

# Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence

K. Schwalme and G. A. Chouinard



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Atlantic cod (*Gadus morhua* L.) were sampled from the southern Gulf of St Lawrence over a 2-year period (1991–1993) to assess the timing and magnitude of seasonal changes in diet composition, stomach fullness, carcass weight, and organ weights. The proportion of fish (mainly *Clupea harengus* L. and *Mallotus villosus* Muller) in the diet of cod was the highest ever reported for this stock. Cod fed very little during the five winter months (December to April) and lost 25–27% of their carcass weight and 76–84% of their liver dry weight during this time. Declines in carcass and liver weights occurred steadily throughout winter and were not specifically coincident with the spring and autumn migrations (approximate one-way distance 500 km) performed by this cod stock. Gonad growth occurred primarily between November and January in males and between January and May in females. Depending on gender and body size, 4–19% of the dry weight lost from the carcass and liver over winter could be accounted for by gonad growth. Therefore, 81–96% of the loss in carcass and liver dry weight over winter was used to meet metabolic energy requirements. The condition factors and hepatosomatic indices of cod in spring were low enough to suggest that winter starvation may cause mortality in this stock. The yield of marketable product (muscle) varied by 39–50% (depending on cod body size) over the course of the study; yields were highest in late autumn and lowest in spring.

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Karl Schwalme: 51 Jasper Drive, Aurora, Ontario, L4G 3C1, Canada. Ghislain A. Chouinard: Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick, E1C 9B6, Canada. Correspondence to K. Schwalme: e-mail: karlsch@hotmail.com

## Introduction

The growth rate of Atlantic cod (*Gadus morhua* L.) has declined significantly throughout much of the northwest Atlantic Ocean during recent decades, the greatest declines being observed in the southern Gulf of St Lawrence. For example, the mean weight of 7-year-old cod in the southern Gulf declined from 2.5 kg in the mid 1960s to 1.2 kg in 1992 (Chouinard and Fréchet, 1994). Southern Gulf cod now exhibit the slowest growth of any cod stock in the northwest Atlantic region (Brander, 1995; Campana *et al.*, 1995). Growth reductions of this magnitude significantly affect stock productivity and reduce the size of commercial catch quotas.

Likely factors implicated in the slow and declining growth rate of southern Gulf cod include low temperature (Brander, 1995; Campana *et al.*, 1995), density-dependent competition (Kohler, 1964; Paloheimo and Kohler, 1968), poor food quality reflected in a low ratio of fish to invertebrates in the diet (Waiwood and Majkowski, 1984; Waiwood, 1986), and size-selective fishing (Hanson and Chouinard, 1992). However, progress in understanding the causes of growth variability in cod has been hindered by incomplete knowledge about the growth implications of seasonal life-history events.

Adult cod in the southern Gulf of St Lawrence migrate seasonally between their summer habitat in the western Gulf and winter habitat east of Cape Breton

Island (Paloheimo and Kohler, 1968), a one-way distance of approximately 500 km (Hanson, 1996). The energetic cost of this migration is unknown, but its impact on growth could be substantial. Gonad maturation can also impact somatic growth, but the published literature contains no data on seasonal variations in the gonad size of southern Gulf cod which could be used to quantify this effect. Finally, the seasonal pattern of food intake in southern Gulf cod, and its implications for growth, are also unknown.

Appreciable declines in the stomach fullness of cod during winter months have been observed in the Labrador and northern Newfoundland banks (Turuk, 1971) and in Passamaquoddy Bay (Tyler, 1971). Poor feeding conditions may also have contributed to over-winter declines in the condition factor or liver weight of Atlantic cod in coastal waters of Nova Scotia (Jangaard *et al.*, 1967) and in Scottish sea lochs (Hawkins *et al.*, 1985). In contrast, Atlantic cod in Norwegian coastal fjords (Hop *et al.*, 1992, 1993), and in the North Sea and areas west of Scotland (Rae, 1967; Daan, 1973), continue to feed actively during winter, although in the North Sea stomach fullness is lowest during January to March (Daan, 1989; Hislop, 1997). In Balsfjorden, northern Norway, liver weight declined between January and March (Eliassen and Vahl, 1982a), even though food intake (indicated by stomach fullness) did not appear to change seasonally (Klemetsen, 1982). Such extensive variability in feeding periodicity indicates that stock-specific empirical data are needed to reliably assess seasonal growth patterns in cod.

Fortunately, the nutrient storage patterns of cod are well suited to the study of seasonal growth processes. The dominant protein depot is the soma which consists predominantly of white muscle (Holdway and Beamish, 1984; Kjesbu *et al.*, 1991). Nearly all the lipid reserves are in the liver (Kjesbu *et al.*, 1991; Lambert and Dutil, 1997a), where lipid concentrations often exceed 50% of wet wt (Jangaard *et al.*, 1967; Kjesbu *et al.*, 1991; Lambert and Dutil, 1997a). Cod white muscle, in contrast, has a lipid concentration of about 1% wet wt (Jangaard *et al.*, 1967; Lambert and Dutil, 1997a), and adipose tissue (either abdominal or intermuscular) is absent.

Seasonal patterns of nutrient storage and depletion in cod can therefore be monitored by quantifying changes in just three body compartments—carcass, liver, and gonads. We used this approach to assess the seasonal timing of body growth and depletion relative to feeding cycles, gonad growth, and migration in Atlantic cod from the southern Gulf of St Lawrence. The diet composition was also quantified to help clarify the causes of long-term growth rate changes in this stock. Seasonal changes in the yield of marketable product (i.e. muscle) were quantified because such changes have implications for commercial harvesting strategies.

## Materials and methods

### Fish collection and dissection

Cod were collected on 24 dates between September 1991 and October 1993, at intervals of approximately 1 month. In September 1991 and 1992, and July and September 1993, cod were collected from their summer range in the southern Gulf during groundfish surveys conducted by the Canadian Department of Fisheries and Oceans. All other samples were taken from the commercial fishery, which follows the cod stock during its seasonal migrations (Figure 1). Cod were taken from the western part of NAFO Division 4T during summer (mid June to early November), from Division 4Vn in winter (December to late March) and from eastern 4T during the migration periods in April, May, early June, and late November.

Although it would have been useful to describe the seasonal growth of individual cod age classes (cohorts), this approach was not practical. As commercial cod fishing methods are very size-selective (Hanson and Chouinard, 1992), the random selection of fish from commercial catches will not yield a random, or even consistently biased, sample of fish from individual age classes. Therefore, cod were selected from commercial and research vessel catches on a size-stratified basis, thereby allowing us to evaluate seasonal changes in body and organ weights on the basis of a standard fish length. This approach underestimates growth when fish are growing in both length and weight. The proportion of different cohorts represented in length-based samples also changes as each cohort grows through the length-based sampling window. On the other hand, length-specific measurements can provide reasonable estimates of loss in organ and body weight brought on by food scarcity because fish fork length probably changes little under these conditions. Most of our conclusions are based on the latter situation.

On each sampling date, we obtained approximately five cod per cm for fork lengths between 40 and 61 cm. This is the size range commonly represented in commercial catches and consists predominantly of cod 4–11 years of age. The commercial catch was sampled at the wharf or fish plant while the catch was being unloaded from the fishing vessel. The samples were usually transported to the Gulf Fisheries Centre in Moncton on the day of collection. If that was not possible, the fish were held overnight in a fish-plant cooler and transported the next day. In summer, cod were transported packed in crushed ice to prevent spoilage. On their arrival at the laboratory, cod were placed into plastic bags (one fish per bag) to prevent desiccation and stored frozen at  $-20^{\circ}\text{C}$ .

