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Cod stocks rebuilding and fish bioenergetics : low productivity hypothesis.

Le rétablissement des stocks de morue et la bio-énergétique des poissons: l'hypothèse d'une faible productivité.

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Abstract

The lack of response of several cod stocks and other species to management regulations expected to promote stock rebuilding is hypothesized to stem from a combined (multiplicative) effect of 3 factors : 1. natural intrinsic productivity is low; 2. natural intrinsic productivity has declined; 3. pressures on production associated with natural and fishing mortality have remained high or have increased relative to these stocks/species rates of production. Annual production per capita and per unit biomass varies among stocks, with northerly distributed stocks or stocks inhabiting cold and sometimes hypoxic environments being notably less productive than other stocks. Cod in less productive stocks grow slowly, recruit at an older age, become sexually mature at a later age and a smaller size and produce fewer eggs. Fish condition is on average lower and varies much more in these stocks compared to other stocks. Environmental conditions have changed progressively after the mid ‘80s with conditions during the moratorium not favorable to cod production in northern areas of the western North Atlantic. Fish stocks in these areas have thus become less productive and hence less resilient, i.e., less able to resist and respond to perturbations, whether man-made or environmental. There are several recent indications that individual performance has improved, but fishing pressure has not been relaxed sufficiently to offset increased predation pressures and low productivity associated with limiting environmental conditions. These stocks are unable to produce new biomass fast and as a result stock rebuilding is expected to take much longer than would be predicted for other stocks living in more favorable environments, particularly if exploited under enduring adverse environmental conditions. Strengths and weaknesses of this hypothesis are discussed.

Résumé

Nous posons l'hypothèse que la lenteur avec laquelle les stocks de morue se reconstituent malgré la mise en place de plans de gestion censés en favoriser le rétablissement s'explique par un effet combiné de trois facteurs : 1- la productivité naturelle de ces stocks est faible, 2- la productivité naturelle est aujourd'hui moindre que par le passé, 3- la mortalité par pêche et la mortalité naturelle sont demeurées élevées ou même ont augmenté exerçant des contraintes majeures sur la production. La production annuelle par individu ou par kg de biomasse diffère entre les stocks, les stocks nordiques ou vivant en milieu froid ou parfois pauvre en oxygène étant nettement moins productifs que les autres. Les morues des stocks les moins productifs ont une croissance lente, recrutent à la pêche à un âge plus avancé, deviennent sexuellement matures à une longueur moindre et un âge plus avancé tout en produisant moins d'oeufs. Leur condition énergétique est moins bonne et varie davantage que chez les morues des stocks les plus productifs. Les conditions environnementales se sont détériorées progressivement vers la fin des années '80 et n'ont pas été favorables à la morue pendant le moratoire dans le nord-ouest de l'Atlantique. Les stocks de cette région sont donc devenus encore moins productifs et moins aptes à résister ou à se remettre d'une perturbation qu'elle soit naturelle ou anthropique. Quelques éléments suggèrent que la performance individuelle s'est améliorée récemment, mais une reprise de la pêche a réduit à néant la lente remontée des stocks dans un contexte où la production était handicapée par une forte prédation et des conditions environnementales peu favorables. Pour ces stocks, la production de nouvelle biomasse est lente de sorte que le rétablissement sera plus lent que pour d'autres stocks vivant dans un milieu moins hostile, particulièrement si on les exploite et que les conditions environnementales restent extrêmes. Les forces et les faiblesses de cette hypothèse sont discutées.

Statement of the low stock productivity hypothesis

The lack of response of several cod stocks and other species to management regulations expected to promote stock rebuilding stems from a combined (multiplicative) effect of 3 factors :

- natural intrinsic productivity of these stocks is low;
- natural intrinsic productivity of these stocks has declined;
- pressures on production associated with natural and fishing mortality have remained high or have increased relative to these stocks/species rates of production.

Below is a detailed account of the supporting evidence for this hypothesis. Some of the material has been submitted for publication, but most of it has already been published and is referenced. Thus we have limited the number of tables and figures which should be viewed as a limited set of examples. For more information, refer to the list of references.

1. Annual production per capita and per unit biomass varies among stocks, with northerly distributed stocks or stocks inhabiting cold environments being less productive

The data from stock assessments were used to compare stock biomass, annual growth (Gs) and surplus production per capita (TSPc) and per unit biomass (TSPb) among 15 cod stocks in the North Atlantic (Dutil and Brander, 2003). TSPc ranged from 99 in the least productive stock up to 1012 g/fish in the most productive stock and averaged 448 g/fish across stocks. TSPb ranged from 140 to 469 g/kg among stocks and averaged 294 g/kg across stocks. Gs varied considerably with low growth production associated with low surplus production. On average, cod produced 724 g/fish in growth annually with cod in the least productive stock producing 7.2 times less than in the most productive stock (Southern Gulf, 248 g; Celtic Sea, 1801 g). Restricting our analysis to age-groups 3 to 5, which are the only age-groups common to all SPAs, increased the range of production figures substantially with five of the stocks accounting for 65% of the cumulative Gs for all 15 stocks. Gs averaged 968 g with a minimum of 238 g for Southern Gulf cod and a maximum of 2477 g for Celtic Sea cod.

Through a cluster analysis, the stocks divided into 4 groups reflecting 4 levels of production (Dutil and Brander, 2003). Celtic Sea, Irish Sea and West Scotland cod (cluster 1) showed the highest levels of production with each fish producing on average 1386 g of fresh weight annually (Table 1). TSPc (806 g/fish) was also much greater than for any other cluster. Clusters 3 and 4 were made of the less productive stocks. Gs was quite similar in clusters 3 and 4 (457 and 386 g/fish in clusters 3 and 4, respectively), but recruitment was less in cluster 4 (267 and 153 g/fish in clusters 3 and 4, respectively). Stock surplus production (recruitment not included) was minimal in both groups with stocks of cluster 3 producing a TSPc of nearly 300 g/fish on average compared to less than 200 g/fish for stocks of cluster 4. Yield to the fishery was lower for stocks of cluster 4 (321 and 218 g/fish in clusters 3 and 4, respectively). Cluster 4 included many Canadian stocks, Eastern Scotian Shelf, Northern Grand Banks, Northern and Southern Gulf of St. Lawrence, and Northeast Arctic cod. Among stocks in cluster 4, Southern Gulf cod would be considered as the least productive stock. Stocks of cluster 1 (Celtic Sea, Irish Sea, West Scotland) account for 45% of Gs, 42% of TSPc and 35% of TSPb for all stocks combined whereas stocks of cluster 4 account for only 12% of Gs, 10% of TSPc and 15% of TSPb for all stocks combined.

Total surplus production (TSPc and TSPb) increased with increasing Gs (Figure 1). The slope was significant in both cases ($P<0.001$) with $r^2= 0.61$ and 0.26 for TSPc and TSPb, respectively. Thus variability among years was great. For Gs values increasing from 0.2 to 1.2 kg/fish, TSPc and TSPb increased by 642 g/fish and 228g/kg, respectively. In contrast, for Gs values increasing from 1.2 to 2.2 kg/fish, TSPc and TSPb increased by 216 g/fish and 77 g/kg, respectively. Among stocks in cluster 4, TSPc and TSPb correlated with Gs in 3 stocks (Northern Grand Banks, Northern and Southern Gulf of St. Lawrence).

2. Less productive stocks live in cold water, sometimes also in hypoxic waters, are characterized by slow growth, recruit at an older age, become sexually mature at a later age and a smaller size and produce fewer eggs. Fish condition is on average lower and varies much more in these stocks compared to other stocks

The exact regime of temperatures cod are exposed to over their life is largely unknown particularly for Canadian stocks as they range over large areas, migrate seasonnally and live in waters characterized by strong temperature stratification. When average surface temperatures over the area occupied by each stock were examined, the least productive Canadian stocks (cluster 4, Eastern Scotian Shelf, Northern Grand Banks, Northern and Southern Gulf of St. Lawrence) were found to inhabit colder areas than other Canadian stocks or any other stock in the North Atlantic (except Northeast Arctic cod, Brander, 1995). Other studies have examined cod distribution and bottom temperature. Gulf cod were found to inhabit cold water (D'Amours, 1993; Swain and Kramer, 1995). They also were found in colder waters in summer than in winter (Swain et al., 1998; Castonguay et al., 1999). During the growth season, a large proportion of the population lived at temperatures as low as 2°C or less.

Some of the poorly productive Canadian stocks (Northern and Southern Gulf of St. Lawrence, and to a lesser extent Eastern Scotian Shelf) either live in hypoxic waters or avoid hypoxic waters and as a result have access to a fraction of the demersal habitats. In the northern Gulf, cod avoided areas with less than 30% oxygen saturation (D'Amours, 1993), which is close to the incipient lethal threshold (28%) determined in the laboratory (Plante et al., 1998). However, a large proportion of the stock was found in waters with 30-70% saturation in 1991

(D'Amours, 1993) and 1995 (Figure 2)(up to 46% of the stock in numbers or 47% in biomass in August 1995, Chabot and Couturier, 2002). Furthermore, cod distribution in 1991 and 1995 was representative of summer distribution at least in the early 90s. Bottom waters in deep channels of the Gulf of St. Lawrence have been characterized by low levels of oxygen for as long as this variable has been measured (several decades, Denis Gilbert, pers. comm.). Thus cod from this stock probably always spent some time in hypoxic waters.

A variable mix of waters from the Atlantic Ocean and the Labrador Current enters the Laurentian channel, with oxygen levels varying between 60 and 70% saturation (Bugden, 1991; Gilbert and Pettigrew, 1997). These waters progress towards the head of the channels, and get progressively more depleted in oxygen : levels of 20–30% saturation are typical of the estuary (part of 4T) and some locations in the deep channels of the Gulf of St Lawrence (Northern and Southern Gulf). Bottom waters of deep basins on the Scotian Shelf also experience mildly hypoxic waters periodically.

