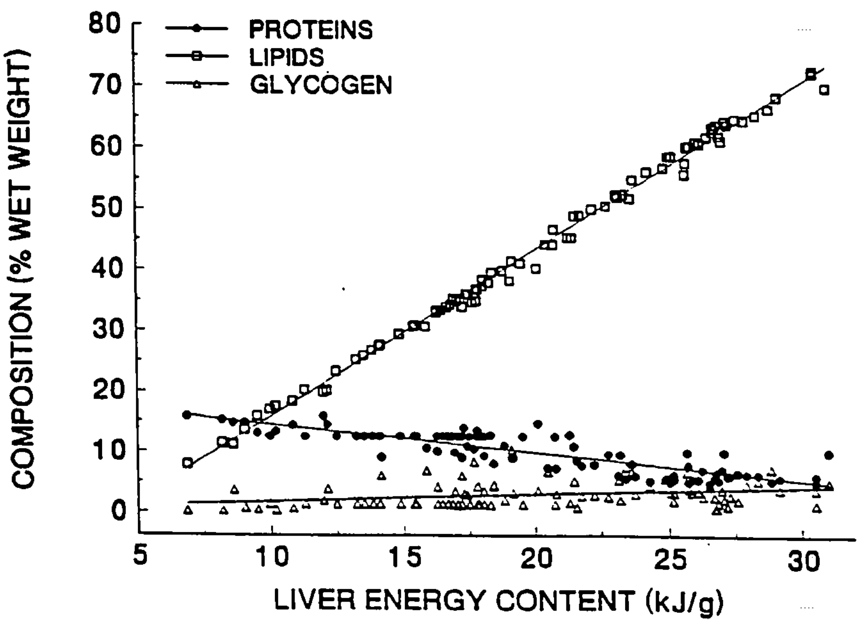

Figure 2. Variations in the protein, lipid and glycogen composition of liver in relation to changes in liver energy content in cod. Liver proteins, lipids and glycogen are expressed as percentages of wet weight.

