Environmental influences on the productivity of cod stocks: some evidence for the northern Gulf of St. Lawrence, and required changes in management practices

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Résumé

Dans ce document, nous examinons à la lumière de projets réalisés à l'IML comment les changements climatiques peuvent avoir affecté la productivité du stock de morue franche (*Gadus morhua*) du nord du golfe Saint-Laurent. La température de l'eau du Golfe varie d'une année à l'autre et une suite d'hivers rigoureux ont entraîné une baisse de la température de la CIF particulièrement prononcée vers la fin des années 1980 et le début des années 1990. Des variations de température ont aussi été observées dans la couche profonde qui se caractérise par ailleurs par de faibles tensions d'oxygène pouvant causer des mortalités chez la morue. Ces changements climatiques ont entraîné un changement de distribution, ce qui a pu avoir un impact négatif sur la croissance, la condition et la maturation en exposant les morues davantage aux faibles tensions d'oxygène. La moins bonne condition des morues à l'automne se traduit en une mauvaise condition au printemps de sorte que les femelles adultes produisent moins d'oeufs à un coût relativement plus élevé, ce qui les rendrait vulnérables à la mort par inanition. Des analyses préliminaires suggèrent d'ailleurs que les oeufs issus de femelles moins bien nourries sont de qualité inférieure et sont moins viables. L'impact sur les larves reste à établir, bien que l'on ait observé un lien entre la croissance des larves et leur activité natatoire. Les changements dans la taille à l'âge entre 1980 et 1996 ont suivi de près les variations des conditions climatiques. Les morues en moins bonne condition sont également celles dont la croissance est lente, ce qui suggère que la mort par inanition chez les poissons en mauvaise condition se produirait surtout chez les stocks à croissance lente. Ces nombreux facteurs limitent la productivité de ce stock qui subit également un taux élevé de prédation par les phoques. Nos décisions doivent prendre en considération les variations temporelles et latitudinales dans la productivité des stocks de morue.

Abstract

The mechanisms linking climatic changes and Atlantic cod (*Gadus morhua*) stock production in the northern Gulf of St. Lawrence are examined through a review of projects conducted at MLI. The average temperature of Gulf waters varies between years and severe winters particularly in the late 1980's and early 1990's caused a marked decline of the CIL temperature. Temperature fluctuations are known to occur in deep waters as well which are also characterized by low oxygen pressures potentially lethal to cod. These climatic changes resulted in a shift in the distribution of cod and this may have had a negative influence on growth, condition and maturation. Declining energy reserves in the autumn result in poor condition in the spring so that females produce a smaller amount of eggs at a relatively higher somatic cost which exposes post-spawners to death through starvation. Preliminary results suggest that eggs produced by poor condition females are less viable due to their poor quality. The impact on larvae hatching from those eggs remains to be documented, but nevertheless larval growth and swimming activity were found to be correlated. Between 1980 and 1996, size at age followed changes in climatic conditions. Poor condition occurred in cod with slow growth rates which may mean that death from poor condition may be limited to cod exhibiting slow growth rates. Northern Gulf cod thus have a low productivity which is further impaired by a high rate of mortality due to predation by seals. Stock management decisions must factor in latitudinal and temporal variations in productivity.

Introduction

Management decisions on Atlantic cod (*Gadus morhua*) fisheries rest on very little biological information; lengths, weights and ages are used essentially in combination with landings statistics. Fluctuations in the marine environment and resulting stock-specific annual variations in production are not factored in the models used to assess the status of a stock. This situation resulted from the widely shared view that cod stocks were all very productive and would persist in spite of large man-made perturbations in the absence of significant environmental perturbations. Cod stocks have long been exposed to heavy fishing pressures (Turgeon 1995; Turgeon 1997). Their persistence under heavy exploitation, with as much as 60% of the biomass being removed annually (Cook et al. 1997), argued up to a recent past in favor of the maximum sustainable yield management strategy. More recently, several stocks have collapsed in eastern Canada showing that cod stocks cannot resist unlimited perturbation. This has raised the question of whether record low abundances in the 1990's resulted from fishing overexploitation (Hutchings and Myers 1994), as high fishing mortality rates suggest, or alternately from a combination of man-made perturbations and changing environmental conditions through decreasing productivity and increasing natural mortality, as a strong coincidence of the declines in both space (northern stocks) and time (early 1990's) would suggest.

This question is not new to fishery literature and fishery managers. Cushing (1982) discussed the case of the West Greenland cod stock. He speculated that favorable climatic conditions in the early 1900's were responsible for the colonization by cod of West Greenland and suggested that cooler temperatures had in turn been responsible for a decline of this stock in the 1970's. Fishing however, was also a candidate cause for the decline (Cushing 1982). Cushing reviewed several instances of conflicts concerning probable causes of collapsed fisheries, some scientists arguing in favor of linking stock declines to natural causes and others to fishing activities. Similarly, declining sizes at age in the northern and southern Gulf of St. Lawrence cod stocks (Chouinard and Fréchet 1994), are also being argued to result from either deteriorating climatic conditions (Dutil et al. submitted) or size selective fishing (Hanson and Chouinard 1992). Interestingly, increasing sizes at age in the northern Gulf of St. Lawrence in the 1960's were also considered as having resulted from increased fishing, through a reduction of intraspecific competition, or from improving climatic conditions (Wiles and May 1968).

The case for an environmental cause or for an interaction between an environmental perturbation and high fishing mortalities to account for a low standing stock biomass was examined for the northern Gulf of St. Lawrence cod stock under two research programs. MLI's multidisciplinary research program was launched in late 1992 under the following working hypothesis: "Environmental conditions have changed in recent years in the northern Gulf of St. Lawrence. Marine habitats have become less favorable to survival, individual growth and sexual maturation of cod. These modifications resulted in a measurable shift in distribution and altered patterns of migration and reproduction. Productivity in turn declined through a deterioration of individual condition, slower growth rates and an increased vulnerability of cod at all stages in the life cycle: larvae, juvenile and adult fish became less efficient in feeding and escaping predation and were more vulnerable to diseases and parasites.". Two years later, a more narrowly focused research program was launched in the DFO Atlantic Zone under the High Priority Funds initiative: "Partitioning total mortality of Atlantic cod stocks". This program was a multi-regional effort to

assess fishing mortality and to partition natural mortality into several components for several stocks on the East Coast of Canada.

The present document does not address the question of whether fishing, natural causes or both factors were responsible for the decline of cod stocks in Eastern Canada. We examine recent evidence showing that environmental conditions did change and we review documented influences on the stock in the northern Gulf of St. Lawrence. Project leaders at MLI were asked to provide sample results from their research under both programs. Potential consequences on future management strategies are also discussed in the context of emerging precautionary approaches to fisheries management.

Changes in the climatic conditions of the Gulf of St. Lawrence over the past decade

Denis Gilbert

In this section we describe some of the key climatic variations that occurred in the Gulf of St. Lawrence over the past few decades, with some emphasis on the period of cod stock decline and collapse to see whether the climatic conditions that prevailed then were typical or not. Information on air temperatures and sea ice cover were obtained from Environment Canada, whereas the information on water temperature and dissolved oxygen comes from historical data collected mostly by scientists from Canada's Department of Fisheries and Oceans.

Air temperature and sea ice cover

Over the past decade, by far the most significant departures from normal air temperatures have occurred during the winter season (Gilbert et al. 1997, Figs. 5 to 8). Colder-than-normal winter air temperatures have been observed over the Gulf of St. Lawrence from 1989 to 1995, and led to more extensive ice cover than usual. Not only has ice extent increased, but the first presence of ice generally occurred earlier and the last presence of ice occurred later-than-normal, so that the total ice cover duration was longer-than-normal by a few weeks (Drinkwater et al. 1996).

Cold intermediate layer

Changes in local winter air temperatures over the Gulf of St. Lawrence influence the properties and the interannual variations of the cold intermediate layer (CIL), a layer of cold water extending roughly from a depth of 30 to 125 m (Gilbert and Pettigrew 1997). Minimum temperatures within the CIL have been below normal since 1984, with the five consecutive years from 1990 to 1994 marked by near-record cold temperatures (Figure 1). A slight warming of the CIL began in 1995 and continued in 1996 and 1997. The region of the Gulf of St. Lawrence most likely to be directly affected by low CIL temperatures is the southern Gulf, where a large expanse of the sea bed lies within the depth range of this cold layer. Bottom areas with estimated bottom temperatures below 0°C and below 1°C exceeded the long-term normals in the southern Gulf from the late 1980s to the mid-1990s (Swain and Wade 1993; Gilbert et al. 1997).

Temperature and dissolved oxygen in the deeper layers (100-300m)

In the 100-200 m layer, the coldest temperatures of the 1985 to 1996 period were observed in 1991 and 1992 (Gilbert 1997). Temperatures had returned to normal by 1994, but then dropped below normal once again in 1995. In the 200-300 m layer, if we look at a time series of temperature over the last few decades at Cabot Strait (Bugden 1991), we find that record low values were reached in the mid-1960s and were followed by relatively warm conditions until about 1988 (Figure 1). Rapid cooling then marked the period through 1991, followed by equally rapid warming in 1992 and 1993. Temperatures have been close to normal since then in this deep layer. With regards to dissolved oxygen, no prolonged period of anomalous conditions has been observed between 1981 and 1995 in the deep waters of the Gulf (Gilbert et al. 1997).
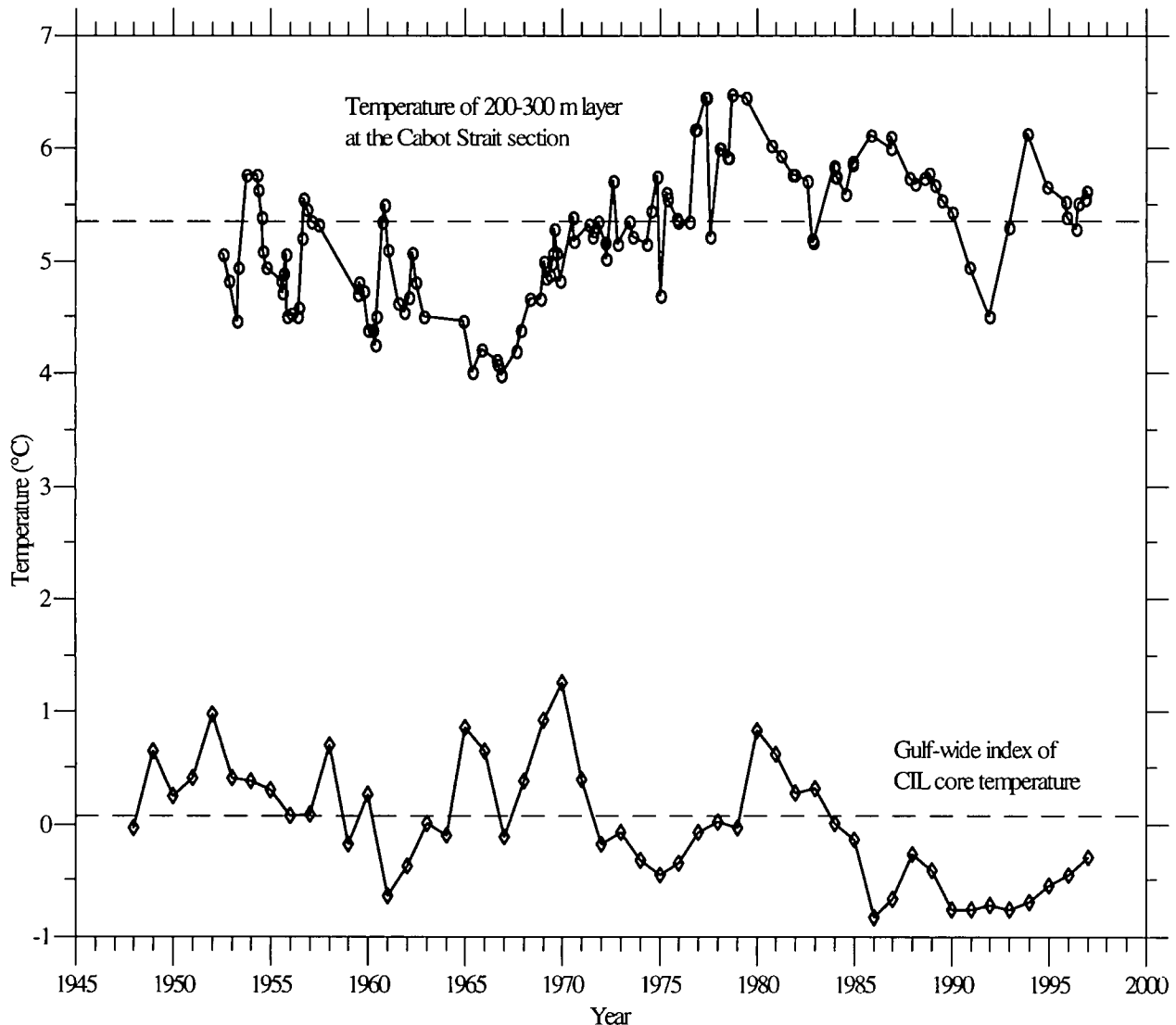

Figure 1. Time series of the Cold Intermediate Layer (CIL) core temperature index (diamonds) and of the average temperature of the 200-300 m layer at the standard Cabot Strait hydrographic section (circles).

Distribution changes in relation to an oceanic cooling

Martin Castonguay

The Gulf of St. Lawrence has been experiencing colder-than-normal water temperatures in the cold intermediate layer (CIL), since the mid 1980s (Gilbert and Pettigrew 1997; Gilbert, this document). We examined how the cooling of the CIL affected the distribution of cod with respect to depth, temperature, and latitude in the northern Gulf in both summer and winter. We tested the null hypothesis that the cooling did not result in exposure of cod to colder water temperature in either January or August.