Cod were dissected after having been warmed at room temperature to a pliable but frozen state, which

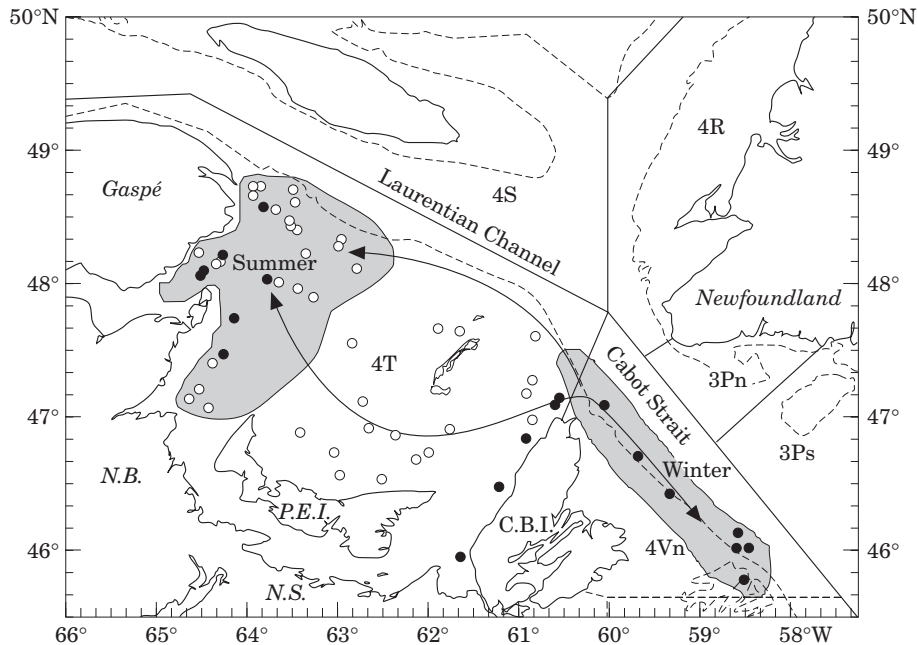


Figure 1. Map of the southern Gulf of St Lawrence showing NAFO divisions, and the main summer and winter distributions (shaded), migration routes, and capture locations of Atlantic cod. ●, capture locations of commercial cod samples; ○, capture locations of cod obtained from September groundfish surveys. N.B., New Brunswick; P.E.I., Prince Edward Island; N.S., Nova Scotia; C.B.I., Cape Breton Island.

prevented leakage of water from the tissues during weighing. After measuring fork length ( $\pm 1$  mm) and body weight ( $\pm 1$  g), the liver, gonads, and stomach (from esophagus to pyloric sphincter) were excised, weighed ( $\pm 0.1$  g), placed into plastic bags (as was the remaining carcass), and returned to frozen storage.

Stomach contents were examined from all cod collected during 18 sampling dates between November 1991 and April 1993. Individual stomachs were thawed and the contents segregated into prey categories which were weighed ( $\pm 1$  mg) and identified to the level of species (fish), and to family, order, or class (invertebrates).

#### Dry weight and ash determination

The dry matter and ash contents of carcass, muscle, liver, and gonads were determined on seven sampling dates between November 1991 and November 1992. On each date, four or five male and female cod in each of three length categories (40–42 cm, 48–50 cm, and 55–57 cm) were selected from the total sample. A 50 g sample of epaxial white muscle, free of small bones and skin, was excised from below the dorsal fin of each frozen carcass. The remainder of the carcass was minced in a meat grinder, the resulting paste mixed thoroughly by hand, and a 25 g portion transferred to a preweighed aluminium pan. Muscle samples, and the entire organ in

the case of liver and gonads, were homogenized in a Waring blender with nine volumes of distilled water. Weighed aliquots of homogenate were then transferred to preweighed aluminium pans. Tissue or organ dry weights were determined after drying to constant weight at 60°C. Ash content was determined by heating pans containing dried tissue at 550°C until all organic matter had been combusted. The dry weight values reported include ash.

#### Sample size, calculations, and statistics

A total of 2505 cod was collected during the study. Cod were divided into two length categories as a means of duplicating the statistical procedure used to detect seasonal changes in carcass and liver weights. Small cod were those from 40.0 to 50.9 cm fork length, inclusive. Large cod were those from 51.0 to 61.0 cm fork length, inclusive. Gender ratios varied among samples because cod could not be sexed prior to their selection from the commercial catch due to time constraints. The mean number of small cod collected per sampling date was 28 females and 33 males. For large cod, mean sample sizes were 26 females and 18 males.

Carcass weight was calculated as total body weight minus the combined weight of the liver, gonads, and stomach. Seasonal variations in carcass weight were

calculated for two standard lengths of fish; 45 cm (small), and 56 cm (large). Regression equations relating carcass weight (W) and fork length (L) were calculated each month for each size group as:

$$\log_{10}(W) = a + b \cdot \log_{10}(L) \quad (1)$$

where a and b are the intercept and slope, respectively. Data from males and females were combined during calculation of weight-length regressions because there were no significant differences in length-specific carcass weight between genders in either size group of cod. The carcass weight of individual fish was then adjusted to weight at a standard fork length of 45 cm (small) or 56 cm (large) using the equation:

$$\log_{10}(W_{\text{STDi}}) = a + b \cdot \log_{10}(L_{\text{STD}}) + e_i \quad (2)$$

where  $W_{\text{STDi}}$  is the standardized carcass weight of fish i,  $L_{\text{STD}}$  is standard fork length (i.e. 45 or 56 cm),  $e_i = \log_{10}(W_i) - [a + b \cdot \log_{10}(L_i)]$ ,  $W_i$  and  $L_i$  are the actual carcass weight and fork length, respectively, of fish i, and a and b are defined as above.

To quantify liver depletion over winter, it was necessary to use actual liver size rather than relative size such as the hepatosomatic index (HSI), which is influenced by changes in body size independent of liver weight. However, variability in liver, gonad, and stomach content weights was so large that regressions of these weights against fork length were often statistically insignificant over the size range of cod in our study. Therefore, organ weight vs. length regressions could not be used to calculate liver, gonad, and stomach content weights at a standard fork length. Liver weights at 45 and 56 cm standard fork length were calculated by multiplying the ratio of liver weight to carcass weight of individual fish by the standardized carcass weight ( $W_{\text{STDi}}$ ) of the same fish.

In contrast to the liver, the weights of gonads and stomach contents were expressed as a percentage of carcass weight (yielding gonadosomatic index, GSI, and stomach fullness index, respectively) because the relative size of these compartments was considered more useful than their actual size. For selected comparisons with the study of Lambert and Dutil (1997b), their formulae were used to calculate condition factor and HSI for critical periods in the seasonal growth cycle. The hepatosomatic index is liver weight expressed as a percentage of somatic weight (total body weight minus the sum of gonad and stomach contents) and condition factor was calculated as  $K = (W \cdot L^{-3}) \cdot 100$ , where K denotes condition factor, W is somatic weight (g), and L is fork length (cm).

The statistical significance of seasonal and gender-related variation in carcass weight, liver weight,  $\log_{10}$  GSI,  $\log_{10}(Y+1)$  transformed stomach fullness index,

and tissue dry matter and ash concentrations was tested using analysis of covariance (ANCOVA) with fork length as the covariate to control for the effect of fish size. All first- and second-order interaction effects were always examined. Non-significant interaction effects were removed from the ANCOVA model prior to testing for treatment effects. The criterion for statistical significance was always  $p < 0.05$ , and seasonal variations were statistically significant unless stated otherwise.

Stomach content data were grouped into three periods (spring/autumn, summer, and winter) to achieve sufficient sample size for diet composition analysis. The prey composition of cod diets was expressed both as percentage of diet weight and as frequency of occurrence. Percentage of diet by number was not used because accurate counts of individual food items were often difficult to obtain and because this method exaggerates the importance of small but numerous prey. The percentage of diet weight contributed by an individual prey group (%  $P_i$ ) was calculated as:

$$\% P_i = \frac{\sum_{j=1}^n W_{ji}}{\sum_{j=1}^n \sum_{i=1}^A W_{ji}} \times 100 \quad (3)$$

where  $W_{ji}$  is the weight of prey group i in stomach j, A is the number of different prey groups in stomach j, and n is the total number of stomachs containing food.