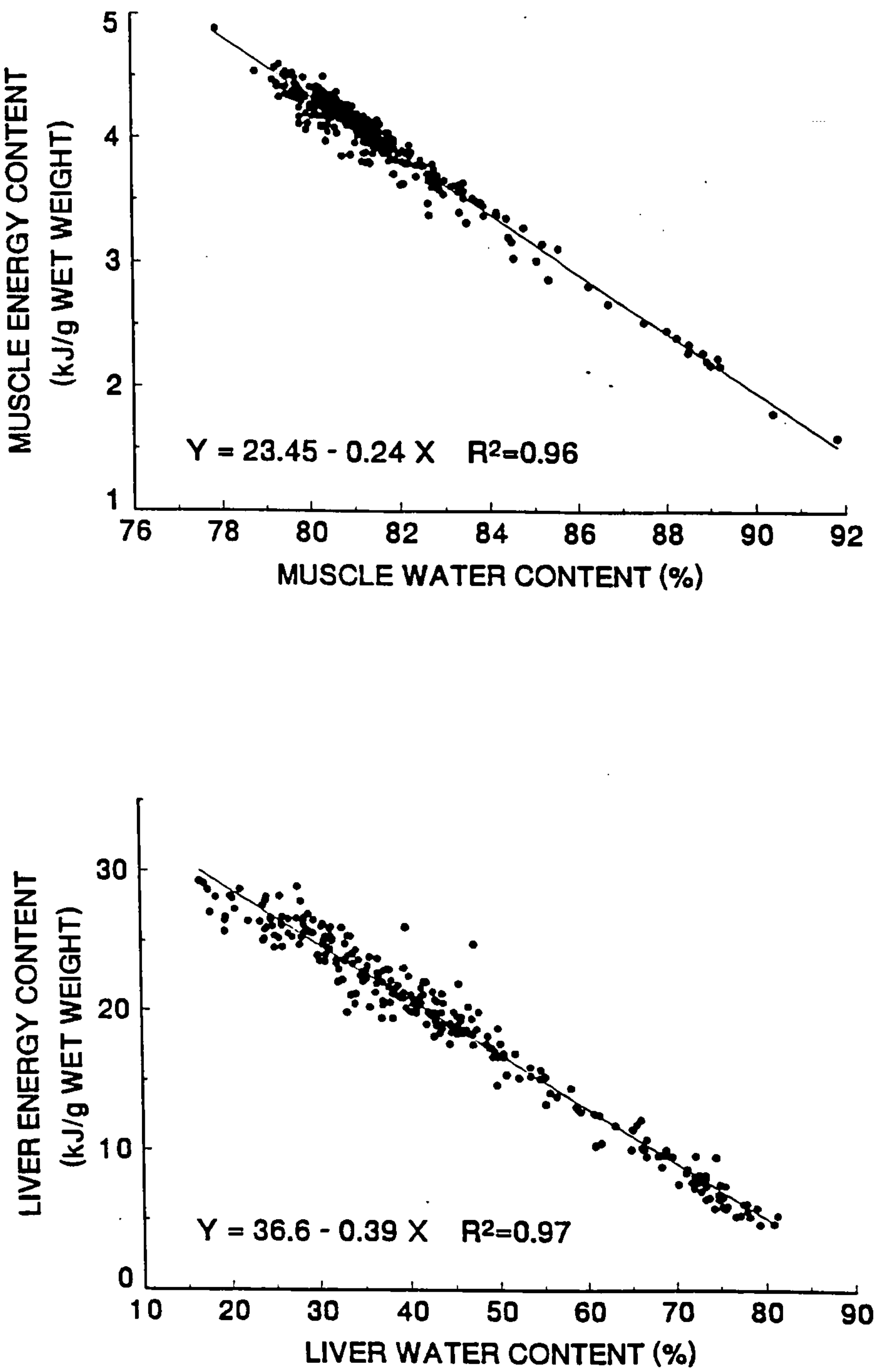

Figure 3. Linear relationships between energy content and water content for muscle and liver tissues in cod. Regression equation and coefficient of determination are presented for each relationship.

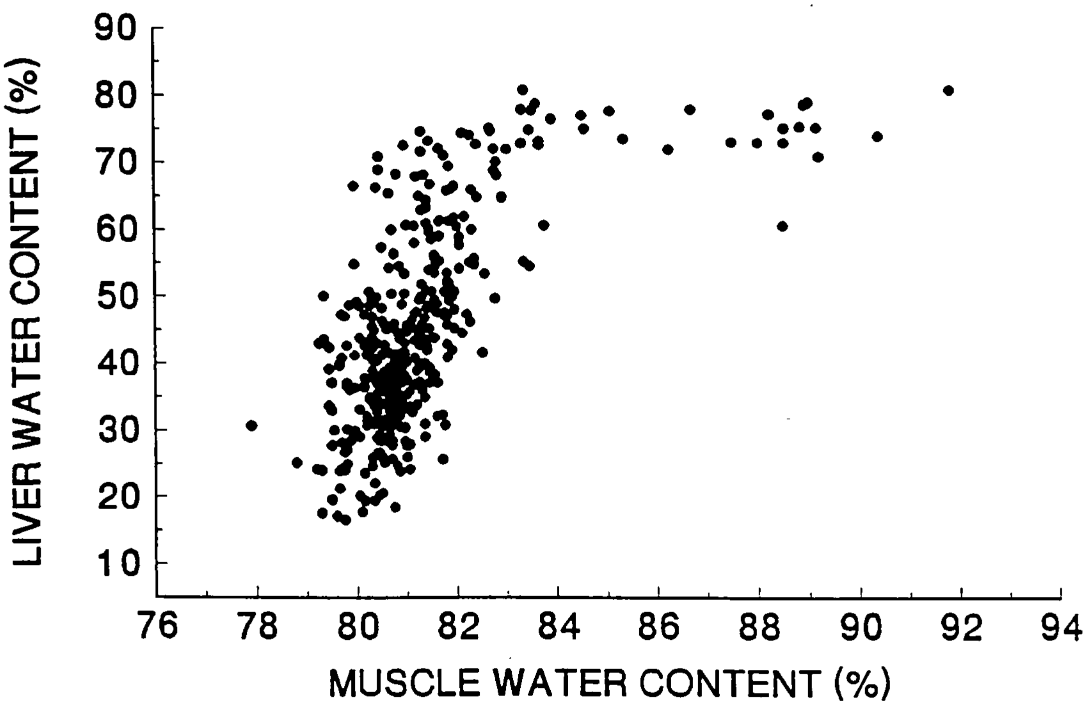

Figure 4. Plot of liver and muscle water content for cod sampled between June 1993 and May 1994 in the northern Gulf of St. Lawrence and for cod used in the starvation experiment in 1994.