We analysed data collected on research vessel trawl surveys in both January (1978 to 1994, except no survey in 1982) and August (1984 to 1995). Cod catch-at-age, calculated for each tow, was expanded to the surface area of the various strata. Near-bottom water temperatures were measured either with Sippican XBT, Applied STD, Guildline CTD, or Sealogs. Temperatures were quality-controlled against mean and SD values for the corresponding month and area from Petrie (1990). For both surveys, we compared distributions of observed (i.e., for all stations sampled during the surveys) and selected (i.e., observed weighted by number of fish caught) temperatures, depths, and latitudes among years (ages 2 to 8+, pooled and disaggregated) (Castonguay et al. submitted). To accomplish this, we implemented Perry and Smith (1994) cumulative distribution function (cdf) method, which statistically compares cdfs of sampled parameters (i.e., 2.5, 50, and 97.5 percentiles of depths, temperatures, and latitudes) with those selected (occupied) by fish.

Distribution in January

We found that the January distribution changed substantially among years. Cod have been distributed 200 m deeper (from about 250 to 450 m) starting in 1989 for ages 6, 7 and 8+, and in 1990 for ages 4 and 5 (Figure 2). Juveniles (ages 2 and 3) also shifted to deeper water in January, but to a lesser extent (Figure 2). However, this depth shift was not accompanied by a change in median selected temperatures, which remained in the 4.4-5.9°C range for all age groups (Castonguay et al. submitted).

Cod have also been progressively located further south in January starting in 1986, such that the median latitude of their spatial distribution by 1993 was 2° (220 km) south of its median location in 1985 (Figure 3). There was a significant positive correlation between the median latitude where cod were found in January and the index of CIL core temperature anomaly in the previous summer (r=0.79, p<0.05, corrected for autocorrelation as per Ebisuzaki 1997) (Figure 3; Castonguay et al. submitted).

Distribution in August

In contrast with the shifts in the January distribution, cod did not seem to change their distribution with respect to latitude, depth, or temperature in August, with the caveat that because waters<92 m (50 fathoms) were not sampled before 1991, they had to be excluded from survey analysis. The
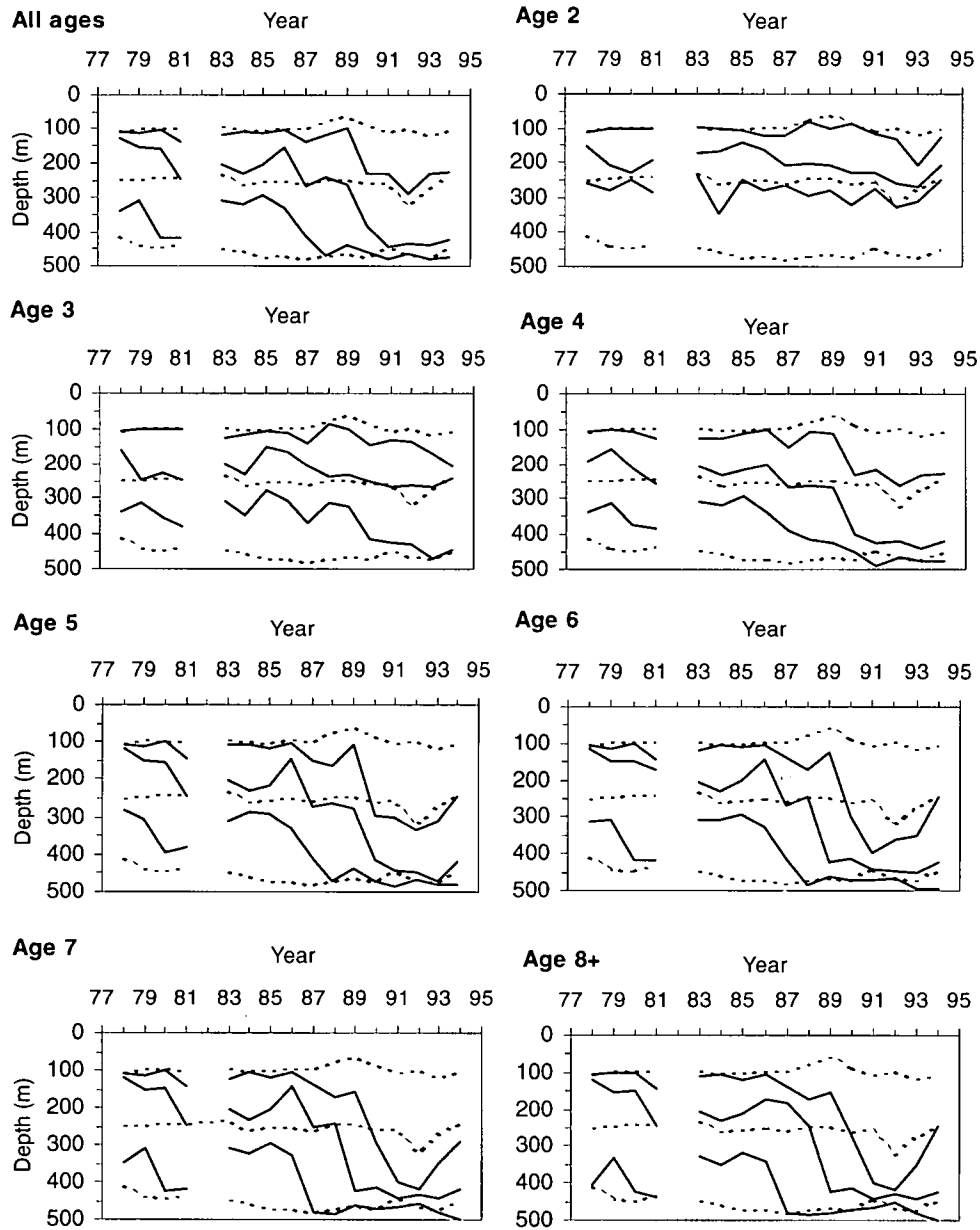
Figure 2. Cumulative distribution functions (cdfs) of depths (expressed as 2.5, 50, and 97.5 percentiles) selected by cod 2 to 8 + years old (and also for pooled ages) versus those sampled by the trawl during the winter survey, from 1978 to 1994 (no survey in 1982). The 2.5, 50, and 97.5 percentiles of selected depth cdfs are represented by the top, middle, and bottom solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled depth cdfs are represented by the top, middle, and bottom dotted lines, respectively.

median depth occupied in August did not exhibit temporal trends or age-related differences and remained in the 144-181 m range, except for 1987 when it was only 119 m. The median temperature occupied in summer did not show a temporal trend either: it fluctuated between 1.4 and 3.5°C, again with the notable exception of -0.1°C in 1987. In years when depths between 37

and 91 m (20-50 fathoms) were also sampled (i.e., 1991-1995), 35% of cod were found above 100 m in the CIL, on average. The median latitude where cod were found in August fluctuated little among years (49.4 to 50.1°N) or between juveniles and adults (Castonguay et al. submitted).
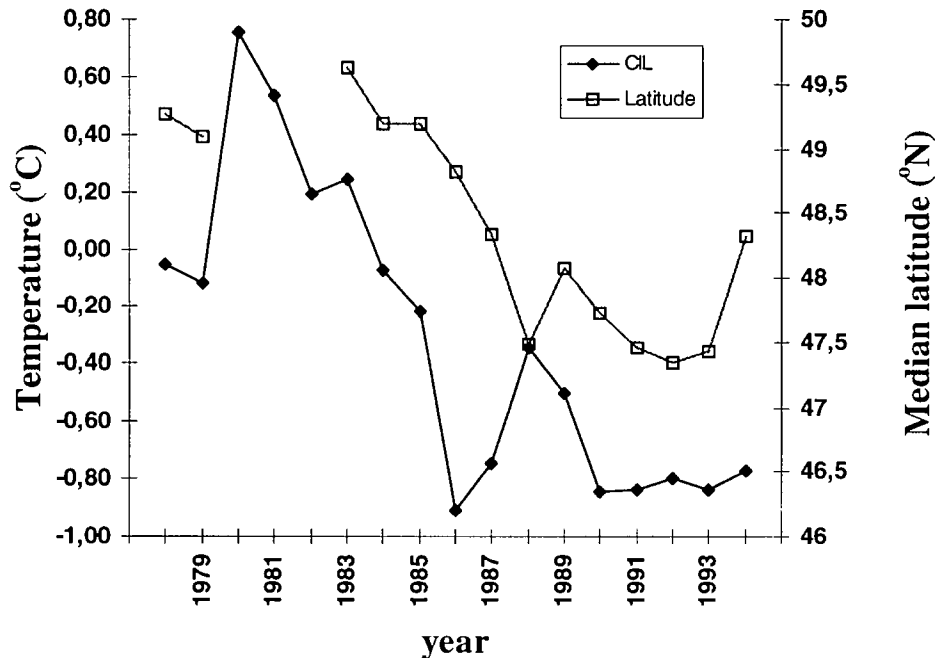

Figure 3. Deviations from the 1948-1994 mean temperature in the cold intermediate layer of the gulf of St. Lawrence in summer (diamonds) and median latitude of cod distribution in January (squares). Latitude data were excluded for 1980 and 1981 because the survey was conducted three weeks later than normal, hence the possible effect on distribution. There was no survey in 1982.

Distribution of cod and CIL temperature

Our analysis showed that we could not reject the null hypothesis, since we found no evidence that cod were exposed to colder temperatures as a result of the cooling of Gulf waters. However, results suggest a cause-effect relationship between summer CIL temperature anomaly and cod spatial distribution during the following winter. This, coupled with the finding that the summer CIL temperature anomaly and cod growth are positively correlated in the northern Gulf (Dutil et al. submitted; Dutil, this document), points to relationships between CIL temperature, cod distribution, and cod growth. Hence we put forward the following hypothesis: the cooling of Gulf CIL waters decreased the duration of the fall feeding period of cod in the northern Gulf and produced an earlier departure to wintering grounds, as reflected by the absence of change in occupied latitudes in August coupled with the southerly occupied latitudes in January. This reduction in the length of the feeding period was in turn largely responsible for the growth decline of cod in the late 1980's and early 1990's (Castonguay et al. submitted). This hypothesis raises the question of whether the earlier wintering migration was caused by direct exposure to cold

water or by a diminished availability of preys, or both. Further retrospective work is planned to test the hypothesis.

The impact of low oxygen values on survival and growth

Denis Chabot

Gilbert (this document) has shown that the waters of the Gulf of St. Lawrence were cooler than average in the late 1980's and early 1990's. Cod has changed its spatial and bathymetric distribution during the same period (Castonguay, this document). Thus, in recent years most of the cod biomass was found in deep waters of the Cabot Strait in early January, whereas earlier in the 1980's they were still in the Gulf of Saint Lawrence at this time of the year. This suggests that cod left the Gulf of St. Lawrence sooner in the fall in recent years than they did previously, and therefore spent more time in late fall and winter in deeper waters. There is also anecdotal evidence from the collapse of the trap fishery along the Lower North Shore that cod are less common in coastal waters in summer and early fall than they were in the early 1980s, and therefore spend more time in deeper waters at this time of the year.

Recent data (Chabot, unpublished) show that cod caught inshore have fuller stomachs than cod caught offshore. The reduced feeding offshore could be due, at least in part, to differences in prey abundance between the inshore and offshore habitats. Hypoxic waters (i.e. waters not fully saturated with oxygen), however, could also be involved. Many studies have shown that the deep waters of the Gulf of Saint Lawrence are hypoxic (D'Amours 1993a; D'Amours 1993b; Gilbert et al. 1997). Because metabolic processes require oxygen, hypoxia can limit metabolism in marine organisms. In fish, mild hypoxia may constrain energetically demanding activities, such as fast swimming or digestion. In more severe hypoxic conditions, fish may suffer a reduced growth and ability to capture prey or evade predators, and even death. Considering that waters with less than 30% O_2 are common in the Gulf, our first objective was to define the lethal hypoxic threshold for cod at temperatures characteristic of the deep water layers. Our second objective was to measure the impact of non-lethal, chronic hypoxic exposure on cod growth.

Lethal hypoxic level for two water temperatures (2 and 6°C) and two size-ranges (small fish, 45.2±0.3 (mean±SE) and large fish, 57.5±0.2 cm) of cod was defined as the level killing 50% of the animals over 96 h (LC_{50}^{96h}), a toxicity test well accepted in the literature (American Society for Testing and Materials 1988). To assess which parts of the Gulf are not available to cod we also calculated hypoxic levels where cod begin to die (5% mortality after 96 h). For each experimental condition, 10 fish were randomly allocated to each one of six 800 l tanks. The six levels of hypoxia used in the tests were 12%, 17.4%, 23.5%, 29.5%, 35.8% and 41.9% O_2. Each experiment was repeated twice for a total of 20 fish per O_2 level. However, one replicate for large cod at 6°C had to be dismissed. Dead fish were counted at 1 h, 3 h, 6 h, 12 h and every 12 h thereafter up to 96 h. Lethal levels (50% and 5%) were calculated for each one of these periods by Probit regression (SAS Institute 1989).

The impact of hypoxia on growth was studied by growing 20 fish at each of six oxygen levels (45, 56, 65, 75, 84 or 93%). Fish were measured and weighed, at the beginning of the study (mean±SE for all 6 tanks: 44.2±0.3 cm, 715±17 g, 0.81±0.009 condition factor, based on total mass). Temperature was set at 10°C in all tanks to obtain good growth rates. Cod were fed

capelin ad lib for 1 h three times weekly. Excess food was removed and weighed after 1 h. After a growing period of 84 days, all fish were remeasured and reweighed, and a condition factor was calculated based on somatic mass.