#### Determination of cod muscle weight (marketable product)

To determine whether the proportion of carcass weight represented by marketable product (i.e. muscle) changes seasonally, 11–16 carcasses were dissected from each of the samples collected in December 1991, June 1992, and September 1992. As the proportion of muscle in the carcass varies depending on whether a fish is relatively light or heavy for its length, the cod selected for dissection were those whose standardized carcass weights were closest to the mean standardized carcass weight of the sample.

Muscle was dissected from frozen, pliable carcasses by first removing most of the trunk musculature as two fillets. To avoid introducing variability related to filleting technique, muscle still attached to the vertebrae, ribs, and head region was also carefully dissected free. However, muscles in the mouth and opercular regions were not removed since these are not commonly marketed. Once it had been separated from all bone, fins, and skin, the swimming musculature was weighed to determine its contribution to total carcass weight.

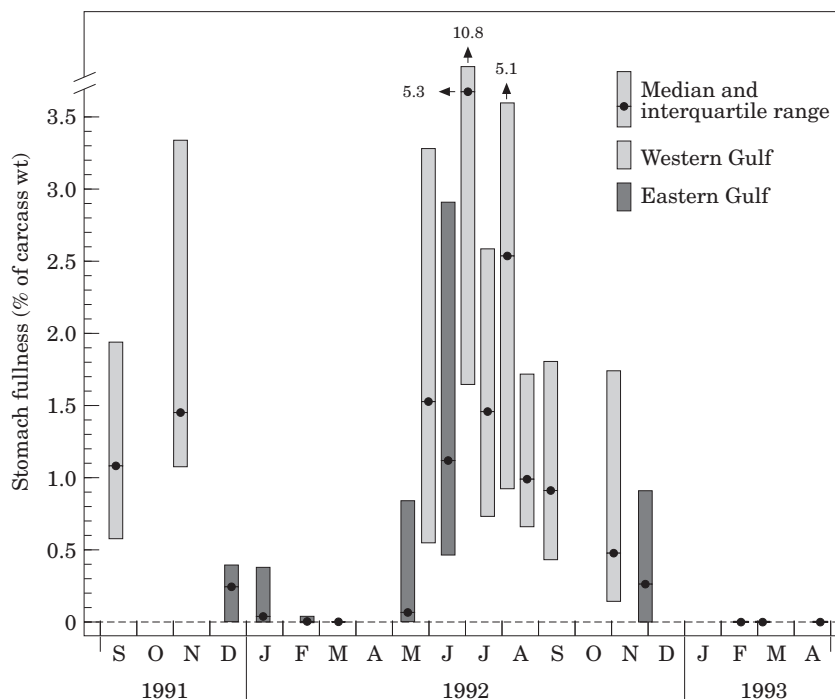


Figure 2. Seasonal changes in the stomach fullness index of Atlantic cod in the southern Gulf of St Lawrence. Data from both genders and size groups of cod are combined. Empty and non-empty stomachs were included in calculation of median stomach fullness and interquartile range. Sample sizes are in Table 1. Medians and upper interquartile limits are indicated by arrows when they exceed the vertical scale.

## Results

### Stomach fullness and diet composition

The stomach fullness of individual cod was highly variable and most samples exhibited a positively skewed distribution (Figure 2). Stomachs contained appreciable quantities of food only during May through November. Maximum stomach fullness occurred in late June and July. During the latter months, food in the stomach amounted to 24% of carcass weight in some cod (data not shown), but median values were much lower, about 1–5% (Figure 2).

Only about 3% of all stomachs collected during summer were empty, but during winter (December to late April) the percentage of empty stomachs rose to 64% (Tables 1 and 2). Consequently, median values for stomach fullness were often zero (Figure 2). Reduction in food intake during winter was indicated by a 61% reduction in feeding frequency (i.e. the proportion of non-empty stomachs decreased from 97% in summer to 36% in winter), and from reductions of 39% (large cod) and 82% (small cod) in the weight of food per non-empty stomach (Tables 1 and 2). Most empty stomachs of cod captured during winter were small and tightly compacted in appearance, probably because the

stomach musculature contracted in response to infrequent feeding.

Significant size-related variation in stomach fullness occurred during spring/autumn and winter when fullness index was greater in larger cod (Tables 1 and 2), the magnitude of the effect depending on sampling date. There were no significant differences in stomach fullness index between males and females for any period, nor were there significant interactions between gender and sampling date or between gender and fork length.

The diet composition was diverse; a total of 47 different prey species was identified. Fish was by far the most important dietary component for large cod at all times of year, comprising 66–83% of the diet by weight (Table 2). Fish was also the dominant component in the diet of small cod during the primary feeding period (summer), when it represented 63% of diet weight (Table 1). During summer, fish were present in 57% (small cod) and 70% (large cod) of all non-empty stomachs examined. Atlantic herring (*Clupea harengus* L.) and capelin (*Mallotus villosus* Muller) were the most important prey species; together, they constituted more than 73% of the weight of all recognizable fish prey (Tables 1 and 2). Herring represented a significant proportion of diet weight at all times of year, whereas

Table 1. Diet composition of small cod (40.0–50.9 cm fork length) in the southern Gulf of St Lawrence (1991–1993).

Item	Spring/Autumn <sup>a</sup>	Summer <sup>b</sup>	Winter <sup>c</sup>	Percent occurrence among non-empty stomachs		
	Percent composition by weight			Spring/Autumn <sup>a</sup>	Summer <sup>b</sup>	Winter <sup>c</sup>
No. of stomachs examined	372	392	383			
Percentage empty	18.0	2.8	64.0			
Stomach fullness index <sup>d</sup>	1.31 ± 0.10	3.15 ± 0.20	0.57 ± 0.10			
Fish (total)	25.5	62.8	15.0	22.6	57.2	9.4
Herring	7.1	13.7	3.8	3.6	7.6	1.4
Capelin	5.7	18.8	0.0	4.9	10.8	0.0
Other identified species	3.5	5.1	0.0	3.0	11.5	0.0
Unclassifiable fish	9.1	25.1	11.2	12.5	31.2	8.0
Invertebrates (total)	61.1	32.2	57.5	90.5	80.3	66.7
Crustacea (total)	36.2	22.2	54.3	72.5	70.6	54.3
Decapoda (total)	21.3	16.7	53.3	43.0	57.5	22.5
Brachyura and Anomura	8.5	1.4	14.2	13.8	6.3	0.7
Caridea	12.8	15.3	39.1	32.1	54.3	21.7
Euphausiacea	2.4	4.6	0.1	8.2	16.5	8.7
Other identified crustacea <sup>e</sup>	12.3	1.0	0.8	44.6	17.8	24.6
Unclassifiable crustaceans	0.2	<0.1	<0.1	2.6	0.3	1.4
Mollusca	12.6	1.4	0.3	14.8	4.5	3.6
Annelida	8.3	4.0	2.9	23.9	23.1	10.1
Echinodermata	2.4	0.1	<0.1	7.5	0.8	2.2
Other invertebrates <sup>f</sup>	1.6	4.4	0.0	4.9	10.8	0.0
Unclassifiable food	13.4	5.0	27.5	34.4	19.9	43.5

<sup>a</sup>Samples collected in May, September, October, and November; all years combined.

<sup>b</sup>Samples collected during June through August; all years combined.

<sup>c</sup>Samples collected during December through April; all years combined.

<sup>d</sup>Mean ± s.e.m. Only stomachs containing food were included in computations.

<sup>e</sup>Includes order Mysidacea, order Amphipoda, subclass Copepoda.

<sup>f</sup>Includes phyla Aschelminthes, Nematoda, Platyhelminthes, Cnidaria, and subphylum Tunicata.

capelin were consumed primarily during summer. The remainder of the recognizable fish prey consisted of 14 different species, each consumed only in small amounts.

