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Report of the ICES/GLOBEC Workshop on the Dynamics of Growth in Cod

Including CD-Rom from ICES ASC 2001

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1 Overview

1.1 Introduction

Growth rate varies widely among cod stocks. Large changes in growth rate have also been observed within many cod stocks and have important consequences for the productivity of these stocks. Variation in growth rate may reflect effects of temperature change, density dependence (i.e., changes in per capita prey availability due to variation in prey or cod abundance), changes in maturation schedules, changes in size-selective fishing mortality, changes in activity of the fish or adaptive (genetic) change. An understanding of the causes of variation in growth rate among and within cod stocks may lead to improved forecasts of stock biomass and productivity, and is required to assess the likely impacts of climate change on cod populations. The ICES/GLOBEC Working Group on Cod and Climate Change held a Workshop on the Dynamics of Growth in Cod in May 2000, with the aim of exploring the causes of growth variability and developing a single growth model for cod that will allow interpretation of information from all parts the geographic range of cod.

As a follow-up to the Workshop, a Theme Session was held at the ICES Annual Science Conference in Oslo in September 2001 on Growth and Condition in Gadoid Stocks and Implications for Sustainable Management. Thirty papers were presented and are included in this Cooperative Research Report as a CD-Rom containing abstracts, extended abstracts or full papers.

Terms of Reference and Justification

Council Resolution 2C12 (C.Res. 1999/2C12) gives the Terms of Reference for the Workshop:

A Workshop on the Dynamics of Growth in Cod [WKDGC] (Co-Chairs: N. Andersen, Denmark, G. Ottersen, Norway, and D. Swain, Canada) will be held in Dartmouth, Nova Scotia, Canada from 8–10 May 2000 to:

a) develop models of growth in order to improve the quality of stock forecasting;

b) describe major sources of uncertainty in the prediction of growth rates and advise on further studies to reduce this uncertainty;

c) assess the contribution of growth rate variability to the observed variability in stock biomass and stock forecasts;

d) recommend standard methods for comparing growth rates;

e) develop specific case studies which will be relevant to the advice of ICES.

WKDGC will report to the Oceanography Committee at the 2000 Annual Science Conference, and to ACFM at its November 2000 meeting.

Justification:

Recent widespread changes in growth rates for many cod stocks have considerable consequences for stock biomass estimation and forecasting. A number of studies have related growth changes to temperature, food availability (per capita), maturation and other factors. These are in turn a consequence of shifts in the distribution and abundance of cod and their prey and possibly also of selection due to fishing. As part of the eventual aim to synthesise our knowledge of cod, a single growth model that attempted to bring together and interpret our information on cod growth from all parts of the range would be a valuable component.

Procedures for estimating ambient temperature have improved recently, with the development of data storage tags, isotopic analysis of otoliths and more sophisticated interpretation of the seasonal distribution of fish in relation to temperature fields.

1.2 Preparations for the workshop

1.2.1 Topics

A list of topics was developed by the co-convenors and the ICES/GLOBEC co-ordinator in order to address the terms of reference:

- Factors explaining interannual variation in growth within cod stocks.
- Single growth model covering all stocks.
- Estimation of "ambient" temperature.
- Effects of size-selective fishing mortality and back-calculation studies.
- Effects of variation in growth on stock biomass.
- Environmental and density-dependent influence on growth during the early pelagic life stages and the consequences of this on later abundance and size.
- Bioenergetic models.
- Genetic variation of growth.

21 Working Documents (WD) were prepared by participants to the Workshop and also by some contributors who were not able to attend. These are listed by topic, in Appendix 4 and are included here as abstracts, extended abstracts or full papers.

Electronic Bulletin Board

The aim with the Workshop was to make WDs available to participants before the meeting and to begin the discussion on the topics before the meeting, so that it could quickly be summarised and applied to the Terms of Reference during the meeting. For this purpose an electronic bulletin board was set up on the ICES website (http://www.ices.dk/globec/workshops-/growth/wkgrowth1.htm). The Terms of Reference, topics to be addressed, data and graphs on size-at-age and abundance were posted on the site for 16 stocks from the Northeast and Northwest Atlantic, and were available for downloading for Workshop analyses. Working papers or abstracts for Workshop presentations were posted in advance of the Workshop and a Discussion Board was set up. At the start of the Workshop, the Discussion Board was structured as follows:

TOPIC 1 - Factors explaining interannual variability - **Doug Swain**
  - Tests of effects of abundance and temperature on growth of southern Gulf of St. Lawrence cod - **Doug Swain**

TOPIC 2 - Single growth model for all stocks - **Keith Brander**
  - Growth potential of cod fed on maximum rations: effects of temperature and size - **Bjørn Bjørnsson**
  - Maturity and growth - **Keith Brander**

TOPIC 3 - Estimating “ambient” temperature - **Geir Ottersen**
  - Ambient winter and annual temperatures of Arcto-Norwegian cod - **Geir Ottersen**
  - Ambient temperature and spatial distribution of Arcto-Norwegian cod - **Geir Ottersen**
  - Seasonal changes in temperature associations and feeding rates of cod - **Doug Swain**
  - Density-dependent temperature selection in southern Gulf of St. Lawrence cod - **Doug Swain**

TOPIC 4 - Size selective fishing and back-calculation - **Martin Castonguay**

TOPIC 5 - Effects of variation in growth on stock biomass –**Keith Brander**
  - Feedback from Working Groups - **Keith Brander**

TOPIC 6 - Environment and density- dependent influence during early pelagic life and consequences of this on later size and abundance - **Geir Ottersen**
  - Developmental Ecology of Marine Animals - **Keith Brander**
  - Early growth of Arcto-Norwegian cod - **Geir Ottersen**
  - Comparison with other cod stocks - **Keith Brander**
  - Is size determined during early life? – **Keith Brander**
  - Re: Is size determined during early life? - **Geir Ottersen and Tara Marshall**
  - Re: Is size determined during early life? - **Geir Ottersen**
  - Re: Is size determined during early life? - **Doug Swain**
  - Re: Re: Is size determined during early life? - **Keith Brander**
  - Re: Re: Is size determined during early life? - **Doug Swain**

TOPIC 7 - Bioenergetic models - **Niels Andersen**
  - How may bioenergetics contribute to our understanding of the growth variations of cod? - **Niels Andersen**
  - Food for thought - **Niels Andersen**

TOPIC 8 - Genetic variation of growth - **Joe Brown**

MATTERS ARISING - **Keith Brander**
  - Correspondence with Bjorn Bjornsson about wild vs pen-reared cod; food limitation; liver condition; common formats for growth rates - **Bjørn Bjørnsson**

1.2.2 Workshop structure and working procedures

The agenda for the Workshop is given in Appendix 2 and the participants are listed in Appendix 1. The Workshop was divided into three sections. On the first day, individual presentations were made by the participants. These were grouped by topic, each with an introduction and followed by a general discussion on the presentations for that topic. On the second day, the participants broke into working groups based on the topics. Discussion was aimed at synthesizing the information on each topic and developing conclusions and recommendations related to the terms of reference. Working group reports were made in plenary. On the third day, working groups based on the terms of reference were formed. These developed conclusions and recommendations based on the Workshop presentations and the work of the working groups on the topics. In one case, additional analyses were conducted using the data posted at the Internet site. The Workshop wrapped up with a plenary session discussing the reports of the working groups on the terms of reference.

2 Factors explaining interannual variation in growth within cod stocks

Wide interannual variation in size-at-age occurs within many stocks of cod. For example, the mean weights of 6-year-old cod in the southern Gulf of St. Lawrence in the mid 1990s were about 45% of the mean weights in the late 1970s (Chouinard *et al.,* 1999). Similarly, the average weight of 5-year-old cod on the Faroe Bank in 1989 was 35% of the average weight in 1985 (Magnussen WD 1.4). An understanding of the factors associated with this variation within populations is required to develop predictive models of cod growth.

2.1 Possible sources of interannual variation in growth within stocks

2.1.1 Temperature

Since they are ectotherms, temperature is a key environmental factor for fish (Fry 1971), controlling the rates of physiological processes including growth (Brett 1979). On unlimited rations in laboratory studies, growth rate increases with temperature to a maximum at some optimum temperature (Brett 1979; Björnsson *et al.,* 2001). As ration decreases, the optimum temperature for growth decreases (Brett *et al.,* 1969; Elliott 1979; Woiwode and Adelman 1991). Thus, the effect of temperature on growth depends on ration level. Growth increases with temperature if rations are maximal, but may decrease with temperature at fixed submaximal rations, because of increasing metabolic demands at high temperatures (Krohn WD 7.2).

A number of studies have reported relationships between temperature and cod growth, both within and among stocks. For example, Brander (1995) found that much of the variation in growth among 17 North Atlantic cod stocks could be attributed to variation in temperature, with growth increasing at higher temperatures. Among these 17 stocks, weight of a 4-year-old cod increased by almost 30% for every 1ºC increase in temperature (Brander 1994). Dutil *et al.* (WD 1.5) reported that size-specific per-capita growth production increased with environmental temperature among several stocks. Similarly, Campana *et al.* (1995) found that spatial variation in length-at-age on the Scotian Shelf and the Magdalen Shallows closely matched variation in bottom temperatures. In North-east Arctic cod, mean individual growth rates and lengths-at-age were highest in year classes experiencing high ambient winter temperatures (Michalsen *et al.,* 1998; Ottersen *et al.,* WD 3.2).

Effects of temperature on growth can be direct or indirect. Direct effects involve changes in the rates of physiological processes associated with growth. Indirect effects include effects on ecosystem productivity, changes in the length of the feeding season, effects on the distribution of cod or their prey, etc. For example, size-at-age and per-capita growth production of cod in the northern Gulf of St. Lawrence tended to be small during a cold period from the mid 1980s to the mid 1990s (Dutil *et al.,* 1999; Dutil *et al.,* WD 1.5). However, there was no evidence that the ambient temperatures occupied by cod changed during the cold period (Castonguay *et al.,* 1999, WD 3.1). Instead, cod appeared to migrate from their feeding grounds to their over-wintering grounds earlier in the fall and shift their over-wintering distribution to deeper waters to remain within their preferred temperature range. Castonguay *et al.* (1999, WD 3.1) suggested that this earlier migration to the wintering grounds may have shortened the autumn feeding period and contributed to the decline in size-at-age.

A literature survey indicated that many cod stocks are apparently feeding well below their maximum consumption rates, and therefore do not appear to be physiologically limited by their temperature-dependent metabolic capacity, at least over much of the year (Krohn WD 7.2). Two bioenergetic studies indicated that growth rates in some stocks are well below the maximum growth rates expected given the temperatures that these stocks are assumed to occupy, suggesting that these stocks are food rather than temperature limited (Krohn *et al.,* 1997; Dutil *et al.,* 1999). These results suggest that the positive relationships between growth and temperature reported within and among stocks may be indirect, due possibly to higher food availability (and/or accessibility) in warmer waters (Krohn WD 7.2). For example, length of the feeding season appears to vary widely among stocks, with some warm water stocks feeding year round and some coldwater stocks (e.g., the Gulf of St. Lawrence stocks) fasting over the winter. These differences in the seasonality of feeding presumably contribute to the differences in growth rate among stocks. They also need to be taken into account in bioenergetic calculations of expected maximum annual growth rates.

Tests for effects of variation in temperature on growth of cod in the wild require accurate estimates of temperature conditions. Direct effects of temperature depend on the actual temperatures occupied by cod ('ambient' or 'cod-weighted' temperatures). Indirect effects may be related to indices of general environmental conditions (e.g., average bottom temperatures in a survey, temperatures at a fixed monitoring site or along a monitoring transect; i.e., temperatures unweighted by cod distribution). Obtaining accurate measures of temperature, particularly ambient temperature, is a difficult challenge (see Section 4). Failure to detect a relationship between growth and temperature in the field may result from inadequate measures of ambient temperature rather than from the absence of a relationship (Brander WD 1.1), though the absence of a positive relationship between growth and temperature in the field could also result from food limitation in the wild (e.g., Buckley *et al.,* WD 6.3).

2.1.2 Density-dependent effects

Food ration, like temperature, is a key determinant of growth rate. It can depend on both the abundance of cod and the abundance of their prey. While estimates of the relative abundance of cod are available for most stocks, time series of the relative abundance of the prey spectrum for cod are not available. This is a particularly difficult problem given the varied diet of cod in many populations. In some cases, variation in growth or condition of cod can be related to variation in the abundance of a preferred prey. For example, Yaragina and Marshall (2000, WD 5.2) demonstrated a relationship between the liver condition index of NE Arctic cod and capelin, their preferred prey. The relationship between the liver condition index (LCI) of cod and capelin stock biomass was nonlinear, with LCI decreasing rapidly when capelin biomass declined below one million tonnes. In other cases, cod growth appears to be inversely related to cod abundance, suggesting that food is limiting cod growth at high levels of abundance. For example, a strong negative relationship between growth and abundance is evident for cod in the southern Gulf of St. Lawrence, even after accounting for effects of temperature and size-selective mortality (Sinclair *et al.,* WD 4.1; Swain *et al.,* WD 1.2). Density-dependent changes in the distribution of southern Gulf cod during the feeding season (e.g., Swain 1999) also suggest competition for food at high abundances of cod in this stock (i.e., that food is limiting when cod abundance is high).

Even though few relationships between cod growth and their abundance or the abundance of their prey have been demonstrated, there are some indications that food limitation and thus density dependent effects on growth may occur in other cases. On the Faroe Plateau, average weight of cod increased by 62% from 1989 to 1995, a period when average annual temperature tended to decrease, suggesting that this increase in growth was more likely due to increases in food availability (Magnussen WD 1.4). Condition of wild cod off Iceland is low compared to that of pen-reared Icelandic cod, and condition of wild cod can be improved by supplementary feeding (Bjornsson, 1999). Growth rates of cod and haddock larvae on Georges Bank show a dome-shaped relationship with temperature, with a maximum at 7°C (Buckley *et al.,* WD 6.3). The decline in growth at temperatures above the 7°C optimum is compelling evidence that larval growth was food limited at higher temperatures on Georges Bank.