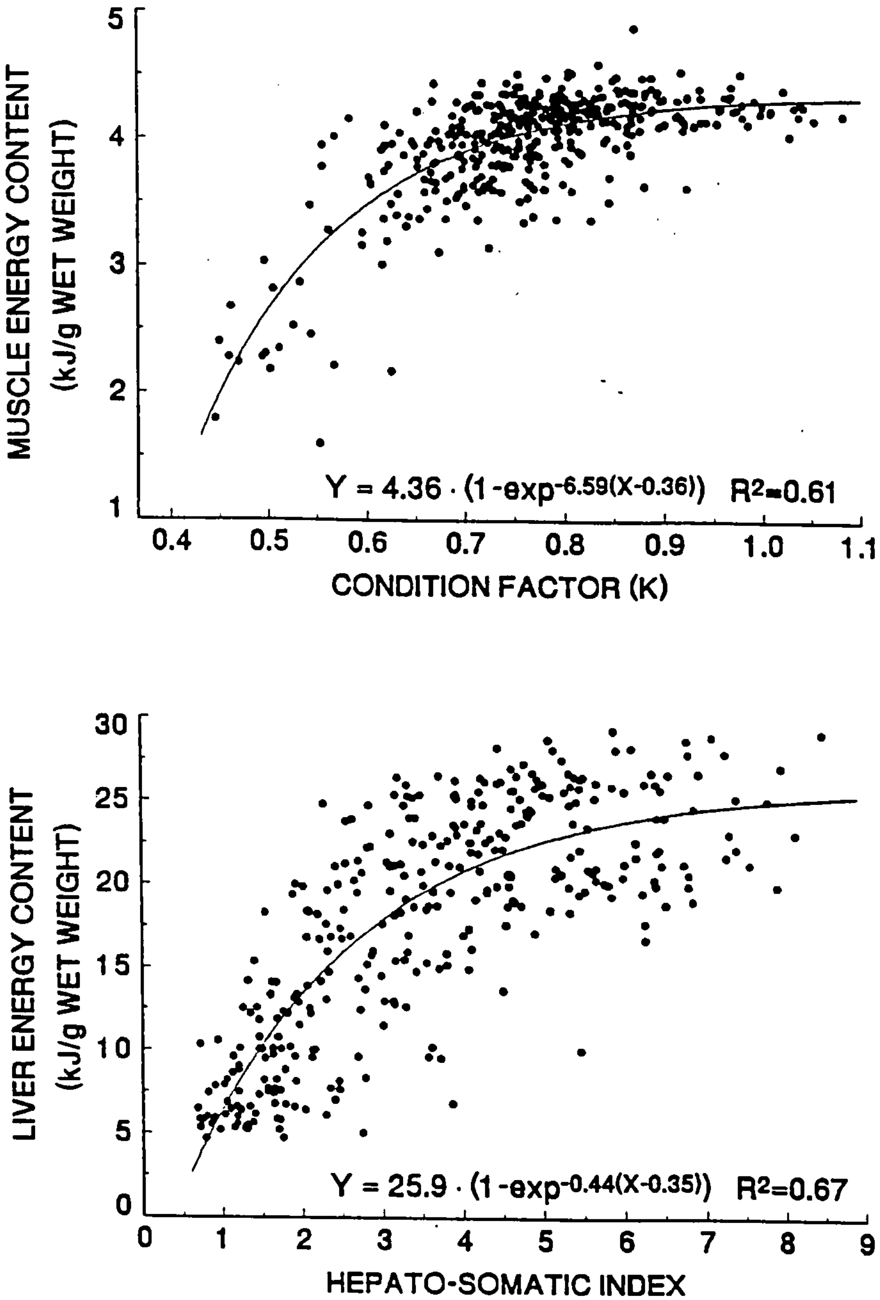

Figure 5. Relationship between specific muscle energy content and condition factor and between specific liver energy content and hepatosomatic index for cod with muscle and liver energy content values covering the full range of energy content for cod. Exponential equations describing the relationships between specific muscle and liver energy content and condition indices (K and HSI) are presented.