Lethal oxygen levels, small and large cod at 2 and 6°C in the laboratory

We found no effect of temperature or size on tolerance to hypoxia and the overall mean lethal level was 21.2% O_2, although small cod at 6°C had a tendency to be more tolerant than the other groups (Figure 4). Figure 4a also shows it takes very low oxygen saturations to kill 50% of the fish very quickly, but the lethal level stabilizes after 24 h. It is unlikely that longer exposures would have led to a very different value of lethal hypoxic level. Figure 4b shows that fish begin to die in waters containing 24.5% O_2 (small cod at 6°C) and 28.5% O_2 (the 3 other groups), for a mean of 27.6% O_2. Again, most fish that survived 24 h were able to withstand prolonged exposures. So in this temperature range (2-6°C) and size range (about 40-60 cm), cod survive up to 96 h in waters at 30% O_2 sat. or more, but 5% of individuals die at 27% O_2, and 50% die at 21.2% O_2. Therefore below 30% O_2 small changes in saturation have major effects on fish survival.
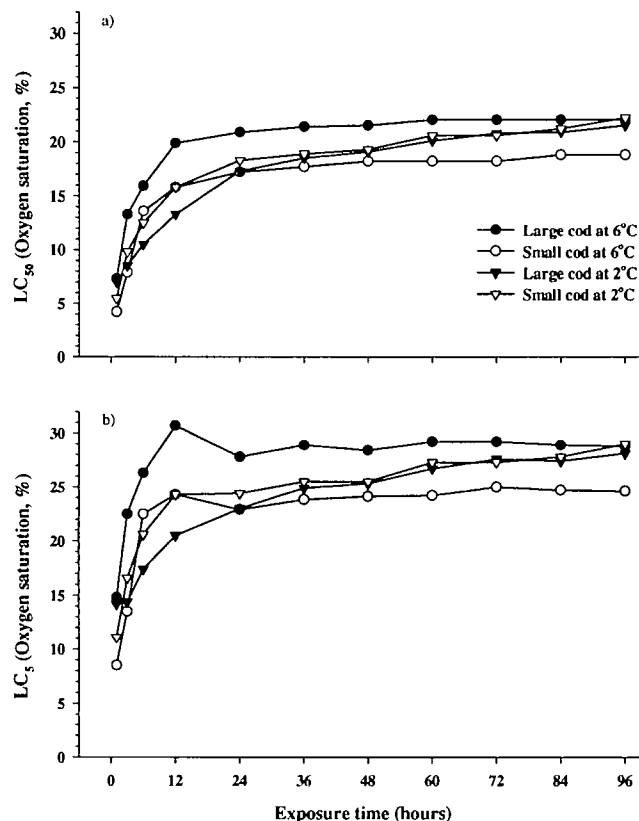

Figure 4. Relationship between lethal hypoxic level and observation time. a) Oxygen saturation that killed 50% of the subjects for each exposure time. b) Oxygen saturation that killed 5% of the subjects for each exposure time.

O$_2$ levels causing a reduction of growth rate in the laboratory

Significant growth in length and mass as well as significant improvements in condition occurred at all O$_2$ levels (Figure 5). Condition factor was significantly less, however, when O$_2$ fell below 70%. Growth in length and in mass was reduced when O$_2$ fell below 60%. In the most extreme treatment (45% O$_2$) growth in length (40.2 mm) and in mass (327 g) was 35% and 52% less, respectively, than for cod raised at $\geq$60% O$_2$ (61.9 mm and 677 g). We also confirmed that swimming activity was proportional to O$_2$, with a reduction in activity being detectable even at 84% O$_2$.
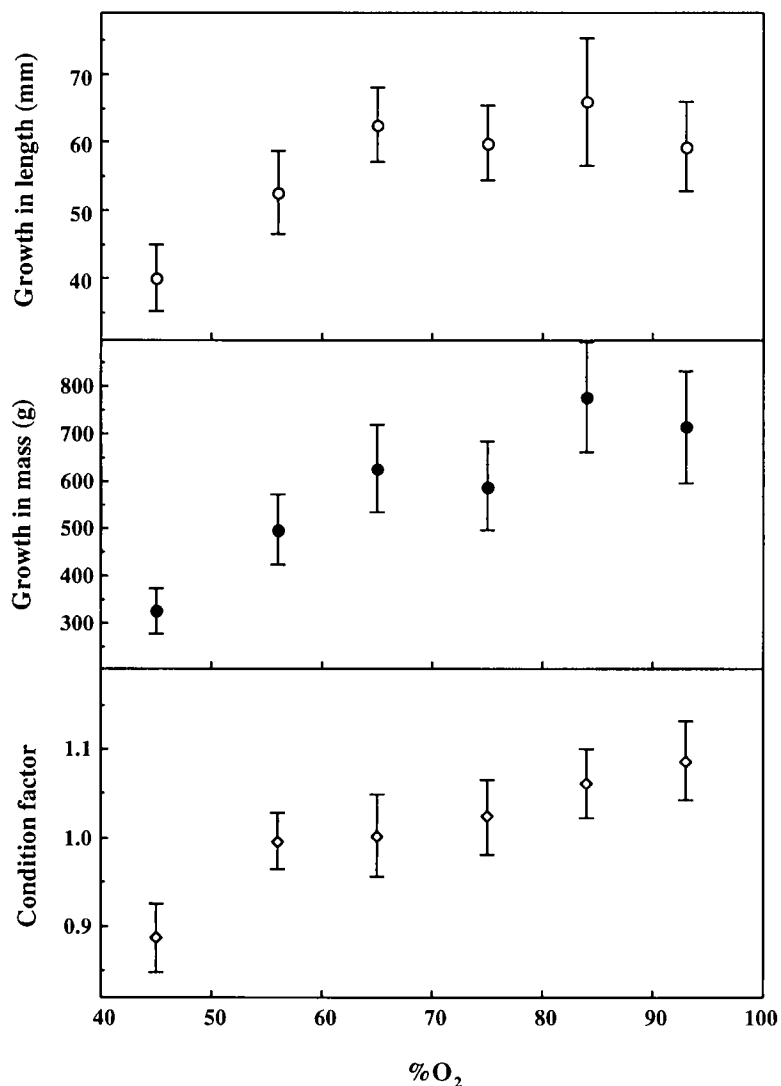

Figure 5. Growth in length and in mass, as well as final condition factor (Fulton's K) at the end of an 84-day growing period at 10°C in cod exposed to different levels of hypoxia and fed ad lib three times weekly.

Hypoxic waters of the Gulf of St. Lawrence limit cod production

These findings show that cod must avoid waters with less than 28% O_2 or risk death. D'Amours (1993a; 1993b) found that 20% and 24.7% of the surveyed area was $\leq 30\%$ O_2 in 1991 and 1992, respectively. In 1995, most of the waters deeper than 200 m were $\leq 40\%$ O_2, and even $\leq 30\%$ O_2 for the Laurentian Channel and the Estuary (Gilbert et al. 1997). Indeed cod are rarely found in waters with less than 30% O2 in the Gulf of St. Lawrence (D'Amours, 1993a, 1993b). Furthermore, growth was reduced when O_2 was below 60%, even though cod did not have to exert themselves to find and catch food, or to avoid predators. Yet cod encounter hypoxic conditions in the field as soon as they leave coastal waters: between 80 and 90% of the sites sampled by D'Amours in 1991 and 1992 had $\leq 60\%$ O_2. In 1995, Gilbert et al (1997) found that although O_2 was near 100% in the first 30 m of water everywhere in the Gulf and estuary, all zones deeper than 200 m had $\leq 60\%$ O_2. Saturation levels were often below 60% in the 100-200 m layer West of Anticosti Island. Cod are often caught below 200 m in the Gulf of St. Lawrence, and hypoxia has always been a constraint they had to deal with. There is no evidence that the deep waters of the Gulf or Cabot Strait have become more hypoxic since the mid-1980's. However the changes in distribution demonstrated by Castonguay (this document) suggest that cod spend more time in late-fall and winter in hypoxic waters, and this could have impacted negatively on growth or gonadal development. Furthermore, the collapse of the trap fishery on the lower North Shore before the fishing moratorium does suggest that cod avoided coastal waters in summer after the mid-1980's, and spent more time in deeper, hypoxic waters during the crucial growing season. For instance most cod in the 1991 and 1992 surveys were in hypoxic waters (D'Amours 1993a, 1993b). This could have had a considerable impact on growth and condition of cod in fall.

Climate and changes in size and condition

Jean-Denis Dutil

Temperature is a key factor of the environment as it limits the metabolic rate of fish and hence their capacity to grow, to swim, to ingest and assimilate food and to accumulate energy reserves in preparation for periods of low food abundance. Atlantic cod tolerate temperatures ranging from -1 to +18°C and exhibit maximum growth rates at higher temperatures within this range (Jobling 1988). Bottom temperatures in the northern Gulf of St. Lawrence range between 2 and 6 °C (Petrie et al. 1996) which is far from promoting maximum growth rates in cod. Temperatures in the intermediate layer (CIL) are colder and recent studies indicate that core temperatures of the CIL have decreased through the 1980's and have been below the long term average since then (Gilbert and Pettigrew 1997; Gilbert, this document). Trends in environmental temperature, growth rates and energetic condition were examined to determine whether changes in size-at-age reflect differences in productivity within and between cod stocks (Dutil et al. submitted). This section compares trends in the CIL temperature anomaly to trends in size-at-age in the northern Gulf of St. Lawrence in the 1980's and 1990's and examines size-at-age and condition relationships for various stocks in the North Atlantic.

Temperature data are from Gilbert (1997) and are expressed as deviations from the 1948-1994 mean core temperature of the CIL (Gilbert and Pettigrew 1997). Lengths-at-age of 4, 6 and 8

year-old cod were standardized using the mean and standard deviation of various time series for both research surveys and landings statistics as described in Dutil et al. (submitted). Then we averaged the standardized values for the 3 age-groups and used this value as a representation of the trend in length for cod having recruited to the fishery. Condition factor and mass of 6-year-old cod were examined for several stocks in which size at age 6 ranged from less than 1 to as much as 12 kg (Brander 1995). Condition factor was calculated as: K = 100 X Total weight (g) / Length $(cm)^3$.

Size of cod and CIL temperature anomaly

During the 1980's, variations in the relative size of cod followed changes in the index of CIL core temperature in the Gulf of St. Lawrence (Figure 6). The decline in the size of cod between 1983 and 1988 matched a similar decline in the relative temperature of the CIL between 1981 and 1986. The short-lived improvement of temperatures in 1987-1988 also resulted in an ephemeral increase in the relative size of cod in 1989-1990, but further cooling of the CIL in 1989-1992 was matched by declining sizes in 1992-1994. Warming of the CIL in 1995-1996 was immediately followed by increasing sizes of cod in the same period.
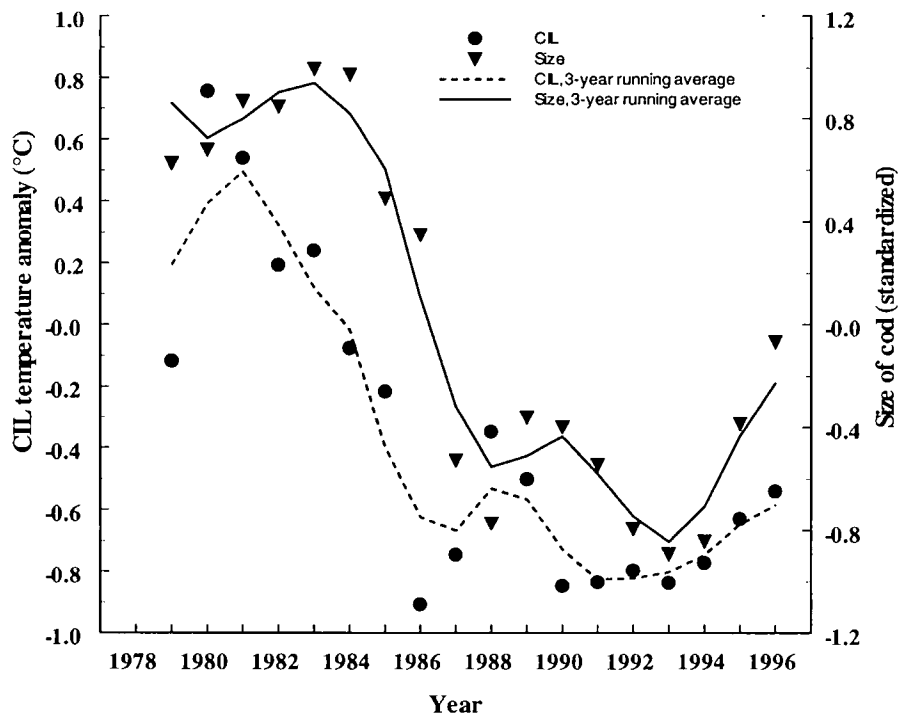

Figure 6. Length of 4-, 6- and 8-year-old Atlantic cod and deviations from the 1948-1994 mean core temperature of the CIL in the Gulf of St. Lawrence for the period from 1979 to 1996. Length data were standardized using the mean and standard deviation of several time series as described in Dutil et al. (submitted). Both commercial landings and research survey data were used.