Slow growth is explained by cold temperatures and low oxygen levels

Length and weight at age vary considerably among stocks and temperature is found to play a major role in explaining such variability. Back in the 50s, significant relationships were found between growth parameters in the Bertalanffy growth equations for cod and mean annual surface temperatures in several locations (Taylor, 1957). Bottom temperature was also found to be a major determinant of weight at age in the landings among 17 cod stocks (Brander, 1995). The weight of 4-year-old cod decreased by 30% for every 1°C decrease in temperature (Brander, 1994). Lengths at age also varied considerably among stocks in the Northwest Atlantic, and bottom temperature was a significant covariate in the length-age relationships (Campana et al., 1995). Stocks characterized by smaller lengths and weights at age exhibit much slower annual growth rates, as determined by changes in average size of the survivors from year to year, with Southern Gulf cod at the low end and Celtic Sea cod at the high end of the spectrum (Dutil and Brander, 2003).

Temperature is a prime determinant of growth rate in laboratory experiments. Weight increments (but not growth rates) are expected to increase as size of fish increases. In contrast, specific growth rates are expected to decrease as fish size increases and as water temperature increases beyond or decreases below a point at which food conversion ratio is optimal. These relationships have been described for cod in laboratory experiments (Jobling, 1988; Björnsson et al., 2001; Björnsson and Steinarsson, 2002). Wild cod grow nowhere close to the maximum rate expected based on laboratory experiments (Figure 3) (Björnsson and Steinarsson, 2002; Dutil and Brander, 2003). Poorly productive stocks do as well as others. Southern Gulf cod achieve 38% of the maximum rate observed at 2 ºC compared to 36% of the maximum rate observed at 10 ºC in highly productive stocks. Thus, poorly productive stocks do not appear to incur greater maintenance and activity costs or to suffer from greater food limitations than other stocks. They simply are limited by cold temperatures.

Cod are expected to grow more slowly when oxygen levels are below 70% saturation (Chabot and Dutil, 1999) than in normoxic and hence shallower waters under similar food and temperature conditions. The impact of low oxygen availability on annual growth production of Northern Gulf cod has been estimated to be about 17-19% in summer, during the peak of the feeding season, and 9% in fall (Chabot et al., 2001; Chabot and Couturier, 2002). These values were obtained by estimating the distribution of cod in relation to dissolved oxygen, and growth rate, as a proportion of growth in normoxic waters, in function of dissolved oxygen. Six oxygen classes were defined: <30% saturation, where survival is compromised and growth is negative, 30-39.9, 40-49.9, 50-59.9, and 60-69.9% saturation, where growth is limited by oxygen availability, and ≥70% saturation when growth is not affected by oxygen availability. Three surveys which sampled the entire northern Gulf of St. Lawrence cod stock were used to assess the relationship between cod distribution and dissolved oxygen during the peak of the feeding season in 1995: two Sentinel Fishery surveys (no. 3, July 25 to August 15, and no. 4, October 6 to November 4) and the Needler groundfish survey (August 11 to September 4). For each survey and each stratum, the number of cod estimated for the stratum was distributed into the six oxygen classes according to the proportion of the stratum's area that was characterized by each oxygen-class. Overall, growth production was estimated to be reduced by 18.5% (survey 3), 16.9% (Needler) and 9% (survey 4) relative to growth in normoxia (Table 2). These early results show that during the peak of the feeding season, a significant proportion of the Northern Gulf stock can be found in waters with levels of dissolved oxygen sufficiently low to reduce growth rate in the laboratory, and suggest that the impact of hypoxia on growth is not negligible.

Poorly productive stocks have a reduced reproductive potential

Because of their smaller size at age (Brander, 1995) and lower size-specific fecundity (Figure 4), cod of many Canadian stocks have a lower egg production potential. Size, age, and condition of individual spawning cod strongly influence the reproductive potential of stocks (Kjesbu et al., 1991; Chambers and Waiwood, 1996; Solemdal, 1997; Trippel et al., 1997; Kjesbu et al., 1998; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Lambert and Dutil, 2000; Vallin and Nissling, 2000; Marteinsdottir and Begg, 2002). Fish size is the factor that most influences potential fecundity. The relationship between potential fecundity and length is usually described by a curvilinear relationship ($Y=aX^b$) with values of b typically ranging between 3 and 5. The values of the parameters describing the relationships can vary with populations, geographic areas, and years (Marteinsdottir and Begg, 2002). Smaller sizes at age in Canadian cod stocks will result in lower egg production. For example, the average weight of a 4-year-old cod in the NGSL is 0.61 kg compared to 3.63 kg in the North Sea (Brander, 1995). Corresponding lengths would be 42 cm and 72 cm, respectively. Relationships between potential fecundity and length for these stocks

(Oosthuizen and Daan, 1974; Lambert and Dutil, 2000) would indicate a 9.4 fold difference in the potential fecundity at age 4 between the two stocks (176800 eggs in NGSL compared to 1664200 eggs in the NS).

Because smaller sizes at age are associated with lower condition factors (Dutil et al., 1999; Rätz and Lloret, 2003) and cold water (Rätz and Lloret, 2003), many Canadian stocks have a lower fecundity at age. Many studies have reported correlations between levels of energy reserves and potential and/or realised fecundity (Lambert et al., 2003). In laboratory experiments, cod with low condition factors produced fewer previtellogenic oocytes and used a smaller fraction of these during vitellogenesis. Actual fecundity was between 20 and 80% of potential fecundity depending on the nutritional status of the fish, and a significant relationship between the percentage of previtellogenic oocytes and Fulton's condition factor was observed (Kjesbu et al., 1991). Laboratory experiments conducted with cod from the northern Gulf of St. Lawrence also indicate that female cod with low energy reserves invest less energy in egg production (Lambert and Dutil, 2000). Realised fecundity and total egg dry weight were significantly reduced in females with lower condition factors. A multiple regression model indicated that length and condition factor explained 72% of the variability observed in realised fecundity. Forty nine percent of this variability was explained by female length, while condition factor explained 23% of the variability. Potential fecundity of Atlantic cod held in sea cages in Newfoundland was greater than in wild cod of the same length captured in the same area (Wroblewski et al., 1999). Differences in potential fecundity were apparently related to better nutritional condition of the caged fish which had a higher nutritional condition (Fulton's condition factor) than wild cod. Moreover, differences in the mean relative fecundity of caged cod from two different locations were directly related to nutritional condition (t-test, $P = 0.015$).

There are also indications that condition has a significant effect on potential fecundity in wild cod (Lambert et al., 2003). Total length and liver weight had direct effects on the potential fecundity of the Arcto-Norwegian cod (Kjesbu et al., 1998). Interannual variations in potential fecundity were directly related to the condition of the females. The significant changes in the annual regressions of whole body weight on total length between 1986 and 1991 were used to define the 1987 spawners as in poor condition and those in 1991 as in good condition. Estimated potential fecundity (regressions between potential fecundity and total length) was found to be 44% lower in 1987 than in 1991.

Marshall et al. (1998) observed a significant effect of both length and condition on the relative fecundity of the Northeast Arctic cod stock. In Icelandic cod, condition (in addition to length or weight) was shown to be significantly related to potential, relative, and batch fecundity (Marteinsdottir and Begg, 2002). Generally, more variation was explained by the hepatosomatic index than by the Fulton's condition factor and, in some years, more variation in relative fecundity was explained by the hepatosomatic index than by length. Up to 92 % of the variation in potential fecundity was explained by length and condition (Marteinsdottir and Begg, 2002). In Baltic cod, temperature and individual condition factor at sampling had a significant correspondence to individual potential fecundity (Kraus et al., 2000). In another study, the variability in potential fecundity of Baltic cod was unrelated to the condition of the fish (Kraus et al., 1997). Growth anomaly and ambient water temperature, however, explained a substantial amount of the observed variance in the annual average relative fecundity of Baltic cod (Kraus et al., 2000). Potential fecundity of Arcto-Norwegian cod was also observed to be significantly correlated with environmental temperature and capelin biomass (Kjesbu et al., 1998). The potential fecundity of a standard female of 90 cm in length was estimated from regressions between potential fecundity and total length using data from 1986 to 1996. This potential fecundity was correlated to the 6-month mean temperature before spawning and the ratio of Barents Sea capelin biomass and Arcto-Norwegian cod spawning biomass.

Egg size which is frequently reported as a measure of egg quality and initial offspring size (Chambers, 1997), is influenced by female age/size, condition, spawning experience and environmental conditions (Lambert et al., 2003). Most of the studies examining the influence of female properties on egg size have shown that egg diameters or dry weights increase significantly with female length, weight, and/or age (Solemdal et al., 1993; Kjesbu et al., 1996; Pedersen et al., 1997; Marteinsdottir and Steinarsson, 1998). A significant relationship between egg size and several female condition indices has also been reported ($0.34<r^2<0.86$) (Chambers and Waiwood, 1996; Marteinsdottir and Steinarsson, 1998; Ouellet et al., 2001).

The size of larvae as well as other parameters associated with larval viability (hatching success, survival, feeding ability, and growth) are significantly related to egg size/weight in many species including cod (Knutsen and Tilseth, 1985; Miller et al., 1995; Pepin et al., 1997; Marteinsdottir and Steinarsson, 1998; Nissling et al., 1998; Trippel, 1998). In several cod stocks female condition affects offspring viability and explains up to 80% of the variance in egg size. The influence of the maternal liver index and condition factor on larval feeding and growth has only been reported for Icelandic cod (Marteinsdottir and Steinarsson, 1998). It seems that the effect of condition on viability plays an important role in stocks exposed to temporal shortages in food supply. For example in Eastern Baltic cod, which experience abundant prey, e.g., sprat stocks are on the highest level on record (ICES, 1999), no impact of female condition on size and buoyancy of eggs was observed (Vallin and Nissling, 2000). In contrast, significant positive relationships have been found in Icelandic and North West Atlantic cod stocks (Chambers and Waiwood, 1996; Marteinsdottir and Steinarsson, 1998; Marteinsdottir and Begg, 2002). The impact of female condition appears, however, to be weaker than the seasonal effect and regulates fecundity rather than offspring quality (Kjesbu et al., 1998; Marshall et al., 1998; Lambert and Dutil, 2000).