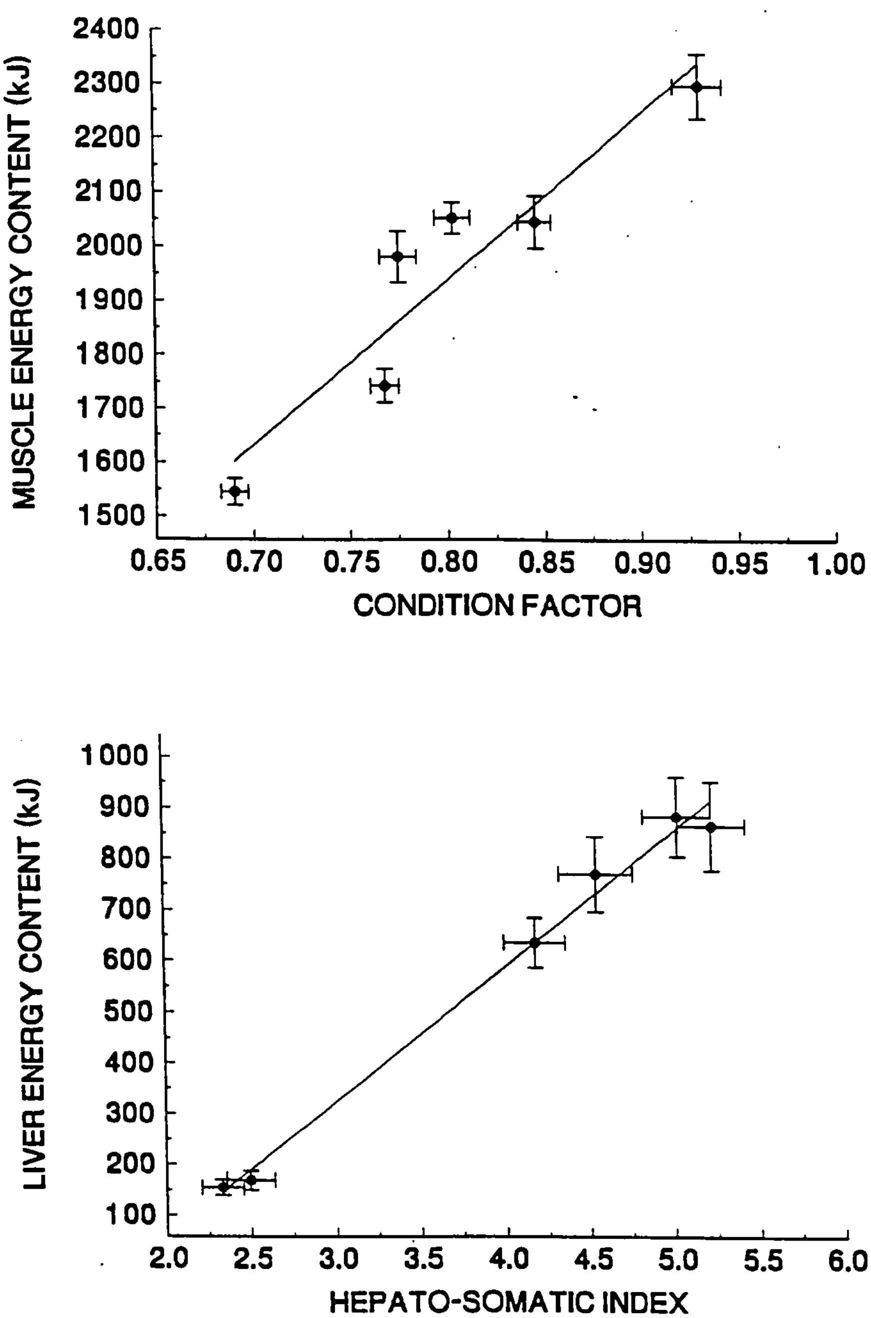

Figure 6. Relationship between total muscle and liver energy content of a 45 cm cod with the corresponding condition factor and hepato-somatic index for the six samples of cod captured between June 1993 and May 1994 in the northern Gulf of St. Lawrence. Total muscle and liver energy contents were calculated from the linear regressions between muscle and liver energy content with length (log transformed data) for each sample. Energy contents and condition indices are presented with standard errors. The number of fish for each sample is between 47 and 76.

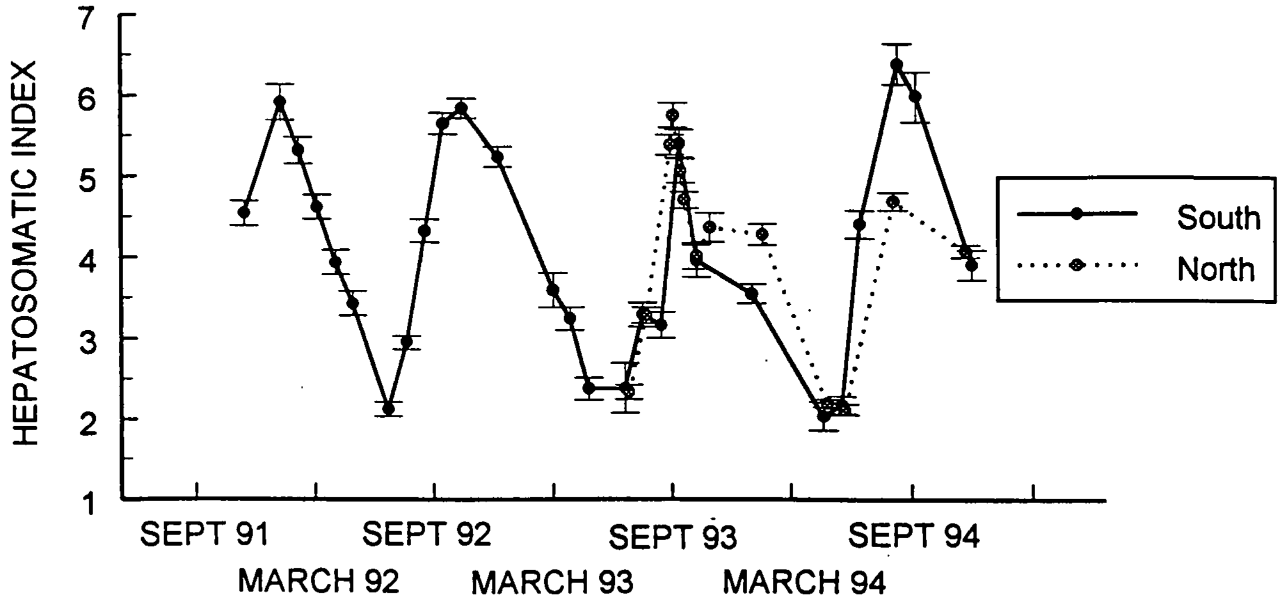

Figure 7. Seasonal changes in hepatosomatic index for 30 - 55 cm cod in the northern Gulf of St. Lawrence and for 40 - 50 cm cod in the southern Gulf of St. Lawrence from 1991 to 1995. The error bars indicate ± 1 s.e..