While variation in food ration is potentially an important cause of variation in growth within and among cod stocks, indices of prey abundance are not available to examine this possibility in most cases. Cod in many stocks eat a wide variety of prey items whose abundance is not monitored. An alternate approach could be to develop indices of stomach fullness to test for effects of food ration on growth in the wild. Such indices would incorporate effects of variation in both the abundance of cod and of their prey, as well as variation in the availability of prey. Such indices should take into account variation in the energy content of different prey species. Seasonal variation in feeding intensity would need to be considered when developing these indices for populations with strong seasonal cycles in feeding, such as the Gulf of St. Lawrence cod stocks (Schwalme and Chouinard 1999). Extensive time series of cod stomach contents are available in some cases. For example, a database with information on over 100,000 stomachs exists for NE Arctic cod based on stomach sampling conducted since 1984 (Filin WD 5.1). These data are being used to model growth of NE Arctic cod based on ration and temperature (Filin WD 5.1).

2.1.3 Size-selective mortality

Population mean size at age will not reflect individual growth rates when mortality is size-selective. Significant changes in the intensity and even the direction of size selection have been demonstrated for the 4T cod stock (Hanson and Chouinard 1992, Sinclair *et al.,* WD 4.1). Sinclair *et al.* (WD 4.1) demonstrated that changes in the direction and intensity of size selective mortality were the most important source of the large interannual changes in length-at-age observed in southern Gulf cod (see below). This topic is addressed further in Section 5.

2.1.4 Early life history

Variation in growth rates at early life history stages may have a strong influence on size at subsequent ages. For example, mean weight of North Sea cod at ages 3 to 6 years shows a strong positive relationship with the bottom temperature experienced during their first year of life (Brander and O'Brien WD 6.1). This topic is addressed below in Section 7.

2.1.5 Energy allocation (e.g., growth versus reproduction)

Somatic growth rate is generally expected to decline with maturation in fishes (e.g., Roff 1983) and differences between populations or years in size at age may reflect differences in maturity schedules or in the allocation of energy between growth and reproduction. This possibility was noted but not investigated during the Workshop.

2.1.6 Other

2.1.6.1 Sampling

Estimates of population mean sizes-at-age come either from samples of commercial fishery landings or from data collected on research surveys. Samples from fishery landings suffer from a number of difficulties. Most fishing gear is size-selective. Fishery landings will provide a biased estimate of size at age until the age when year classes are fully recruited to the fishery. Spurious trends in mean size at age can results from changes in gear (e.g., mesh size, hook size), in composition of the fishery (e.g., fixed gear versus mobile gear), or in timing or spatial distribution of the fishery.

Although research survey gear is also size-selective, in most cases cod are fully recruited to this gear at a younger age. Changes in gear are well documented and often adjustments for any changes in fishing efficiency can be applied. Fishing is conducted using standard methods, usually at the same time each year, and following a statistical design that permits the estimation of population mean sizes-at-age.

For western Atlantic stocks, weight at age is usually based on research vessel survey data. The weight at age data available from eastern Atlantic assessments are usually based on commercial catch information. In addition the assessment data are arithmetic mean values, derived in a variety of ways for different stocks. The limitations of these data need to be taken into account when attempting to model effects of environmental conditions or compare with results from laboratory experiments on individuals.

Usually, weight data are derived values, based on measurements of length, and the application of a regression relationship between weight and length. Immediately, a component of the variability in weight at length has been eliminated from the derived data set. The expression of size at age in terms of arithmetic mean weights at age further distorts the variability, because neither length nor weight at age are necessarily normally distributed.

2.1.6.2 Stock structure

Many cod populations consist of a number of stock components differing in growth rates. Two examples are northern (2J3KL) cod and 4X cod. Changes in the proportions of these stock components will result in changes in mean size at age aggregated over the components, even when there is no change in growth within the stock components. Aggregating over stock components can thus produce spurious changes in size at age (or obscure real variation in growth within stock components). These possibilities need to be ruled out before using aggregated data on size at age.

2.2 Methods of identifying factors explaining interannual variation in growth

A number of Workshop presentations tested for effects of potential explanatory factors on interannual variation in growth within cod stocks. The dependent variable in these tests was either size-at-age (i.e., length-at-age or weight-at-age) or some measure of recent growth (i.e., the annual growth increment, the instantaneous annual growth rate, or a condition index). Measures of recent (annual) growth were related to indices of conditions (i.e., temperature or prey abundance) during the year in which this growth occurred. Two approaches were used to test effects on growth using size-at-age. One was to test size-at-age against measures of lifetime conditions up to the age of capture (e.g., the sum of annual temperature indices up to the age of capture). The second was to model growth with parameters that depended on the explanatory variables. Models were modifications of the three parameter von Bertalanffy model, given by:

$$L_t = L_\infty(1-ae^{-kt})$$

where L_t is the expected length-at-age t. Effects of potential explanatory factors on growth were tested following Millar and Myers (1990). In their model, L_∞ depends on the explanatory factors X_j:

$$L_{yt} = L_{\infty_{y1}}(1-ae^{-k}) + \sum_{i=2}^{t}((L_{\infty_{yi}} - L_{y,i-1})(1-e^{-k})$$

where

$$L_{\infty_{yi}} = L_{\infty_0} + \sum_{j} \beta_j X_{j_{yi}}$$

where L_{yt} is the expected length-at-age t for year class y, and $X_{j\ yi}$ is the index for explanatory factor j (e.g., temperature or cod abundance) for year class y at age i. Thus, in this approach, observed length-at-age is predicted by summing environmentally-dependent predicted growth increments to the observed age. An equivalent linear analysis can be conducted using the data available from back-calculation studies (Sinclair *et al.,* WD 4.1).

In most cases, tests of factors affecting growth were conducted on single stocks (though in some cases the same approach was applied to several stocks). A difficulty with this approach is that the dynamic range of the explanatory factor (e.g., temperature) may not be great for single stocks. This is a particular problem for factors that may not be well estimated such as ambient temperature. One approach in response to this problem is to try to increase the signal to noise ratio by pooling data from several stocks together in the same analysis. This approach has been used in analyses of the effect of temperature on cod growth (Brander 1995, WD 1.1). The advantage is that dynamic range is increased substantially by the large differences in ambient temperature that can occur between stocks. A potential difficulty is that differences in ambient temperature may be confounded with other differences between stocks (e.g., duration of the feeding season, extent of seasonal migrations, etc.).

2.3 Confounding between factors affecting growth: simultaneous tests of competing hypotheses

The need for simultaneous tests of the various potential factors affecting cod growth was also raised at the Workshop. The various factors that may affect cod growth (temperature, food availability, etc.) all vary over time and confounding between these factors may obscure effects or generate spurious relationships if only the effect of a single factor is examined. A number of studies presented at the Workshop simultaneously tested the effects of two or more factors on interannual variation in cod growth.

Swain *et al.* (WD 1.2) simultaneously tested for density-dependent and temperature-dependent growth in each of the four cod stocks on the Scotian Shelf and in the Gulf of St. Lawrence using the Millar-Myers approach described above. For the southern Gulf (4T) stock, two indices of temperature were used, the ambient or cod-weighted temperature during the feeding season (T_C) and the average bottom temperature available in the environment (T_E). Effects of both abundance (negative) and temperature (positive) were highly significant for the 4T stock. The single variable providing the most substantial improvement in model fit was T_C. This variable is apparently itself density-dependent for southern Gulf cod (e.g., Swain and Kramer 1995) and thus may incorporate aspects of both density-dependent and environmentally-induced variation in growth. On the other hand, when abundance was already included in the model, addition of T_E resulted in greater improvement in the model than did addition of T_C. T_C should provide a better indication of the temperatures experienced by cod during the feeding season than T_E. This suggests that the superior fit of the model incorporating abundance and T_E may be related to mechanisms that do not involve direct effects of the temperatures experienced during feeding. In this case, the significance of the abundance term may be related to density-dependent changes in both food ration and the temperature occupied during the feeding season (with both ration and occupied temperature declining as abundance increases) while the significance of the T_E term may be related to other climate-related effects like duration of the feeding season.

Measures of ambient temperature were available only for the 4T stock, so the comparative analysis of effects on growth of the four Scotian Shelf (4X, 4VsW) and Gulf of St. Lawrence (3Pn4RS, 4T) stocks used indices of general temperature conditions. Results differed between stocks. The 4T stock stood out as a stock for which age alone accounted for an unusually small percent of the variation in length (58% compared to 79–95% for the other stocks). The 4T stock was also the only stock in which growth was strongly density-dependent. Mean research survey catch rates reach much higher levels in the 4T stock than in the other stocks. Thus, the 4T stock may be the only one of these four stocks in which densities reach high enough levels for competiton to result in substantial declines in average food ration. A slight and marginally significant density-dependent effect was also detected for the 4VsW stock after accounting for the effect of temperature. Growth was positively related to temperature for all stocks except the 4X stock. For the 4X stock, age alone accounted for 95% of the variation in mean lengths, and abundance and temperature accounted for negligible amounts of variation. The 4X stock occupies relatively warm waters compared with the other stocks, so temperatures may never have been cold enough to limit growth in this stock. Residuals from the growth models for the 4T, 3Pn4RS and 4VsW stocks were strongly patterned, tending to be positive in the mid to late 1970s and negative in the 1990s. This suggests the operation of factors not accounted for by the models. The strong pattern in residuals from the growth model for 4T cod is eliminated if an index of size selection is included in the model (see below).

Sinclair *et al.* (WD 4.1) extended the analysis for 4T cod by including indices of size-selective mortality in the analysis. Size-selective mortality appeared to be the most important cause of interannual variation in size-at-age in this stock. All factors were statistically significant in the nonlinear analysis, though the influence of the temperature indices was slight. Measures of the relative importance of the various factors in explaining interannual variation in size-at-age were: direct size selection (19.9), population density (5.9), cumulative size selection (5.8), T_C (2.2), and T_E (0.8). (Direct size selection refers to size selection during the year that a growth increment is put on, while cumulative size selection refers to size selection between age 3+ and capture.) The most parsimonious linear model was obtained using the size selection and population density variables; neither temperature variable was significant in the linear model after accounting for effects of size selection and population density. Failure to account for the effects of size-selective mortality led to incorrect conclusions about the effect of temperature on interannual variation in growth, particularly in the linear model.

2.4 Interactions between effects: temperature and food ration

Interactions between the factors affecting growth complicate attempts to understand the causes of interannual variation in growth in the wild. The interaction between the effect of temperature and food ration poses a particularly difficult problem. An increase in temperature will accelerate growth if food is not limiting but reduce growth if it is. Further, whether food is 'limiting' may depend on temperature. There is an optimum temperature for growth at any particular food ration. If temperature is below this optimum, then food is not limiting and an increase in temperature will accelerate growth. If temperature is above this optimum, then food is limiting and an increase in temperature will decelerate growth. The possibility that temperature preferences may depend on food availability further complicates the issue (Swain and Kramer 1995; Despatie *et al.,* WD 2.2). Food may not be limiting at the cold temperatures occupied by cod, but they may choose to occupy these cold waters because they cannot afford to occupy warmer waters given the available food. Estimates of food availability are rarely available for cod in the wild. However, food is clearly limiting at some times in some cod stocks (e.g., Yaragina and Marshall 2000; Buckley *et al.,* WD 6.3), and appears to be in others (i.e., 4T cod) in some time periods based on the evidence for density-dependent effects on growth and distribution (Swain *et al.*, WD 1.2, Swain 1999).

Cod in some populations (e.g., the Gulf of St. Lawrence stocks) show a marked seasonal cycle in feeding, with little feeding occurring in the winter (Schwalme and Chouinard 1999; Lambert and Dutil 1997). In these stocks the effect of temperature on growth and condition may reverse between seasons in the same year. If food is not limiting during the feeding season, then an increase in temperature will result in greater growth during this season. In contrast, an increase in temperature during the over-wintering period (when the fish are fasting) will have the reverse effect, resulting in greater weight loss over winter.

A number of approaches to studying effects on cod growth in light of these complications were suggested at the Workshop. One approach is to model the interaction between food ration and temperature using bioenergetic models. Another suggestion was to use indices of condition (e.g., liver condition indices) to infer whether food is limiting. It may be possible to conclude that food is not limiting when these indices exceed some level. In this case, interpretation and tests of effects of temperature on growth would be more straightforward. In stocks with a strong seasonal cycle, this needs to be incorporated into investigations of variation in growth. Instead of using annual mean sizes, it would be better to obtain estimates of mean weight at age at the beginning and end of the feeding season and compare the change in weight with the temperature distribution of cod during the feeding season. The seasonal cycle in feeding and condition should be documented for additional stocks, in particular for some fast growing stocks to complement the information that has been collected for slowing growing stocks (Schwalme and Chouinard 1999; Lambert and Dutil 1997).

2.5 Conclusions and recommendations

- The factors accounting for interannual variation in growth appear to vary between cod stocks. In some cases, density-dependent effects due to variation in prey availability or cod abundance appear to be important. In other cases, effects of variation in temperature appear to be important. Both factors appear to be important for some stocks, while neither factor accounts for much interannual variation in growth of other stocks.
- In some cases, relationships between temperature and size at age between or within stocks appear to reflect indirect effects (e.g., involving changes in the duration of the feeding season or distribution of cod) rather than a direct effect on the rates of physiological processes related to growth.
- Variation in size-selective mortality can have a strong effect on interannual variation in size at age, and failure to consider this effect can lead to incorrect conclusions about effects of other factors on growth.
- Wherever possible, effects of the various potential factors that may affect size at age should be tested simultaneously in order to take confounding between these factors into account. If this is not done, effects of untested factors may be spuriously attributed to the tested factor (or may obscure effects of the tested factor).
- Possible effects of aggregating over stock components with different growth rates need to be assessed before using aggregated data.
- When using size at age data from fishery landings, possible bias caused by changes in the fishery (e.g., gear changes, timing or distribution changes in the fishery) needs to be considered.
- The interaction between effects of food ration and temperature is an important consideration in studies of causes of variation in cod growth. The effect of increasing temperature on growth will be positive if food is not limiting and negative if it is. The effect of temperature on growth can thus be in opposite directions in different seasons in populations with strong seasonal cycles in feeding. Bioenergetic modelling may provide a useful approach for taking this interaction into account in studies of effects on cod growth.