First-time spawners perform poorly compared to second-time spawners. In the laboratory, they breed for a shorter period, produce fewer egg batches, exhibit lower fecundity, and produce smaller eggs with lower fertilization and hatching rates (Trippel, 1998). The inclusion of age diversity has been shown to improve substantially the stock-recruitment relationship of Icelandic cod (Marteinsdottir and Thorarinsson, 1998). Recruitment of Eastern Baltic cod was demonstrated to be significantly influenced by the age structure of the adult stock (Cardinale and Arrhenius, 2000) and egg production of age group 5+ (Vallin and Nissling, 2000). However, no evidence of the influence of age structure on cod recruitment in the southern Gulf of St. Lawrence was found (Swain and Chouinard, 2000).

Fish condition is on average lower and varies much more in less productive stocks

Poor condition is associated with poor growth both in laboratory experiments (Dutil et al., 1998b) and in the field (Dutil et al., 1999; Rätz and Lloret, 2003). When condition factor, as determined for cod caught in the fall period, was plotted against weight at age, poorly productive stocks differed from other stocks. Condition factor was smaller and more variable in slow-growing cod compared to fast-growing cod which maintained condition factor values above 1.00 (Figure 5) (Dutil et al., 1999). Furthermore, condition and bottom temperature correlated with stocks living in cold water having lower condition factor values in the fall (Rätz and Lloret, 2003). Thus stocks living in colder areas build lower energy reserves over summer, both as a result of a smaller size and a lower energy build up relative to their size. This puts them in a more precarious situation in preparation for starvation and maturation which take place in winter and this has a negative impact on fecundity (section above). These relationships may in part stem from a positive relationship between condition factor and length, such as observed in Southern Gulf cod (Dutil et al., 1995). Nevertheless they reflect lower energy reserves for cod of the same age-class across stocks.

3. Environmental conditions have changed progressively after the mid ‘80s with present conditions less favorable to cod production in northern areas of the western North Atlantic

The NAO index captures large scale variations in climate in the North Atlantic. High index years are associated with cooling and low index years with warming in northern seas. Historically, the NAO index has shifted from positive to negative values over short periods of time. In the last 50 years, persistent negative index values were observed in the 50s, 60s and 70s. More recently, a suite of strong positive index values were observed starting in the 80s. Record high values were reached in the 90s until recently, except in 1996 when the NAO index was negative. This climatic event has driven a large scale cooling of waters in Labrador, over the Grand Banks, in the Gulf of St. Lawrence and over the Scotian Shelf. For instance, below normal temperatures were observed in the late 80s on the Newfoundland and Labrador shelves, minima were reached in

1991 and temperature remained low up to 1995. The recent period was warmer than normal (Colbourne, 2002). A similar pattern was observed in southern Newfoundland where near 0°C waters occupied a larger proportion of bottom surface areas in the 90s. This situation started to improve in 1998 (Colbourne, 2002). Temperature of the CIL in the Gulf of St. Lawrence also decreased markedly in the 90s and a series of very cold years occurred and persisted through the 90s with warming occuring as late as 1999 (Gilbert and Pettigrew, 1997). The area of the bottom covered with cold water in the northeastern Scotian Shelf was maximum in 1991 and has remained high up to 1998 (Neilson et al., 2002).

Low temperature was pointed out as a key factor of the environment which might have contributed to increased natural mortality of cod. Several instances of mass mortalities of cod in the northern Gulf of St. Lawrence and in the North Atlantic have been considered as potentially related to unusually cold waters, but firm evidence is lacking (Templeman and Fleming, 1965; Harden Jones and Scholes, 1974). Temperature and stock declines on the Labrador and Newfoundland shelves have taken place roughly simultaneously (Lilly, 1994). Thus massive mortalities were hypothesized to have occurred suddenly, due to cold lethal temperatures. Myers and Cadigan (1995) tested whether an increase in natural mortality had occurred in 1991. They examined both research survey and commercial catch-at-age data, but found no evidence that natural mortality increased in the first half of 1991. They rejected the mass mortality hypothesis and ruled out temperature as a factor explaining the concurrent collapse of several stocks in the Northwest Atlantic. They argued that cold water temperatures in 1991 were not atypical for the period 1800 to 1950 and finally concluded that the stock decline had been gradual, had begun in 1985 and was unrelated to temperature (Hutchings and Myers, 1994; Myers and Cadigan, 1995). Temperature in this case was viewed as a factor having had a sudden direct negative impact on survival. There is no direct evidence that massive die-offs have occurred due to a cold spell in the Northwest Atlantic in the early 1990's. Cod inhabit areas where subzero temperatures occur, particularly in areas of high food availability (Lilly, 1994). They survive prolonged exposures to 0°C water (Harden Jones and Scholes, 1974). They also produce antifreeze glycopeptides (Hew et al., 1981) which favor their survival at temperatures as low as -1.35°C (Goddard et al., 1994). Lilly's (1994) analyses showed no relation between the disappearance of cod north and west of 2J and 3K and low bottom temperature.

4. Fish stocks in these areas have thus become less productive and hence less resilient, i.e., less able to resist and respond to perturbations, whether man-made or environmental

Growth : cold environments and cooling events would be expected to be more detrimental to smaller fish than to larger fish

That cod mortality did not increase as a direct result of exposure to extreme low temperatures does not mean temperature played no role in the collapse and more recently lack of rebuilding of these stocks. Temperature has pervasive effects on stocks because of its major effects on metabolism. When exposed to cold temperatures in laboratory experiments, cod have a lower metabolic rate, activity is reduced, ingestion and digestion slow down, and growth rate declines accordingly (Jobling, 1988). Temperature - growth relationships of Icelandic cod have been examined recently (Björnsson et al., 2001; Björnsson and Steinarsson, 2002). Temperature requirements in terms of fast growth were found to correlate negatively with fish size. In small juvenile cod (2 g), maximum growth was observed at 16°C. In contrast, maximum growth was observed at a much lower temperature (8°C) in 2 kg cod. Thus in terms of growth, cold environments and cooling events would be expected to be more detrimental to smaller fish than to larger fish as a result of a larger gap between actual temperatures and temperatures promoting maximum growth. This has major consequences : 1- recruitment would be predicted to be more problematic in cold environments as the small fish would have a greater difficulty to find optimal growth conditions all year round, and 2- growth production would be expected to decrease as average fish size in the stock decreases. Thus environmental conditions in the 90s were unfavorable to juveniles and to small fish left by the fishery. For a comparison of actual and predicted maximum growth rates of cod of different sizes at different temperatures, refer to Dutil et al. (1999) and Dutil and Brander (2003).

Growth : causes for smaller sizes at age are debated, but declines in size at age are consistent with observed changes in temperature and their potential impact on growth rates

Not only do cod in poorly productive stocks have slow growth rates, they also experienced declining growth rates (Figure 6). When population abundance declined in the late 80s and in the 90s, individual cod did not benefit from a presumably relaxed intraspecific competition. Growth rates decreased at high densities, but did not increase at low densities in the 90s in the southern Gulf of St. Lawrence (Swain and Wade, 1993). Sizes-at-age on the contrary declined in the northern and southern Gulf of St. Lawrence (Chouinard and Fréchet, 1994), on the Eastern Scotian Shelf (Mohn and MacEachern, 1992), and in Labrador and on the Grand Banks (Krohn and Kerr, 1997). The decline was much more pronounced in 2J than on the Grand Banks (Davis et al., 1997; Lilly, 1997). Traditionnally, declining sizes-at-age in heavily exploited stocks have been explained by size-selective fishing (Hanson and Chouinard, 1992). The relative effects of size-selective mortality, density-dependent growth and temperature on growth were examined for Southern Gulf cod. The strongest effect was size-selective fishing with a weak positive effect of temperature (Sinclair et al., 2002). Temperature effects were highly significant on the other hand, when changes in length at age were tested for density and temperature effects, with lower temperature resulting in slower growth, i.e., smaller lengths at age, in three out of four stocks (Northern and Southern Gulf and Eastern Scotian Shelf)(Swain et al., 2003). In the northern Gulf of St. Lawrence, coincident changes in long-term average temperatures (Gilbert and Pettigrew, 1997), median latitude of cod distribution in winter (Castonguay et al., 1999) and size-at-age (Chouinard and Fréchet, 1994) also suggest that climatic conditions played a role in this reduction of growth rates (Dutil et al., 1999). On the Faroe Plateau, year-to-year differences in weight at age were influenced, perhaps largely controlled, by temperature (Brander, 1995).

Annual surplus production figures (Dutil and Brander, 2003) indicate a synchrony in surplus production patterns between stocks in the Gulf of St. Lawrence (Figure 7) and on the eastern Scotian Shelf, suggesting these poorly productive stocks were affected by common factors. The period starting in 1986 appears to have been a period of low per capita surplus production in the 3 stocks, with several years resulting in negative figures. Surplus production and growth production correlate significantly both for the Northern and Southern Gulf stocks ($P<0.001$) and growth production explains 64% of the variability in surplus production in both cases.

Condition : low condition factors observed in poorly productive stocks and declining condition factors observed during cold water years indicate that the environment was not very favorable to production in the post-moratorium period

Declining growth rates in the mid-80s were followed by declining energy reserves in the late 80s and early 90s in cod in the northern Gulf of St. Lawrence (Figure 8)(Lambert and Dutil, 1997b), eastern Scotian Shelf (Neilson et al., 2002) and north of the Grand Banks (Lilly, 1996; Lilly, 1997; Lilly, 2001). Jorgensen (1992) described a similar situation for Northeast Arctic cod which exhibited a sharp decline in length-at-age (ca 15 cm) and a 20% decline in condition factor between 1984 and 1989. In contrast, condition factor was high and did not decline in cod of the south Scotian Shelf and Bay of Fundy (Neilson et al., 2002), a stock which has not been exposed to colder waters and has not experienced a decline in size-at-age over the last 30 years.