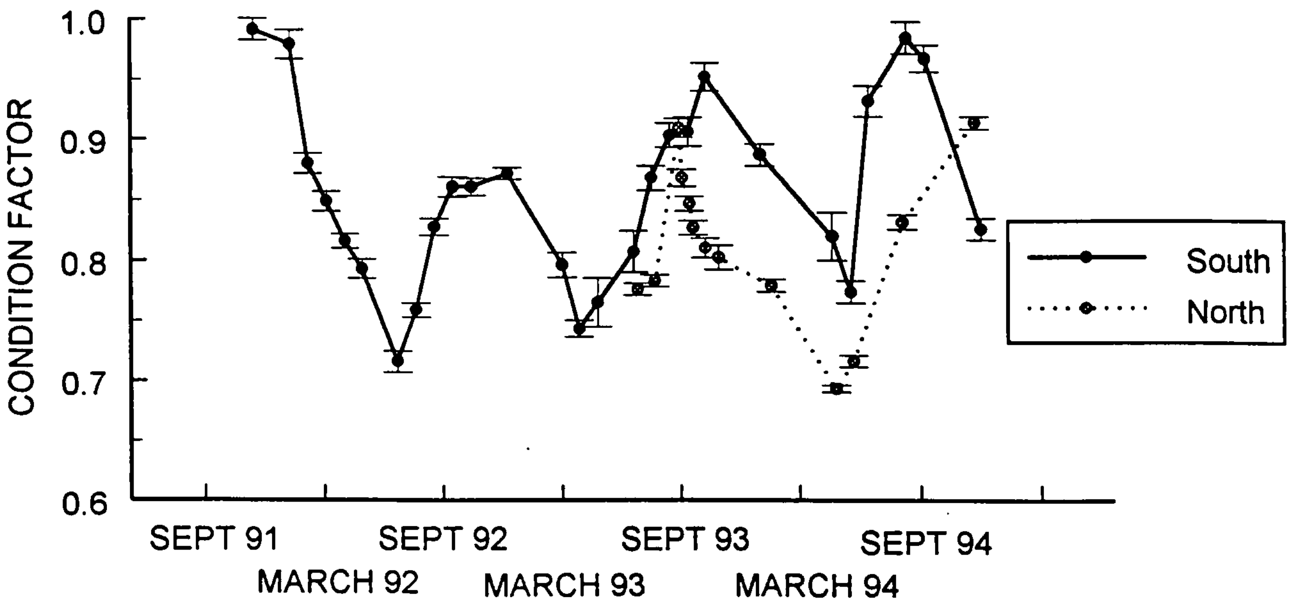

Figure 8. Seasonal changes in condition factor for 30 - 55 cm cod in the northern Gulf of St. Lawrence and for 40 - 50 cm cod in the southern Gulf of St. Lawrence from 1991 to 1995. The error bars indicate ± 1 s.e..