Irrespective of time of year or cod size, invertebrates always occurred in a greater percentage of stomachs than did fish prey. During the spring/autumn and summer periods, invertebrates occurred in 68–91% of all non-empty stomachs examined (Tables 1 and 2). However, despite their high frequency of occurrence, invertebrates never comprised more than about 28% of diet weight in large cod (Table 2). Invertebrates were somewhat more important in the diet of small cod, accounting for 58 and 61% of diet weight during winter and spring/autumn periods, respectively (Table 1). The dominant invertebrates were crustaceans, mainly decapods (caridean shrimp plus brachyuran and anomuran crabs). Caridean shrimp were always consumed by a greater percentage of cod, and comprised a greater proportion of diet weight, than the crabs. Cod also consumed small quantities of several non-decapod crustaceans including euphausiids, mysids, amphipods, and copepods. These groups were most prevalent in the diet of small cod during the spring/autumn period (Table 1). Other invertebrates included molluscs, annelids, echinoderms, and several groups of very minor importance. Non-crustacean invertebrates, especially molluscs, made

their greatest contribution to the diet during the spring/autumn period (Tables 1 and 2).

### Gonad maturation

Gonad maturation in both males and females began in late November (Figure 3) as cod were migrating to their wintering area in NAFO Division 4Vn. The growth of male gonads was largely complete by January, but maximum GSIs of females were not attained until late April or May. Reductions in GSI associated with spawning occurred during June and July, after cod had returned to the Gulf of St Lawrence from wintering areas, and after they had resumed feeding (Figure 3).

Gonad weights varied widely between individuals. For example, coefficients of variation for GSI in samples collected between December and May were 41–78% in males, and 56–86% in females. Over the 40–61 cm size range of cod used in this study, there was no significant relationship between  $\log_{10}$  GSI and fork length in either gender for any month during the maturation period (December to May). Therefore, data from large and small cod were pooled to illustrate the seasonal cycle of gonad maturation in Figure 3.

Large variability in GSI during the maturation period was partly due to some exceedingly small and undevel-

Table 2. Diet composition of large cod (51.0–61.0 cm fork length) in the southern Gulf of St Lawrence (1991–1993).

Item	Spring/Autumn <sup>a</sup>	Summer <sup>b</sup>	Winter <sup>c</sup>	Percent occurrence among non-empty stomachs		
	Percent composition by weight			Spring/Autumn <sup>a</sup>	Summer <sup>b</sup>	Winter <sup>c</sup>
No. of stomachs examined	216	276	350			
Percentage empty	18.5	3.3	63.7			
Stomach fullness index <sup>d</sup>	2.34 ± 0.25	3.61 ± 0.28	2.20 ± 0.32			
Fish (total)	65.7	72.4	82.9	47.2	70.4	40.2
Herring	46.5	25.0	35.0	18.8	18.0	11.0
Capelin	0.1	19.5	0.0	0.6	12.4	0.0
Other identified species	7.0	2.4	12.3	4.5	6.4	7.1
Unclassifiable fish	12.1	25.5	35.6	25.0	40.1	23.6
Invertebrates (total)	28.1	18.6	7.8	68.2	72.3	49.6
Crustacea (total)	12.5	14.0	6.3	50.6	62.2	37.8
Decapoda (total)	10.3	8.8	5.8	38.1	50.2	17.3
Brachyura and Anomura	4.9	1.8	<0.1	17.0	7.5	1.6
Caridea	5.4	6.9	5.8	26.1	44.9	15.7
Euphausiacea	0.2	3.7	0.1	3.4	9.4	7.9
Other identified crustacea <sup>e</sup>	1.9	0.8	0.3	14.8	8.6	14.2
Unclassifiable crustaceans	<0.1	0.8	<0.1	1.7	3.4	1.6
Mollusca	11.8	1.8	0.9	19.3	8.6	5.5
Annelida	2.8	0.7	0.5	18.8	12.7	8.7
Echinodermata	0.4	0.1	<0.1	3.4	1.9	3.1
Other invertebrates <sup>f</sup>	0.6	2.0	0.0	2.3	7.1	0.0
Unclassifiable food	6.2	9.0	9.3	31.3	24.7	40.2

<sup>a</sup>Samples collected in May, September, October, and November; all years combined.

<sup>b</sup>Samples collected during June through August; all years combined.

<sup>c</sup>Samples collected during December through April; all years combined.

<sup>d</sup>Mean ± s.e.m. Only stomachs containing food were included in computations.

<sup>e</sup>Includes order Mysidacea, order Amphipoda, subclass Copepoda.

<sup>f</sup>Includes phyla Aschelminthes, Nematoda, Platyhelminthes, Cnidaria, and subphylum Tunicata.

oped gonads which occurred in both genders and size groups. The presence of these small gonads resulted in bimodal frequency distributions for male GSI between January and May and female GSI between March and May. The lower mode of the GSI distributions represented gonads that weighed less than about 1.0% of carcass weight. These low GSIs suggest that some cod may not mature gonads and spawn each year. In samples exhibiting bimodal GSI distributions, gonads in an apparently immature state occurred in 7–29% of male cod, and in 20–40% of female cod (Figure 3).

#### Liver and carcass wet weights

A large decline in liver weight occurred in both genders and size groups of cod during winter. Between November 1991 and May 1992, and again from November 1992 to April 1993, small male and female cod lost 75 and 65% of their initial liver weight, respectively, and large male and female cod lost 72 and 56%, respectively (Figure 4). Males experienced greater percentage reductions in liver weight over winter than females because in both cod size groups liver weights were significantly lower in males than in females throughout spring and summer. During the summers of

1992 and 1993, liver weights in both genders and size groups increased fully to the levels of the previous autumn (Figure 4).

Cod also exhibited large declines in carcass weight over winter. Between September 1991 and early June 1992, small and large cod lost 27 and 25% of their initial carcass weight, respectively (Figure 5). The carcass weight of small cod increased during the summer of 1992, but did not reach the peak levels of the preceding autumn. However, even though small cod entered the winter of 1992/1993 in leaner condition compared to the previous year, their carcass weights in the spring of 1993 were no lower than in 1992. They rapidly increased in weight during the spring and summer of 1993, and by October carcass weights were nearly as high as in September of 1991. Seasonal fluctuations in the carcass weight of large cod, although slightly more erratic than those of small cod, followed the same pattern of weight loss over winter, and weight gain in summer (Figure 5).

#### Tissue dry matter and ash content

Liver dry matter concentration declined from 69% wet wt in December 1991 to 40% in May 1992 before increasing again to 67% by November 1992. As