Condition exhibited a marked seasonal cycle in the period following the decline in energy reserves. This was documented for 4 cod stocks, Northern and Southern Gulf, Southern Newfoundland (3Ps) and Labrador and Grand Banks (2J3KL). The energetic condition in cod is primarily determined by the amount of lipids stored in the liver and proteins in the swimming muscles. Relationships between levels of energy reserves in the liver and muscle and simple indices such as condition factor, liver-somatic index and water contents of liver and muscle, have been described for cod (Dutil et al., 1995; Lambert and Dutil, 1997a). Energy reserves of individual cod in the southern Gulf of St. Lawrence were low during the period when this stock collapsed, between 1991 and 1993, and exhibited a strong seasonal cycle (Schwalme and Chouinard, 1999). Southern Gulf cod fed very little and lost 26% of their carcass weight and as much as 76 to 84% of their liver dry weight during winter. Less than 20% of this loss could be accounted for by gonadal growth. Similarly in the northern Gulf, cod experienced marked seasonal variations in condition between June 1993 and June 1995; minimum energy contents occurred in spring during spawning, and maximum energy contents occurred in fall (Lambert and Dutil, 1997b). Northern Gulf cod were in very poor condition, particularly in May and June: some individuals had similar energy contents as cod starved during a prolonged period of time in laboratory experiments. Feeding activity decreased during that period (Dutil et al., xxxx). Cod sampled in fall also had lower energy contents than well-fed cod in laboratory experiments, which indicated that food availability or the length of the growth season (Castonguay et al., 1999; Dutil et al., 1999) were such that cod in poor condition were unable to fully replenish their energy reserves during summer (Lambert and Dutil, 1997b; Dutil and Lambert, 2000). Finally, a marked seasonal cycle in the condition factor and liver index was also described for the southern Newfoundland cod for 1995, i.e. in the absence of any exploitation (Lilly 1996). Seasonal cycles in energy reserves may be a prominent and unique feature of cold water poorly productive stocks and would seem to occur every year (Figure 9)(Lambert and Dutil, 1997b). They have not been described however for healthy stocks characterized by faster growth rates : faster growth rates might be predicted to result in cycles of smaller amplitude.

Northern Gulf cod have experienced some good years in terms of growth, as indicated by changes in condition and weight at age, during the post-moratorium period. Condition was slightly better starting in 1995 (Figure 8). This had a positive impact on weights at age which increased in the fishery and in the surveys from record low values in the early 90s to above average in 1999 (Figure 6). The more spectacular increase observed in the commercial fishery may have resulted from fish being landed exclusively from the fixed gear fishery after the moratorium. Weight at age declined in 2000 and 2001.

Condition : documented effects of poor condition include natural mortality, metabolic breakdown, decreased capacity for aerobic and anaerobic swimming (increased catchability/vulnerability), lower condition factors at the end of summer, and decreased fecundity.

Mortality

Determining how many fish died from energy exhaustion in the spring period in the early 90s is not a simple task. Massive deaths of lean fish have never been reported. Emaciated fish are more vulnerable to predation and may never be found dead on the bottom. Alternately, deaths would occur over several weeks and over large areas in late winter and might never be noticed. Three observations suggest that die-offs are likely to have occurred in the early 90s and may have contributed significantly to increased natural mortality in the recruited segment of the population in the Gulf of St. Lawrence. First, there has been a decline in the spring condition factor, as discussed above. Second, a fraction of the population exhibited condition factors associated with deaths in laboratory experiments. Third, a fraction of the population exhibited low condition factors as late as in late August when fish are expected to have built up large energy reserves in preparation for winter.

The extent of energy depletion in the spring and early summer period (1993-1995) was examined in Northern Gulf cod by comparing several indices of condition in wild fish and in fish that either survived or did not survive to a prolonged period of starvation in laboratory experiments (Dutil and Lambert, 2000). Discriminant analyses classified only a small fraction of the wild fish as similar to cod that did not survive (0.4%) and a much larger proportion as similar to cod that were starved but survived (38.2%). This percentage increased from April to June and peaked in June 1993 (52.7%) and 1994 (65.5%). The low percentage of wild fish classified as similar to cod that died in the laboratory experiments is a direct evidence that condition was low enough to directly result in mortalities in the early 90s. This is not an estimate of the proportion of fish that died from energy exhaustion for two reasons : 1- dead fish cannot be sampled due to predation and scavenging; 2- mortalities may occur at higher condition factor values in the wild.

The small fraction of cod which classified as deceased-like in the spring period (0.4%) had extremely low chances to recover and survive. The large fraction of cod which classified as starved (38.2%) may have recovered. Some of them did not perform very well however : when Northern Gulf cod collapsed, individuals in poor condition were also found in the fall and a fraction of the sampled population was considered as unable to survive a prolonged period of food privation (Dutil and Lambert, 2000). Slow growth rates, even in the summer period in the Gulf of St. Lawrence, may have contributed to that situation (Guderley et al., 1996). Muscle lactate dehydrogenase activity provided a distinct measure of metabolic condition and suggested that cod had experienced a prolonged period of negative growth early in 1993, 1994 and 1995 in the northern Gulf (Dutil and Lambert, 2000). This is consistent with Schwalme and Chouinard's (Schwalme and Chouinard, 1999) finding, based on stomach contents analyses, that food privation in Southern Gulf cod lasts for at least five months (late November to early May). This is not meant to say that no feeding takes place during winter and early-spring : rates of energy loss were less in the wild on average than expected in food-deprived cod at two temperatures (2 and 6 ºC) (Dutil et al., xxxx). One potential interpretation could be that the annual cycle in condition is a normal event but that cod in the wild may feed just to maintain themselves if energy reserves become dangerously low. This may be met with various degrees of success depending on years and individuals.

Natural mortality from poor condition was assessed for the northern Gulf stock only, but low condition factor values reported for other stocks indicate that a similar situation prevailed elsewhere (Schwalme and Chouinard, 1999; Lilly, 2001).

Metabolism

Low values of the condition factor are problematic because they may reflect a lack of energy to carry out vital processes, but several publications have shown that low condition factors are associated with lower metabolic capacities. Measures of condition factor rest on the postulate that changes in the weight of the fish relative to its length reflect changes in energy content. Metabolic demands and food availability change relative to one another and explain variations in storage and utilization of macromolecules, particularly proteins and lipids. These molecules are needed to fuel metabolic processes such as maintenance, swimming activity, somatic growth and reproduction. The condition factor responds to changes in protein and lipid contents and adequately describes the level of energy reserves in individual fish (Lambert and Dutil, 1997b). Poor condition is also associated with other problems in cod. Several studies have shown that as condition factor decreases, enzyme systems of major tissues are depressed. In many cases, only correlations were shown, but more recently causal relationships were established between growth for instance and enzyme activities suggesting that enzymatic capacities needed to be restored following food deprivation before growth capacities are fully restored. The following references provide some examples in cod: Bélanger et al. (2003), Couture et al. (1998), Dutil et al. (1998a), Lemieux et al. (1999), and Martinez et al. (2003).

Swimming

The mobilization of energy reserves in the muscle during starvation might impair sprint and endurance swimming in cod, and low and declining condition factors in poorly productive stocks may have contributed to their low productivity through a reduction of their capacity to outswim preys and predators. Their capacity to escape fishing gears may have changed leading to a biased estimate of abundance.

Catchability is estimated for each age-group and each index used in the assessment and therefore is adjusted for differences in gear selectivity (e.g. trawl vs longline) and seasonal variations in fish characteristics which vary seasonnally (e.g. size at age). The assumption is made however that catchability does not vary from year to year for a given index. For research surveys, when vessel and gear characteristics are modified, the index is recalibrated to meet the assumption. Catchability however may vary from year to year and this, apparently, is not taken into consideration when determining numbers at age. For instance, if size at age 5 has decreased steadily over time, catchability at age 5 in a trawl would have increased. The figure used to determine the abundance of 5 year olds is an average value that would tend to underestimate (in the current year) the abundance of 5 year old fish in years when they were large and overestimate their abundance in the current year if their length at age is below average.

Poorly productive stocks have experienced declining sizes at age over time. They have also exhibited variations in condition and may have been exposed to colder temperatures. These factors may all have increased catchability over time in poorly productive stocks leading to a biased estimate of abundance. Size and temperature effects on swimming capacity are already well documented in the litterature. Condition effects were not and experiments were conducted to assess how condition might have an effect on sprint and endurance swimming in cod. During starvation, cod mobilize energy reserves from different tissues including muscle. White muscle, which is required for sprint swimming, is used preferentially, whereas red muscle, which is required for aerobic swimming, is spared (Black and Love, 1986; Martínez et al., 2003). Cod in good condition were able to swim over longer periods of time than cod in poor condition. Decreased endurance in poor condition fish was ascribed to their incapacity to make kick-glide movements as a result of muscle atrophy (Martínez et al., 2003). The picture was not as clear with sprint swimming. Sprint swimming speeds increased with feeding, but decreased little when the same individuals were food-deprived (Martínez et al., 2002). Food-deprivation during longer periods however decreased sprint swimming capacity.

Growth

Cod have an innate capacity for catch up growth in response to periods of food shortages, but catch up growth is impaired when critically low levels of condition are reached such as in least productive stocks, particularly if food availability varies in space and time during summer and if the growth season is short, a likely feature of least productive stocks.