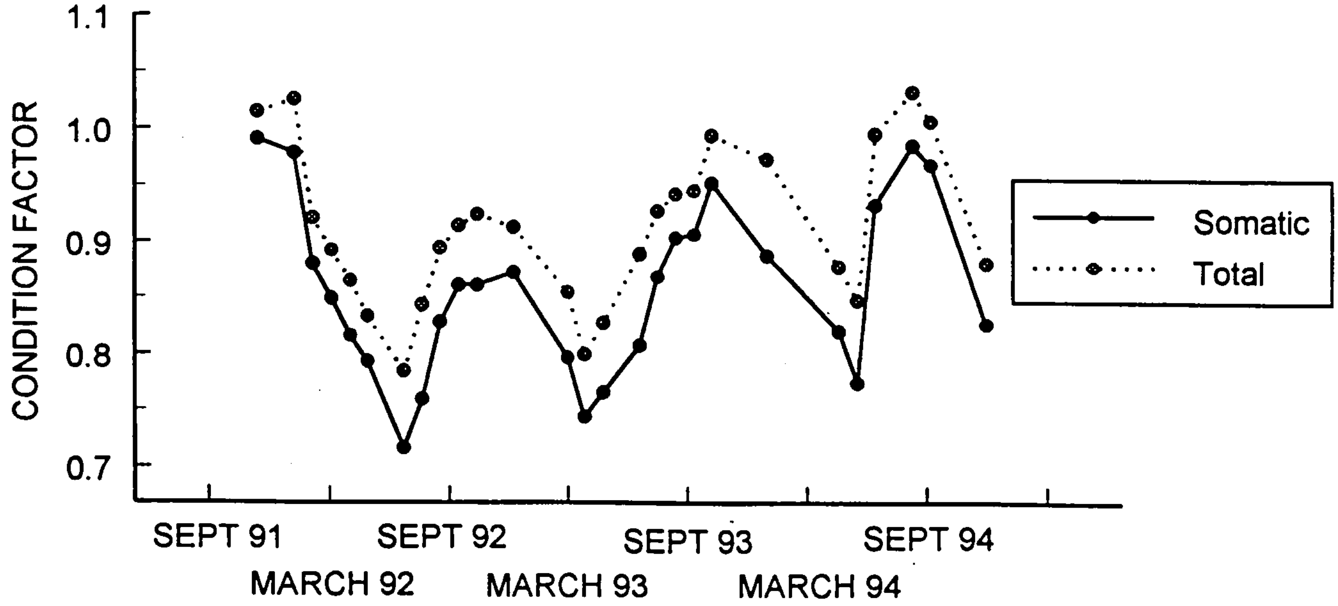

Figure 9. Seasonal condition factor calculated from somatic and total weight for cod in the southern Gulf of St. Lawrence.

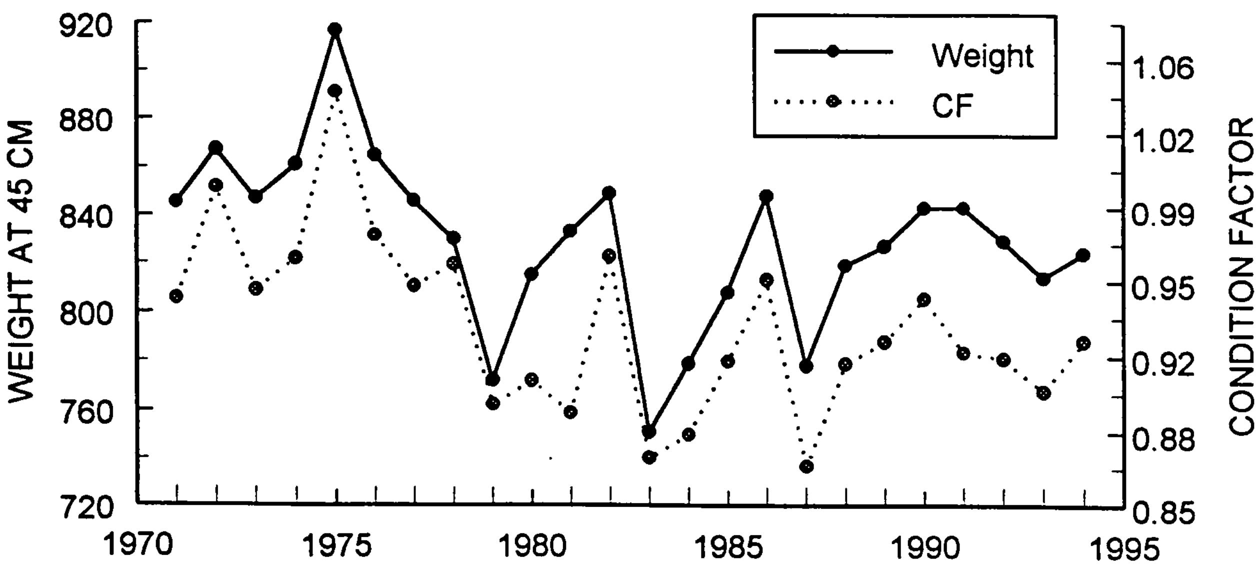

Figure 10. Total weight at 45 cm and condition factor calculated from total weight for cod sampled from annual groundfish surveys in the southern Gulf of St. Lawrence.

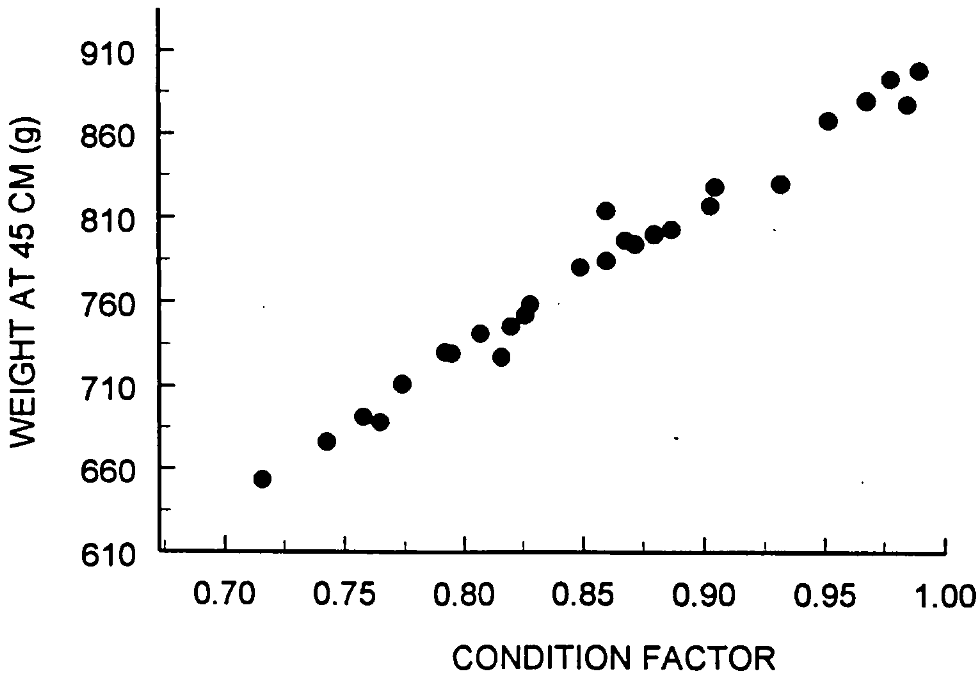

Figure 11. Somatic weight at 45 cm and condition factor calculated from somatic weight for seasonal samples of cod in the southern Gulf of St. Lawrence.