Relationship between size and condition

The condition factor, which reflects the level of energy reserves in cod (Lambert and Dutil 1997a), varies with size-at-age (Figure 7). Stocks that have faster growth rates and reach a large size by age 6, for instance cod stocks around the U. K., tend to maintain higher condition factors than stocks living in colder waters, such as the northern and southern Gulf cod stocks (Figure 7). Condition factors above 1.05 on average are common in faster growing cod whereas they are not found in slow growing cod. The range in condition factor also increases in slow growing cod; cod smaller than 4 kg at age 6 for instance had condition factors ranging from 0.80 to 1.05 in research surveys conducted in fall and low condition factors showed a tendency to diverge from the general relationship.
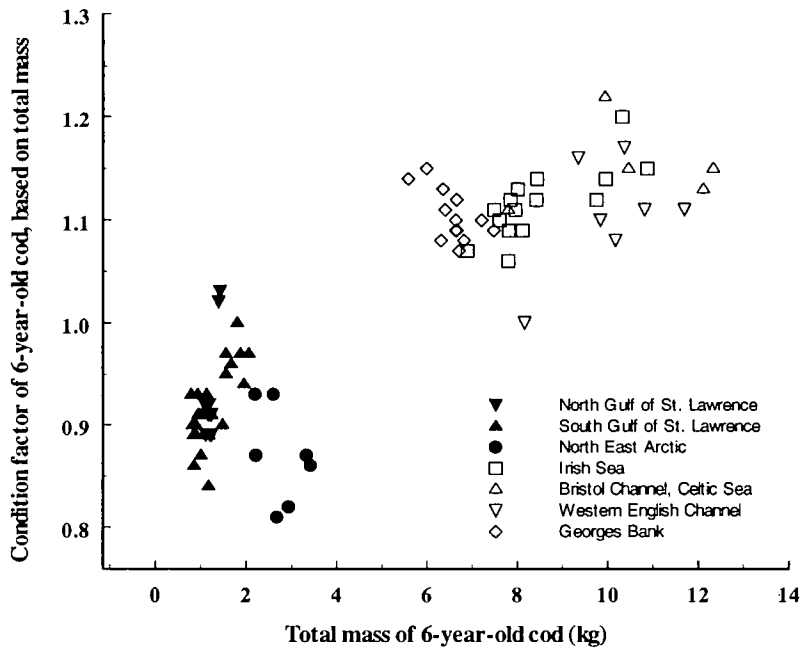

Figure 7. Condition factor and corresponding mass of 6-year-old Atlantic cod. Full symbols represent data from research surveys and open symbols data from landings. Sources of data are described in Dutil et al. (submitted). North Gulf of St. Lawrence, August sur survey (1987-1996); South Gulf of St. Lawrence, September survey (1972-1994), weights from Table 11 in Sinclair et al. (1996) and lengths from length-weight relationships in assessment documents; North East Arctic, USSR survey (November-December, 1984-1990)(ICES 1992); UK, landings 1982-1996, Myrtle Boon, pers. comm.; Georges Bank, landings 1978-1991, from Table 7 (Hunt and Buzeta 1992).

Colder temperatures, slower growth rates and poor condition

Size-at-age varies considerably between stocks and temperature has been shown to explain a large proportion of this variability in the North Atlantic (Brander 1995) and on the East Coast of Canada (Campana et al. 1995). Cod size-at-age (Chouinard and Fréchet 1994) and condition

(Dutil et al. 1995; Lambert and Dutil 1997b) have decreased in the Gulf of St. Lawrence through the 1980's and in the early 1990's. Declining sizes at age have been ascribed to size-selective fishing mortality (Hanson and Chouinard 1992). In contrast, size-selective fishing mortality cannot account for declining condition factors. Furthermore, back-calculations based on otoliths from both commercial and research survey samples indicate that cod did not sustain detectable size-selective mortality in the northern Gulf of St. Lawrence. This supports the view that declining sizes-at-age must have resulted from lower growth rates during the 1980's and early 1990's (Dutil et al. submitted). Biochemical correlates of growth rate also support the view that cod did not experience fast growth rates in the 1990's, even in summer (Dutil et al. in press; Guderley et al. 1996).

Bottom temperatures have been shown to explain a large proportion of the variability in size-at-age between stocks (Brander 1995; Campana et al. 1995). Figure 6 indicates that environmental temperatures could also drive year to year variations in the size-at-age of cod in the northern Gulf of St. Lawrence. The mechanism linking CIL core temperature to size-at-age however is unknown. The analysis of time series further suggests that individual condition declined once size-at-age had declined in cod of the northern Gulf of St. Lawrence. Figure 7 shows that cod with faster growth rates, i. e. cod with larger sizes-at-age, are less likely to experience periods of poor condition. Mortality from poor condition could thus be restricted to stocks exhibiting slow growth rates and marked seasonal variations in condition (Dutil and Lambert in preparation), such as in the northern and southern Gulf of St. Lawrence (Dutil et al. 1995; Lambert and Dutil 1997b).

Energetic consequences of reproduction in situations of lower available energy reserves.

Yvan Lambert

Substantial energy reserves are required for maturation and reproduction in cod. As in many spring spawners, cod build up energy reserves during summer and fall which will later be used for overwintering, maturation and spawning. Changes in environmental conditions, particularly temperature (Gilbert and Pettigrew 1997) and in migration pattern may influence the levels of energy reserves in fall and hence patterns of energy allocation between growth, maintenance and reproduction. Reproductive fish may respond to lower energy reserves by following various strategies: reproductive investment could be maintained at the expense of somatic condition, in which case the risk of mortality due to exhaustion of energy reserves would increase; reproductive investment could be reduced by decreasing fecundity in order to limit the loss in somatic condition; and finally, in extreme situations, fish could simply skip reproduction.

Condition and energy reserves of cod at the onset of winter declined in the early 1990's in the northern Gulf of St. Lawrence (Lambert and Dutil 1997b). This decline began in 1989 with the lowest values being observed between 1992 and 1994. This indicated that lower energy reserves were available for overwintering, maturation and reproduction in recent years. Field sampling and laboratory experiments were used to assess the consequences of such reductions in energy reserves on reproductive investment and post-spawning condition.

Two laboratory experiments were conducted between 1994 and 1996. Cod measuring between 45 and 65 cm were maintained in large tanks at temperatures between 2 and 6°C between the months

of September to March. During that period, groups of fish were fed two different feeding regimes in order to obtain cod with different levels of condition. Cod were then anaesthetized, measured, weighed, scanned to identify sex, and paired (1 male, 1 female) into smaller tanks to follow egg production of individual females through the spawning period. Condition (Fulton's condition factor) was measured before and after spawning, and for each batch of eggs produced, fecundity, egg diameter, dry weight and energy content were determined. For more details on rearing conditions in 1995 and 1996, see Ouellet, in this document. Field samples collected in the northern Gulf of St. Lawrence in May of 1994, 1995 and 1997 were used to assess relations between condition and reproductive status in wild cod. The condition factor expressed as the ratio between somatic mass (g) and length³ (fork length in cm) was used as an index of condition (Lambert and Dutil 1997a). The fecundity of wild cod was measured in 1995 to assess reproductive investment in the northern Gulf of St. Lawrence. Finally, field observations were interpreted in the light of laboratory results for cod of different levels of condition.

Fecundity and costs of reproduction in relation to condition, in the laboratory

Laboratory experiments revealed a significant relationship between pre-spawning and post-spawning condition (Post-K = 0.0127 + 0.8141 • Pre-K; r^2=0.67). Greater losses were observed for cod with poorer levels of condition. Pre-spawning cod with lower levels of condition lost 30% of their somatic mass compared to 20% for cod in better condition (Figure 8). Corresponding somatic energy losses varied between 70% and 20% with greatest losses being observed for cod with poorer levels of condition. The proportion of somatic energy reserves lost by cod in poor condition during spawning was similar to that lost by semelparous species like Pacific salmonids during migration and reproduction (70 to 80%). Cod in poorest condition (condition factors below 0.6) had liver (70-80%) and muscle (86-91%) water contents characteristic of cod dying from exhaustion of energy reserves (Dutil and Lambert in preparation).

Lower available energy reserves also have a significant influence on the reproductive investment of cod. A positive relationship was observed between female condition and the total number of eggs produced during reproduction in the laboratory (Figure 9). The fecundity of females in poor condition was 5 to 7 times lower than that of females in good condition.

Fecundity and condition at spawning, in wild cod

Significant differences (p < 0.006) were observed in the condition of pre-spawning, spawning and spent female cod in the wild (Figure 10). The condition of immature cod was also significantly higher than the condition of spent females.

The potential fecundity of pre-spawning female cod in the wild in the spring of 1995 indicates that the fecundity of cod in the northern Gulf of St. Lawrence was characteristic of cod with low levels of energy reserves (Figure 11). Individual fecundities were in the range observed for cod fed a low ration in the laboratory. Few females in the wild reached fecundities comparable to those reached by well-fed cod in the laboratory (Figure 11).
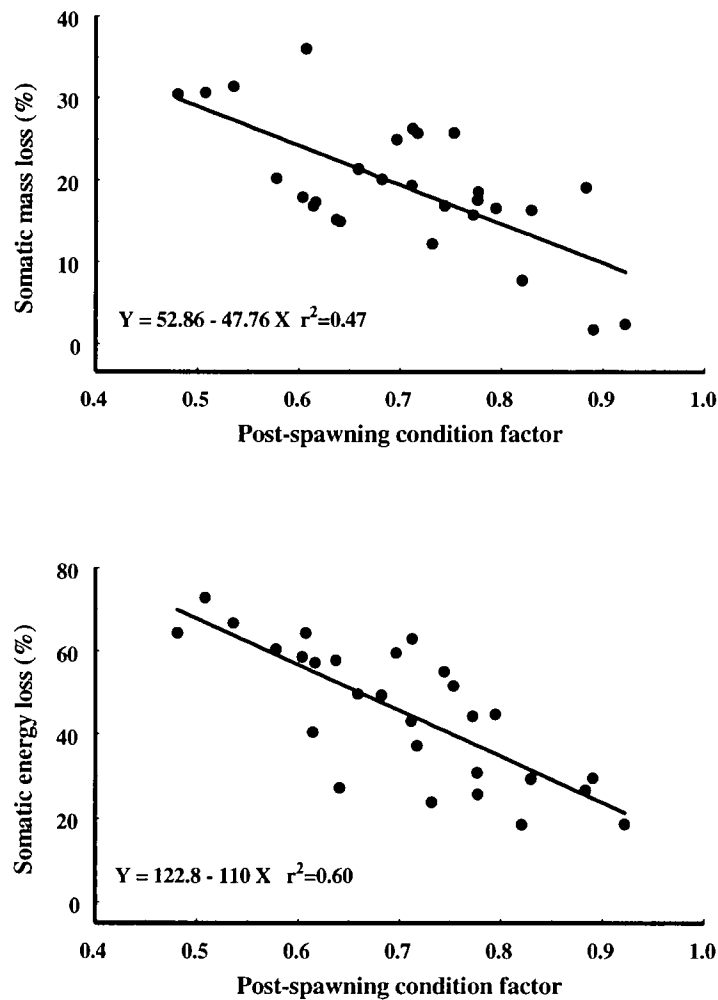
Figure 8. Somatic mass and energy losses of female cod during reproduction in relation to post-spawning condition for the two laboratory experiments conducted between 1994 and 1996. Somatic mass and energy losses are expressed as percentages of somatic mass and energy before reproduction.

Potential consequences of poor condition during reproduction

Laboratory experiments show that female cod with low energy reserves invested less in reproductive products. However, even at reduced reproductive output, the loss in somatic mass and energy in these poor condition females was higher, in relative term, than the losses experienced by females in good condition. Consequently, the reserves of energy committed to reproduction by poor-condition females may increase their risk of mortality. Relationships
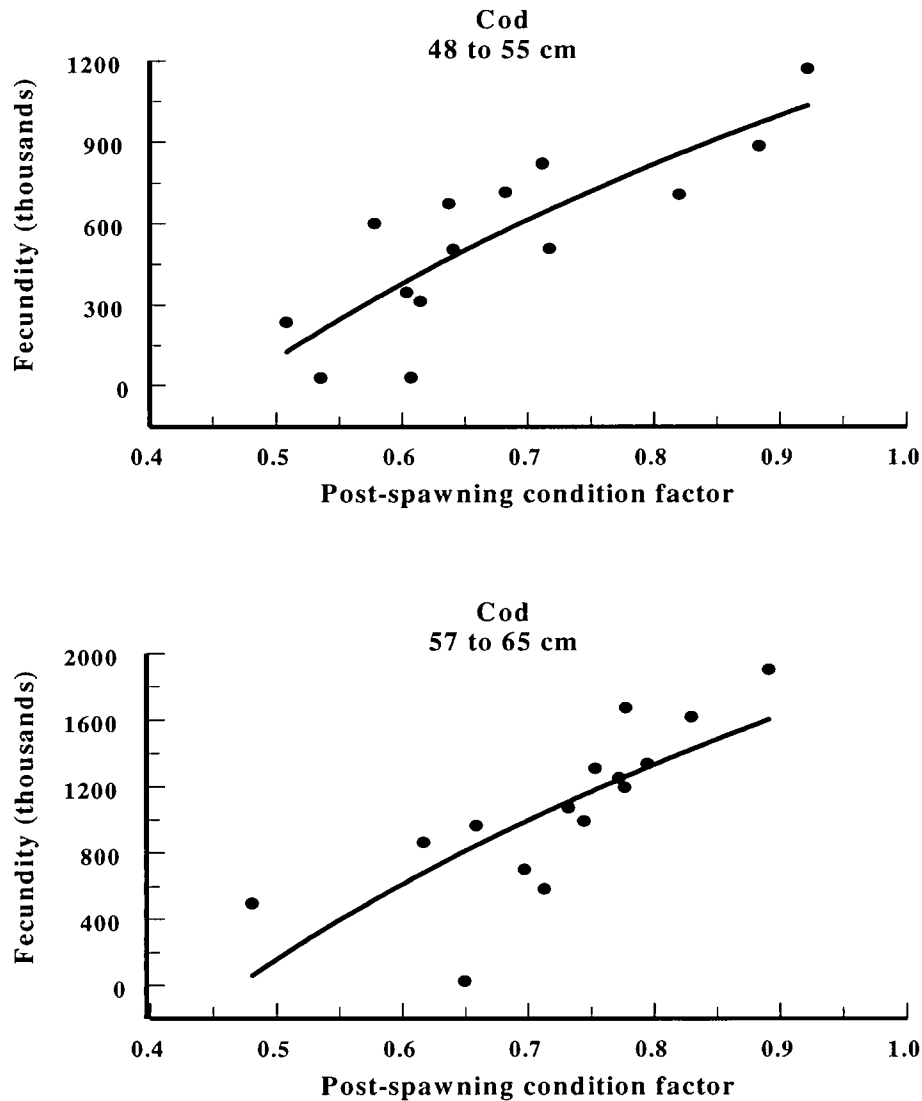
Figure 9. Relationship between fecundity and post-spawning condition for female cod between 48 and 55 cm and between 57 and 65 cm in length.