Following periods of weight loss due to food shortages, refed fish experience a period of fast growth which may compensate for negative growth periods. The increased relative mass of the pyloric caeca and intestine relative to body mass following food deprivation suggests that growth compensation is associated with an increased capacity of cod to produce digestive enzymes and to absorb nutrients across the gut wall (Bélanger et al., ; Lemieux et al., 1999). Prolonged starvation however was hypothesized to have a detrimental effect on the growth capacity of fish with sub-lethal condition factor values (Dutil et al., 2001). Cod were food-deprived so as to achieve a range of condition factors. Size was measured before refeeding and after 3, 6, 9 and 12 weeks of *ad libitum* feeding. Maximum growth occurred in the first 3 weeks in controls and declined after 6 weeks with very slow growth being observed in the last 3 weeks of the experiment. In contrast, cod with low condition factors experienced very slow growth in the first 3 weeks and maximum growth after 6 and 9 weeks of feeding. Overall, weight gains over a period of 12 weeks were nearly identical in all groups so that fish with lower initial condition factors ended the experiment with lower energy reserves. The duration of the feeding experiment (12 weeks) was representative of the duration of the feeding period in the northern Gulf of St. Lawrence in 1994, when condition factors were minimal in June and peaked in late-August (Lambert and Dutil, 1997b). These fish would thus be at a greater risk of mortality over winter (Dutil and Lambert, 2000). Furthermore, fish in the laboratory experiment were fed to satiation 3 times a week. In situations where food is limited or distributed unevenly in time and space, fish in poor condition may not recover to the point where catch up growth takes place. The first few weeks after spawning in the spring and early summer period would thus appear to be critical to the survival of adult cod that have strong seasonal cycles in condition. This experiment supports the field observations of condition vs size at age as discussed above (Dutil et al., 1999). Such a situation is indicative of limited growth capacity in poorly productive stocks, a situation which is not likely to occur in more productive cod stocks.

Reproduction

Individual fecundity was low in the northern Gulf of St. Lawrence in the 90’s (Figure 10)(Lambert and Dutil, 1997b; Lambert and Dutil, 2000). The condition factor of cod decreased in the early 90’s with lowest values being observed between 1992 and 1994 (Lambert and Dutil, 1997a). The mean value for the condition factor of pre-spawning females in 1994 was 0.71. Based on laboratory experiments, these pre-spawning females should have expended a large proportion of their energy reserves and ended reproduction with condition factors between 0.5 and 0.6; levels where risks of mortality increase rapidly (Dutil and Lambert, 2000). The higher condition factors observed for pre-spawning females in 1998 than in 1995 were associated with higher potential fecundities in 1998 (Lambert et al., 2000). The potential fecundity of female cod in the northern Gulf of St. Lawrence in 1995 was comparable to the realized fecundity observed in the laboratory for female cod with poor post-spawning condition factors. Comparisons between these estimates of potential fecundity and those for other stocks have to be treated cautiously. Different size ranges were used to calculate fecundity-length relationships. Female size in the northern Gulf of St. Lawrence varied between 37 and 58 cm compared to minimum sizes above 50 and even 60 cm in other studies (Buzeta and Waiwood, 1982; Pinhorn, 1984; Marteinsdottir and Begg, 2002). The actual fecundity of wild cod may even have been lower since oocytes may be resorbed in cod in poor condition (Kjesbu et al., 1991). Actual fecundity of cod deprived of food during spawning was between 20 and 80% of the potential fecundity depending on the nutritional status of the fish (Kjesbu et al., 1991). These observations suggest that egg production by cod in the northern Gulf of St. Lawrence in 1995 was low compared to the potential fecundity of females in good condition, based on laboratory experiments. The situation could have been even worse in 1994 when female condition was significantly lower. Female commitment to reproduction in the northern Gulf of St. Lawrence in the 90's indicates that when lower energy reserves are available, higher somatic costs and increased risks of mortality are expected in cod. Energy investment in reproduction at a small size could also have negatively affected the future growth of the fish as there were indications that immature cod were in better condition than spent fish (Lambert and Dutil, 2000).

Stock fecundity was lower in the 90's than in earlier times. Spawning condition was significantly related to fish size in Northern Gulf cod (Ouellet et al., 1997). A negative relationship between the proportion of maturing females per length-class and length indicated that more females in the smallest length-classes were still in the maturation process at the time of sampling in the spring of 1994 and 1995. Consequently, in both years, a higher proportion of females in the smallest length-classes had not yet begun to spawn. A reduction in the size at maturity was also observed during that period. The mean length at maturity varied between 34 cm and 42 cm in 1994 and 1995 (Ouellet et al., 1997) compared to historical values between 46 cm and 50 cm (Wiles and May, 1968; Minet, 1977). Theses changes in the timing of spawning and size structure of the spawning fish undoubtedly affected the egg production of Northern Gulf cod. Available data on proportions of fish at age, sizes at age, maturity ogives, condition factors and fecundity give indications of important variations in the total egg production of Northern Gulf cod. On a relative basis, egg production between 1984 and 1988 was twice as high as egg production in the period between 1992 and 1994 (Lambert et al., 2000). Considering that spawning stock biomass between 1992 and 1994 was estimated to correspond to only 10% of the level observed between 1983 and 1986 (Fréchet and Schwab, 1998), egg production of the Northern Gulf cod during the 1992 to 1994 period may have represented only 5% of egg production for the period between 1983 and 1986.

The fewer eggs produced had low chances of hatching due to the presence of the CIL. In the northern Gulf of St. Lawrence, a high proportion of cod eggs were located in the mid-water column at very low water temperatures (Ouellet, 1997). The low hatching success observed for eggs incubated at 0°C in the laboratory would suggest that only ca. 2 to 5% of all eggs found in the cold intermediate layer (CIL) in the spring of 1993 and 1994 (Ouellet et al., 1997) would have hatched normally. Moreover, in the laboratory experiments, the few larvae that hatched at 0°C were small and often abnormal, indicating that survival rates for cod eggs located in the CIL would be very low (Ouellet et al., 2001). The CIL is a permanent feature of the Gulf and little is known as to the relative proportions of the eggs released above and below the CIL.

5. Fishing pressure has not been relaxed sufficiently to offset increased predation pressures and decreased productivity associated with poor or deteriorating environmental conditions

Between 1986 and 1993, i.e. before the moratorium was imposed, fishing mortality per capita was more or less constant (except for high values in 1992 and 1993), but surplus production per unit biomass was below average, possibly as a result of increasing natural mortality (Figure 11). The reference level ($F_{0.1}$) was not reduced to take into account lower surplus production after 1985.

Since the moratorium was imposed in 1994, surplus production per unit biomass has been above average in 1996 and 1998, but it has been below average for that stock in 1995 and has remained below average from 1997 to 2000. Meanwhile, fishing mortality per capita increased from 1997 to 2000. While fishing mortality per capita was still below average compared to historical times, it exceeded surplus production in 1997, 1999 and 2000. The stock could not have rebuilt under such conditions (Myers et al., 1997).

6. Compounding effects of poor growth and condition on removals associated to a constant TAC

The impact of lower growth rates and condition factors on the number of fish required to make up a TAC was assessed for Northern Gulf cod. For a hypothetical TAC of 50,000 tons, 29 million cod had to be landed in 1975; 46 million had to be landed in 1993 (just prior to the moratorium), and 27 million had to be landed in 2002. This was calculated based on the age distribution and mean weights at age in the catch in each year. Half of the increase from 1975 to 1993 was explained by smaller size at age in 1993 (32%) and the other half (26%) by lower condition in 1993. In 2002, 27 million cod had to be landed, a figure very similar to 1975. But in fact, older fish and thus larger fish made up the catch in 2002. If the different age groups had been caught in similar proportions in 1975 and 2002 as in 1993, then the outcome of such a calculation would be : 34 million fish for 1975 and 2002, and 46 million in 1993. This is consistent with a high condition factor and above average weights at age in 2002. Projections done to derive TAC's typically use recent average weights at age from the commercial fishery while changes in condition are not implicitly used. Here we show that condition may have a compounding effect on projections.

This hypothesis relative to other hypotheses : strengths and weaknesses

The low productivity hypothesis is consistent with the slow increase in biomass observed during the moratorium and the decline observed when the fisheries were reopened. It is also consistent with the increased predation hypothesis.

Predation by seals would have similar effects as fishing mortality : constant mortality in a situation of declining productivity or increased mortality in a situation of low productivity would have similar negative effects whether due to natural or man-made causes. Furthermore, it is not inconsistent with the lack of response of individual cod to decreased intra-specific competition. Finally, it is not inconsistent with the overfishing hypothesis. When productivity declined, the stocks were experiencing high fishing mortality which quickly reduced the abundance of the stocks. Despite the large reduction in fishing effort, productivity declined to such low levels that even low exploitation rates were unsustainable.

The reasons for the collapse and lack of recovery of depleted stocks during and after the moratorium are complex and no single factor can explain all observations. The present hypothesis offers a general background for understanding why different stocks respond differently. We need to be aware of all these aspects to provide realistic means and time-lines for rebuilding our stocks. Some key issues would require more information. For instance, comparative studies between highly and poorly productive stocks are required : information on seasonal cycles of condition in highly productive stocks is lacking, and relative effects of fishing mortality, size selective fishing and stock productivity should be compared across stocks. Furthermore, the impact of poor condition on subsequent growth and survival needs to be better understood.

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Table 1. Growth per capita (Gs, g/fish) and surplus production per capita (TSPc, g/fish) and stock biomass (TSPb, g/kg) for cod grouped into four clusters. S. Gulf of St. Lawrence SG, N. Gulf of St. Lawrence NG, Northern Grand Banks NC, Eastern Scotian Shelf ES, East Baltic EB, Northeast Arctic NA, West Baltic WB, Iceland IC, Western Scotian Shelf BF, Faroe Plateau FP, Georges Bank GB, West Scotland WS, Irish Sea IS, North Sea NS, Celtic Sea CS.

	Cluster number and list of stocks in each cluster			
	1 CS IS WS	2 BF FP GB IC	3 EB NS WB	4 ES NA NC NG SG
Gs	1386	847	457	386
TSPc	806	609	296	194
TSPb	442	278	340	190

Table 2. Estimation of the biomass and number of cod present in each class of dissolved oxygen and on the average growth production relative to growth in normoxia (from Chabot and Couturier, 2002).