Seasonal cycles in feeding and condition should be characterised for a number of stocks, including both fast- and slow-growing stocks.

3 Single growth model for all cod stocks

3.1 Purpose of trying to construct a common model

The purpose of constructing models of growth rates is to understand what causes variability in growth and, if possible, to predict the consequences of changes in the main factors on future growth rates. The main factors influencing growth rate are size, temperature and food availability (Brett, 1979), but a number other factors also play a part including light environment (Suthers and Sundby, 1996), turbulence (Leising and Franks 1999), previous feeding history, conditions during very early life (See Section 7). Obtaining appropriate data on all these factors is rarely possible. Because of this, and in order to begin with parsimonious models, only size and temperature are included in the preliminary studies presented here.

Growth rate is partly genetically determined, but the small number of studies (see Section 9), which compare growth rates of cod from different stocks under the same conditions, indicate that differences between stocks are minor compared with the effects of other factors, including size, temperature and food. It therefore seems worthwhile to construct a common model and test it against available data from all stocks, rather than only fitting separate models for each stock.

A common growth model will facilitate comparisons between stocks. If the observed growth rates for a particular stock deviate from the common fit in a systematic way then the causes, such as stock dependent factors, missing factors (i.e., incomplete model) or inappropriate estimates of important variables can be investigated.

3.2 Combining data from all stocks

3.2.1 Standard methods for comparing within and across stocks

The instantaneous growth rate (g) can be expressed as $\ln(\text{Weight}_{t+1}/\text{Weight}_t)$. Since many growth experiments on small fish are conducted over short time periods it is recommended that t is expressed in days and all rates are expressed as daily rates. The instantaneous coefficient, which is in units of d^{-1} is sometimes multiplied by 100 to reduce the number of leading zeros. This is close to, but not the same as growth rate expressed as % per day.

Growth rates derived from field data (e.g., annual mean weight at age) for older fish can also be expressed in the same way, in order to include them in a common model. However it is important to remember that this method produces a constant instantaneous rate throughout the year and the “true” growth rate may vary seasonally and with the size and age of fish.

Similarly, growth in length can be compared using the instantaneous rate, although growth in length is not exponential. Length may represent the structure of fish in a more conservative way than mass, but production is expressed in mass, not length.

3.2.2 Assembly and preliminary analysis of data from many stocks

Data on stock weight at age were assembled from all cod stocks assessed in the ICES area (not including NW Atlantic stocks at this stage) and used to fit common models of growth rates. The temperatures for each area, which were taken from Brander (1994) and Sparholt (1996). The number of values of weight at age is given in the Table 3.1 below:

Table 3.1 Cod stocks and number of weight-at-age estimates used to fit growth rate models.

Stock area	Mean Bottom Temp	N
W Baltic	6	189
E Baltic	6	35
North Sea	8.6	384
Celtic Sea	11	70
NE Arctic	4	208
Faroe Plateau	7.4	333
Iceland	5.8	312
Irish Sea	10	120
Kattegat	7.5	165
W Scotland	10	224

Growth rates were estimated as recommended above and are plotted against geometric mean (GM) weight during the year in Figure 3.1. The decline in growth rate with size is evident. An exponential model (equation shown on the left hand plot in Figure 3.1) accounts for 75% of the variance in growth rates.

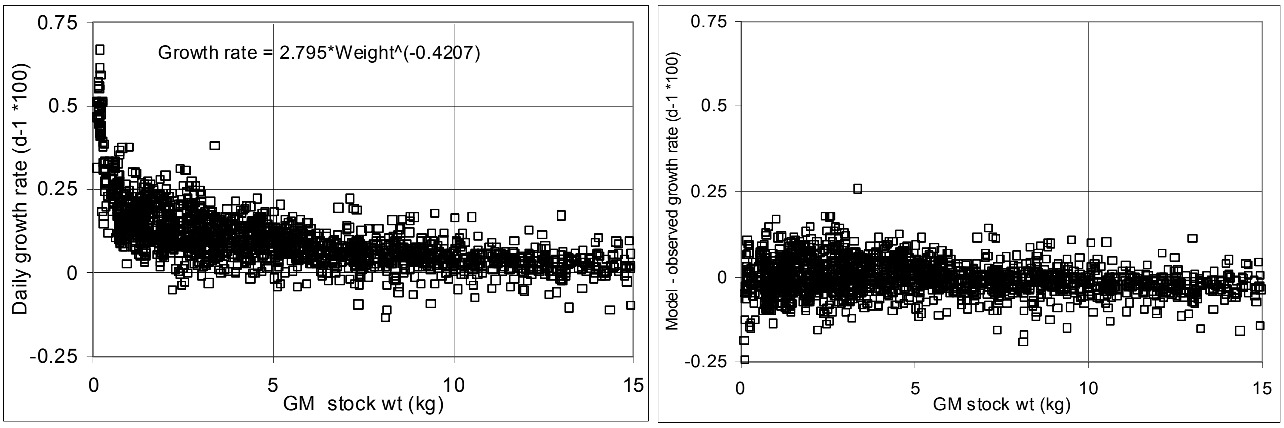

Figure 3.1 An exponential model of growth rate as a function of size and the residuals.

It is likely that the stock effect is due to temperature (see Figure 3.2). Temperature data for individual years have not yet been assembled, to allow a further step in the analysis and modelling.

The difficulty of estimating ambient temperature has been discussed under Section 4. The data on weight at age which have been used for the analysis shown here are from the assessment reports and derive from market sampling of the commercial fishery. They are therefore subject to bias due to selection by the fishery and they are highly aggregated in space and time. Because of this, they are less than an ideal data set for growth rate analysis. Nevertheless they have to be examined, because they are used directly in the assessment calculations of spawning stock biomass and we need to consider the variability and predictability of such aggregated estimates, if the same kind of assessment models continue to be used.

It would of course also be desirable to include other factors, particularly food, if it is limiting, but field data are rarely available.

3.3 Review and comparison of existing models

Previous experimental (Jobling 1988) and field (Brander 1994, 1995, 2000, WD 1.1) studies combined data from several stocks in order to construct common models of growth, showing the effect of temperature and body size. In the light of recent experimental work reported below, these models are probably structurally inadequate, since they assume that temperature at which the maximum rate of somatic growth occurs is independent of body size.

Experiments with Icelandic cod ranging in size from <1g to several kg and fed to satiation at temperatures from 1.3 to 16^{o} C show that the effect of temperature on growth rate is far greater for small fish and that the optimal temperature for growth declines with increasing size of fish (Bjornsson *et al.*, 2001 WD 2.1). The growth rates achieved in these satiation experiments are at least twice as fast as those estimated for wild fish (Figure 3.3). A large part of the difference is probably because wild fish are more active as they feed, migrate and avoid predators. The hepato-somatic index of wild fish rarely exceeds half of the level achieved by fish fed to satiation in captivity, even when the amount of food available to the wild fish is not apparently limiting growth (Yaragina and Marshall, 2000). Although there are therefore likely to be large, systematic differences between experimental and field growth rates, the functional form of the relationship with temperature established in the Icelandic rearing experiments is probably applicable to wild populations.

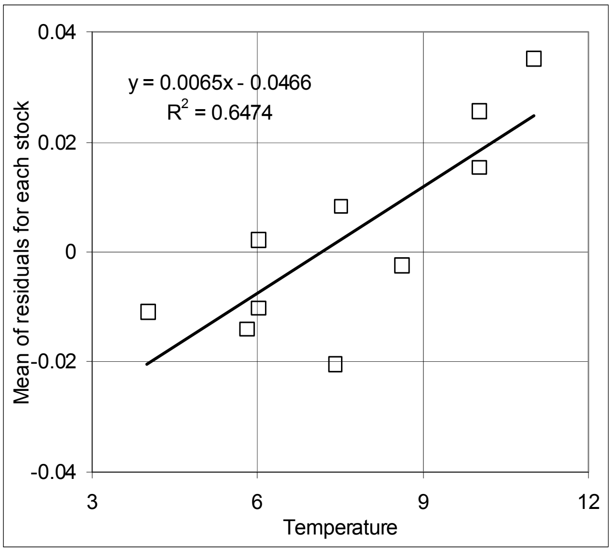

Figure 3.2 Mean residuals for each stock as a function of temperature.

Bjornsson and Steinarsson (WD 2.1) used a four parameter function to model their experimental data:

g = (A*temperature + B) * Weight^(C*temperature+D)

Their fitted values are A=0.701; B=-0.973; C=-0.026; D=-0.147. The temperature for zero growth rate is -B/A = 1.39^{o} C, but there were only two experiments at temperatures below 3^{o} C (1.1^{o} C and 1.3^{o} C respectively), both of which gave positive growth rates, therefore it

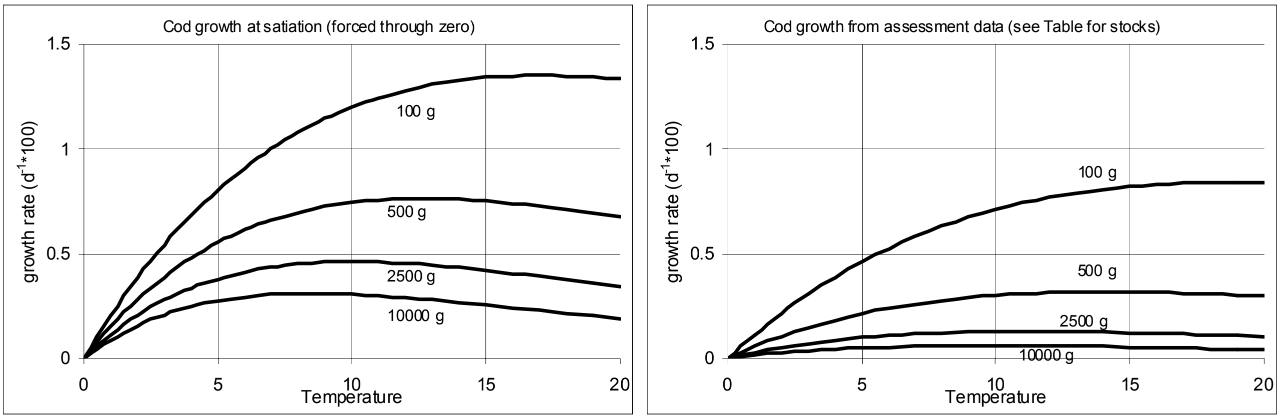

Figure 3.3 Three parameter growth model fitted to Bjornsson's satiation reared cod and to assessment data.

may be sensible to set B=0. (The other parameters then become A=0.469; C=-0.0128; D=-0.0169). The same model can be fitted to the assessment data set for the stocks listed in Table 2.1. The parameter estimates are A=0.830; C=-0.0114; D=-0.420.

3.4 Other approaches to constructing a single growth model

At least two other approaches to modelling cod growth have been applied recently and seem worth pursuing. Individual-based models (Leising and Franks, 1999) have been used to resolve the variability in temperature, prey size and turbulence forcing which cod larvae may encounter within small time and space scales. An individual-based approach would be useful to explore the consequences of realistic spatial and temporal variability in temperature on the growth model used in the previous section.

A life history model (Cook *et al.*, 1999) was used to explore the interrelationship between rates of growth, natural mortality and maturity for North Sea cod. The authors conclude that the observed changes in maturity with age and size are explicable from a model which maximises egg production over an individual lifetime It would be useful to extend the analysis to other stocks, particularly since North Sea cod show rather little variability in growth and maturity.

The authors also conclude that growth rate of North Sea cod may be density dependent, but an alternative explanation (Brander and O'Brien, WD 6.1) is that the changes are due to temperature experienced during the first year of life.

Finally, a very preliminary attempt was made to use neural networks and genetic algorithms to develop alternative models of growth, during the preparations for this Workshop. The latter, in particular, may be useful to provide new insight into the functional forms most applicable to single growth models.

All of the modelling approaches in this section have their particular uses, but progress is likely to be slow until a larger data set on the growth and environment of individual fish is available against which to develop and test the models. Several of the proposals and recommendations for further work address this need.

4 Estimating ambient temperature

4.1 Background

Temperature and food rations are the two primary factors driving growth in fishes. Although growth of fishes is dependent on the availability of prey, quantitatively as well as qualitatively, growth is also the integration of a series of processes (feeding, assimilation, metabolism, transformation, and excretion) where rates are all controlled by temperature (Michalsen *et al.*, 1998). Brander (1995), who examined 17 North Atlantic cod stocks, found that most of the observed variability in growth was due to temperature. The main conclusion he drew was: "More attention should be paid to quantifying the effect of temperature on growth of cod (and perhaps other species), because it probably has significant effects on stock assessment, catch forecasting, and evaluation of the consequences of climate change. In order to investigate the effect in detail for individual stocks, data on temperature and fish distribution need to be analysed jointly". An example of this temperature-growth link is given in WD 6.1 (Figure 4.1) for North Sea cod.

Based on this it was natural for the Workshop to examine the temperature representations currently used in growth models and tests, to evaluate these measures and, if necessary, suggest improved approaches. Questions that we asked ourselves prior to the Workshop (and posted on web) include the following: What is the best measure of temperature to use? How well does interannual or geographic variation in "environmental" temperature reflect variation in the temperatures occupied by cod (i.e., "ambient" temperature, or "cod-weighted" temperature)? How should seasonal variation in the temperature distribution of cod be incorporated in growth models and tests, especially when feeding rates vary seasonally (i.e., there is a distinct feeding season)? How well do snapshots of cod temperature distribution from research surveys reflect the temperature distributions indicated by data-storage tags or suggested by isotopic analyses of otoliths?

4.2 How do we define ambient temperature?

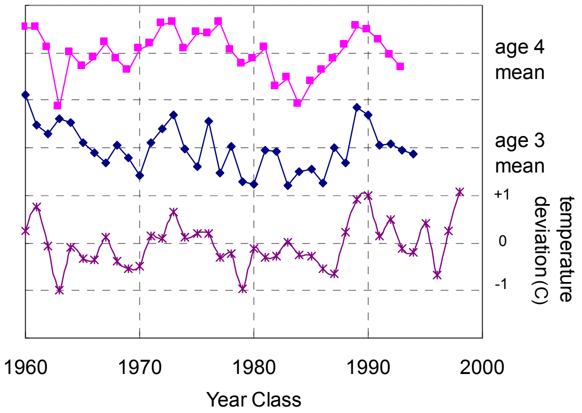

Figure 4.1. Deviations from the mean weight at ages 3 and 4 and mean bottom temperature for North Sea cod. The horizontal dashed lines correspond to 20% deviations from the mean weight (from WD 6.1).