between pre- and post-spawning condition suggest that pre-spawning cod with condition factors below 0.75 have an increased risk of mortality following reproduction. In wild cod in the northern Gulf of St. Lawrence, somatic costs associated with reproduction resulted in poorer condition and greater risks of mortality in reproductive than in immature individuals. This situation was particularily true in 1994 when the condition factor of reproductive females in the wild was close to the level from which mortality risks are found to increase rapidly in the laboratory.
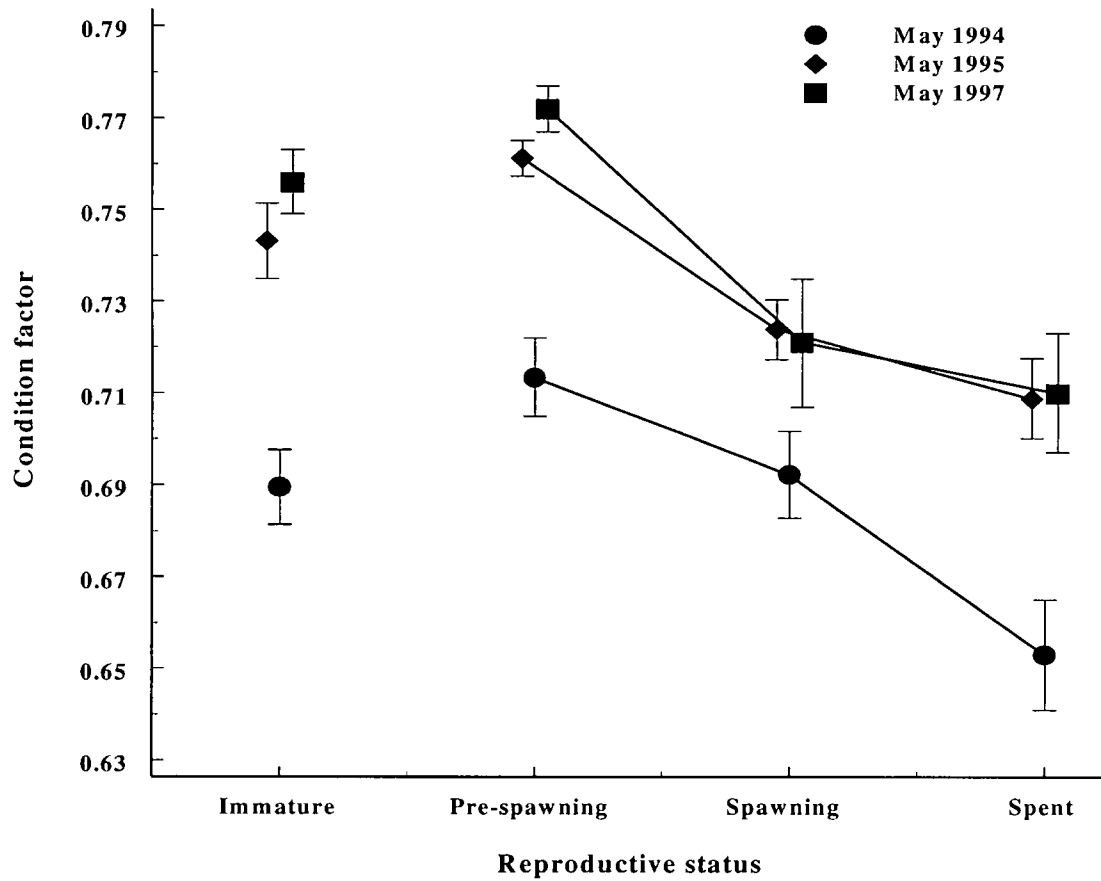
Figure 10. Condition factor of immature, pre-spawning and spent female cod captured in May 1994, 1995 and 1997 in the northern Gulf of St. Lawrence (NAFO division 3Pn4RS).

The significant decline in available energy reserves of cod at the onset of winter in the northern Gulf of St. Lawrence during the early 1990's had a negative impact on the energy budget of adult females in the spring. Reproductive females had lower fecundities and greater energetic expenses, and were in worse pre- and post-spawning condition. The condition of spent females suggested a greater impact of changes in environmental conditions of the habitat on adult than on immature cod. Based on laboratory experiments, many reproducting adults reached lethal or near-lethal levels of condition. Stock recovery, population reproductive potential, and possibly recruitment may have suffered from that situation.
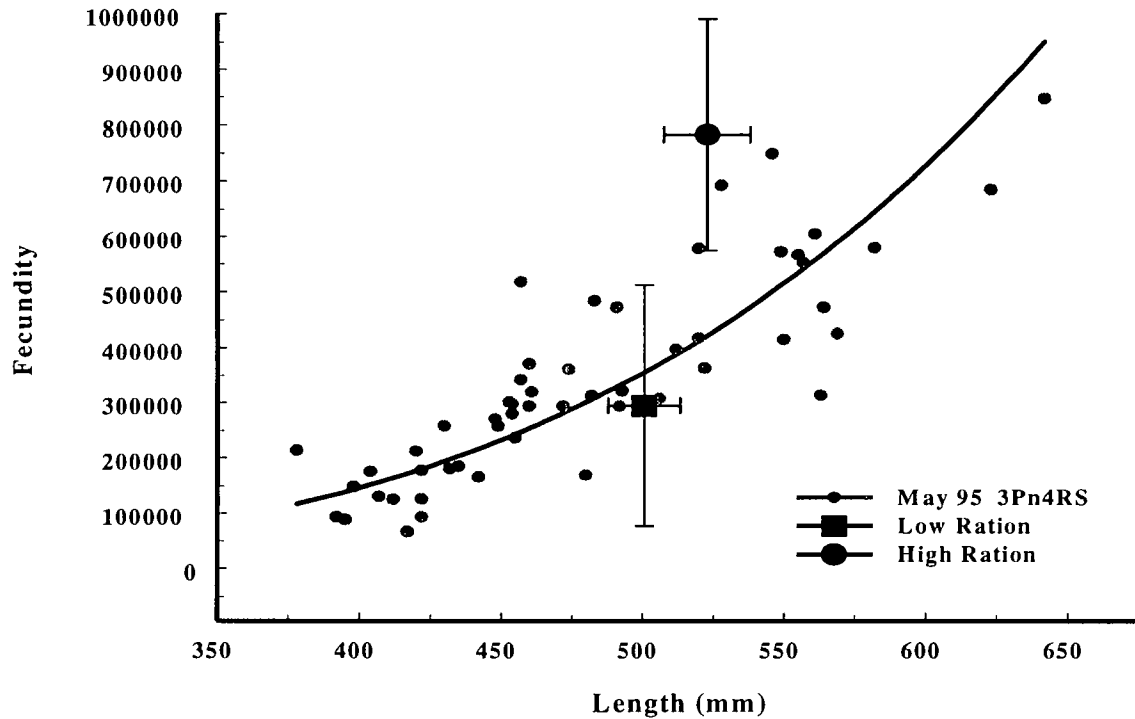
Figure 11. Relationship between fecundity and length for cod captured in May 1995 in the northern Gulf of St. Lawrence and fecundity at length for cod fed a low or high ration level in the laboratory. Mean post-spawning condition of female cod under low and high rations were o.58 and 0.74, respectively.

The effect of maternal condition on egg quality and hatching success

Patrick Ouellet

Female cod characteristics, such as age, size, and nutritional condition, influence egg production both quantitatively and qualitatively (Trippel in press; Chambers and Waiwood 1996; Kjesbu et al. 1996). Low incubation temperatures, such as observed in the upper water column in early spring on a cod spawning ground in the northeastern Gulf of St. Lawrence (Ouellet et al. 1997), could negatively influence egg development and larval survival (Pepin et al. 1997; Ouellet and Bérubé, unpublished). However, the effect of reproductive-female low nutritional condition on viability of their eggs has never been clearly documented. If such a relationship exists and can be quantified, it could be used to assess more accurately the reproductive potential of a stock from routine estimation of spawning biomass and individual fish condition. The objectives of this

project were to test the specific hypotheses that a decline in the condition of female cod is responsible for the production of eggs of poor quality and that survival of those eggs is reduced, especially when incubated at low temperature. This report briefly summarizes the main results from two years of experiments on the effects of maternal condition on egg characteristics and survival.

Female cod were individually monitored for the duration of their spawning cycle. In 1995, variability in condition (Fulton's K: $(W/L^3)*100$) among a group of cod (mean length: 567.2 ± 41.4 mm, range: 466-641 mm, n: 19) was created by feeding the fish during the maturation period one of two feeding regimes (low ration: satiation feeding once every 10 days; high ration: satiation feeding twice a week); for each ration, 2 temperature regimes were used (low: 2 - 6°C, high: 6 - 10°C), hence producing four groups of cod with initial condition factors varying from 0.76 to 1.24 (Lambert, this document). In 1996, feeding regimes were similar (high and low rations) but only one temperature regime (6 - 10°C) was used, and the fish were distributed in two distinct size classes (small: mean length 515.3 ± 16.0 mm, n = 12; large: mean length 613.7 ± 22.6 mm, n = 10; t-test $p < 0.0001$; Figure 12). The average female pre-spawning condition factors were not different between years (t-test $p = 0.88$; Figure 12). Pre-spawning and post-spawning conditions are based on total and somatic mass, respectively.
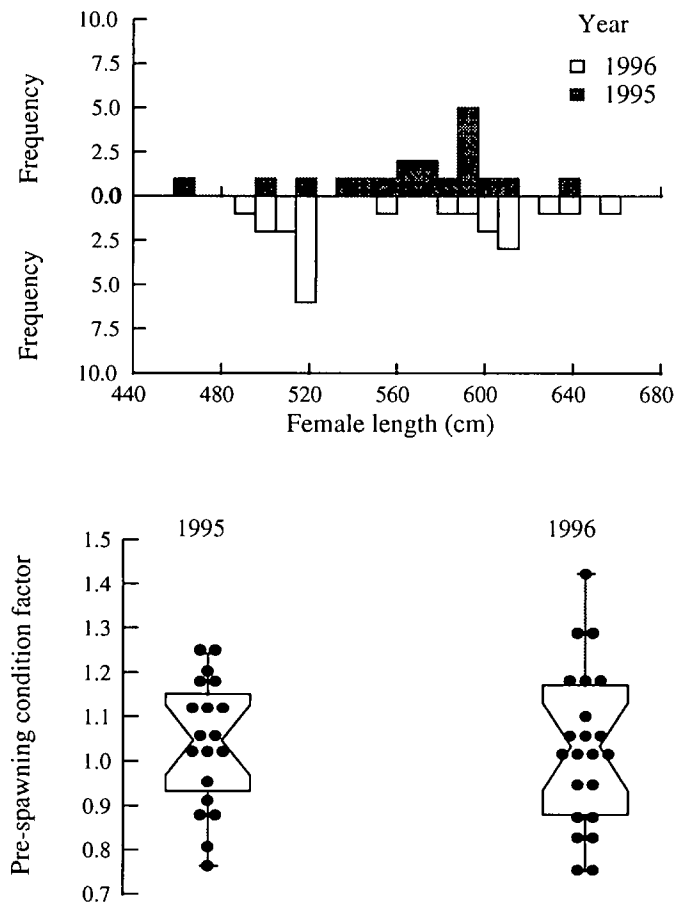

Figure 12. Pre-spawning length-frequency distribution and condition factor statistics (box-plots) of female cod in the egg incubation experiments in 1995-1996.

Each year, the spawning activity of each female was monitored by recording the number of egg batches spawned and their volume (mL). For each batch, two subsamples (10 to 20 mL) of eggs were preserved for estimation of mean size (diameter, mm) and mass (dry-weight, $\mu g \cdot egg^{-1}$). For each female, weighted estimates of mean egg diameter and dry mass were calculated by weighting the means for each batch by the number of eggs in the batch.

In 1995, subsamples of eggs from different egg batches and from females of varying condition, were isolated in incubation chambers (500 mL) at 4°C and 0°C to monitor survival and development up to hatching. In 1996, to reduce the possible effect of differences among egg batches when comparing the effect of maternal condition on egg viability, egg incubation experiments were conducted on batches number 3 and 6 only for each female.

Number of egg batches spawned and female condition

Although fecundity is strongly correlated to maternal condition (Lambert, this document), the number of egg batches spawned was significantly related to pre-spawning condition only in 1995 ($R^2 = 0.46$, $p = 0.001$; 1996: $p = 0.128$ - Figure 13). For unknown reasons, in 1996, some females in good pre-spawning condition spawned few egg batches. Moreover, one female in good condition died during the experiment. In both years, the regressions of the number of egg batches on post-spawning maternal condition were not significant (Figure 13).
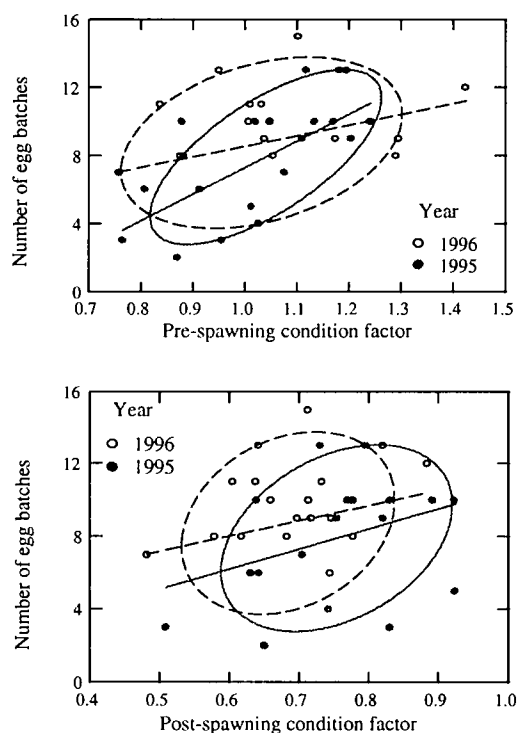

Figure 13. Number of egg batches spawned by each female in relation to pre-spawning (top panel) and post-spawning (bottom panel) condition factor. Confidence (± one standard deviation) ellipses were drawn for each distribution. Each ellipse is centered on the sample mean, and the standard derivations of each variable determine the major axis. The sample covariance (i.e. correlation) between the variables determines the orientation. In addition, the linear regression estimation is illustrated for each distribution.