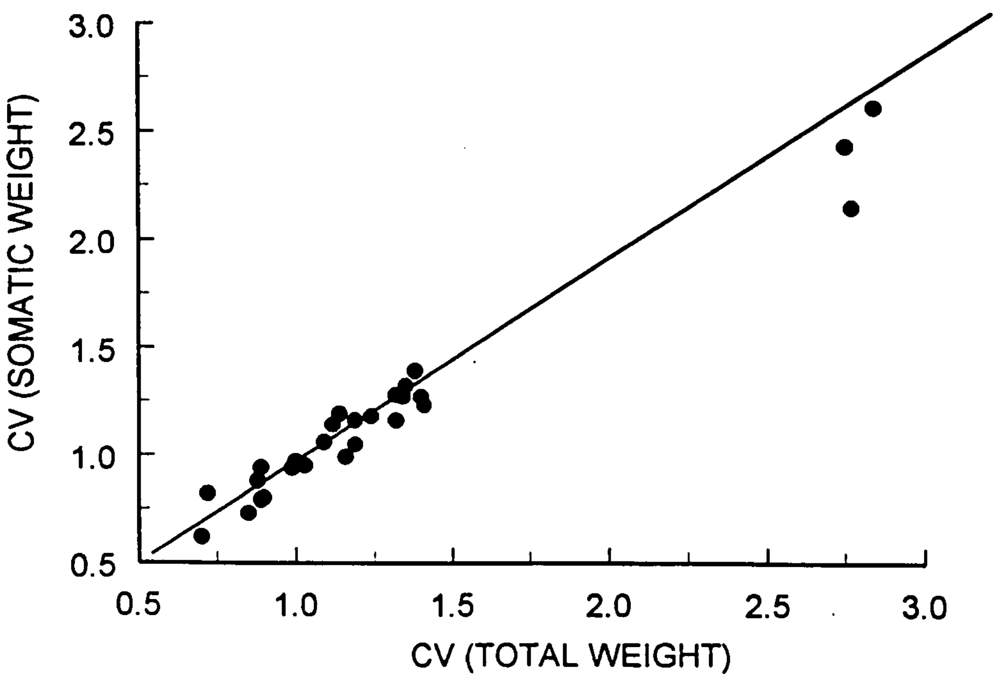

Figure 12. Coefficient of variation of the condition factor calculated using somatic and total weight.