When studying the effect of temperature on growth an appropriate estimate is the ambient temperature, which can be defined as the temperature actually experienced by the fish (WD 1.1). In an experimental system, failure to regulate or at least monitor the ambient temperature would almost certainly lead to the results being rejected. If similar criteria were applied to field studies then very few would be published. It is not sufficient to have a time series of temperature from fixed stations, or even complete horizontal and vertical temperature fields for the entire ocean; in addition, the distribution of fish in relation to that temperature field must be known (Heessen and Daan, 1994).

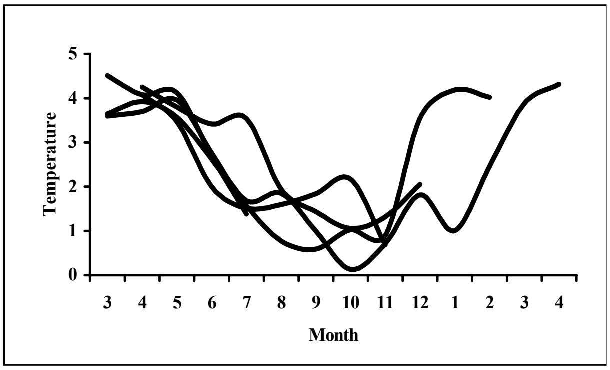

Figure 4.2. Seasonal variability in ambient temperature of Arcto-Norwegian cod as measured by data storage tags. Smoothed means of measurements done every two hours are shown. From WD 3.2.

Ambient temperature may be defined as a fish density weighted temperature mean estimated by the following equation:

$$T_{amb} = \frac{\int \left[\rho(x,y,z,t) \quad T(x,y,z,t)\right] dxdydzdt}{\int \rho(x,y,z,t) dxdydzdt} \qquad (1)$$

where $\rho(x, y, z, t)$ is fish density at position (x, y, z) and time t, $T(x, y, z, t)$ the corresponding temperature, and the integration is done, separately for each age group, over the whole distribution volume of the fish and the time period in question (Ottersen *et al.,* 1998).

In practice regional coverages of both temperature and fish density are done by scientific surveys and such data are seldom available for more than one or at best two periods a year. This means that we only get a "snapshot" of the temperature conditions that the fish live in. The seasonal temperature variation at the depths where cod mainly are found may in many areas be rather small for any given fixed location. However, the seasonal migration undertaken in many stocks may impose large differences in ambient temperature through the year.

An alternative approach for estimating ambient temperature is the use of electronic data-storage tags, which measure depth and temperature in the surroundings of an individual fish with fixed (short) temperature intervals. This method gives a good estimate of the temperature history of a few single fish, but a large number of tag returns is necessary for the mean values to be reliable estimates for the whole population or age group. An example of the use of data storage tags on Barents Sea cod is given in WD 3.2 (Figure 4.2).

A third method is isotopic ratio analysis of cod otoliths (Weidman and Millner, in Werner *et al.,* 1999). This method gives an estimate of the temperature history throughout the fishes life and is less expensive than data storage tags. However, the precision is a lot coarser and such an analysis on a large number of fish time consuming.

4.3 Examples of growth models and tests including ambient temperature

Growth models need to incorporate representative measures of ambient temperatures experienced by the fish to account adequately for environmental variability. On the basis of winter and summer research surveys the relation between various temperature indices and size-at-age of Northern Gulf of St. Lawrence cod were studied in WD 3.1. They concluded that in the case of northern Gulf cod, ambient temperature did not seem to be the key variable driving changes in growth.

Michalsen *et al.* (1998) related mean length and weight at age of 2–6 year old Arcto-Norwegian cod to their ambient winter temperature. Mean individual growth rate was highest for year classes experiencing high temperatures. Mean lengths at age increased with increasing life-time accumulated ambient winter temperature.

Swain *et al.* (1998a) also show the importance of using 'ambient' or 'cod-weighted' temperature indices in tests of possible impact of temperature conditions on cod growth. In tests of effects of abundance and temperature on the growth of Southern Gulf of St. Lawrence cod, they demonstrated that the effect of 'cod-weighted' temperature is twice as strong (in terms of explained variation in growth) as the effect of either 'available' (unweighted) temperature or abundance in models containing a single explanatory variable.

On the other hand, measures of general or available temperature conditions may capture effects not captured by cod-weighted temperature (e.g., length of the growing/feeding season, productivity, etc). In models including two explanatory variables, the model including abundance (density dependence) of Southern Gulf cod and available temperature explained somewhat more of the variation in growth than the model including ambient temperature and abundance. This may be in part because the abundance term accounted for density-dependent changes in temperature distribution (Swain *et al.*, 1998a).

4.4 "Ambient" versus "Environmental" temperature

The temperature as measured at fixed locations may often not reflect the ambient temperature, i.e., the temperature actually surrounding the fish. Since cod often inhabit regions of relatively large horizontal temperature gradients they may, depending on their movements, experience temperature variations which are quite different from those in any geographically fixed point (Ottersen *et al.*, 1998).

Temperatures at the Kola section and mean bottom temperatures in the Barents Sea have been compared with mean ambient winter temperatures for Arcto-Norwegian cod. As expected, the interannual variability in ambient winter temperature was found to be larger than in "environmental" temperatures. Furthermore, ambient temperatures were found to increase with the age of the fish. While the ambient temperatures for cod of ages 1, 2 and 3 were significantly lower than the corresponding Kola section temperature, the differences between ambient and "environmental" temperatures were not statistically significant for ages 4 and 5. and the ambient temperatures of 6 and 7 year old cod higher than the Kola section temperature (Ottersen *et al.,* 1998).

While the above was an example of how variability in ambient temperatures of cod may not be detected by only studying temperature, a different relation has been described for Southern Gulf of St. Lawrence cod. Here variation in environmental conditions may occur without variation in the temperature conditions experienced by cod (i.e., in their 'ambient' temperature) being observed. For example, bottom temperatures on the Magdalen Shallows in the in the early 1980s were the warmest in the 1971–2000 time series, but the temperatures occupied by cod were average to cool. In contrast, environmental conditions were unusually cold in the 1990s, but the temperatures occupied by cod were not (Swain, 1999).

In some areas, environmental temperature seems to be a better indicator of ambient temperature. The results of Heessen and Daan (1994) indicate that a shift in the average North Sea winter bottom temperature results in an about equally large shift in the ambient temperature of cod, i.e., North Sea cod show no systematic pattern of change in the spatial distribution to compensate for interannual temperature variability.

4.5 Density-dependent temperature selection

Bioenergetic considerations suggest that temperature selection by fishes should be density-dependent. On limited rations, the temperature yielding the highest growth rate decreases as ration size decreases (Brett *et al.*, 1969; Elliott, 1975; Woiwode and Adelman, 1991). Therefore, if fish select the habitat that maximises their growth rate, the optimal temperature for fish growth decreases as food supply decreases (Elliott, 1975; Crowder and Magnusson, 1983; Swain and Kramer, 1995). Thus, if food supply is density dependent (due to competition at high abundance), then the proportion of a population occupying habitats of lower temperature should increase with population size (Swain and Kramer, 1995).

The distribution of southern Gulf of St. Lawrence cod during their feeding season on the Magdalen Shallows has been monitored since 1971 by an annual bottom-trawl survey. Density-dependent changes in the distribution of cod during their feeding season were consistent with the predictions above. Distribution shifted from warm shallow inshore waters at low abundance in the 1970s to colder waters at intermediate depths when abundance was high in the 1980s (Swain 1993; Swain and Kramer 1995). Coincident with the decline to low abundance in the 1990s, distribution shifted back to the low abundance pattern of the 1970s (Swain, 1999). This independent support for the hypothesis of density dependence reduces the likelihood that the connection between southern Gulf cod abundance and their distribution is spurious.

In WD 1.3 lower growth rates of Arcto-Norwegian cod during periods of high abundance is proposed to be a result of a decrease in ambient temperature. This again is due to density-dependent mechanisms causing the geographic range of Arcto-Norwegian cod to extend eastwards into colder water masses. Such a distributional response to fluctuations in abundance may be seen in the light of the theory of density dependent habitat selection (MacCall, 1990). The hypothesis thus states that density-dependent growth is imposed on immature Arcto-Norwegian cod by density-dependent habitat selection.

4.6 Interannual variations in ambient temperature and distribution patterns

There seems to be little doubt that for most cod stocks there tends to be a connection between interannual changes in temperature conditions and distribution. The mechanisms involved are, however, complex and the causal relations not fully understood. A shift in distribution may lead to changes in ambient temperature, but temperature variability may also induce distributional responses.

Mountain and Murawski (1992) showed that interannual changes in temperature affect the distribution pattern of cod on Georges Bank. They compared the mean bottom water temperature in the region during spring Northeast Fisheries Center surveys with the mean temperature at which cod were caught in the surveys. The findings could suggest that the cod compensated for about 40% of the interannual temperature variability by changing their spatial distribution. This compensation could, however, not be explained simply by north-south or between-depths movements of fish (Serchuk *et al.*, 1994).

Ottersen *et al.* (1998) studied variability in ambient winter temperature for immature Arcto-Norwegian cod for the period 1988–1995. Their ambient temperature displayed a pronounced interannual variability suggested to be related to the year-to-year differences in the distributional pattern of the fish. The results of Shevelev *et al.* (1987) and Ottersen *et al.* (1998) indicate that at high abundances the fish may extend their distribution towards the east, thus shifting the centre of mass of distribution eastwards, apparently independently of the temperature conditions. However, Ottersen *et al.* (1998) did not reach a clear conclusion with regards to the involved mechanism(s): "Further study is required to determine whether changes in distributional pattern can be regarded as a response to temperature directly, to abundance, or to other temperature-related environmental factors (abiotic and biotic), e.g., temperature-induced changes in distribution of prey organisms as hypothesized by Shevelev *et al.* (1987)".

Rose *et al.* (1994) and Rose *et al.* (2000) show pronounced variability in the distribution of Canadian Northern (2J3KL) cod relative to thermal conditions for the years 1980–1992. They found that the cod was consistently located substantially further to the north in warmer ocean periods than in cold. The mean latitude of cod concentration from autumn surveys and winter trawl fishery was positively correlated with the annual sea temperature signal as assessed at Station 27.

4.7 Seasonal variations in ambient temperature

Many cod stocks undertake seasonal spawning and feeding migrations. For some populations these movements are minor, while others cover 100's of kilometres resulting in dramatic variability in the surrounding environment.

For Arcto-Norwegian cod in the Barents Sea and Svalbard waters annual mean temperatures range from 6–8°C at the spawning grounds along the west coast of Norway (Aure and Østensen, 1993) down to 0 or even -1°C along the polar front in the northern and north-eastern parts where the fish feed during summer and autumn (Mehl *et al.*, 1985). Cod is mainly found at depths below 100 metres (Korsbrekke *et al.*, 1995) where seasonal variations at fixed locations are rather small, 1–3°C (Ottersen and Ådlandsvik, 1993). This implies that the seasonal variation in ambient temperature is mainly determined by how the fish move and to a lesser extent by the rather limited seasonal temperature variation in fixed points. Consequently the majority of adults, more than 7 years of age, experience significantly higher temperatures during their migrations to and from the spawning grounds in November-May than during summer-autumn when feeding as indicated by Jørgensen (1992). A less extensive seasonal migration takes place for the immature fish, ages 3–6 years, which prey on capelin migrating towards the coasts of Russia and Northern Norway in winter-spring (Mehl *et al.,* 1985). Seasonal migrations of 1 and 2 year old fish appear to be smaller. In accordance with these seasonal movements through the temperature field, ambient temperatures of the various age groups of Arcto-Norwegian cod have been demonstrated to be higher during winter-spring than summer-autumn. One would also expect that ambient winter temperatures are higher for older fish as demonstrated by Nakken and Raknes (1987) and Shevelev *et al.* (1987).

In some populations of cod, marked changes in both temperature associations and feeding rates occur among seasons. For example, in southern Gulf of St. Lawrence cod, most feeding occurs during summer and early fall; during the winter months (December to April), these cod feed very little and undergo marked declines in weight and condition (Schwalme and Chouinard 1999). These cod occupy relatively cold waters during the summer feeding season and (paradoxically, like the Arcto-Norwegian cod) relatively warm waters during the over-wintering period (Swain *et al.*, 1998b). How should interannual variation in temperature be integrated over the year to account for or predict interannual variation in growth in such populations? During the summer feeding season, an increase in temperature would be expected to result in increased growth if food is not limiting, or perhaps decreased growth if food is limiting. During the over-wintering period, when the cod are fasting, an increase in temperature might be expected to result in decreased growth (i.e., accelerated weight loss).

Recommendations

Estimates of ambient temperature need to be further refined. Approaches that should be undertaken include:

- To generate temperature time series from isotopic analyses of otoliths, if the signal-to-noise ratio is high enough to produce meaningful results (e.g., problems with salinity can be dealt with).
- To implement a data storage tag program on a wider scale, in particular in the NW Atlantic.

5 Effects of size-selective mortality

5.1 Changes in the intensity and direction of size-selective mortality of southern Gulf of St. Lawrence cod

Population mean size at age will not reflect individual growth rates when mortality is size-selective. Both fishing and natural mortality can be size selective. Fisheries are usually assumed to selectively remove the faster-growing individuals in a population (e.g., Parma and Deriso 1990). However, Hanson and Chouinard (1992) demonstrated reversals in the direction of size-selective fishing for southern Gulf of St. Lawrence cod based on comparisons between length frequency distributions of the landings and of the population (estimated from research survey catches). Fishery removals were disproportionately high for slow-growing fish for the 1967–1972 year classes and for fast-growing fish for the 1977–1982 year classes. Hanson and Chouinard (1992) noted that the reduced mean lengths-at-age of the 1977–1982 year classes compared with the 1967–1972 year classes were consistent with this change in the selectivity of the fishery.