Egg size and female condition

A positive and significant relation between mean egg size and female condition was observed in 1996 (pre-spawning: $R^2 = 0.25$, $p = 0.019$; post-spawning: $R^2 = 0.3$, $p = 0.008$), but not in 1995 (Figure 14). Similarly, a positive and significant regression of egg dry mass on maternal condition was observed in 1996 (pre-spawning: $R^2 = 0.39$, $p = 0.002$; post-spawning: $R^2 = 0.48$, $p < 0.001$), but not in 1995 (Figure 14). Overall, female cod in good condition in 1996 spawned larger and heavier (with higher organic content) eggs. On the other hand, female length had no effect on egg size (1996: $p = 0.076$; 1995: $p = 0.682$) and mass (1996: $p = 0.139$; 1995: $p = 0.656$). However, in 1995, although they spawned on average the same number of egg batches, female cod maintained at low temperatures produced significantly larger eggs (mean: 1.406 ± 0.03 mm) than cod at high temperatures (mean: 1.313 ± 0.059 mm, t-test, $p = 0.001$). Larger eggs usually mean larger larvae at hatching (Miller et al. 1995), hence, potentially, an ecological advantage for larger eggs (Browman, this document). Moreover, larger eggs are apparently better in maintaining their buoyancy, therefore controlling their vertical distribution in the water column (Bérubé, unpublished).
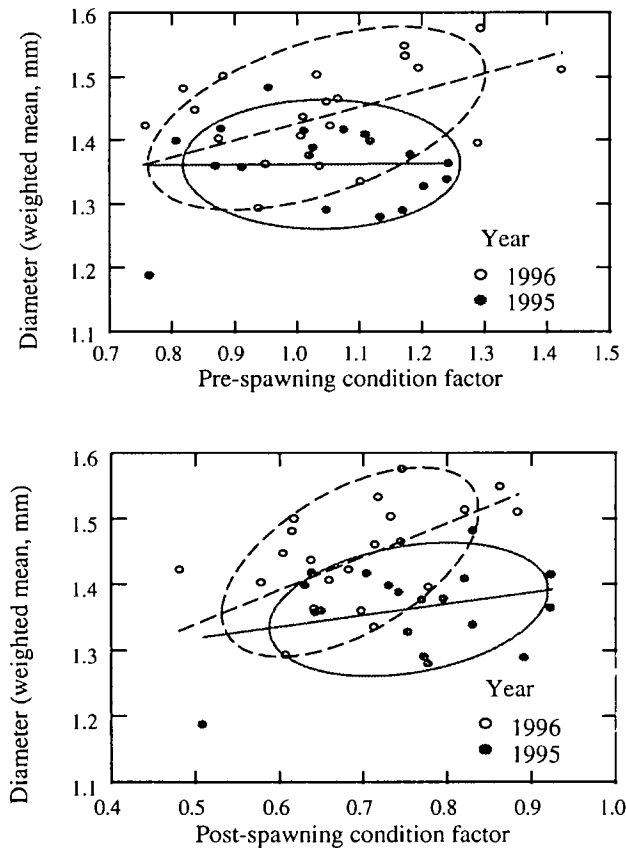

Figure 14. Average diameter of eggs for each female in relation to pre-spawning (top panel) and post-spawning (bottom panel) condition factor. Confidence (± one standard deviation) ellipses were drawn for each distribution. Each ellipse is centered on the sample mean, and the standard deviations of x and y determine the major axis. The sample covariance (i.e. correlation) between the variables determines the orientation. In addition, the linear regression estimation is illustrated for each distribution.
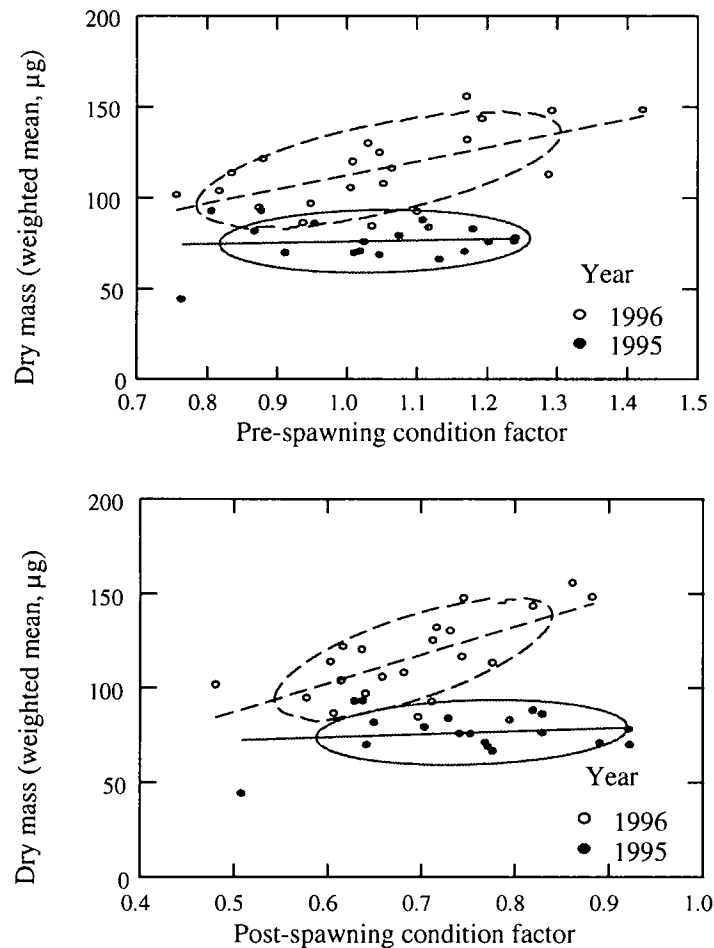
Figure 15. Average dry mass of eggs for each female in relation to the pre-spawning (top panel) and post-spawning (bottom panel) condition factor. confidence (± one standard deviation) ellipses were drawn for each distribution. Each ellipse is centered on the sample mean, and the standard deviation of x and y determine the major axis. The sample covariance between the variables determines the orientation. In addition, the linear regression estimation is illustred for each distribution.

Hatching success at 0 and 4°C and female condition

Since hatching was almost null for eggs incubated at 0°C, only the results for cod eggs incubated at 4°C are presented in this summary. Hatching success was estimated as the ratio of the number of larvae hatched in each incubation chamber over the number of eggs incubated. The proportions were arcsin-transformed for the statistical analysis. Hatching success tended to increase in egg batches spawned later in a female spawning cycle, but for both years these relations were not significant (1995: $p = 0.124$; 1996: $p = 0.468$). Pre-spawning maternal condition had a significant positive effect on hatching success in 1996 ($R^2 = 0.231, p = 0.032$, Figure 16). The regressions of hatching success, either for egg batches 3 and 6 or all egg batches, on maternal condition (pre- or post-spawning) were not significant in 1995 (Figure 16).
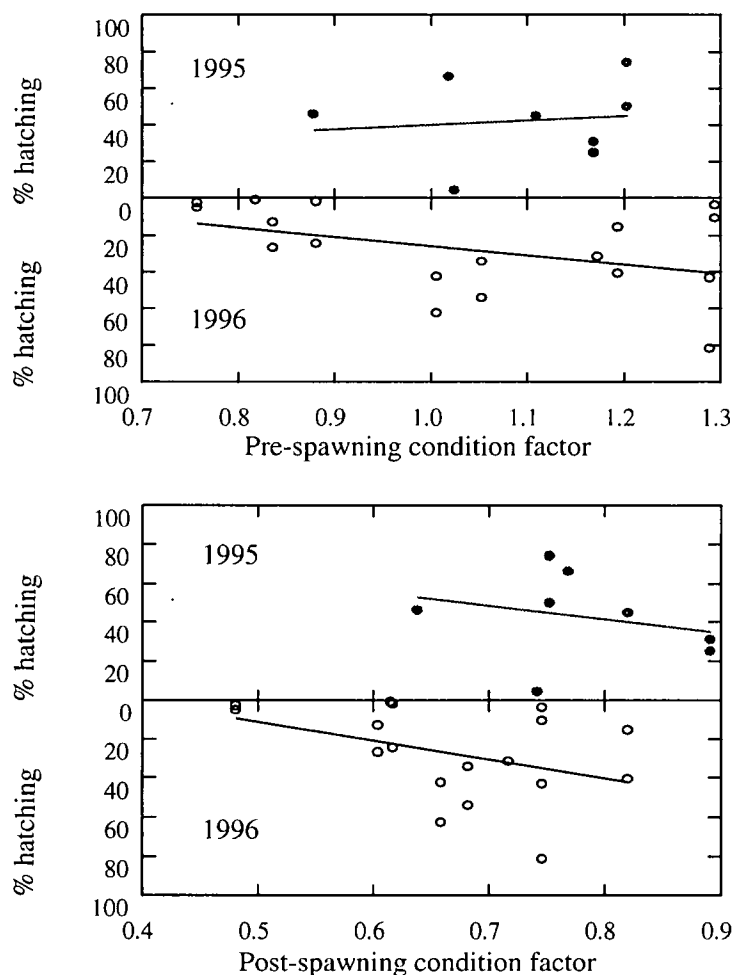
Figure 16. Hatching success in relation to female cod condition factor before (top panel) and after (bottom panel) spawning. The linear trend in the data is illustrated for each distribution.

Potential consequences on spawners biomass and recruitment relationships

Maternal condition had a significant effect on cod egg characteristics and hatching success in 1996, but not in 1995. Nevertheless, the results support the hypothesis that the quality of female (size/age, condition) cod had a significant effect on the quality and viability of the eggs. That would suggest that annual estimates of the biomass of spawners as an indicator of potential recruitment need to be examined in conjunction with data on female condition during the maturation and spawning periods as condition will influence the net reproductive output from those spawners.

A full discussion of the results is beyond the scope of this document. However, one potential explanation for the difference between years may be the increased importance of small fish in 1996 relative to 1995 (see Figure 12). That would imply a combined effect of size and condition on cod eggs that was more evident in 1996.

The influence of maternal condition and thermal history on larval performance

Howard I. Browman

The number of individuals that survive through the larval period is a major determinant of recruitment in many marine fish populations (e.g. Houde 1987; Sinclair 1988; Leggett and Deblois 1994). Current hypotheses on the underlying mechanisms of variability in survival and recruitment in fish populations concentrate on the importance of differential growth and survival of individual larvae (e.g. the "Stage Duration" and the "Bigger is Better" hypotheses; see Chambers and Leggett 1987; Houde 1987; Litvak and Leggett 1992; Chambers 1993; Pepin 1993). Maternal environmental and nutritional histories are likely related to the viability of individual larvae, yet fisheries scientists have only recently begun to examine these relationships in detail (e.g. Chambers et al. 1989). MLI's multidisciplinary research program represents an attempt to evaluate these relationships.

Cod females are highly fecund determinate spawners that release their eggs in batches (Kjesbu 1989). The relationships between female condition and the number and quality of eggs that they produce have only recently been characterized for cod (Kjesbu 1989; Kjesbu et al. 1991; Kjesbu 1994; Kjesbu and Holm 1994; Ouellet, this document). For females in good condition, these studies indicate that (1) 17-19 egg batches are spawned per female over a period of four to six weeks, (2) the number of eggs liberated in each batch varies significantly and generally follows a smooth dome-shaped curve, (3) egg size and dry mass decrease from the first to the last batch, (4) egg diameter of the first batch is positively correlated with female length and (5) there is an inverse relationship between egg diameter and mortality. Further, cod females with high condition factors produce more previtellogenic oocytes and use a larger fraction of them during vitellogenesis than females with low condition factors (Kjesbu et al. 1991). Overall fecundity is also related to female condition; females with low condition factors produce fewer eggs than those with high condition factors (Kjesbu et al. 1991; Lambert, this document).

Inter-batch and inter-female differences in egg quality may be translated to the larvae that they produce. Preliminary evidence indicates that the feeding performance (numbers of prey ingested) of cod larvae hatching from small eggs is poorer than that for larvae hatching from larger eggs (Per Solemdal, Norwegian Institute of Marine Research, personal communication). Similar results have recently been reported for other species (e.g. Cerda et al. 1994). Further, eggs liberated towards the end of a given female's spawning cycle (i.e. those from the last few egg batches) appear to produce larvae whose overall activity is less than that for larvae from earlier egg batches (Per Solemdal, personal communication). Because activity and feeding rates translate into rates of growth and survivorship, these observations imply that cod larvae hatching from different egg batches, and/or from different females, may be more-or-less viable.

Spawning in batches over a relatively long 4-6 week period is thought to increase the chances that the larvae of any given female will encounter feeding conditions adequate to support rapid growth and an increased chance of survival. However, the preliminary results outlined above indicate that, for example, larvae produced from eggs released late in a female's spawning cycle will be less likely to take advantage of good feeding conditions than larvae released during the middle of the same female's spawning cycle.

Following from the above, the major thrust of our project was to test the following null hypotheses.

(1)   Female nutritional and thermal histories are not related to the performance of early larvae that they produce. These experiments were undertaken during the 1995 field season;

(2)   Female spawning and nutritional history are not related to the performance of early larvae. These experiments were undertaken during the 1996 field season.

Fertilized eggs were obtained from spawning couples that had been maintained under the feeding and thermal regimes described in Lambert and in Ouellet (this document). Egg batches were transferred to an incubation system within a few hours of their release. At hatching, larvae were transferred to 60 litre black rearing basins. The rearing basins were stocked with algae (*Nanochloropsis sp.*) and larvae were fed nutritionally enriched (Artemia Systems' Super Selco) rotifers (*Brachionus sp.*). Eggs and larvae were handled so as to maintain those from any given male-female cross and spawning batch event in isolation. Temperature was held at 6 °C and photoperiod was 14 h L : 10 h D.