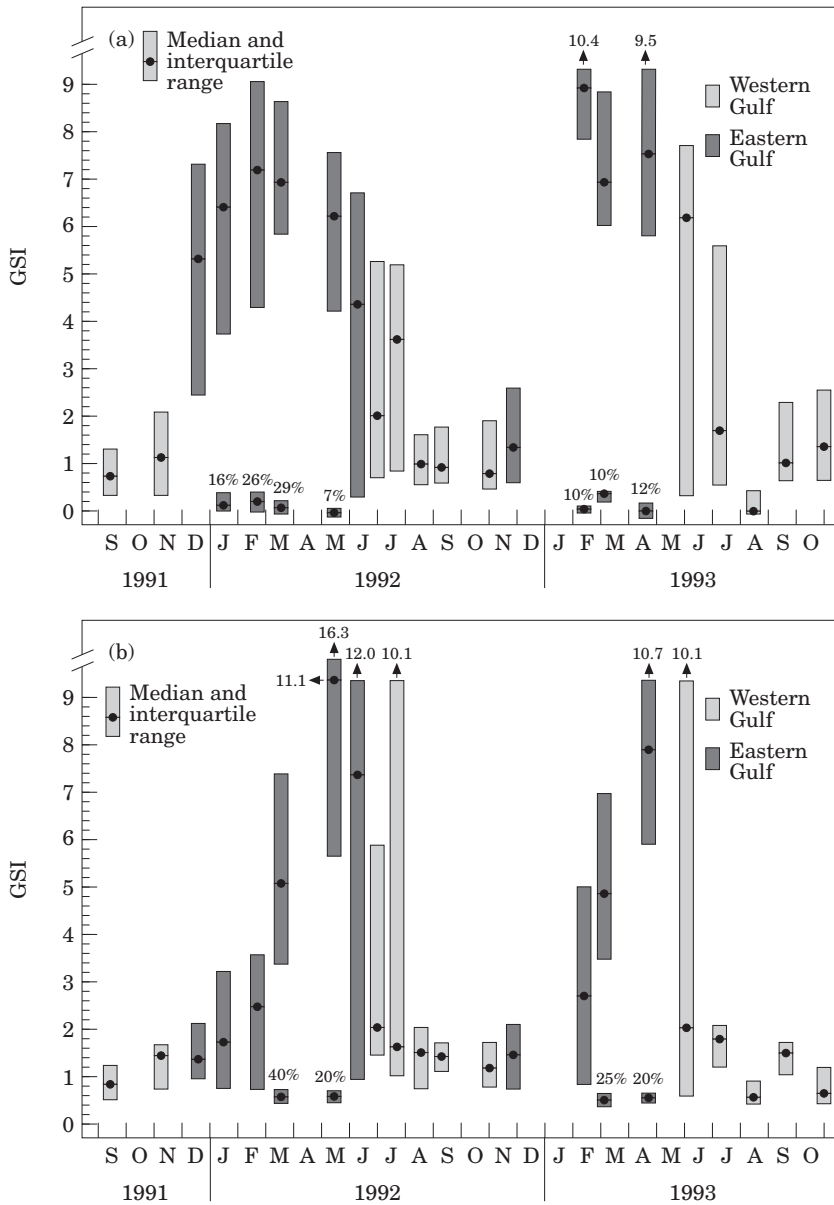


Figure 3. Seasonal changes in the gonadosomatic index (GSI) of male (a) and female (b) Atlantic cod in the southern Gulf of St. Lawrence. Data from both size groups of cod are combined. Samples of male cod collected between January and May, and female cod collected between March and May contained some fish with small, non-maturing gonads. For these samples, separate calculations of the median and interquartile range were done for maturing and non-maturing fish. Percentage values inside each panel indicate the proportion of fish with non-maturing gonads in the total sample. Medians and upper interquartile limits are indicated by arrows when they exceed the vertical scale.

reductions in liver weight and dry matter concentration occurred concurrently, the true extent of liver depletion over winter was greater than that indicated by wet weight changes alone (Figure 4). Accordingly, male and female cod lost 84 and 76%, respectively, of their initial liver dry matter content between late autumn (September to November) and spring (April to May).

The latter values are averages calculated over both size groups and both winters encompassed by the study.

Between December 1991 and May 1992, the dry matter concentration of muscle decreased from 19.8 to 17.7% wet wt and that of carcass declined from 21.5 to 19.9% wet wt. Muscle and carcass dry matter concentrations both increased again to previous values by the



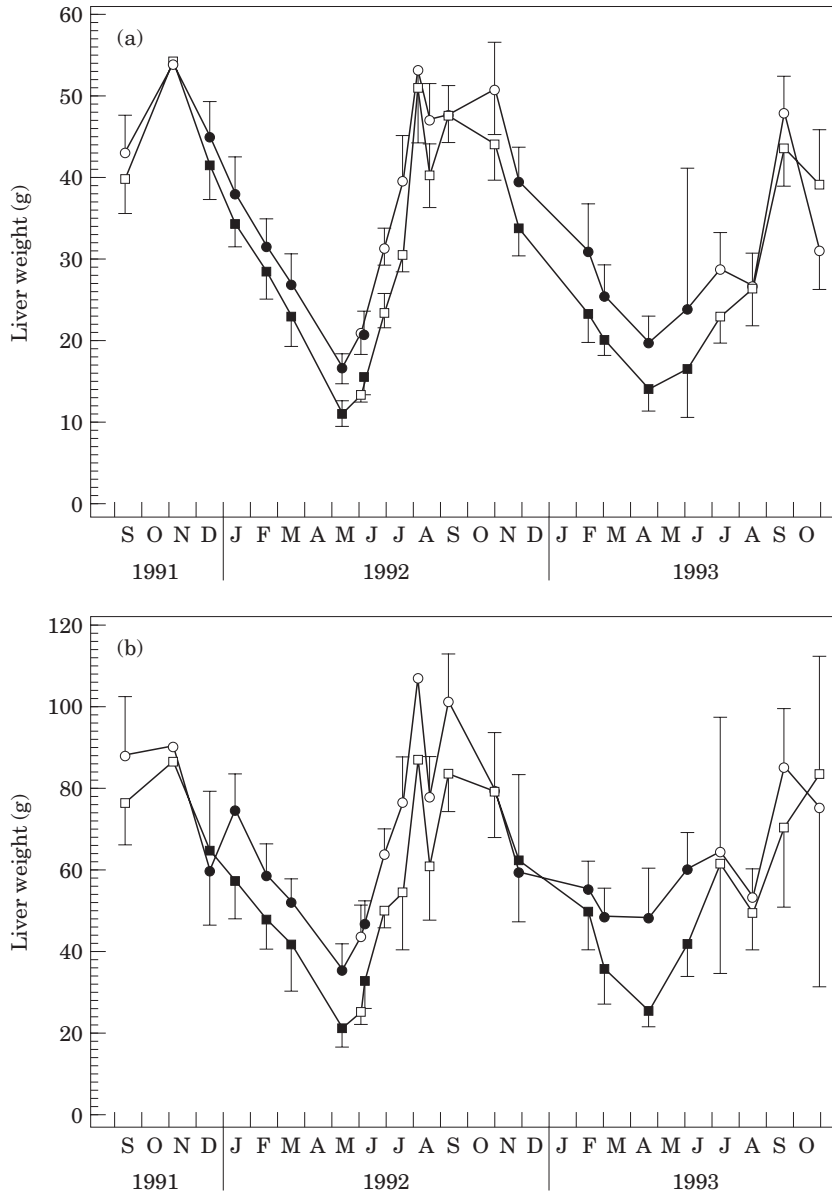


Figure 4. Seasonal changes in the standardized liver weight of (a) small and (b) large Atlantic cod in the southern Gulf of St Lawrence. Means and 95% confidence intervals are shown. ●, female cod, eastern Gulf; ○, female cod, western Gulf; ■, male cod, eastern Gulf; □, male cod, western Gulf.

autumn of 1992. Ovary dry matter increased from 19.6 to 23.9% wet wt during the early portion of ovarian maturation from November 1991 to March 1992 and decreased to 19.0% by the following May. The rapid growth in cod testes between November and December 1991 was accompanied by a decline in dry matter concentration from 20.1 to 17.4% wet wt. A second decline in testis dry matter, to 15.1% wet wt, occurred between March and May 1992. With the exception of the gender-related differences in gonad dry matter con-

centrations noted above, tissue dry matter concentrations varied little with length or gender. There was also very little seasonal, length, or gender-related variation in tissue ash concentrations, which were 0.6–1.8% wet wt in the liver, muscle, and gonads, and 3.3–3.9% wet wt in the carcass.

From 4 to 19% of the over-winter depletion in carcass and liver dry matter could be accounted for by gonad growth (Table 3). Gonad growth made a slightly greater percentage contribution to somatic depletion in females