An otolith back-calculation study confirmed this reversal in the direction of size selection for this stock (Sinclair *et al.,* WD 4.1). This study was based on back-calculations on over 13,000 otoliths collected between 1971 and 1998. Size selection was examined by comparing back-calculated lengths at age *i* between fish in the same year class caught in the annual research survey at age i^+ and age $(i+3)^+$. There was a highly significant change in the direction of size selective mortality. During the early to mid 1970s, back-calculated length-at-age *i* tended to be greater for fish caught at age $(i+3)^+$ than for those caught at age i^+ (i = 3–8), indicating greater mortality for slower-growing fish. During the 1980s and early 1990s, this difference was reversed (i = 3–7), indicating greater mortality for faster-growing fish.

Sinclair *et al.* (WD 4.1) used back-calculated lengths to calculate yearly size-selection indices at age for this stock. They calculated two indices of size selection, a cumulative index *C,* which measured the cumulative effect of size-selective mortality between age 3 and the age of capture, and an annual index *S*, which measured the effect of size selection in the year before capture (the direct effect on the mean growth increment used in the analyses described in Section 2.3):

$$C_{i,y} = L_{3,i+y,y} - L_{3,3+y,y}$$

and

$$S_{i,y} = L_{i-1,i+y,y} - L_{i-1,i+y-1,y}$$

where *i* indexes age, *y* indexes year class and and $L_{j,k,y}$ is the back-calculated length at the *j*th annulus for fish in year class *y* caught in year *k*. Using these indices, they demonstrated that changes in the direction and intensity of size selective mortality were the most important source of the large interannual changes in length-at-age observed in southern Gulf cod (see Section 2.3). Conclusions regarding the role of factors such as temperature on interannual variation in growth were altered by consideration of the effects of size selection (see Section 2.3).

The studies by Hanson and Chouinard (1992) and Sinclair *et al.* (WD 4.1) demonstrate phenotypic selection for length of southern Gulf cod. The extent of any genetic response to this phenotypic selection will depend on the heritability of growth in this population, which is unknown. Size-at-age remains low in this population despite low population sizes and low fishing mortality since the early 1990s. Severe environmental conditions (cold temperatures, delayed feeding seasons) in the early to mid 1990s may contribute to the recent small size-at-age in this population. However, environmental conditions have recently moderated. Continued small size-at-age in southern Gulf cod may indicate that a genetic response has occurred to the strong selection against fast-growing fish in the 1980s and early 1990s.

5.2 Conclusions and recommendations

Changes in population mean length or weight with age do not give unbiassed estimates of growth rates if mortality is size-selective. Evidence of size-selective mortality has been presented for Norwegian coastal cod (Kristiansen and Svåand 1998), and Krohn and Kerr (1997) suggested that size-selective fishing mortality may have played an important role in declines in weight at age of northern cod. Size-selective mortality, and changes in its intensity and direction, have been demonstrated for the southern Gulf of St. Lawrence (4T) cod stock. These changes in size-selective mortality accounted for a large fraction of the substantial interannual changes in length-at-age observed in this population. Failure to consider effects of size-selective mortality can lead to incorrect conclusions about the role of other factors such as density or temperature in determining interannual variation in size at age. The possibility that changes in the intensity or direction of size-selective mortality are an important source of variation in mean size at age should be investigated in other stocks. Likely candidates for such an effect would be slow-growing stocks that recruit to the fishery over a protracted period.

Back-calculation studies should be conducted to estimate individual growth histories from scales or otoliths. These studies could provide unbiassed estimates of the growth of survivors. These studies would also be a good method of investigating size-selective mortality and variation in its intensity and direction. Data need to be corrected for effects of size-selective mortality before investigating effects of environmental factors on growth using data on wild cod (i.e., from research survey or fishery catches). This is true even if back-calculated growth histories of survivors are used in analyses (because size selection will affect whether fast- or slow-growing fish survive to be included in analyses). Effects of size selection could be accounted for in analyses by using indices of the type described by Sinclair *et al.* (WD 4.1).

6 Effects of variation in growth on stock biomass

Variation in growth within stocks can have a substantial effect on stock biomass. This can occur in several ways: (1) adult growth rate has a direct effect on the rate of change in harvestable biomass or spawning stock biomass (SSB), (2) size and condition affect reproductive output and thus subsequent recruitment and biomass, and (3) year class strength appears to be related to growth rates during the larval and pelagic juvenile stages in cod.

6.1 Adult growth

Dutil *et al.* (WD 1.5) conducted production analyses for selected cold-water and warm-water stocks and assessed the contribution of variability in growth production to variability in surplus production within and between stocks. Five different stocks covering a wide spectrum of sizes-at-age were examined using the data posted at the Workshop website: Irish Sea, a fast-growing stock, Northeast Arctic and NAFO 4X, two stocks exhibiting intermediate growth rates, and the northern (NAFO 3Pn, 4RS) and southern (NAFO 4T, 4Vn) Gulf of St. Lawrence which are two slow-growing stocks.

Per-capita growth production (GP) was greatest in the Irish Sea stock, intermediate in the Northeast Arctic and NAFO 4X stocks and lowest in the Gulf of St. Lawrence stocks. This was reflected in differences in per-capita surplus production (SP) between stocks (Figure 6.1).

Within stocks, SP was not correlated with GP in the warmer water stocks (Irish Sea, NAFO 4X) suggesting that variation in recruitment rate had a more important effect than GP on variability in surplus production in these stocks (Figure 6.2A,B). However, in the two slow-growing Gulf of St. Lawrence stocks, SP was positively related to GP (Figure 6.2C,D), indicating that variability in growth contributed strongly to interannual variation in surplus production in these stocks.

It was felt that the production analysis should be discussed and developed further. One suggestion was to distribute the analysis for each stock to the experts on those stocks for validation. Alternative analyses were also suggested, e.g., length-based rather than age-based analyses, consideration of mature versus immature biomass, incorporation of risk analyses, etc. For Northeast Arctic cod, analyses had to be restricted to recent years (late 1980s and the 1990s) because annual information on weight at length was not yet available for earlier years. This emphasized the importance of ongoing efforts to retrieve historical data on interannual variation in length-weight relationships in order to update weights at age for these earlier years.

The effect of variation in growth on stock biomass was investigated further for cod in the southern Gulf of St. Lawrence. This stock declined to low levels of

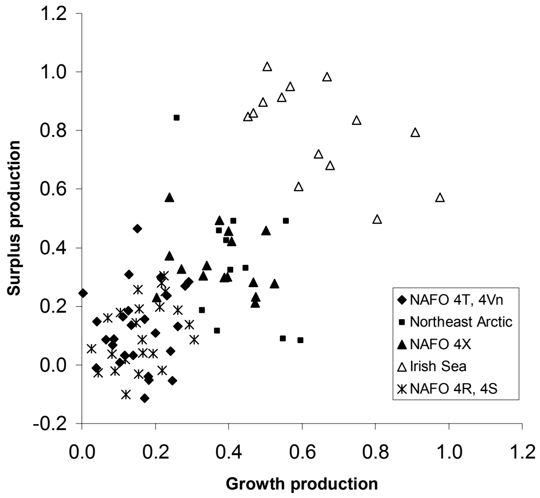

Figure 6.1. Surplus production in year t+1 and growth production of survivors from year t to year t+1 on a per capita basis for five different cod stocks.

abundance in the mid 1970s and again in the early 1990s. Recovery from the stock collapse in the 1970s was very rapid while recovery from the recent collapse has been slow (Figure 6.3A). Weight at age varied widely between these two periods (Figure 6.3B). This apparent difference in growth contributed strongly to the difference in recovery rate between the two periods. This was demonstrated by simulating the recovery of this stock from low abundance using the weights at age from either the mid 1970s or the early 1990s. Recruitment was predicted using a Ricker stock-recruitment model fitted to the SPA estimates of stock and recruitment for 1950–1997, natural mortality was set at the recent estimate of M=0.4, and fishing mortality was set to zero. In the simulation using the weights at age from the mid 1970s biomass increased at about five times the rate obtained using the weights at age from the early 1990s (Figure 6.3C).

Given the very slow growth currently exhibited by the southern Gulf stock, it has been important to reduce exploitation to a very low level to allow SSB to increase.

Northeast Arctic cod provides another example where changes in individual growth are strongly reflected in the harvestable biomass and in spawner biomass (Filin WD 5.1). This effect of changing individual growth rates needs to be taken into account when developing fishing strategies for this stock. Models incorporating this effect are currently under development using time series of stomach content data (Filin WD 5.1).

The effect of rapidly changing growth rates on stock projections was discussed. Projections usually use the average weights at age in recent years. Considerable error could be introduced into projections if weights at age are rapidly changing (e.g., as occurred in the southern Gulf stock in the late 1970s and early 1980s and in the Northeast Arctic cod during the period from 1984 to 1995). For example Figure 6.4 shows the prediction error which results from using weight at age data for the previous year. For North Sea cod the interannual variability in weight at age is fairly small, but for Northeast Arctic cod it is substantial and gives rise to large errors in the prediction.

6.2 Reproductive output

Variations in growth rate contribute to variation in spawner biomass and thus to variation in reproductive output and subsequent recruitment to the harvestable biomass. However, spawner biomass alone is not a sensitive measure of reproductive output (egg production) and recruitment potential (Marshall *et al.*, 1998, 1999, WD 5.3). Reproductive output depends on the quality as well as the quantity of spawner biomass. Relative fecundity (fecundity per unit of body weight) tends to be greater in larger cod, so that the same spawner biomass will lead to greater egg production if it is composed of larger fish. Cod in poor condition have reduced fecundity (e.g., Kjesbu *et al.,* 1998; Lambert and Dutil 2000; Lambert *et al.,* 2000). Marshall *et al.* (1998) also present evidence of skipped spawning in poor-condition years.

Marshall *et al.* (1999) argue for the replacement of spawner biomass by more accurate measures of reproductive potential, which incorporate effects of variation in growth and condition. Total lipid energy provides a better proxy than spawner biomass for total egg production. Strong seasonal cycles in liver condition exist in some stocks. An understanding of these cycles is needed in order to incorporate condition indices into indices of reproductive potential. Measurement of the seasonal cycle of liver condition was recommended for a few stocks covering a range of growth rates, including some fast-growing stocks (to compare with the cycles demonstrated for slow-growing stocks). There is also a need to periodically estimate and update maturity ogives in order to obtain better estimates of spawner biomass (or total lipid energy of mature females).

6.3 Growth at early life history stages (see also topic 6, Section 7)

Evidence has accumulated suggesting that growth in the first several months of life in Atlantic cod and other species is related to year class size (Campana 1996, Ottersen and Loeng, 2000). This period encompasses the larval and pelagic juvenile stages. Variations in growth rate have been related to temperature and food availability. While temperature is easily measured, estimation of food availability is more problematic. Fortunately variations in temperature explain a large proportion of the observed variability in growth (Campana and Hurley 1989, Buckley *et al.,* in prep.). Field and laboratory studies have shown that the relationship between temperature and growth may be parabolic with a distinct optimum temperature (T_{opt})

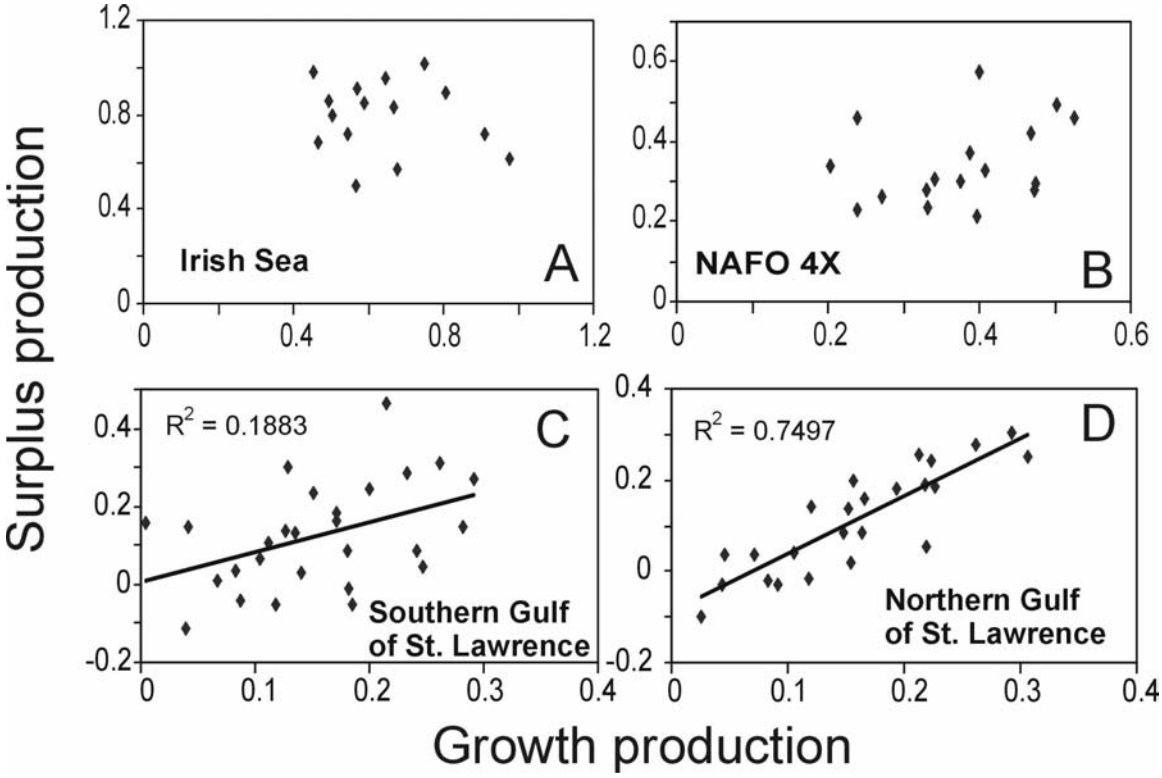

Figure 6.2. Relationships between per-capita growth production and per-capita surplus production for selected cod stocks.