We attempted to fill a 2 X 2 X 2, three replicate experimental design, for a maximum of 24 larval groups. In 1995, the treatments were: maternal ration (condition) X maternal thermal history X egg batch number. In 1996, the treatments were: maternal ration (condition) X maternal size X egg batch number. Three of the five or six male-female pairs from each of the four ration-temperature treatment groups (in 1995), or ration-size treatment groups (in 1996) were targeted as sources of fertilized eggs. As much as possible, these were the same pairs and egg groups targeted by Ouellet's egg project (this document). Two egg batches from each of these females were targeted, the second or third (typically of relatively poor quality) and the fifth or sixth (typically of relatively high quality) of any given female's spawning. All of the experiments were conducted at 6 °C.

Larvae from all targeted groups were subsampled at various intervals. Larval size was determined from measurements on live larvae under a microscope. Immediately after the standard length measurements, specimens were dried at 50°C for 24 hours and then weighed on an electrobalance to the nearest 0.001 mg. Drying was continued until there was no further change in mass. For each egg batch, 10 to 12 larvae were collected from the rearing basins on approximately day six post-hatch (PH). At least three such measurements were obtained prior to day 20 PH. Mean length and dry mass were used to calculate the specific growth rate for mass (SGR$_m$) and for standard length (SGR$_l$), as follows (Ricker 1979):

$$SGR_m = \frac{BM_f - BM_i}{BM_i(T_f - T_i)} \times 100$$

and

$$SGR_l = \frac{BL_f - BL_i}{BL_i(T_f - T_i)} \times 100$$

where BM$_f$ and BL$_f$ are mean body mass (mg) and body length (mm) for the last day of measurements, BM$_i$ and BL$_i$ are for the first day of measurements and T$_f$ and T$_i$ are the ages of the larvae on the first and last day on which they were measured.

The overall activity levels (percent time actively swimming) and swimming patterns (swimming speed, frequency and duration of stops, repositioning turn angles) of the larvae were evaluated, on day three and day six PH, using silhouette video photography (SVP). An SVP recording platform similar to that described in Browman & O'Brien (1992a; 1992b), along with a computer-controlled motion analysis system, were used to obtain these data. These observations were conducted on free-swimming cod larvae in a 20×20×20 cm aquarium. Path analysis (see Bell 1990; Browman and O'Brien 1992a; Browman and O'Brien 1992b) was used to evaluate whether there were any discernable differences in activity levels or swimming patterns among the treatment groups. Fifty larvae were used in each trial, and there were three replicates per trial. All data were evaluated by two way ANOVA. At this writing, only the observations obtained during the 1995 field season have been analyzed. We expect to complete the 1996 analysis by late summer 1998.

Growth of larvae issued from females differing in condition factor and thermal history

The range of pre-spawning condition factors (Fulton's K, based upon total mass) in the females for which larval groups were followed varied between 0.88 and 1.25. There was no significant relationship between the SGR (based upon either dry mass or total length) of larvae and female condition factor or thermal history (Figure 17). Nor was there any significant relationship between larval activity or larval swimming speed and female pre-spawning condition factor, on either day three or day six PH (Figure 18) or thermal history (Figure 19). There was a mildly significant (p = 0.038) treatment interaction effect (female ration with temperature) on larval SGR.
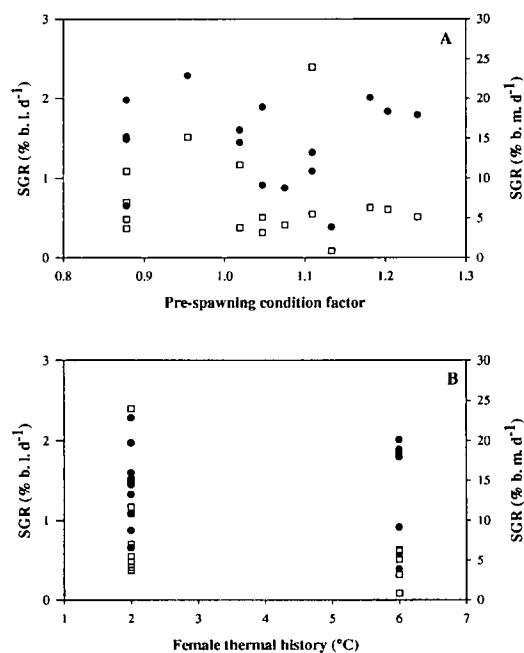

Figure 17. Atlantic cod, 1995 experiment series. The relationship between specific growth rate, as percent body length (closed circles) and percent body mass (opened squares0 per day, and (A) female pre-spawning condition factor annd (B) female thermal history.
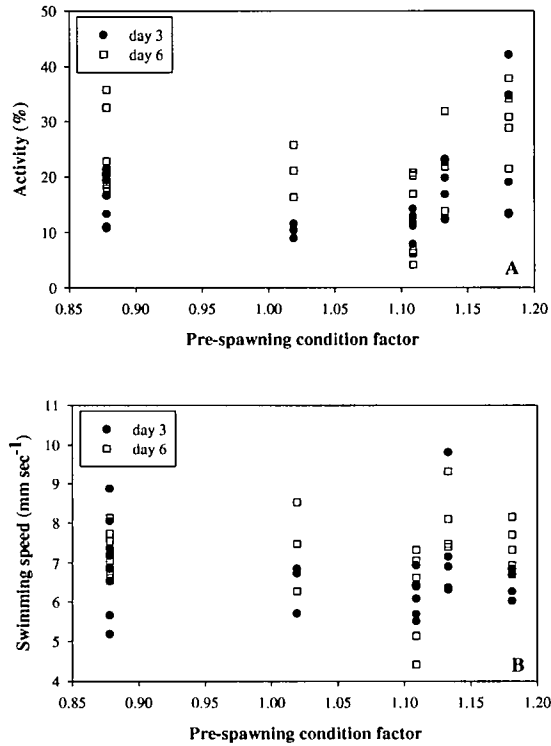
Figure 18. Atlantic cod, 1995 experiment series. The relationship between female pre-spawning condition factor and (A) the percentage of time larvae were actively swimming and (B) swimming speed.
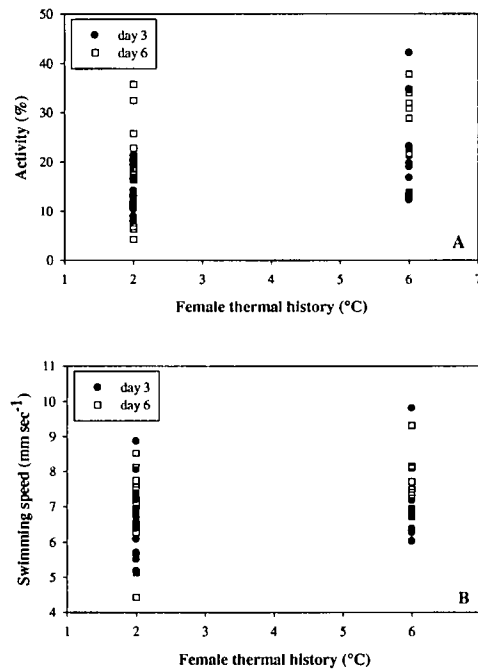

Figure 19. Atlantic cod, 1995 experiment series. The relationship between female thermal history and (A) the percentage of time larvae were actively swimming and (B) swimming speed.

The results for 1995 indicate only a weak effect of female condition factor and thermal history (combined) on the larval performance variables that were measured. This result conforms with those reported by Ouellet (this document): for 1995 there were only weak effects of maternal condition and thermal history on the egg quality variables measured. There are a number of likely explanations for the lack of a more consistent effect: the fact that the majority of egg groups that we followed were the progeny of females with relatively high pre-spawning condition factors; the relatively small range of pre-spawning condition factors for these females; the fact that we were unable to follow the full complement of egg groups.

Larval growth rate and performance relationships

The relationship between larval SGR, overall activity and swimming speed were also evaluated. With only one exception (dry mass vs. larval activity on day 3 PH), all of these were significant: there were direct relationships between larval SGR and both activity and swimming speed (Figure 20 and Figure 21). The significant positive relationships between larval SGR and activity or swimming speed support the use of these variables as reasonable indicators of larval performance.
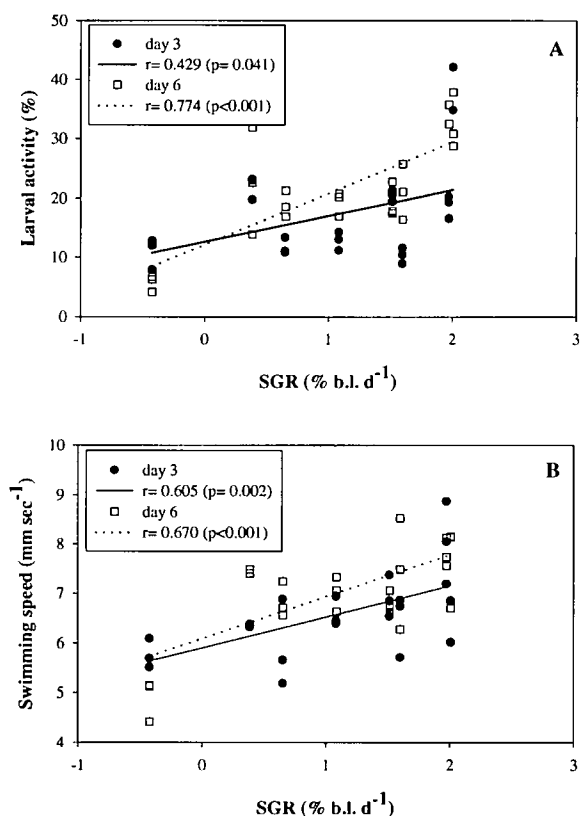

Figure 20. Atlantic cod, 1995 experiment series. The relationship between larval specific growth rate (expressed as percent body length per day) and (A) the percentage or time larvae were actively swimming and (B) swimming speed.
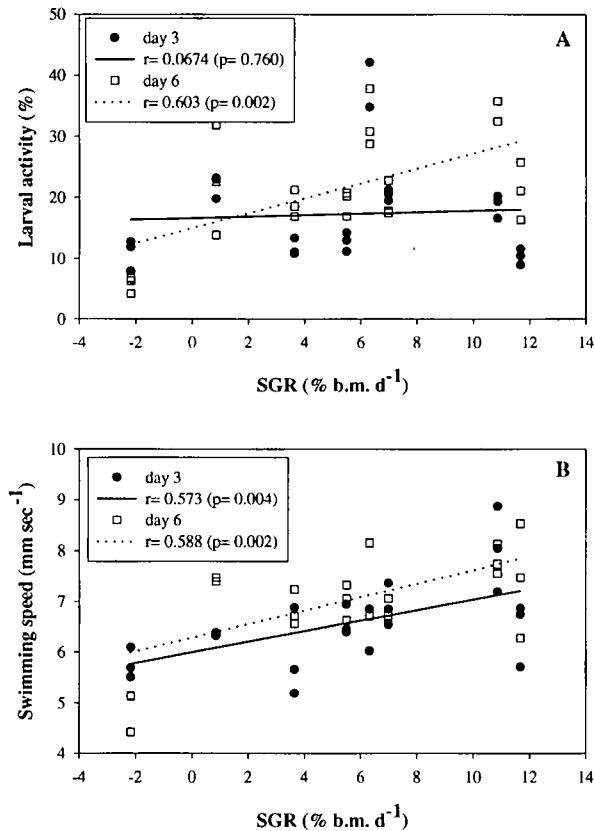
Figure 21. Atlantic cod, 1995 experiment series. The relationship between larval specific growth rate (expressed as percent body dry mass per day) and (A) the percentage of time larvae were actively swimming and (B) swimming speed.

Albeit tentative, these results represent one of the first demonstrations of a link between female condition and the performance of her progeny. The condition factors of the females for which egg batches were followed in 1996 were considerably greater than those for 1995 and included more egg groups from those in poor condition. We are hopeful that this will allow us to discern more conclusive effects of maternal condition and spawning history on larval performance. We will also determine, for 1995 and 1996, whether there is any relationship between the larval performance variables that we measured and post-spawning female condition factor.

A brief summary of seal predation

M.O. Hammill

In spite of a moratorium on fishing since the early 1990's, many cod stocks in eastern Canada show little sign of recovery, possibly as a result of continued high mortality, (due to unfavourable environmental conditions, seal predation, continued unreported fishing activity or lack of massive recruitment). In Atlantic Canada, there are estimated to be over 5.4 million seals divided between harp (4.8 million), hooded (500,000), grey (150,000), and harbour seals (<20,000). Evaluating

their impact on commercial species involves estimating mortality (consumption) caused by seals and the magnitude of this predation compared to total mortality (Mohn and Bowen 1996).

Fish consumption

An initial step is to determine total consumption, which requires information on the dynamics of the predator population, their energy requirements, diet composition and distribution in relation to the prey population (Hammill and Stenson submitted; Harwood and Croxall 1988). Recently, Hammill and Stenson (submitted) estimated that pinnipeds consumed ≈ 3.4 million tonnes of fish in an area extending from the southern Labrador coast (NAFO divisions: 2J3KL) to the Nova Scotia coast (NAFO division: 4X) and including the Gulf of St. Lawrence (NAFO divisions: 4RST). Sixty-three percent of this consumption consisted of capelin, sand lance and arctic cod, species with little or no commercial value. However, assuming that there is little or no error in the estimates of seal abundance, energy requirements, diet composition and the seasonal distribution of the animals, then in 1996 seals may have consumed 68,000 t of Atlantic cod, 27,000 t of Atlantic herring and 98,000 t of redfish in the northern Gulf alone (Table 1)(Hammill and Stenson submitted).

Table 1. Estimated fish consumption (tonnes) by seals in Atlantic Canada in 1996 (modified from Hammill and Stenson, submitted).