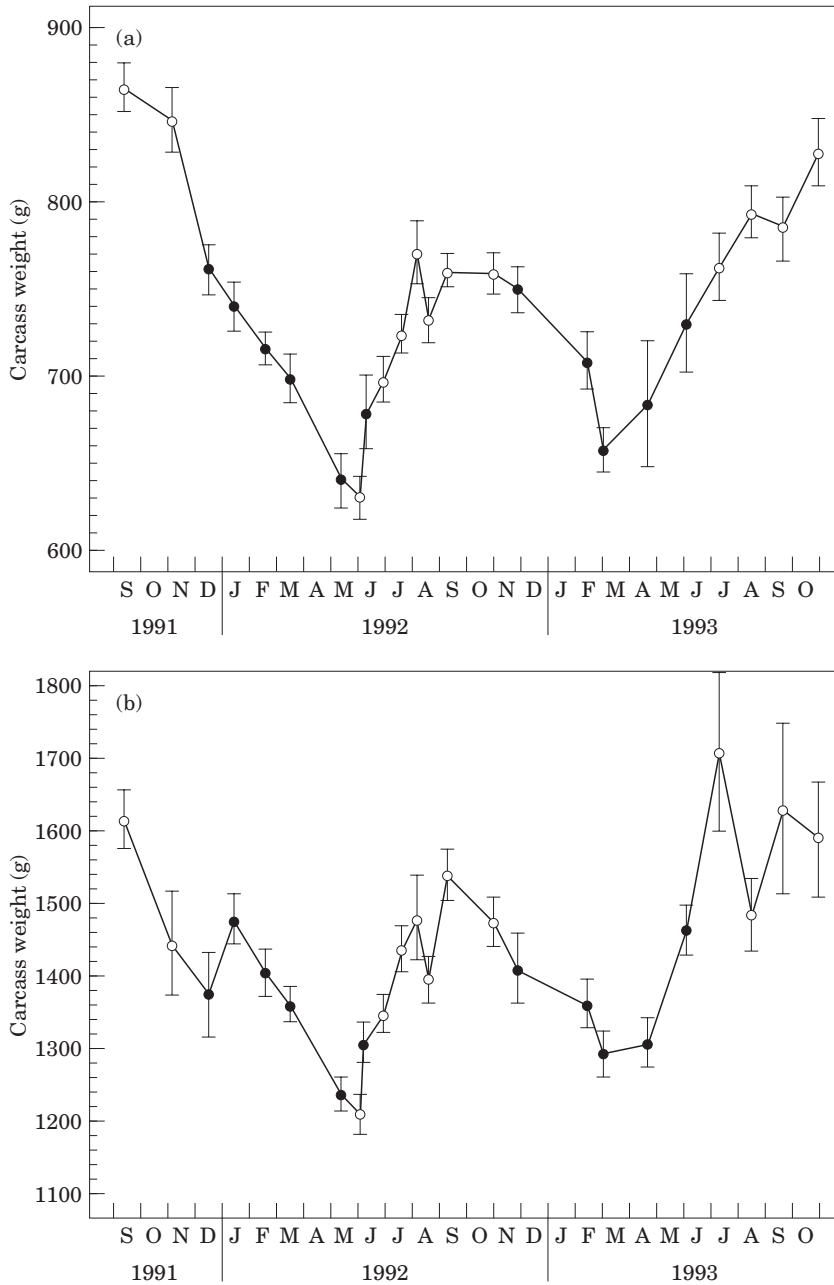


Figure 5. Seasonal changes in the standardized carcass weight of (a) small and (b) large Atlantic cod in the southern Gulf of St. Lawrence. Means and 95% confidence intervals are shown. Data from male and female cod were combined. ●, eastern Gulf; ○, western Gulf.

than in males because females had slightly (non-significant) higher peak GSI values, slightly lower percentage reductions in liver weight over winter, and higher gonad dry matter concentration relative to males. Likewise, the contribution of gonad growth to somatic depletion was greater in large than small cod. Again, this resulted from slightly (non-significant) greater GSI and

slightly less over-winter somatic depletion in the large cod.

#### Yield of marketable product

The procedure used to estimate seasonal variations in the weight of marketable product (muscle), in cod is

Table 3. Over-winter changes in the dry weights of carcass, liver, and gonads of cod in the southern Gulf of St Lawrence.

Date	Carcass dry wt (g)	Liver dry wt (g)	Gonad dry wt (g)	Changes between November and April or May			
				A Decrease in carcass dry wt (g)	B Decrease in liver dry wt (g)	C Gain in gonad dry wt (g)	C as % of A+B
Small male cod							
6 Nov 1991	179.3	35.3	2.8	—	—	—	—
13 May 1992 <sup>a</sup>	127.2	4.4	6.0	52.1	30.9	3.2	3.9
2 Nov 1992	160.5	29.5	3.3	—	—	—	—
22 Apr 1993 <sup>a</sup>	135.9	5.5	6.6	24.6	24.0	3.3	6.8
Small female cod							
6 Nov 1991	179.3	35.0	2.0	—	—	—	—
13 May 1992 <sup>a</sup>	127.2	6.6	10.5	52.1	28.4	8.5	10.6
2 Nov 1992	160.5	33.7	1.9	—	—	—	—
22 Apr 1993 <sup>a</sup>	135.9	7.9	7.8	24.6	25.8	5.9	11.7
Large male cod							
6 Nov 1991	306.1	56.4	1.9	—	—	—	—
13 May 1992 <sup>a</sup>	245.8	8.9	9.9	60.3	47.5	8.0	7.4
2 Nov 1992	312.4	53.5	3.8	—	—	—	—
22 Apr 1993 <sup>a</sup>	260.0	10.4	14.9	52.4	43.1	11.1	11.6
Large female cod							
6 Nov 1991	306.1	58.7	4.8	—	—	—	—
13 May 1992 <sup>a</sup>	245.8	14.2	24.9	60.3	44.5	20.1	19.2
2 Nov 1992	312.4	53.9	4.0	—	—	—	—
22 Apr 1993 <sup>a</sup>	260.0	19.5	19.9	52.4	34.4	15.9	18.3

<sup>a</sup>Ovary dry weights were maximal on these dates.

presented in Table 4. Columns A and C in Table 4 show that cod whose carcasses were dissected to determine relative muscle weight were neither markedly plumper nor skinnier, on balance, than the average condition of all fish in the respective sample. Therefore, measurements made on the dissected fish should accurately reflect the mean muscle weight of the entire sample.

When cod were in relatively good condition, as in December 1991 and again in September 1992, epaxial muscle comprised 64–66% of carcass weight (Table 4). If the loss of carcass weight over winter had been taken equally from all carcass compartments, then loss of muscle should likewise account for about 65% of the decline in carcass weight. However, dissections of cod in June 1992 showed that muscle represented only 60–62% of carcass weight (Table 4), which indicates that muscle contributes disproportionately to carcass depletion over winter. Muscle loss accounted for 82% (large cod) and 91% (small cod) of the decline in carcass weight between December 1991 and June 1992 (calculated from values in Table 4).

Changes in muscle weight within a 1-year period were 21–38% in small cod and 19–32% in large cod (Table 4). Absolute changes in muscle weight are even greater when comparisons are made over longer periods of time. For example, small and large cod exhibited 44 and 38%

greater muscle weight, respectively, in September/October 1993 than in June 1992 (calculated from Table 4). Although the body weight of large cod was greatest in July 1993 (Figure 5), comparisons involving this value are not recommended because the sample size on that date was small (10 fish).

## Discussion

### Historical patterns in cod diet and growth

Historically, the diet of cod in the southern Gulf of St Lawrence has been strongly linked to the abundance or availability of fish prey. An early example of this relationship occurred in 1954–1955 when cod predation on herring increased due to an epizootic fungal disease in the Gulf herring population which made herring more vulnerable to predation (Powles, 1958; Kohler, 1964). Herring were also prominent in the diet of cod in the early 1960s, when herring were quite abundant in the southern Gulf (Kohler and Fitzgerald, 1969). When Gulf herring populations subsequently declined to historically low levels by the late 1970s, herring all but disappeared from cod diets (Waiwood *et al.*, 1980; Waiwood and Majkowski, 1984). By the early 1990s, the fall spawner biomass of herring in the southern Gulf of

Table 4. Calculation of changes in the wet weight of muscle (marketable product) in cod over a seasonal cycle.