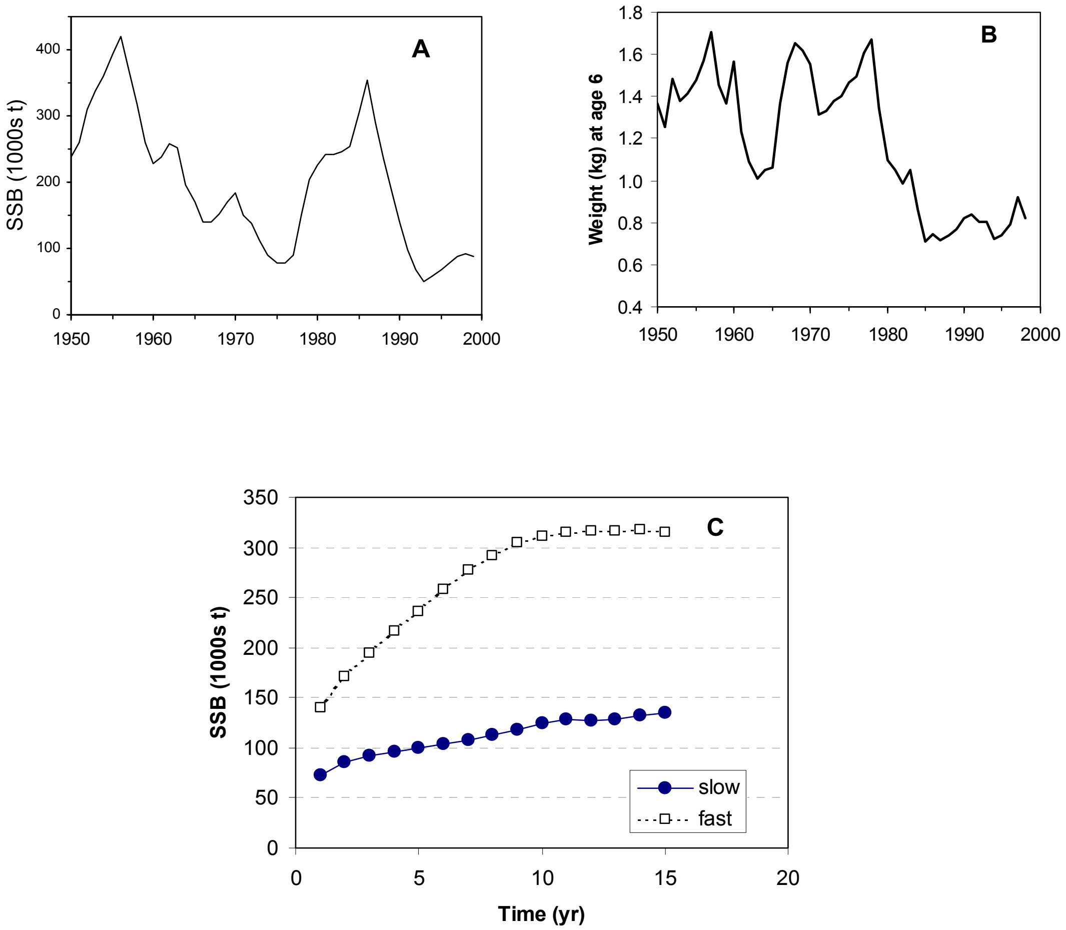

Figure 6.3. Effect of variation in growth on biomass of southern Gulf of St. Lawrence cod. A. Spawning stock biomass (SSB). B. Weight at age 6. C. Simulated recovery from stock collapse assuming either the fast growth rates of the mid 1970s or the slow growth of the early 1990s.

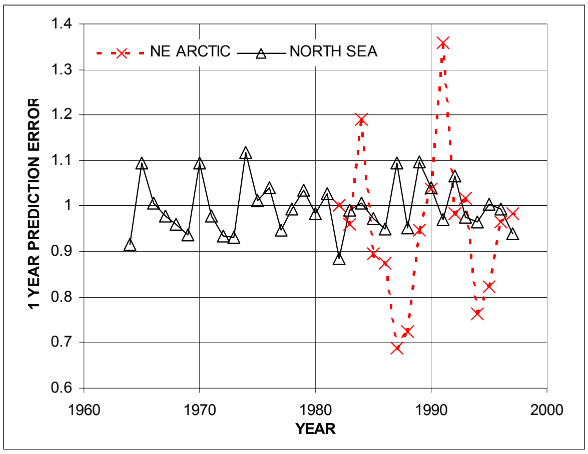

Figure 6.4 Error in prediction of total stock biomass due to using weight at age for the previous year.

corresponding to maximum growth (G_{max}) (Figure 3.3, WD 2.1, Bjornsson and Steinarsson 2002). Above and below T_{opt} growth falls off rapidly. Size at age can be determined from otolith microstructure analysis. By the time juveniles are caught in fall research trawl surveys, the relationship between size and year class strength may be obscured by density-dependent growth as benthic juveniles.

Two types of studies are recommended: 1) studies of larval and juvenile growth and size at age, and 2) studies of the relationship between size and age through the juvenile and adult periods. In both cases an emphasis is placed on determining the relationship between temperature and growth. Studies of larval and early juvenile growth can be accomplished through dedicated sampling of these stages as was completed in the US GLOBEC-Northwest Atlantic Georges Bank Program or through back calculation of size at age of juveniles caught in fall research trawl surveys. This level of analysis is not possible in older (1+) juveniles since the early daily rings become obscured. Studies of the effects of year class size on size at age through the juvenile and adult periods can again be accomplished by direct sampling or from back-calculation of size at age in this case using annual rings. A variety of approaches are available to estimate temperature ranging from direct observation to remotely sensed data to elemental and isotope ratios in fish otoliths.

The larval and early juveniles studies should provide the earliest possible estimates of year class size and lead to a better understanding of the physical and biotic factors affecting recruitment variability. These studies could lead to the development of a suite of simply measured proxies (e.g., temperature, size at age 60 days) for prediction of year class strength. Studies of growth and size at age in juveniles and adults could help to explain the observed variation in production and fishery yield.

6.4 A case study: incorporating growth into the assessment for Northeast Arctic cod

The Arctic Fisheries Working Group posed the following issues pertaining to Northeast Arctic cod:

1) Despite an increase in the capelin abundance (and consumption of capelin by cod) the size at age of cod has increased very little in the last couple of years. Some people claim that this is because the fishing mortality on small fish has increased considerably, so that the largest fish at a given age is caught and does not show up in the surveys.
2) Growth at ages 0–3 has been down in the last few years compared to earlier periods. Why?
3) Variation in growth rate for NEA cod may contribute strongly to variation in biomass and production.

These issues were addressed within the frame of the Workshop and a response to some of them was prepared:

Capelin is the most important prey species for cod in arcto-boreal ecosystems. The importance of capelin varies with respect to age. When abundant, capelin constitutes a high proportion of the diet of cod age 3 and older, whereas, younger cod feed on species also eaten by capelin (e.g., amphipods and euphausids). High capelin stock biomass will increase growth in older cod but may decrease growth in young cod through increased competition.

Since 1973 the abundance of the Barents Sea capelin has varied between 100,000 to 8 million tonnes. This variability affects the growth, condition (Yaragina and Marshall 2000), maturation (Marshall *et al.,* 1998), fecundity (Kjesbu *et al.,* 1998) and cannibalism of NA cod. Although central to the population dynamics of NA cod, information about the current and future status of the capelin stock cannot presently be incorporated into the assessment.

For the past two years, projections of capelin stock biomass for the upcoming year have been provided to the ICES Arctic Fisheries WG. This has stimulated interest in developing models, which utilize this information to forecast weight- and (or) maturity-at-age. Several different approaches have been investigated. Bioenergetic models have been developed based on estimates of the consumption of capelin and other prey species (Ajiad 1996). Empirical models, such as that of Ozhigin *et al.* (1994), which include capelin abundance, temperature and a term for observed length in the previous age class, have also been developed. Ecosystem models describing the impact of variation in capelin stock biomass and temperature on weight-at-age, are also currently under development (Filin WD 5.1). While progress has been made towards predicting

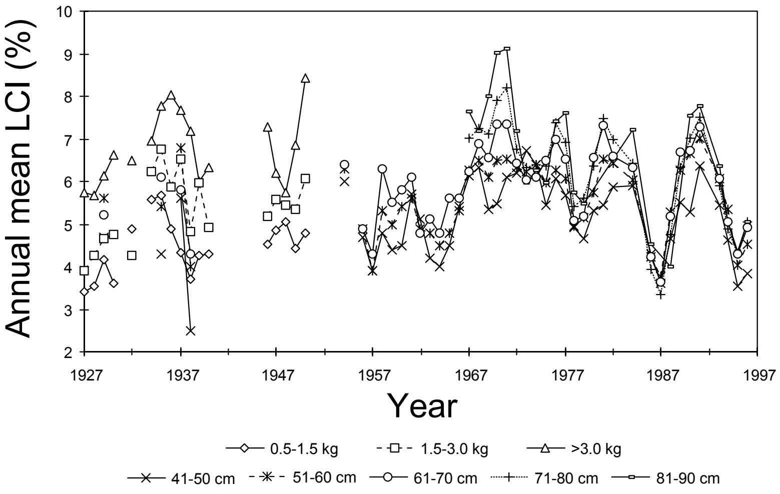

Figure 6.5 Time series of annual mean liver condition indices (LCI) (%) of Northeast Arctic cod. Capelin biomass was known to be below 1 million tons from 1985-1989 and from 1993–1996.

weight at age, very little research has been directed towards forecasting maturities.

Research related to hindcasting the proportion mature and weight-at-age is being conducted in parallel to the development of forecasting models. Currently the assessment assumes constant proportion mature and weight at age for the time period 1946 to 1982. Observations of size and maturity at age exist for historical time periods (Ozhigin *et al.,* 1994; Ponomarenko and Yaragina 1994). In future these data will be collated into a single series. Statistical models which predict proportion mature and length from capelin stock biomass (e.g., Marshall *et al.*, 1999) could also be used.

Traditionally, weight-, length- and maturity-at-age have been used to nowcast cod growth. Alternative indices of growth can provide a more detailed description of stock dynamics. For example, the Russian liver condition index (LCI) database provides a dynamic index of growth that responds rapidly to variation in the ecology in the Barents Sea and, in particular, capelin stock biomass (Figure 6.5 Yaragina and Marshall 2000). Although this information does not currently affect management directly, there is the possibility of developing new biological reference points based on bioenergetic considerations.

The ultimate goal of these efforts is to develop new biological reference points or refine existing biological reference points so that environmental and ecological factors that affect the long-term sustainability of the NA cod stock can be used to formulate management strategies. The harvest control rules should be sensitive to variation in growth rate.

6.5 Conclusions and recommendations

- Variation in growth rate can contribute substantially to variability in stock biomass, especially in cold-water stocks. This needs to be taken into account when setting fishing targets and reference points. This could be investigated further using the approach described by Dutil *et al.* (WD 1.5). Retrospective analyses of the effects of variation in growth on stock projections are recommended for stocks and periods when growth is changing rapidly.
- Variation in growth and condition can have a large impact on reproductive output. Variation in the quality (e.g., condition) of spawner biomass needs to be considered in addition to its quantity. Indices that take this into account, such as total lipid energy of mature females, will provide a better measure of reproductive potential than spawner biomass.
- The seasonal cycle of condition needs to be measured for additional stocks, especially fast-growing stocks.
- Maturity ogives and weight at length/age should be updated annually.
- Year class strength appears to be related to growth during early life history stages. Studies of larval and juvenile growth and size-at-age and their relation to size and abundance at adult stages are recommended.
- It may be possible to forecast weight, condition and proportion mature from indices of prey availability and temperature. Such work is on-going for Northeast Arctic cod and may lead to the development of new biological reference points that incorporate environmental and ecological factors and to harvest control rules that are sensitive to variation in growth rate.

7 Environmental and density-dependent influences during early pelagic life and consequences of this for later size and abundance

The issues motivating the discussion of this topic were:

- Is growth determined by abundance or environment?
- Is size as O-group an indicator of size at later stages?
- Is size at O-group an indication of abundance at later stages?

There are a variety of analytical stock-recruitment models, but all imply that density dependent mortality or growth is very influential in determining recruitment. In most cases we know little of how or when these processes operate in the early life history.

7.1 Stage-by-stage list of main factors influencing growth and survival

We structured the discussion stage-by-stage. Firstly we list the factors we concluded are most important for size at stage. This is followed up by a more elaborate overview of some of the topics in focus.

Eggs:

- Female condition, age and size of females, stage in the spawning season, temperature during gonad development.
- Temperature during egg development – egg stage duration.
- Exposure to contaminants.
- Egg surveys – Lofoten, Iceland, Irish Sea, Georges Bank (US GLOBEC), North Sea 1992.
- Dispersal.

Yolk sac larvae:

- Swim bladder, eye development related to egg size and female spawning history – may indicate a survival differential between recruit/repeat spawners.
- MARMAP surveys show correlation between early larval abundance and subsequent recruitment (in Werner *et al.,* 1999).
- Small larvae may suffer lower initial survival than large larvae.

Larvae:

- No evidence that growth is density dependent.
- Temperature is in general the major explanatory variable of spatial and temporal patterns in growth rate of larvae.
- Sometimes food appears to be limiting, sometimes not.
- Food availability may be affected by food concentration, turbulence, turbidity, irradiance.
- Larvae have a trade off between high temperatures and food availability.
- Vertical distribution/feeding – interaction between daylength/irradiance and wind stress.
- Passive drifters.

Pelagic juveniles:

- Response to predators changes with development.
- Aggregated in response to environmental gradients.
- Refuge response - hide under jellyfish and debris.

Settlement:

- Schooling behaviour begins.
- We expect compensatory processes to cut in at settlement – but did not define the most important processes.
- Habitat must be important in setting the carrying capacity.
- Do compensatory processes affect survival or growth or both – how?

7.2 Egg stage

The reproductive potential of a stock (*sensu* total egg production) integrates many factors affecting the growth and reproduction of spawners (Marshall *et al.,* 1998). Maturity and fecundity are influenced by density-dependent (Ware 1980) and/or density-independent (Rijnsdorp *et al.,* 1991) factors affecting growth. Variation in the physiological condition of spawners affects fecundity (Hislop *et al.,* 1978; DeMartini 1991; Koslow *et al.,* 1995; Ma *et al.,* 1998; Kjesbu *et al.*, 1998) and poor condition can result in skipped spawning seasons (Burton *et al.,* 1997). The size and condition of spawners influences offspring viability (Chambers 1997; Trippel *et al.,* 1997; Trippel 1998; Marteinsdottir and Steinarsson 1998).