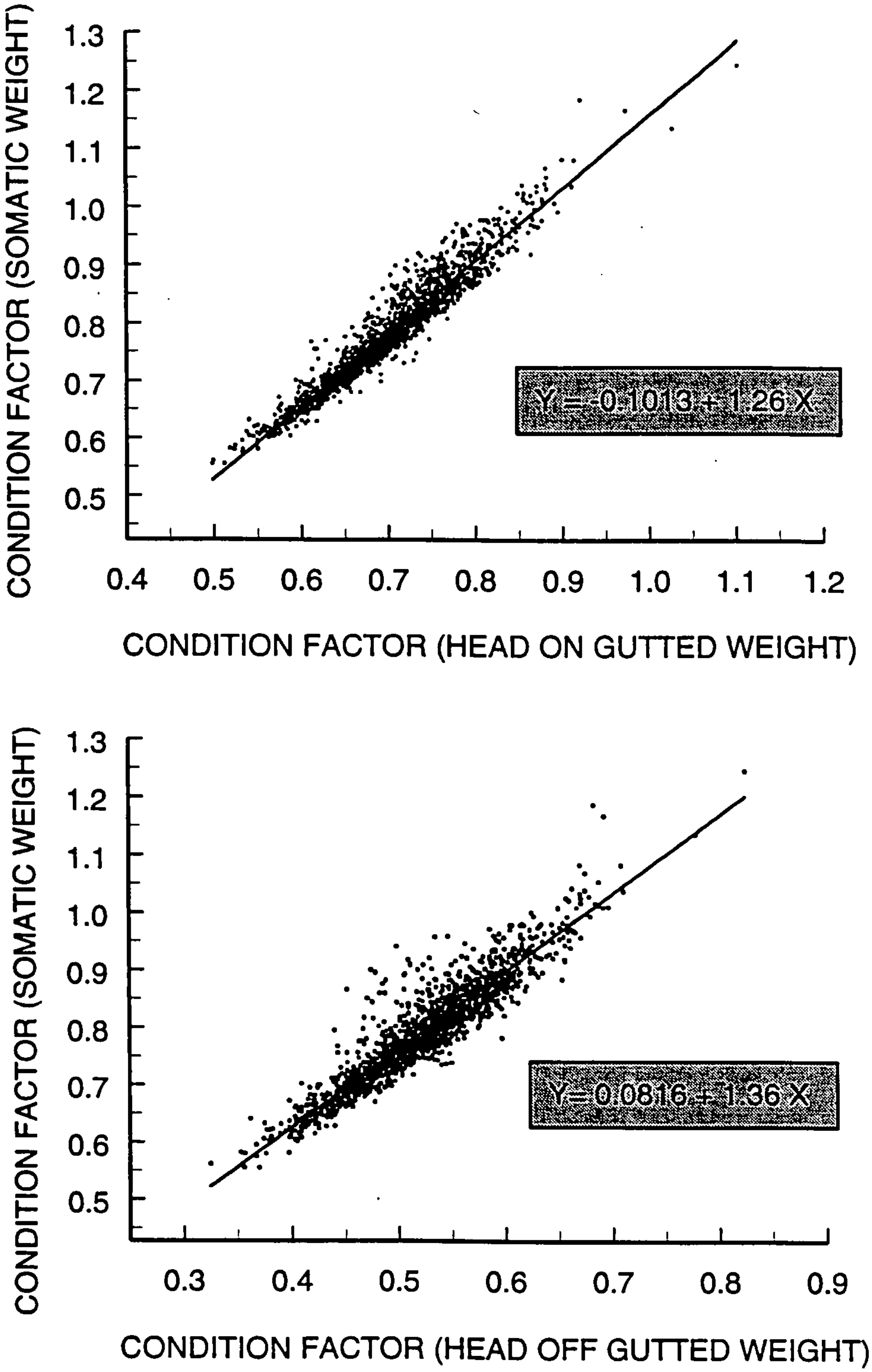

Figure 13. Linear relationships between condition factor calculated using somatic weight and either head-on gutted or head-off gutted weight in cod sampled in the northern Gulf of St. Lawrence.

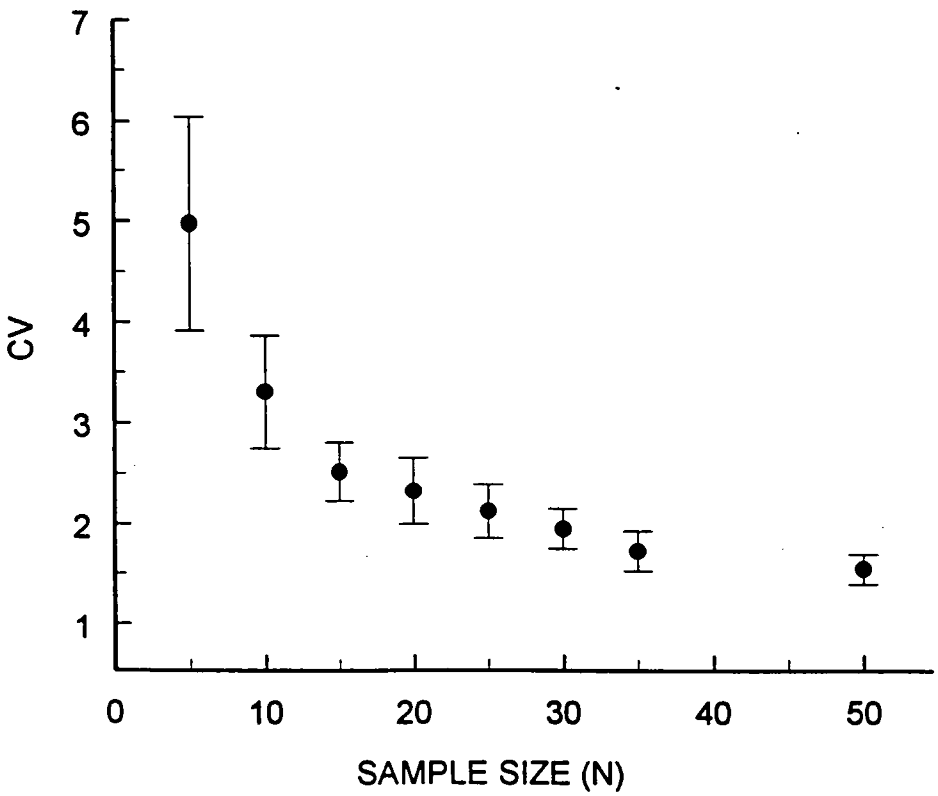

Figure 14. Coefficient of variation around the mean condition factor (somatic weight) for 30 sub-samples for a given size of sample. Sub-samples were drawn from a sample of 208 cod ranging from 40 to 50 cm and taken in June in the southern Gulf of St. Lawrence. Bars are 95% confidence intervals.