Size category	Date	Contribution of muscle to carcass wet weight			Total sample	
		n	Standardized carcass wt (g)	Muscle wt as % of carcass wt	Standardized carcass wt (g)	Muscle wt (B · C/100)
Small	17 Dec 1991	7	756	65.2	760	496
	4 Jun 1992	8	629	60.0	629	377
	11 Sept 1992	8	762	65.9	759	500
Large	17 Dec 1991	4	1350	64.3	1372	882
	4 Jun 1992	8	1211	61.8	1208	747
	11 Sept 1992	8	1555	64.0	1537	984

Maximum changes in muscle wet weight (marketable product) during the study						
Size category	Date	Standardized carcass wt (g)	Percentage change in carcass wt between dates	Estimated muscle weight		Percentage change in muscle wt between dates
				(%) (from column B)	(g)	
Small	13 Sept 1991	865	—	65.6 <sup>a</sup>	567	—
	4 Jun 1992	629	-27	60.0	377	-34
	11 Sept 1992	759	+21	65.9	500	+33
	4 Mar 1993	656	-14	60.0 <sup>b</sup>	394	-21
	30 Oct 1993	826	+26	65.6 <sup>a</sup>	542	+38
Large	13 Sept 1991	1614	—	64.2 <sup>a</sup>	1036	—
	4 Jun 1992	1208	-25	61.8	747	-28
	11 Sept 1992	1537	+27	64.0	984	+32
	4 Mar 1993	1289	-16	61.8 <sup>b</sup>	797	-19
	20 Sept/30 Oct 1993 <sup>c</sup>	1608	+25	64.2 <sup>a</sup>	1032	+29

<sup>a</sup> Mean of December 1991 and September 1992 values.

<sup>b</sup> June 1992 values.

<sup>c</sup> Data from September and October 1993 are combined to achieve greater sample size (n=29 for the two months combined).

St Lawrence had increased seven-fold above the low levels of the late 1970s (Claytor *et al.*, 1996), and herring were again the predominant fish prey of cod (Tables 1 and 2).

The extensive feeding of cod on capelin in our study appears to reflect changes in capelin distribution associated with a widespread cooling of water masses throughout the northwest Atlantic. Capelin is considered a subarctic species (Rae, 1968; Lilly, 1982) whose distribution is closely linked with the cold intermediate water layer (CIL) that occupies large areas of the northwest Atlantic Ocean during summer (Lilly, 1982; Frank *et al.*, 1996). Historically, capelin distribution in the Gulf of St Lawrence has been centred within and north of the Laurentian Channel, presumably because large areas of the southern Gulf are too warm for capelin in summer (Dunbar *et al.*, 1980; de Lafontaine *et al.*, 1991). However, widespread cooling of the northwest Atlantic Ocean during the early 1990s led to expansion of the CIL in the Gulf of St Lawrence until it covered most of the southern Gulf (Swain, 1993a; Gilbert and Pettigrew, 1997). Whereas capelin were rarely caught in September research surveys in the southern Gulf during the 1970s and early 1980s, they have been caught each year since

1988 (Frank *et al.*, 1996). Cod apparently exploited capelin as food in the southern Gulf after capelin became abundant there due to a widespread reduction in water temperature. The return of abundant herring and capelin populations to the southern Gulf may explain why the proportion of fish in the diet of cod in 1992 was the highest observed since the mid 1950s (Table 5).

A low ratio of fish to invertebrates in the diet is believed to be an important reason for the slow growth of 4TVn cod compared to other cod stocks (Waiwood and Majkowski, 1984). This inference is based on the premise that invertebrates are energetically inferior to fish as food for cod. Increased fish consumption has been correlated with improved growth rate in southern Gulf cod; once in the mid 1950s during the herring epizootic (Powles, 1958; Kohler, 1964), and again during the late 1960s when improved growth in cod coincided with increased consumption of capelin (Waiwood, 1986). Accordingly, the fish-rich diet of cod in our study (Table 5) should have produced high growth rates. In reality, cod growth rates, which have declined steadily since 1978, remained at historically low levels during the early 1990s (Chouinard and Fréchet, 1994). This suggests that the influence of diet composition on cod

Table 5. Historical comparison of cod diet composition in the southern Gulf of St Lawrence.

	Study			
	Powles (1958)	Kohler and Fitzgerald (1969)	Waiwood and Majkowski (1984)	Present
Year(s)	1956	1959–1962	1980	1992
Period	late May–early Sept	May–Aug (50+ fathoms)	May 25–Sept 16	May 13–Sept 12
	<b>Small cod</b>			
Cod length range	31–50 cm	30–49 cm	43.8–53.4 cm	40.0–50.9 cm
Sample size (n)	84	845	335	600
	Percent composition by weight			
Fish	25.0	17.0	26.6	58.5
Crustacea (total)	58.0	47.0	41.3	27.5
Decapoda	24.0	—	20.3	19.1
Other crustacea <sup>a</sup>	34.0	—	21.0	8.4
Mollusca	8.0	13.0	7.2	1.5
Annelida	5.0	7.0	4.6	3.7
Echinodermata	4.0	2.0	5.5	0.1
Other food	0.0	14.0	14.8	8.7
	<b>Large cod</b>			
Cod length range	51–70 cm	50–69 cm	53.5–61.4 cm	51.0–61.0 cm
Sample size (n)	71	813	162	407
	Percent composition by weight			
Fish	32.0	48.0	27.9	73.7
Crustacea (total)	46.0	27.0	38.5	13.9
Decapoda	16.0	—	25.5	9.4
Other crustacea <sup>a</sup>	30.0	—	13.0	4.5
Mollusca	14.0	7.0	9.8	1.7
Annelida	6.0	3.0	1.7	1.0
Echinodermata	2.0	3.0	5.8	0.1
Other food	0.0	12.0	16.3	9.6

<sup>a</sup>Predominantly the orders Euphausiacea, Mysidacea, and Amphipoda.

growth in the southern Gulf may have been overestimated, or outweighed by more potent factors in recent years.

The initial decline in the growth rate of 4TVn cod beginning in the late 1970s (Chouinard and Fréchet, 1994) preceded, and cannot be attributed to, the recent period of anomalously cold conditions in the Gulf of St Lawrence (Gilbert and Pettigrew, 1997). Perhaps the initial growth decline was caused by a high proportion of invertebrates in the diet (Waiwood *et al.*, 1980; Waiwood and Majkowski, 1984) or density-dependent selection of cooler water temperatures by cod (Swain and Kramer, 1995). The continuance of slow growth in cod during the present study, despite an increased prominence of fish in the diet, could be related to low water temperature. Note that the cooling trend which began in the southern Gulf in the late 1980s occurred primarily in the shallow depths occupied by cod in summer rather than the deeper waters frequented by cod in winter (Gilbert and Pettigrew, 1997). Hence, temperature-induced growth reductions in summer would not be offset by reduced weight loss due to cooler conditions in winter.

### Seasonal feeding periodicity

Although the metabolic effect of seasonal temperature oscillation is an important factor governing food intake in temperate freshwater fish (Weatherley and Gill, 1987), it is probably not the main cause of seasonal feeding periodicity in southern Gulf cod. September groundfish surveys in the southern Gulf show that commercial size cod (age 4 years and older) are most abundant within the upper part of the CIL (Swain, 1993b; Swain and Kramer, 1995) which is characterized by temperatures <3°C (Gilbert and Pettigrew, 1997). During spring and autumn, Jean (1964) found that although commercial size cod in the western Gulf occurred in temperatures up to 8°C, the majority of cod were at depths where temperature was 1°C. During winter, cod in Area 4Vn were concentrated in deeper waters along the western slope of the Laurentian Channel at temperatures of 1–3°C (Jean, 1964). A winter survey in Area 4Vn during 1994 found that the majority of cod occupied temperatures of 5–6°C (Chouinard, 1994). Therefore, cod in the southern Gulf experience small seasonal changes in temperature (a reasonable estimate being 0–4°C) and

may experience slightly warmer conditions in winter than in summer. It is difficult to believe that the large seasonal fluctuations in stomach fullness of Gulf cod result primarily from the metabolic effects of such small seasonal variations in temperature.

A scarcity of suitable prey is a simpler and more plausible explanation for why cod in the southern Gulf feed little during winter. Levels of primary and secondary productivity in the southern Gulf are highest in the extreme western region along the northern coast of New Brunswick from the Gaspé peninsula southward to Miramichi Bay (Steven, 1975; Dunbar *et al.*, 1980; de Lafontaine *et al.*, 1991). This area corresponds closely to the preferred summer habitat for the 4TVn cod stock (Swain and Wade, 1993). The high productivity of this region results from a combination of factors including nutrient input by the Gaspé current, shallow depth, and relatively warm surface temperatures during summer (Steven, 1975; Dunbar *et al.*, 1980; de Lafontaine *et al.*, 1991). Benthic invertebrates are probably more abundant here than in the deeper, less productive waters on the slope of the Laurentian Channel east of Cape Breton Island.