In Atlantic cod the size, age and condition of females affects the size of eggs and larvae (Kjesbu 1989; Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1998). Larvae from large eggs have morphological attributes, which may result in higher growth and/or survival (Knutsen and Tilseth 1985; Solemdal *et al.,* 1992; Marteinsdottir and Steinarsson 1998). Positive correlations have also been detected between female condition and larval feeding success and growth rates (Marteinsdottir and Steinarsson 1998). Parental effects on offspring could also interact with environmental conditions. For example, in Atlantic cod, older/larger females begin to spawn earlier in the season and continue longer than younger/smaller females (DeMartini and Fountain 1981; Parrish *et al.*, 1986; Buckley *et al.,* 1991; Hutchings and Myers 1993). The removal of older/larger females from the stock, e.g., via high fishing mortality, will shorten the spawning season and change the temporal profile of egg production. This could affect degree to which larvae overlap in time with optimal conditions for survival (Kjesbu *et al.,* 1996).

A number of structural characteristics of fish are set early in life and appear to have long-term consequences for growth performance. These include vertebral numbers and myotomes. Temperature during the egg stage seems to be a determinant of these properties.

7.3 Larval stage

Buckley (WD 6.3) described work from Georges Bank which shows that field growth of cod and haddock larvae follows a parabolic relation with temperature, but with an optimum way below that which is determined in the laboratory. However, both field and laboratory rates coincided at the field optimum temperature. The observed decline in growth at temperatures above the 7°C optimum was taken as evidence that larval growth was food limited at higher temperatures on Georges Bank. That the food demands of larvae could not be met in the field explains why the relation between growth and temperature deviates from that for laboratory situations with unlimited food.

We rarely find close links between fish growth and zooplankton abundance, but it is expected that they exist. Partly this may be because we are unable to adequately measure the appropriate components of the zooplankton for each development stage of larvae or juveniles. Zooplankton signals may also be confounded with temperature effects. Furthermore, earlier studies have indicated that larvae are too dilute to impact the overall production of their planktonic prey and that it is the concentration or availability of prey rather than the total prey biomass that is limiting.

Otterlei *et al.* (1999) show that larval growth is not exponential – a Gompertz curve is more applicable. Weight specific growth increases with temperature, but as ration is reduced the optimum temperature decreases.

Skreslet (WD 6.4) described a new programme called UVAC to investigate the effects of ultra-violet radiation (UVR) on cod egg and larval development. The main possible ways in which UVR may effect cod are through:

1) Lethal effects on cod eggs and larvae.
2) Sublethal effects that restrict function of organs and reduces individual growth.
3) Effects that reduce survival and growth of food organisms.

7.4 Pelagic early juveniles

Suthers and Sundby (1996) compared the growth rate of Arcto-Norwegian pelagic early juvenile cod in the Barents Sea with that of the Canadian 4X stock, off southwestern Nova Scotia. They found that the growth rate of the former stock was more than twice that of the latter. While water temperature and zooplankton biomass were found to be important factors, as expected, and genetic differences could be of importance, they concluded that the difference in light conditions plays a decisive role. Between early May and mid-July there is 48% more time for visual feeding at latitude 70° of northern Norway compared with 43° of south-western Nova Scotia. The hypothesis that longer days enhance the growth of larval and juvenile cod is supported by laboratory experiments (Folkvord, 1991; Folkvord and Otterå, 1993). Furthermore, recent work by Helle (2000) found no diurnal patterns in stomach fullness or degree of digestion in Barents Sea cod juveniles. This suggests that feeding is continuous throughout the day and night, allowing for faster growth than is achieved by conspecifics further south.

Campana (1996) showed that for Georges Bank cod size at the pelagic juvenile stage is highly correlated with year class strength. Differences in growth rates and associated exposure times to high larval mortality rates were sufficient to account for much of the 4-fold difference in adult abundance among the year classes.

Size dependent prey mortality was discussed and there was general agreement that “bigger is better”, i.e., smaller fish are more prone to predation than larger conspecifics. This applies to several stages.

7.5 Pelagic 0-group and later stages

Ottersen and Loeng (2000) and WD 6.2 address the general hypothesis that survival of a cohort is directly related to growth rates during the pre-recruit period for marine fish (Anderson, 1988; Anon., 1965; Cushing, 1974; Meekan and Fortier, 1996). A close link between length and year class strength at the 0-group stage was found for Arcto-Norwegian cod and haddock. Furthermore, the connection holds also between length at the 0-group stage and abundance at age 3. Both length and abundance were closely related to temperature (Loeng *et al.*, 1995). Interannual variability in the temperature conditions was concluded to be the underlying cause of the covariability between growth and year class strength (Ottersen and Loeng, 2000). They furthermore suggest that for stocks at the high latitude end of the overall range of the species the environmental signal generally tends to over-ride density-dependent effects on growth. High temperature will cause a high production of prey items leading to higher growth rates and higher survival through the vulnerable larval and juvenile stages. The duration of the high-mortality and vulnerable stages is also decreased by higher temperature directly increasing the development rate.

Brander and O'Brien (WD 6.1) compared trends in weight at ages 1 to 4 for North Sea cod with the deviation in bottom temperature during the year in which they were spawned. It appears that temperature during the year in which they were spawned determines 30% or more of the subsequent variability in weight at age. The trends in weight at ages 1 and 2 do not match the temperature trend as well as is the case for ages 3 and 4, but are still statistically significant. The fitted regressions up to age 6 can be used to forecast the weights at age up to five years ahead, however the analysis assumes a linear relationship, which may be misleading at warmer temperatures (see Figure 3.3).

An alternative explanation of the interannual variability in weight of North Sea cod is provided by Cook *et al.* 1999, who related it to total stock biomass, indicating a density dependent effect. This result depends on data for the most recent years in the analysis, for which the full age composition was not available, and should therefore also be treated with caution.

However, the strong positive relationship seen in North Sea and Barents Sea cod between temperature conditions during the cod’s early life stages and subsequent growth is not present for all stocks. Campana (1996) found that temperature was a significant, but not necessarily a primary, source of within-year and between-year variations in growth of Georges Bank cod. Furthermore, Swain (see WD 6.5) found no positive relation between temperature in their first year and weights at subsequent ages for southern Gulf of St. Lawrence cod. Indeed, air temperatures during their first spring and summer were *negatively* correlated with weights at subsequent ages for southern Gulf cod. Variation in size at age of southern Gulf cod appears to be strongly influenced by size selective mortality and density dependent growth. For this stock, these factors appear to exert a stronger effect on variation in size at age than temperature conditions during early life history stages. It is possible that confounding with these other factors obscured any effect of early temperature conditions on later weight at age of southern Gulf cod.

8 Bioenergetics models

A prerequisite for bioenergetics modelling being a tool with sufficient power to explain growth variations in fish stocks is the establishment of a model where the swimming activity as well as the dynamics of lean soma, energy stores, and gonads enter as variables which depend on body size, food availability, photoperiod, and temperature. This implies, of course, that the model takes the internal regulation of energy allocation to the dependent variables into consideration.

A simple, traditional model may however be applied to elucidate the effects of some of the variables causing growth variations. The daily increment of somatic energy of a fish may be described as:

$$\begin{aligned} G_s &= \kappa f C_{max} - M_{st} - M_a - G_g = \\ &(1 - \alpha)\, \beta f C_{max} - M_{st} - M_a - G_g = \\ &K(f,W,T)\, f H(W,T) - N(W,T) \\ &- A(V,WT) - P(\,t,W) \qquad (8.1) \end{aligned}$$

where C is the food (energy) consumption rate [the feeding level f ($0 \le f \le 1$) multiplied by the maximum consumption rate $C_{max} = H(W,T)$], T the temperature, t the time of the year in daily steps, V the swimming pattern (modes and speeds), W the body weight, β the absorbed part of the consumed food, α the total costs associated with processing of the consumed food, $(1 - \alpha)\ \beta = K(\,f,W,T)$ the net conversion efficiency (κ), $N(W,T)$ the standard metabolism (M_{st}), $A(V,WT)$ the swimming activity costs (M_a), and $P(\,t,W)$ the increment in gonadal energy (G_g). The gonadal production is set to zero in juvenile fish and is put into a cyclic time (t) function in adults. The increment in gonadal energy is described by an optional function (e.g., linear or exponential) from onset of gonadal growth and until spawning, and the total gonadal energy is released instantaneously around the middle of the spawning season.

Different versions of this model concept have mostly been used to predict growth under well known feeding regimes in aquaculture production (From and Rasmussen, 1984) and to produce approximate estimates of food rations of fish populations in the natural environments (Kitchell *et al.*, 1977; Kerr, 1982; Hansson *et al.*, 1996). One major problem encountered in the latter case is the general lack of information about swimming costs (e.g., Krohn *et al.*, 1997), which restricts considerably the precision of the model. The possibility of food limitation may however be evaluated by comparing $C_{max,}$ as estimated from laboratory experiments, with the food consumption rates quantified by use of the gastric evacuation method in which field data on amount and composition of stomach contents are combined with information about gastric evacuation rates. Further, approximate figures for swimming costs may be obtained by calibrating the bioenergetics model to these consumption rates. These approaches are examplified by a study on saithe (*Pollachius virens*) in Andersen (WD 7.1). Performance of the exercises on a

Table 8.1. Comparison of maximum daily ration values as calculated from different literature sources.

Body weight	Temperature	C_{max} (kJ fish^{-1} day^{-1})		
(g)	(°C)	Jobling (1988)	Krohn *et al.* (1997)	Vestergaard and Andersen (submitted)
1000	1	63	53	
1000	4	86	75	
250	10	47		45

variety of cod stocks where appropriate data are available may give some general trends or ideas about food limitation and swimming costs. However, in the long view a more elaborated model, in which the regulation of energy acquisition is taken into consideration, should be developed and the necessary data basis be collected. The suggestions of Broekhuizen *et al.* (1994) and Van Winkle *et al.* (1997) may give some ideas about construction of the conceptual framework for development of such a model.

8.1 Limitation of growth by food/temperature

8.1.1 Maximum food ration, C_{max}

Allometric and temperature relationships

C_{max} forms the upper limit of the feeding capacity of a fish. The influences of temperature and fish size have been examined in some studies on cod.

Jobling (1988) described this relationship by a polynomial function of temperature and a power function of body weight estimating the parameters from data on cod fed capelin (*Mallotus villosus*) which were acquired from Johnsen (1981) and Braaten (1984):

$$\ln C_{max} = (0.104\ T - 0.000112\ T^3 - 1.500) + 0.802 \ln W \quad (n=50;\ R^2 = 0.91)$$

C_{max} is expressed in kJ day^{-1}, T is the temperature in °C (range 3–16°C), and W is the weight of the fish in grams (range 35–750 g). The equation describes the temperature optimum as being independent of fish size. However, Jobling (1988), referring to McKenzie (1934), also points out that appetite appears to peak at a higher temperature in small (30–45 cm) than in large (70–80 cm) cod, appetite being maximal at 16°C for small and 14°C for large cod.

Krohn *et al.* (1997) described the maximum ration consumed by a 1 kg cod as:

$$C_{max} = 97.9\ (0.075\ T + 0.468)$$

This expression (kJ day^{-1}) was based on feeding rates measured in grammes (at 1°C and 4°C from Waiwood *et al.* (1991) feeding shrimp (*Pandalus montagui*) to the cod), which were converted into energy figures using the energy density of 4.66 KJ/g for the food of North Sea cod of 40–49 cm (Daan, 1975), and further multiplied by factor of 1.2 to correct for the feeding regime applied by Waiwood *et al.* (1991). They fed the cod to satiation once a day, while Braaten and Gokstad (1980) found that cod fed more often than that could on average eat 1.2 times more.

Vestergaard and Andersen (submitted) fed a group of cod (0.25 kg b.w.) to satiation once a day with sandeel [energy density: 5,99 kJ (g ww)$^{-1}$]. The average C_{max} over time (46 days) was 45 kJ fish^{-1} day^{-1}.

The above findings are compared in the Table 8.1. The C_{max} values calculated from Jobling (1988) are 15–20% higher than those from Krohn *et al.* (1997). The may be due to the (slower digested) crustacean food applied in the experiments on which the results of Krohn *et al.* (1997) are based.

Björn Björnsson (WD 2.1) has performed an extensive set of growth experiments on cod fed capelin to satiation. Body size of the cod and temperature were varied between experiments. Unfortunately, there are no energy measurements of the cod, but the energy density of the prey has been measured. Therefore, it is recommended that the parameters of a model describing the effect of temperature and body size on C_{max}, are estimated from these data.

Influence of prey characteristics

In bioenergetics modelling it is usually assumed that maximum energy intake is unaffected by the prey type. The feeding capacity of a fish is presumably closely related to its gastric evacuation performance. Andersen (1998, 1999) demonstrated that gastric evacuation of ingested fish or small crustaceans (euphausids) can be described independently of meal size by a simple square root function of total stomach content weight and that gastric evacuation of amounts of energy is almost unaffected by the energy density of these prey. So far, there is no discrepancy between the evacuation capacity and the model assumption concerning maximum energy intake. However, medium size crustaceans like *Pandalus* and *Crangon* are evacuated considerably slower than might be expected from their energy densities (evacuation took almost twice as long as that of fish prey of similar energy density) - presumably because their exoskeletons work as a barrier against chemical and mechanical break down. Echinoderms and large crustaceans (e.g., *Nephrops norvegicus*) seem to be evacuated at an even slower rate (Bromley, 1991). The range of energy densities covered by Andersen (1999) (and including some subsequent experiments) is 3.4–6.5 kJ g^{-1} wet weight for the fish prey. Some of the main prey of North Sea cod and Baltic cod (herring and sprat), obtain energy densities close to 12 kJ g^{-1} ww. It is not known whether the energy control of gastric evacuation is maintained at such high energy densities or whether it breaks down as it was the case for cod fed processed (formulated) food (dos Santos and Jobling, 1988). At the moment, there are ongoing gastric evacuation experiments at the Danish Institute for Fisheries research (DIFMAR) on cod and whiting fed prey of very high prey energy densities (sprat; 11.5 kJ g^{-1} ww).