Dissolved oxygen (%)	Cod biomass (kg)	Cod biomass (% of total)	Cod number	Cod number (% of total)	Production growth (% relative to normoxia)	Growth x cod number
Sentinel fishery, July-August 1995						
<30	346731	1.05	344008	0.76	3.3	1135295
30-40	2389431	7.21	3164556	7.01	29.9	94580430
40-50	3590185	10.83	5375367	11.91	49.7	267401340
50-60	3569794	10.77	4960555	10.99	65.6	325423369
60-70	4801864	14.49	6581443	14.59	78.8	518633656
>70	18444115	55.65	24692663	54.73	100.0	2469266269
Total	33142120	100.00	45118592	100.00		3676440359
					Average growth relative to normoxia (%)	81
					Decrease in growth due to hypoxia (%)	19
A. Needler August-September 1995						
<30	30927	0.26	29063	0.21	3.3	95914
30-40	710049	5.94	783729	5.61	29.9	23423631
40-50	1212497	10.15	1350228	9.66	49.7	67168030
50-60	1276650	10.69	1497134	10.71	65.6	98215309
60-70	2400859	20.10	2794650	19.99	78.8	220225207
>70	6316553	52.87	7523001	53.82	100.0	752300070
Total	11947535	100.00	13977805	100.00		1161428160
					Average growth relative to normoxia (%)	83.1
					Decrease in growth due to hypoxia (%)	16.9
Sentinel Fishery, October 1995						
<30	139384	0.48	171586	0.35	3.3	566266
30-40	625152	2.16	775852	1.56	29.9	23188220
40-50	2069680	7.16	2612753	5.27	49.7	129973207
50-60	2695704	9.32	3124703	6.30	65.6	204987421
60-70	4693170	16.23	5654529	11.40	78.8	445590593
>70	18702456	64.66	37248043	75.12	100.0	3724804263
Total	28925546	100.00	49587465	100.00		4529109970
					Average growth relative to normoxia (%)	91.3
					Decrease in growth due to hypoxia (%)	8.7

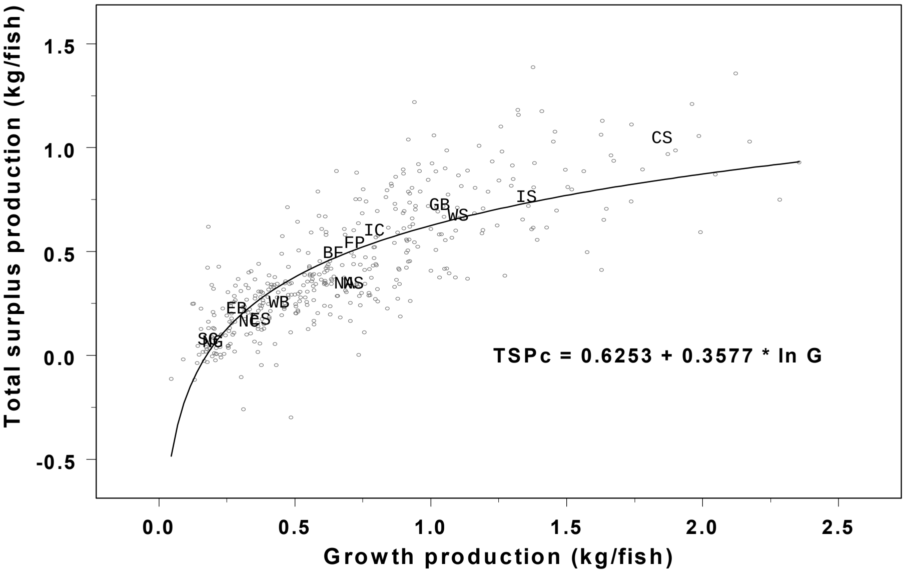

Figure 1. Total surplus production per capita (log10 fit) and growth production for 15 cod stocks in the North Atlantic and adjacent areas. The codes are defined in Table 1.

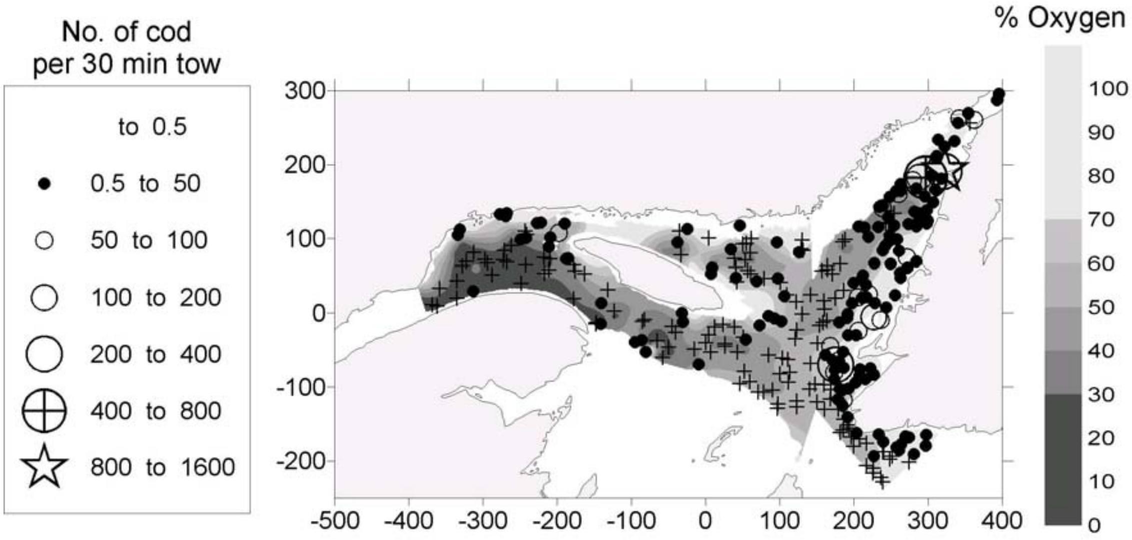

Figure 2. Number of cod caught in each 30 min tow during the Sentinel Fishery survey no. 3 carried out between 25 Jul 1995 and 15 Aug 1995, in relation to bottom level of dissolved oxygen. Coordinates are in km relative to 49°N and 69°W (from Chabot and Couturier, 2002).

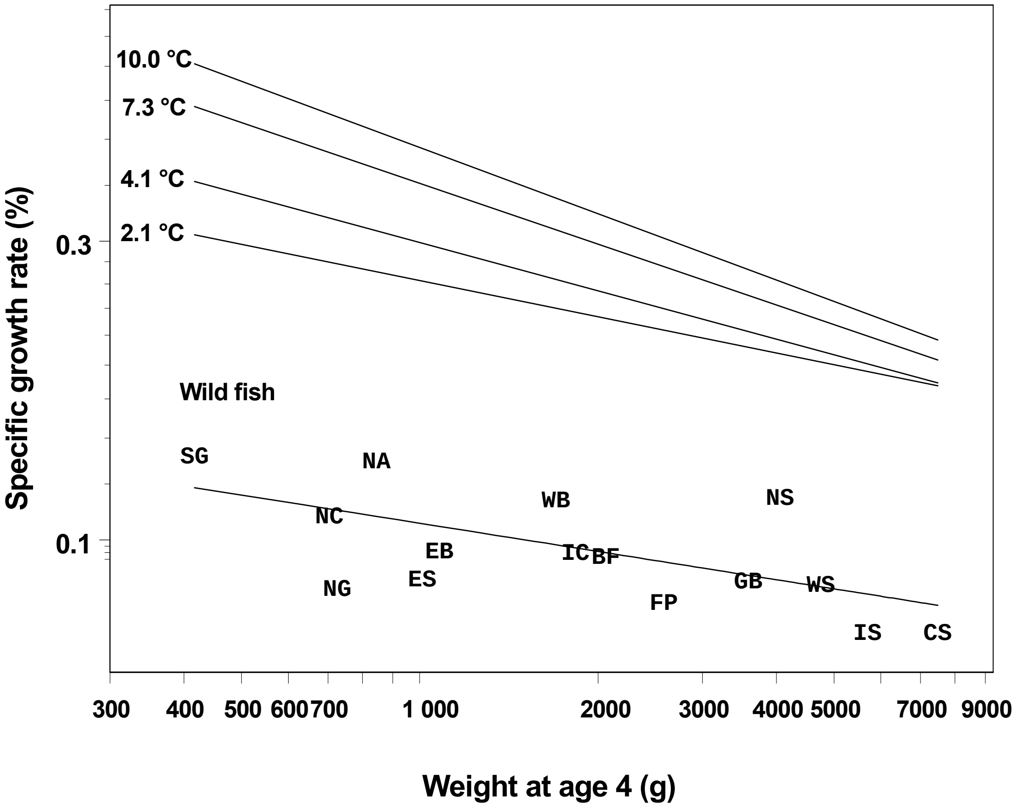

Figure 3. Specific daily growth rate (%) from age 4 to age 5, based on size in the catch, for 15 cod stocks in the North Atlantic and adjacent areas as a function of mean size at age 4 in the catch. The data for the stocks are compared to the food-unlimited growth rate of cod at 4 temperatures, as in Bjornsson and Steinarsson (2002).