The scarcity of fish in cod stomachs during winter is more difficult to explain because many forage fish species, including Atlantic herring, also over-winter outside the Gulf. However, a groundfish and herring survey conducted in Cabot Strait during January 1994 found that herring were mainly distributed between 150 and 200 m whereas cod occupied depths between 200 and 250 m (Chouinard, 1994). More importantly, 70% of all herring were caught at temperatures of 1°C or less (i.e. high in the water column), whereas nearly all cod were caught at temperatures above 5°C (i.e. low in the water column). Hence, there may be a temperature-related vertical separation of cod and herring during winter.

### Seasonal factors governing the cod growth cycle

Food intake is the dominant factor driving seasonal cycles in the carcass and liver weights of southern Gulf cod, rather than migrational energy costs or gonad growth. If the energy cost of migration had been a significant factor underlying these cycles, large and abrupt declines in carcass or liver weight should have occurred during the relatively brief autumn (November to December) and spring (late April to early June) migrations. A relatively large decline in carcass weight occurred in small cod between 6 November and 17 December 1991 (Figure 5). Overall, however, carcass and liver weights of cod declined steadily throughout the entire winter period (October to April).

Evaluating the contribution of gonad growth to somatic depletion was complicated by the presence of some cod whose gonads were not maturing (Figure 3). A study of gonad histology by Burton *et al.* (1997) sug-

gested the existence of three non-reproductive states in cod; an immature stage, a female adolescent stage intermediate between the immature and mature stages, and an adult stage in which fish omit a spawning. Most of the non-maturing fish in our study were probably adolescents or adults in spawning omission because most immature cod are shorter than 41 cm (Burton *et al.*, 1997). Maturing and non-maturing cod were combined to compare gonad growth with somatic depletion (Table 3) because they could not be reliably separated in the autumn. Cod gonads can grow rapidly, which means that small size and immature appearance in autumn is insufficient evidence that a gonad will not mature by the following June.

On a dry weight basis, gonad growth could account for only 4–19% of somatic depletion over winter (Table 3). The contribution of gonad growth to somatic depletion on an energetic basis was estimated based on proximate composition analyses of liver, carcass, and gonads in May and November 1992 (data not shown). Only 3.6–13% of over-winter somatic energy depletion could be accounted for by gonad growth. Gonad growth accounted for a lower percentage of somatic depletion on an energy rather than dry weight basis because much of the energy lost from the soma is due to depletion of liver lipids (which typically comprise 50–60% of liver wet wt), whereas gonad growth consists primarily of protein, the lipid content of ripe gonads being 2–3% wet wt. If some of the nutrients used for gonad growth originated from food eaten over winter, the contribution of gonad growth to somatic depletion would be even less than the above values. Therefore, it can be concluded that at least 81–96% of the depletion in somatic dry matter of cod during the winters of 1991 and 1992 was used to meet metabolic energy requirements rather than to supply substrates for gonad maturation.

Similar results were obtained by Eliassen and Vahl (1982a, b) for Atlantic cod in Balsfjorden, northern Norway. They estimated that gonad growth could account for only 10% of the energy lost from cod carcass and liver between January and April. Consistently smaller livers in male than female cod (Figure 4) may have resulted from earlier gonad maturation in the males (assuming gonad growth influences liver weight) or from hepatic hypertrophy in females in response to estrogen secretion by the developing ovary (Ng and Idler, 1983).

### Management implications

Diminished food intake, 76–84% depletions of the cod's main energy depot (i.e. liver), and 25–27% losses in carcass weight (Figure 5), suggest that cod could die from starvation and energetic depletion over winter. By starving captive cod to exhaustion, Lambert and Dutil (1997b) found that a condition factor less than 0.7 and a HSI less than 2.0 was characteristic of cod in poor

Table 6. Maximum and minimum values for condition factor and hepatosomatic index (HSI) of cod during the study. Q1 and Q3 denote lower and upper quartiles, respectively.

Date	n	Mean	Median	Q1	Q3	Min	Max
Condition factor (sexes and sizes combined)							
13 Sept 1991	136	0.99	0.98	0.94	1.05	0.68	1.27
4 Jun 1992	106	0.71	0.71	0.67	0.75	0.56	0.84
HSI – males							
13 May 1992	58	1.73	1.54	1.19	2.03	0.73	3.81
7 Aug 1992	21	6.34	6.19	5.47	7.67	3.20	8.33
HSI – females							
13 May 1992	91	2.72	2.55	1.84	3.10	1.09	12.75
7 Aug 1992	23	7.02	6.74	5.85	8.24	4.19	10.94

condition and at increased risk of mortality. A condition factor of 0.7 also marked the transition point below which muscle energy content ( $\text{kJ g}^{-1}$  wet wt) declined very rapidly with further decreases in condition (Lambert and Dutil, 1997a).

To facilitate comparisons with studies by Lambert and Dutil (1997b) we calculated condition factors and HSI values for our cod when these indices were at their highest and lowest levels. In June 1992, condition factors as low as 0.56 were observed in cod from the southern Gulf of St Lawrence, and more than 25% of all cod exhibited condition factors less than 0.7 (Table 6). Fifty percent of all male cod collected in May 1992 exhibited HSIs below 1.5%. Although HSIs of female cod were somewhat higher, more than 25% had HSIs less than 2.0 (Table 6). Thus, a significant proportion of cod in the southern Gulf appear to be in poor condition during spring and at increased risk of mortality.

Lambert and Dutil (1997b) reported that the collapse of the northern Gulf of St Lawrence cod stock in the early 1990s coincided with declines in the condition factor of cod during January groundfish surveys. Similarly, fall research surveys indicated that the collapse of cod stocks off Labrador (NAFO Division 2J) and on the Newfoundland shelf (NAFO Division 3K) beginning in 1989 was accompanied by reduced HSI (2J only) and condition factors (Taggart *et al.*, 1994). Although these studies suggest a link between the physiological condition of cod and increased mortality, the evidence to date is largely circumstantial and clouded by competing causes such as over-fishing and low temperature.

Large seasonal cycles in cod carcass weight have implications for stock assessment procedures. Currently, sequential population analyses of commercial catch data are calibrated with annual research vessel surveys to estimate population numbers for each length and age class of cod (ICES, 1993). A weight-length relationship determined from research surveys is then used to estimate stock biomass and to set commercial catch quotas. As annual September research surveys in the southern

Gulf of St Lawrence coincide with the peak of the cod's carcass weight cycle, stock biomass will be consistently overestimated relative to the remainder of the year. Seasonal variability in carcass weight also means that catch quotas based on weight will lead to removal of greater numbers of cod from the population if catches are made in spring rather than in autumn.

From the perspective of the fishing industry, seasonal cycles in cod carcass weight translate into large variability in the yield of marketable product. In practical terms, the muscle mass of a standard length cod was 39–50% greater in September 1991 than in June 1992 (Table 4). Although these comparisons indicate the maximum changes in cod muscle weight observed during our 2-year study, it is clear that substantially greater yields of marketable product can be obtained from a given number of cod if those cod are harvested in late autumn rather than in spring. We realize that practical issues such as the need to spread employment and income over the entire year may make it unfeasible to harvest cod only in the autumn. Nevertheless, it is important to be aware of how seasonal harvesting strategies affect product yields.

## Summary

This study has shown that cod in the southern Gulf of St Lawrence lose much of their carcass and liver weight over winter, and that these losses result primarily from restricted food intake rather than from gonad growth or migrational energy costs. Over-winter losses occurred even though cod consumed a high quality diet (i.e. high proportions of herring and capelin) during the preceding summer. The losses were severe enough to suggest that winter starvation may cause mortality in this cod stock. Seasonal cycles in carcass weight also impact stock assessment procedures and the yields of marketable product obtainable from cod. The near absence of food intake by cod in their wintering area emphasizes the

critical importance of the western Gulf of St Lawrence as summer feeding habitat for cod.

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