	2J3KL	4VsW	4R	4S	4T	Other	Total
Atlantic cod	**142649**	**19430**	**42657**	**24988**	**10135**	**11736**	**251596**
Capelin	805856	163	318660	3709	655	858	1129902
Sandlance	187954	65682	5951	551	23788	18958	302884
Arctic cod	604454	0	1003	1267	0	0	606724
Atlantic herring	90808	11080	18819	9124	4056	3281	136468
Redfish	28480	849	96414	1851	323	1450	129366
Other fish	649308	25290	103981	50763	12536	36472	879048
Invertebrates	329953	5800	58303	951	1675	5926	402609
Total fish	**2509509**	**122494**	**587485**	**92253**	**51493**	**72755**	**3435988**
Total prey	2839462	128294	645788	93204	53168	78681	3838597

Considering overall levels of fish consumption by seals in Atlantic Canada, these estimates may adequately reflect an order of magnitude of consumption. However, some caution needs to be exercised. For example, the redfish consumption (98,000t) is based on extrapolating forward to 1996, diet composition data obtained from 1990-93 (Lawson et al. 1995). Given current redfish biomass estimates, it is possible that this consumption is grossly overestimated.

Cod consumption

To evaluate impact, consumption must be estimated at the level of the fish stock (Table 1). Here, information on diet and seasonal distribution becomes very critical. For example harp seals are responsible for 55% (42,657 t) of the total estimated cod consumption in the Gulf of St Lawrence (77,780t). Although they occur on the Magdalen Shelf in 4T, the fraction of the population in this area, outside of the whelping season, is unknown. Therefore, we assumed that they feed only in 4R. However, if one month of harp seal consumption were shifted from 4R into 4T, then 4R cod consumption would decrease from 42,657 t to 35,547 t.

Size of cod consumed by seals

Consumption consists largely of non-commercial sized fish . Harp seals feed primarily on fish 10-20 cm in length, while grey seals feed on larger fish (25-40 cm). There are some indications that seals do not always target the same size class (Figure 22), therefore knowledge of fish size is important when trying to evaluate impact on particular year classes.
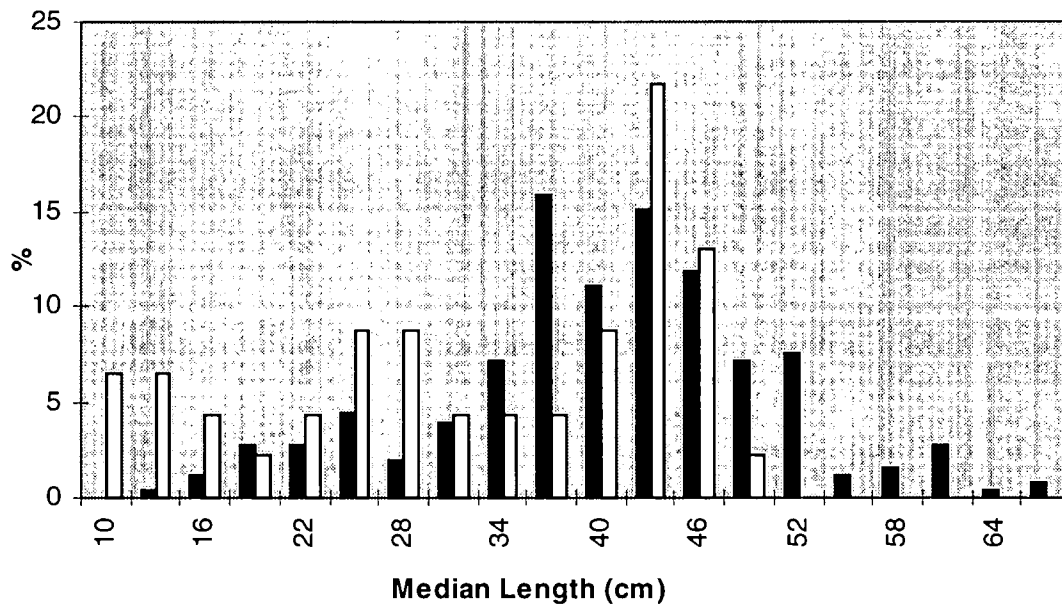

Figure 22. Size frequency of cod consumed by grey seals in 4S during May-July 1988 (black columns) and August-September 1992 (white columns).

Seal populations are at their highest level since the 1960's. The greatest change likely occurred during the 1980's with a decline in harp seal harvests and a rapid increase in grey seal populations. These changes coincide with the most recent decline of the cod fishery. Although it is possible to quantify consumption, and the size classes consumed, we are unable to quantify the impact of this mortality on the failure or the recovery of the fishery. Nevertheless, the increase in mortality from predation does show that the use of a constant natural mortality estimate of 0.2 in fish stock assessments is not appropriate.

Discussion

Biological information

Not only does the Gulf of St. Lawrence exhibit marked seasonal fluctuations in its physical characteristics, particularly temperature and patterns of stratification, it also clearly exhibits long-term trends in climatic conditions (Gilbert and Pettigrew 1997). Both the CIL and the deeper layer showed trends in temperature with colder than long-term average temperatures being observed from 1984 onward in the CIL and in 1991 and 1992 in the deeper layer. These changes in climatic conditions most likely affect the biological processes in the Gulf, and results strongly suggest that year-to-year fluctuations affected cod productivity in the Gulf of St-Lawrence.

The hypothesis put forward in MLI's multidisciplinary research program is not rejected. There are several indications suggesting that changes in the cod environment have affected production. Climatic conditions have changed (Gilbert, this document) and this has resulted in a shift in distribution with cod being less present inshore in shallower waters as indicated by the early decrease in catches in the trap fishery. Cod were more present in deeper waters and started moving out of feeding grounds in the northern Gulf earlier in the fall when the CIL cooling started. This shift in distribution resulted in a shorter feeding season (Castonguay, this document) and cod were exposed to less favourable growth conditions, including lower oxygen availability. Dissolved oxygen is probably the single most under-estimated variate in ecological studies in the northern Gulf. Not only are lethal hypoxic conditions a permanent feature of deep waters in the Estuary, but oxygen availability in deep waters of the Gulf limits cod growth (Chabot, this document).

This is consistent with the observed decline in size-at-age (Dutil, this document) and condition. The nearly perfect correspondence between time trends in size-at-age of cod and the index of the CIL core temperature anomaly in the period between 1980 and 1996 suggests that environmental conditions act as a controlling factor of cod growth in the Gulf (Dutil et al. submitted). Temperature-growth relationships in laboratory studies have shown that temperature acts as a controlling factor in fish (Jobling 1988). Between-stocks comparisons have also shown that differences in size-at-age in cod are mainly attributable to temperature (Brander 1995; Campana et al. 1995). Declining sizes at age in southern Gulf cod have been ascribed to size selective fishing mortality (Hanson and Chouinard 1992), but back-calculations based on otoliths do not support this conclusion for northern Gulf cod (Dutil et al. submitted). Furthermore, declining condition factor values in the early 1990's (Lambert and Dutil 1997b) support the contention that deteriorating environmental conditions were responsible for declining sizes at age during that period (Dutil et al. submitted).

Growth rate and condition are in fact closely related. Laboratory studies show that experimental protocols in which cod are given above-maintenance rations for several weeks result in both positive growth rates and higher condition factor values, with condition factor and growth rate being highly correlated (Dutil et al. in press). Wild cod would appear to exhibit similar relationships. Stocks which experience slower growth rates are characterised by lower condition factor values (Dutil et al. submitted). Field and laboratory studies suggest that northern Gulf cod, with slow growth rates and poor condition (Guderley et al. 1996; Lambert and Dutil 1997b), are

more likely to suffer increased natural mortality (Dutil and Lambert in preparation) from energy exhaustion when climatic conditions deteriorate.

Poor condition in turn has pervasive influences on reproduction. Females in poor condition have a lower fecundity and invest less energy in gonads while spending proportionately more energy in reproduction (Lambert, this document). Hatching success is nil at temperatures such as occur in the CIL and egg quality and viability are influenced by female condition (Ouellet, this document). Larval growth rates correlate with larval activity and swimming speed, but the link between female condition and larval performance, through differences in egg quality, remains to be established (Browman, this document).

Predation is one additional factor that contributes independently to lower the resilience of cod stocks. Seal populations throughout Atlantic Canada have increased considerably since the late 1970's with an increase of about 700% for grey seals (Mohn and Bowen, 1996) and 100% for harp seals (Shelton et al. 1996). Predation on cod by seals was estimated to have been 78 000 tons in 1996 in the Gulf of St. Lawrence, with harp seals and grey seals targeting on different size ranges (Hammill, this document). The increase in seal predation should have resulted mostly in an increase in natural mortality in immature fish (ages 2 to 4) whereas the decline in condition would have caused an increase in natural mortality mostly in mature fish (since condition is greatly linked to reproductive costs in cod). The impact on natural mortality cannot be neglected, particularly in situations where deteriorating environmental conditions may increase mortality in the egg , larval, juvenile or adult stages. While unfavourable environmental conditions, particularly cold temperatures, decreased the capacity of cod stocks to produce new biomass, predation by seals took an additional substantial amount of that production. The two factors, poor condition and high predation, increased the vulnerability of the stock to fishing overexploitation.

Management issues

Current management strategies (e.g. $F_{0.1}$, MSY) of groundfish stocks ignore the production dynamics of the stock and concentrate on managing the standing crop under the assumption that production is a constant property of the existing biomass. Our findings on cod in the Gulf of St. Lawrence and by other studies which examined several stocks in the Atlantic is that stocks vary considerably in their capacity to produce new biomass. Further, this variability does not appear to occur randomly in time, and period of low or high productivity may persist for periods of several years. The decline of cod stocks in the Northwest Atlantic and subsequent low productivity have lasted well over ten years, but the management strategies, target levels, and expectation from the fishery were not modified. These were established when stocks were very productive and were considered to be representative of "normal" conditions.

We have shown in this document several relationships between size-at-age, condition and reproduction which suggest that the low biomasses of cod in the northern Gulf were associated with a much reduced capacity of the stock to produce new biomass. However, estimates of surplus production were not attempted during the course of the assessments of this resource. In retrospect, we can conclude that the exploitation rates (35-45%, Fréchet et al. 1994) were well above the capacity of the stock to replenish itself during that period. These exploitation rates are also well above the target rate ($F_{0.1}$ about 16% - based on steady state mechanisms) but there is no guarantee that even an exploitation at $F_{0.1}$ would not have exceeded the productivity of the stock.

Results presented herein have shown that cod growth and condition are closely related to the environmental conditions in the Gulf of St. Lawrence, probably through shifts in habitats and physiological constraints. This has resulted in an increase in natural mortality and certainly in reduced fecundity; finally the survival of the few offspring of these cod was probably negatively affected. The driving mechanism behind these changes in productivity appears to be related to the CIL. The CIL is a long lasting feature of the Gulf of St. Lawrence, which evolves over many years. Though it is not possible to predict precisely stock productivity over time, the link with multi-year environmental features (*i.e.* the CIL) makes possible the use of relatively simple correlates of stock production (size-at-age, condition, fecundity) in the decision making process.

This needs to be acknowledged in the determination of the stock status and should be taken into consideration as well as the size of the population when making projections and decisions on exploitation rates and harvesting levels. It is already known that short term trends in productivity can impact on the predictions in the exploitation pattern that a stock will undergo because of the discrepancies between the predicted catch numbers corresponding to a TAC (in biomass) assuming constant production and the realised numbers for the same catch weight under a different production scenario. For instance, Rivard and Foy (1987) have shown that decreasing trends in growth and recruitment have led to systematic overrun of target fishing mortalities in the Northwest Atlantic. In a similar fashion, we can predict that targeting fish in poor condition (in spring for instance) will result in higher fishing mortality than harvesting the same fish biomass in better condition, not to mention low yields in processing plants (see Fréchet et al., Working Paper 98/1-1). Long term variations will be more difficult to incorporate. The research program aimed at assessing natural and fishing mortality produced the kind of information that could be integrated in models used to assess population size and make projections. For instance, natural mortality has always been considered constant in stock assessment models, the same rate being applied to all cod stocks for a wide range of ages and for all years. It becomes necessary to incorporate in the possibility of having natural mortality vary in relation to an increase in predation or to a decrease in condition. Moreover, recruitment was obviously much lower in recent years than when productivity was higher. Projections used to estimate future recruitment to the fishery should be adjusted to some biological parameters such as individual condition and actual fecundity to produce more realistic prospects for the near future (see Fréchet et al., Working Paper 98/1-1).

Current thoughts about resource (and fisheries) management call for assessing the risks of exceeding some predefined target (*i.e.* biomass level, or fishing mortality) given the uncertainties in the assessment and selecting management options with predetermined acceptable risk levels (e.g. Cordue and Francis 1994; McAllister et al. 1994; Punt and Hillborn 1997). In this context, long term fluctuations in productivity could be factored in by a) selecting different target levels appropriate to the productivity condition of the stocks (*i.e.* higher minimum biomass, lower exploitation at low production levels, etc.) or by b) adjusting the degree of acceptable risk at the different production levels. There are clearly needs to investigate the implications of variation in productivity on how fishery advice is provided.

This document presented a short review of several studies which were undertaken to understand the collapse of the fishery in the northern Gulf of St. Lawrence. Like many other cod and fish stocks around the world, northern Gulf cod have been heavily exploited for centuries and particularly so in recent decades. The exact cause of the concomitant collapse of several stocks

has been and still is largely debated. What our results suggest is that a deterioration of environmental conditions could have contributed to the collapse by making this vulnerable stock much more vulnerable in the recent past. Cod in the Gulf of St. Lawrence are much less productive than other cod stocks in the Atlantic. Alternative management measures such as those suggested in this document may be more imperative for vulnerable stocks such as the northern Gulf cod stock, considering that such stocks are less resilient as they live in more extreme conditions for the species.

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