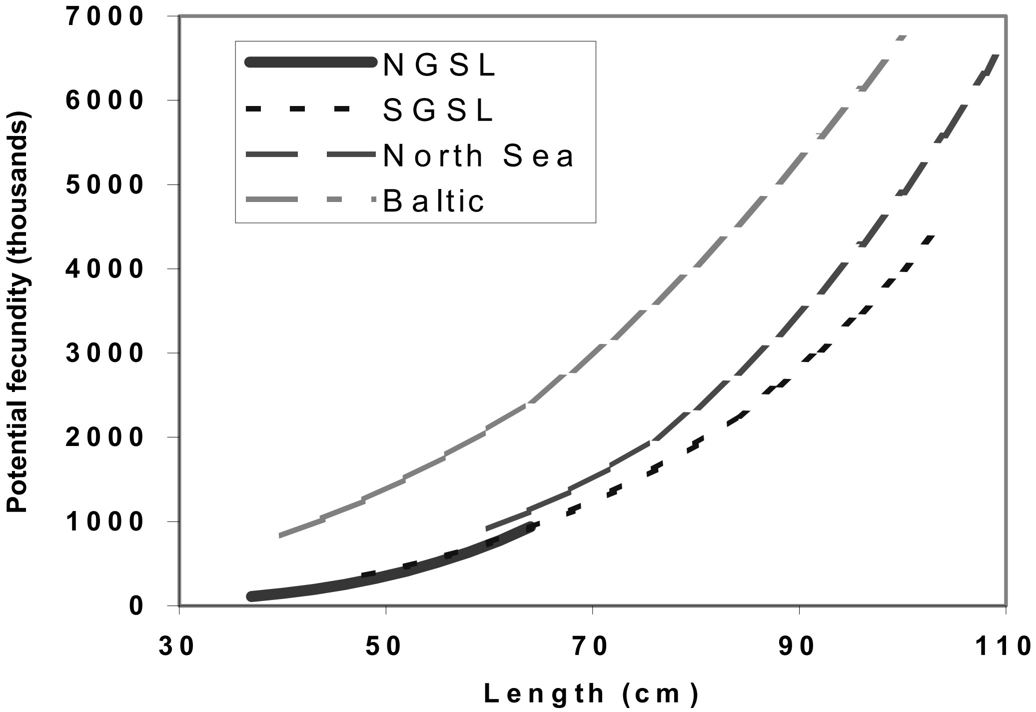

Figure 4. Relationships between potential fecundity and length for cod from different areas of the Gulf of St. Lawrence (NGSL and SGSL), the North Sea and the Baltic. Data from Lambert and Dutil (2000) for the northern Gulf of St. Lawrence (NGSL), Buzeta and Waiwood (1982) for the southern Gulf of St. Lawrence (SGSL), Oosthuzien and Daan (1974) for the North Sea and Kraus et al. (2000) for the Baltic.

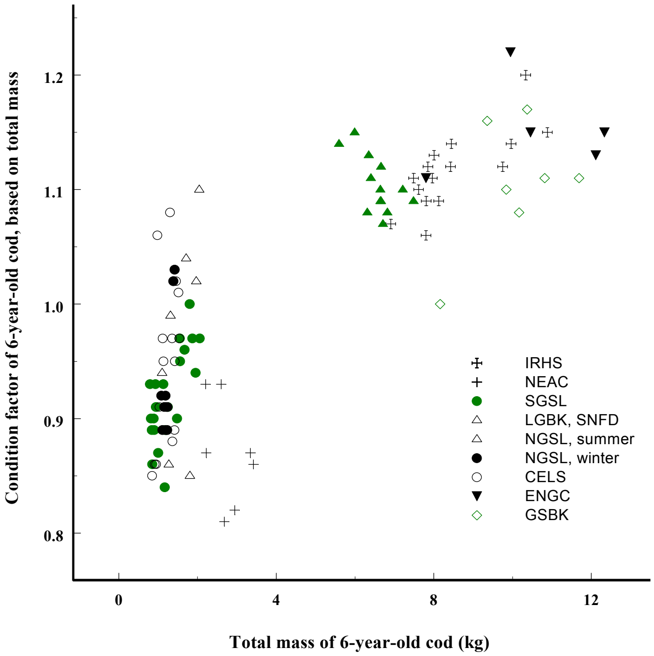

Figure 5. Condition factor and corresponding weight of 6 year old cod. Refer to figure 9 in Dutil et al. (Dutil et al., 1999).

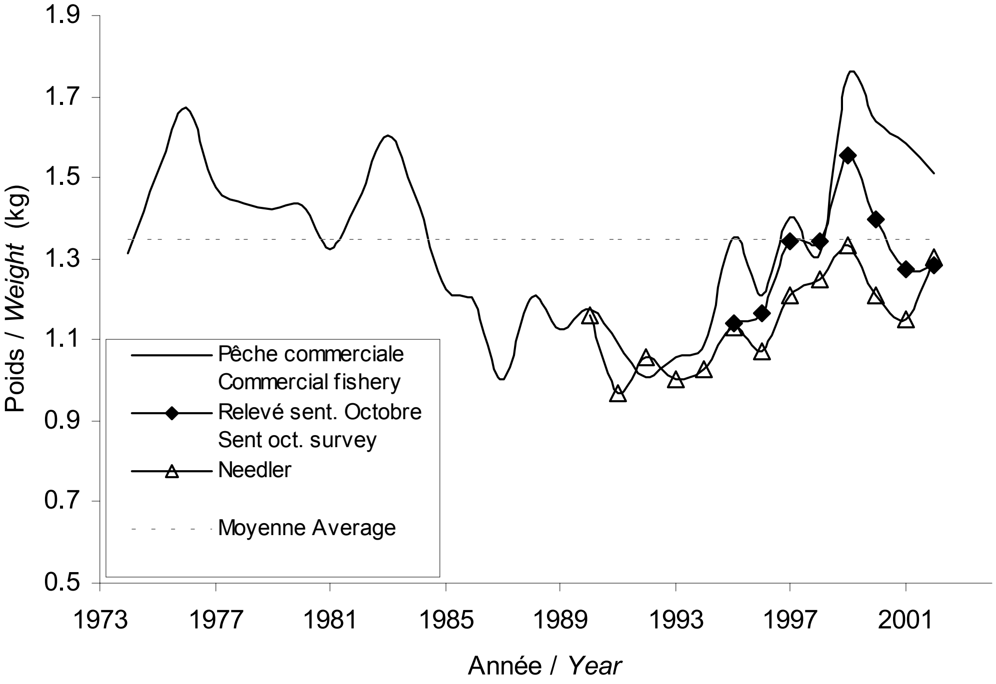

Figure 6. Weight of cod at age 6 in the northern Gulf of St. Lawrence, based on different surveys. The long-term average for the commercial fishery is also shown.

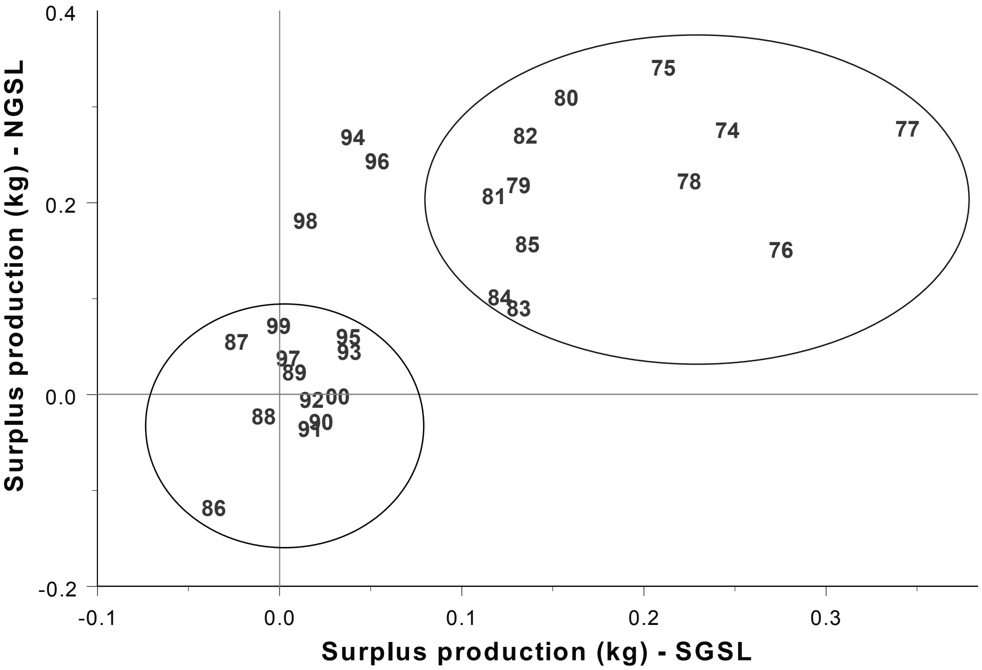

Figure 7. Per capita surplus production of cod in the northern and southern Gulf of St. Lawrence.

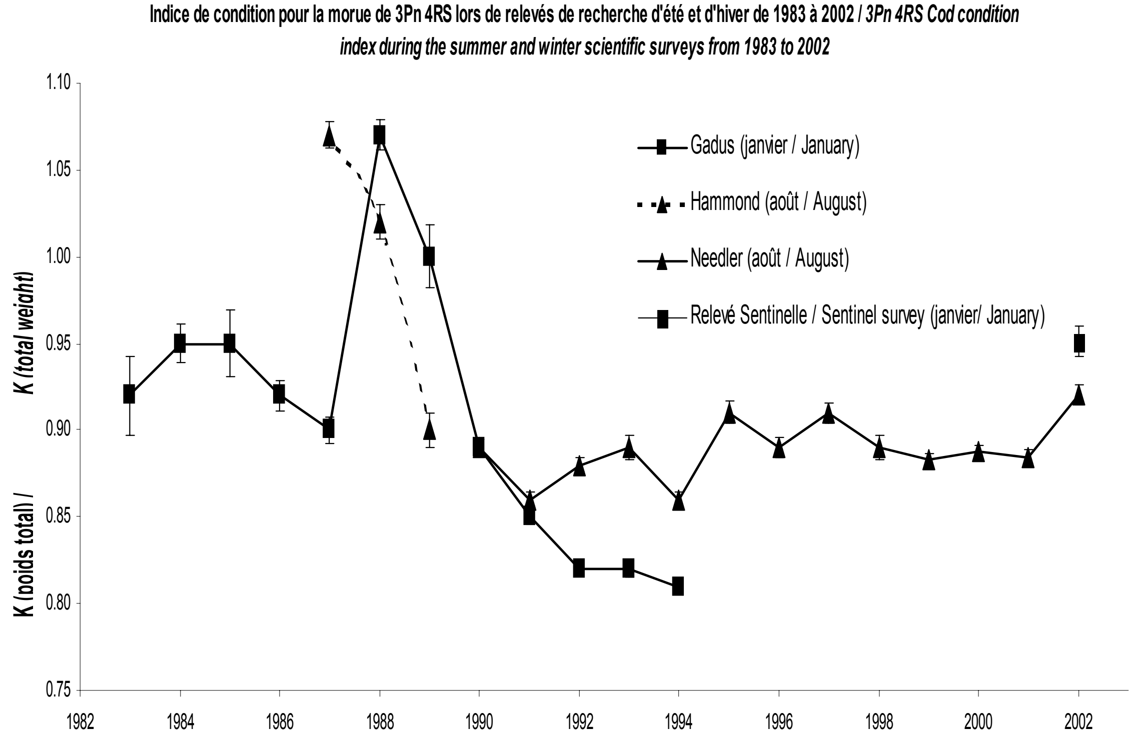

Figure 8. Condition factor of cod in the northern Gulf of St. Lawrence based on total weight (mean and standard error) for cod ranging in length from 30 to 55 cm, from 1983 to 2002. Length effects were checked for the Needler series : year effect was significant ($F_{8,3227}$= 13.37, P < 0.001), but not length as a covariate ($F_{1,3227}$= 1.40, P = 0.24) nor the year-length interaction ($F_{8,3219}$= 0.88, P = 0.54).

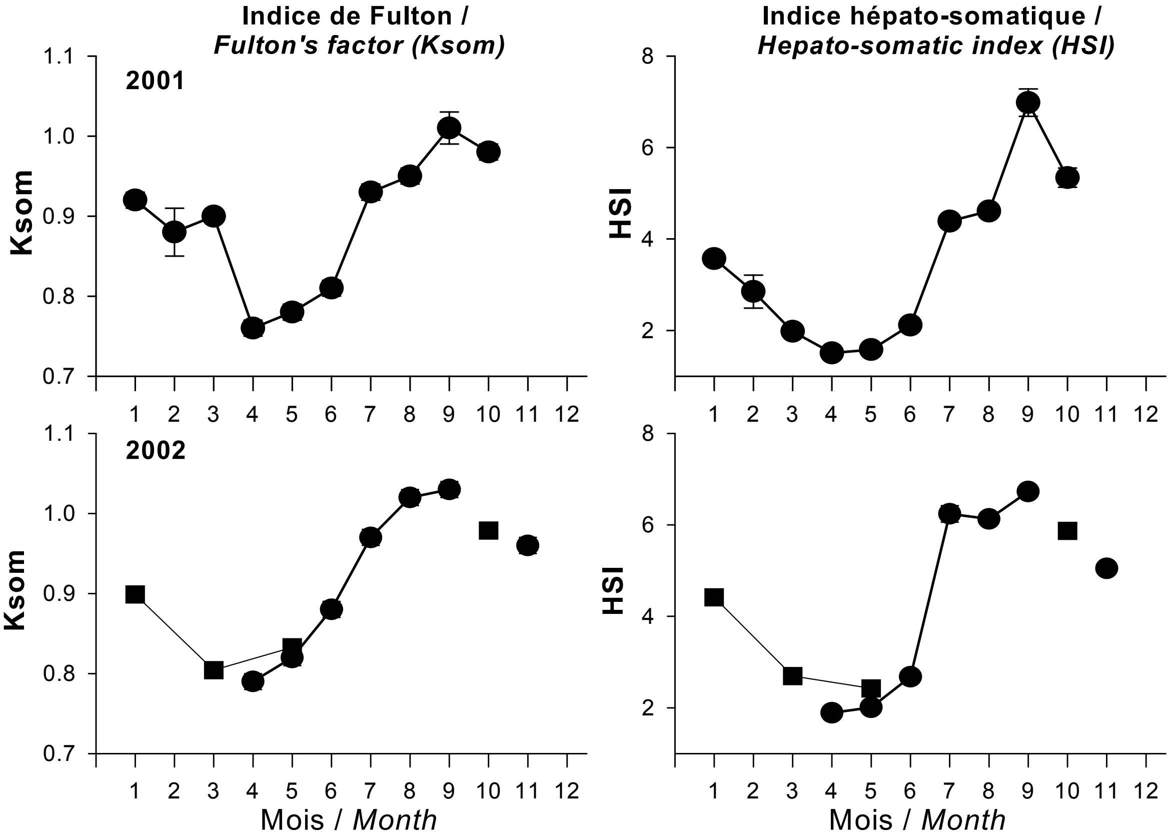

Figure 9. Seasonal changes in the somatic condition factor and liver-somatic index of cod in fixed gears (□) and mobile gears for 2001 and 2002.

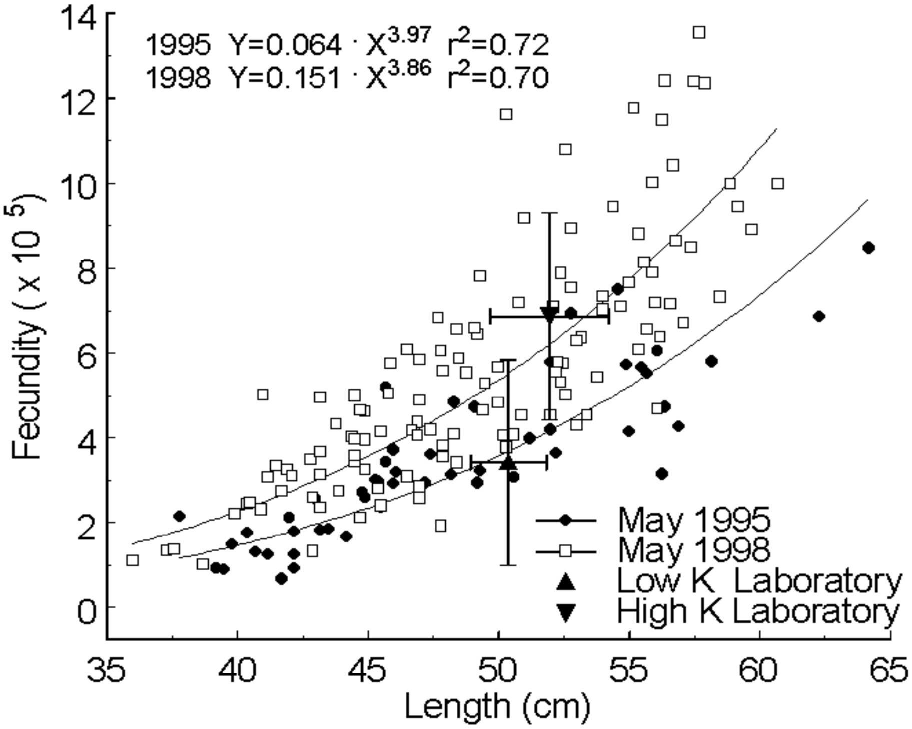

Figure 10. Relationship between potential fecundity and length for female Northern Gulf cod and realized fecundity at length for female cod with low (Low K) and high (High K) condition factors in the laboratory. Post-spawning condition factor varied between 0.51 and 0.64 for females with low K, and between 0.69 and 0.92 for females with high K. For each group (Low and High K), mean fecundity and length with standard deviations are presented. The figure is taken from Lambert at al. (Lambert and Dutil, 2000).

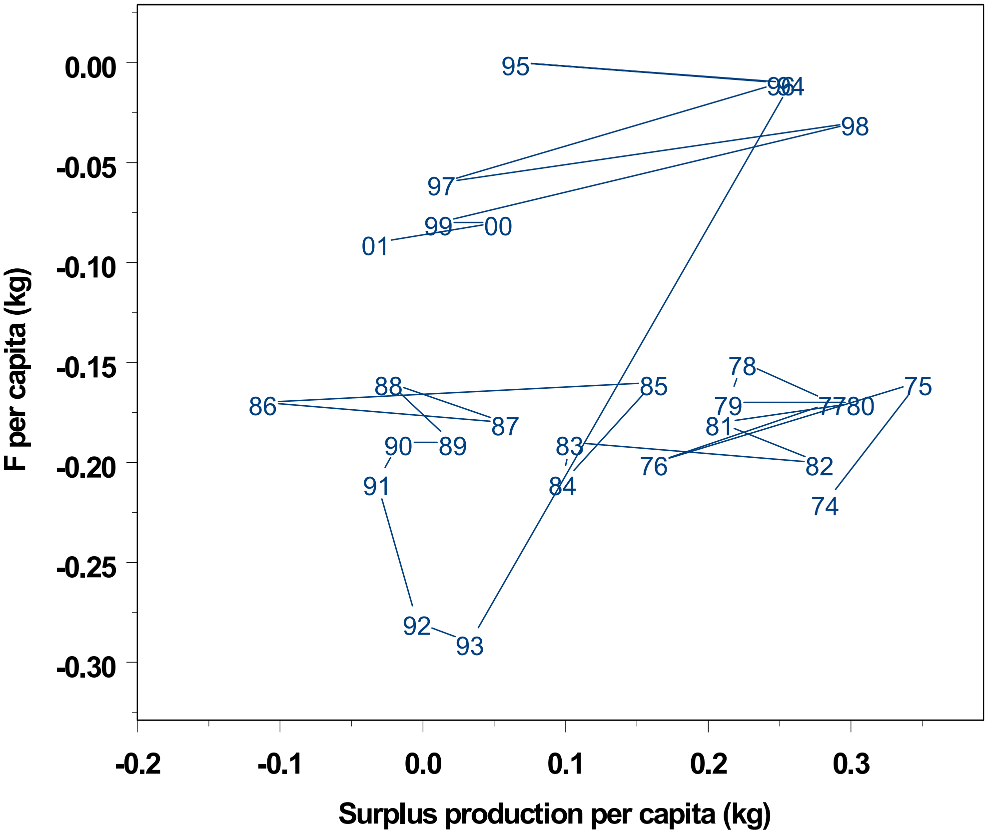

Figure 11. Yield to fishery and surplus production in Northern Gulf cod.