In conclusion, it may be expected that the assumption of C_{max} being independent of prey energy density is valid for fish prey and small crustaceans only. Therefore, food limitation ought to be redefined as a more complex concept, where some kind of prey 'quality' is included also.

Another issue, which is not taken particularly into consideration in bioenergetic modelling, is that echinoderms and larger crustaceans give a considerable egestion loss (influencing the β term of equation 8.1). There is clearly a need for more data.

The slower evacuation combined with the lower nutritional value of echinoderms and larger crustaceans should be reflected in lower growth rate of cod which are relying to a large extent of these prey types compared to cod which are feeding primarily on fish prey. In particular, it might be interesting to examine the growth pattern of cod in the period of its life where the transition from invertebrate to vertebrate food occurs. Differences in cod stocks regarding the body size at which this transition takes place as well as the duration of the transition period may be reflected in different growth characteristics.

8.1.2 Food rations of natural populations as estimated by the gastric evacuation method

The change of stomach content in a cod during time as a function of food intake and gastric evacuation may be described by:

$$dS/dt = C - \rho S^{\alpha} \text{ g h}^{-1}$$

where S is total weight of the stomach content, t is the time, C is the consumption rate, and ρ and α are the parameters in a power model describing gastric evacuation. We have no consistent information about the meal sizes ingested in the field. It is therefore crucial that the evacuation model describes gastric evacuation independently of meal size, i.e., evacuation depends on the instantaneous amount of stomach contents only. As mentioned in Section 8.1.1 a square root version (α=0.5) of the model has been shown to posses this ability. Temperature, body size, and prey characteristics influence the rate constant ρ (Andersen, 1999; Andersen et al., submitted) and a universal set of parameter values applies to different predatory gadoids including cod:

$$\rho = 0.00132\, L^{1.44}\, e^{0.078\, T}\, E_d^{-0.875} \text{ g}^{0.5} \text{ h}^{-1}$$

where L is the total length (cm) of cod, T is the ambient temperature (°C), and E_d is the energy density of the stomach content (kJ g^{-1} wet weight). Over time and population the average consumption rate may then be estimated by:

$$C_{\text{avg}} = \text{avg}\,[\,\rho S^{0.5}\,] \text{ g h}^{-1}$$

where S is the total stomach content of a cod stomach sampled in the field and avg denotes either a simple average over samples and time when random stomach sampling are undertaken or a more elaborated average for stratified sampling designs. In the North Sea, the stomach contents are usually pooled into cod length groups. In that case the calculations become more complicated and some bias will inevitably be introduced (Andersen, WD 7.1).

8.2 Acquisition of information about swimming activity costs

Approximate figures for the swimming costs may be obtained by calibrating the swimming activity term of the bioenergetics model to the gastric evacuation derived consumption rates. The parameter values of the gastric evacuation model appear from Section 8.1.2. The terms and parameters in the bioenergetics model (equation 8.1) needed for the exercise are described below:

Maximum food ration, C_{max}

See Section 8.1.1.

Net conversion efficiency, κ

For a carnivorous fish Brett and Groves (1979) enumerate the average energy partitioning of the dietary energy. The energies of faeces, exogenous excretion, and costs of food processing (heat increment) amount to 20, 7, and 14% of the ingested energy, respectively, which give a value of 0.59 of the net conversion efficiency κ. Hansson *et al.* (1996) find corresponding figures of 17, 7, and 14% for cod (κ = 0.62), while a value of κ of 0.67 can be calculated from Krohn *et al.* (1997) who use other literature sources (heat increment: 13%; faecal + excretion loss: 20%).

From experimental food conversion data on saithe fed Norway pout (*Trisopterus esmarki*), Andersen and Riis-Vestergaard (submitted) find that κ depends on feeding level as well as body size (Figure 8.1) - ranging f. ex. from 0.47 for a saithe of 1 kg at a feeding level f of 0.2 to 0.70 for a saithe of 3 kg fed to satiation. This trend could be explained by an increased deposition of lipid at higher food rations (incorporation of lipid is less costly than that of protein). Estimates of κ may be expected to be different when other food types are applied [e.g., egestion (see Section 8.1.1) and heat increment for larger crustaceans and fat prey fish, respectively]. Thus, the net conversion efficiency varies quite a lot, and there seems to be much room for improvement - even with this simple bioenergetics model approach. From and Rasmussen (1984) and Elliot (1976) (*cited in* Anon., 1997) also demonstrate the variation in the terms entering the calculation of κ. If, for simplicity, a constant κ is required, then a general value of 0.66 is obtained from the data on saithe, which is within the range of the findings on cod of the above authors.

Standard metabolism

A variety of measurements covering a temperature range of 3–15°C have been performed on cod ranging from 80 g to 3 kg body weight (e.g., Saunders, 1963; Bushnell *et al.*, 1994; Steffensen *et al.*, 1994; Schurmann and Steffensen, 1997). The findings are generally high according to new results by Jens Peter Herrmann, Hamburg University (pers. comm.). More work based on new refinements in the applied methodology is needed. Meanwhile, it is recommended to scrutinise the present literature and to set up a common equation relating standard metabolism to temperature and body size.

Somatic growth in natural populations

Data on the total somatic energy content of a cod by age, preferably on a seasonal (monthly–quarterly) basis, are needed. These may be obtained by combining quarterly ALKs with matching LW-relationships and energy densities. It is acknowledged that energy density data are scarce. These may be obtained indirectly in cases where HSI-indices are available. Alternatively, yearly figures for total somatic energy have to be used. Then, data on cod subsequent to spawning are preferred because the use of data at that state of the annual cycle of cod growth and maturation eases the modelling work and minimises the assumptions that have to be made.

Costs of gonadal production

The energy of the total egg production of a cod by age (fecundity times energy content of an egg) is combined with the maturity index to give an estimate for females. Males may be treated separately along the same lines ortheir reproductive costs may be assumed equal to those of females.

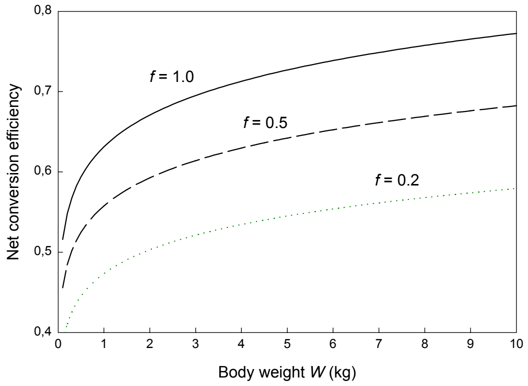

Figure 8.1. Net conversion efficiencies in saithe fed Norway pout. Effects of body size and feeding level.

Energy densities of the main preys

The consumption rates estimated by the gastric evacuation method have to be converted from wet weight to energy figures before they can be applied as input to a bioenergetics model. It is therefore necessary to have information about the energy densities of the main preys of the cod stock on a seasonal basis matching the stomach contents data (according to Sections 8.1.1 and 8.1.2, these energy densities are actually needed in advance for estimation of the consumption rates).

8.3 Identification of cod stocks which may serve as case studies (for Sections 8.1 and 8.2)

There are available data on the seasonal dynamics of stomach contents as well as on seasonal dynamics of body parts and gonads for cod in the southern Gulf of St Lawrence (Schwalme and Chouinard, 1999) and for the north-east Arctic cod (Yaragina and Marshall, 2000; Yaragina, personal comm.). For the latter area, extensive time series studies have been performed. Appropriate data on stomach contents are available for cod in the North Sea and in the Baltic, while the seasonal dynamics of the different body parts are not so well described for cod in these areas. However, it should be possible to use these two stocks also to evaluate food limitation and swimming activity level.

8.4 Towards a mechanistic bioenergetics model: partial substitution of data by causal relations

Incorporation of mechanisms for regulation of energy acquisition and allocation into the model may significantly improve the power to predict growth *variations*. It is suggested that four state variables are included:

- length
- lean soma
- energy storage
- gonads

The regulation of energy acquisition and allocation may be based on the following rules:

> A nutritional state index is used to provide feed back in the formulations for consumption and mortality, and for energy allocation: respiration, somatic growth, sexual maturity and spawning.
>
> Allocation of energy to gonadal development and respiration is treated as a daily demand function (demand of energy for gonadal development is modulated as a function of nutritional state).
>
> Allocation of energy between increment of length and body storage is controlled by the nutritional state index as is depletion of energy from the different body parts.

Concerning energy allocation there are data available for commencement of the modelling work. For example, together with some minor sets from the northwest Atlantic cod the extensive data on northeast Arctic cod (Yaragina and Marshall, 2000) may provide material to answer questions like: how much energy does a fish need in order to enter spawning modus (and how is the allometric relationship)? Above this threshold value: is fecundity dependent on the nutritional status or is it exclusively an either-or situation?

A general revision of the protocols for collection of data on routine surveys to meet the above data needs (i.e., length, total weight, gutted weight, liver weight, maturation index, and gonadal weight of individual fish) would be of invaluable importance. This applies not only to development of the mechanistic model but also to acquisition of the necessary understanding of the dynamics and variations of growth in general. The model is just the framework.

Allocation of food into lean soma and energy stores depends on a complex interaction of a variety of variables as reflected in the net conversion efficiency**.** Larger (adult) fish deposit relatively more lipid than do smaller (juvenile) fish), which may be modelled as a function of ration level (Andersen and Riis-Vestergaard, *submitted*). Laboratory work is a great help in providing more data on the general energy allocation as a function of a variety of internal (body size, nutritional state, activity level) as well as external (food ration and quality, temperature, photoperiod) variables. For example, do adult cod give priorities to deposition of protein and lipid the same way throughout the feeding season or is there an intrinsic mechanism, which brings about a favour of deposition of lipid at some time before over-wintering and spawning? Does a change in activity level primarily affect the deposition of lipid?

The relationships between food availability and activity and food consumption rates as well as locomotion in general are probably the most difficult parts to model because of the scarcity of data and the concomitant low level of knowledge. Different approaches have been applied in order to quantify the costs of locomotion. They have primarily been based on theoretical considerations (optimal foraging theory, stochastic search strategies, optimum sustained swimming speeds at migrations etc.) together with few field measurements of swimming speed and laboratory determinations of swimming costs. In some studies, activity levels measured as a function of food consumption in the laboratory (Edwards *et al.*, 1972; Björnsson, 1993) have been extrapolated to field situations (Kerr, 1982; Krohn *et al.*, 1997). Recently, hydro-acoustic methods have been used to measure swimming speeds of individual fish in the field [Arrhenius *et al.*, 2000; Pedersen (*submitted*)]. All approaches applied hitherto have their own limitations. However, the development of ultrasound transmitters or data storage tags connected to different types of sensors seems to offer outstanding possibilities for acquisition of extensive datasets on f. ex. locomotion and feeding of individual fish. Such types of data would be a great step towards development of activity models describing the relationship between food availability and activity as well as other types of behavioural patterns associated with for instance spawning and feeding migrations, and avoidance of low/high temperatures and other changes in environmental variables.

8.5 Recommendations

According to the above sections it is recommended to:

1) Compare laboratory derived maximum consumption rates with consumption rates estimated from field data on stomach contents for selected cod stocks.
2) Calibrate activity levels in an existing bioenergetic model by use of the above field estimates of food consumption rates.
3) Develop a mechanistic model containing a number of state variables as well as rules for regulation of the acquisition and allocation of energy in cod. It is further recommended to produce revised protocols for collection of data on research vessels and to conduct more experimental work in order to meet the data demand and to parameterise the model.

9 Genetic variation of growth

Geographical variation in life history traits has been observed among stocks of cod. One observed trend is for faster growth and lower age at maturity for cod which occur in warmer water (Brander 1994, Hutchings and Myers 1994, Figure 9.1). Genetic evidence for population differences among cod have been reported using nuclear DNA (Bentzen *et al.*, 1996), microsatellite DNA (Ruzzante et al 1996), mitochondrial DNA (Carr *et al.,* 1995) and allozymes (Mork *et al.,* 1985). However, these analyses vary in their sensitivity to detect population differences and do not provide information on the phenotypic variation among stocks. An approach reported on at this Workshop has been used to untangle environmental and genetic contributions to phenotypic variation among populations of Atlantic silverside which occur along the east coast of North America (Conover *et al.,* 1997). This experimental approach uses "common garden or environment" experiments to examine the importance of environmental and genetic factors to observed phenotypic differences. In a set of experiments we used common garden experiments to determine the response of cod originating from the Gulf of Maine (larger size at age) and from the Grand Banks off Newfoundland (smaller size at age) to different temperatures. Evidence for a stock-related growth response to temperature was found for the larval stage while differences in energy allocation and food conversion efficiency were found for 0 group juveniles. These responses may be stock specific and could be related to ecological factors (i.e., growing season) which are particular to the different stocks. This approach may be useful in determining the relative contribution of environment or genetics to the growth variation observed among the various populations of cod stocks.

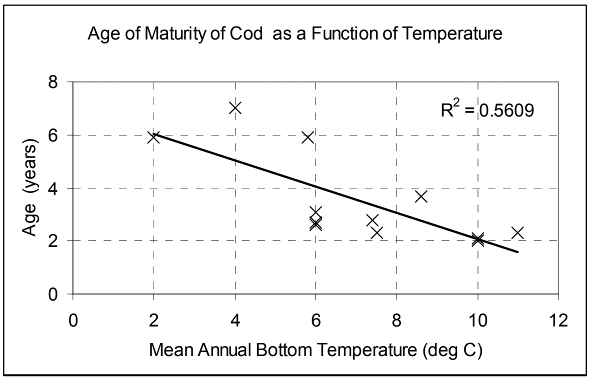

Figure 9.1. Age of maturity for the stocks included in the Workshop database.

A similar study which compared Norwegian coastal and northeast Arctic cod found stock-specific difference in mean weight at age, but no countergradient latitudinal variation in growth capacity of the two larval cod stocks (Otterlei *et al.,* 1999). Differences in growth rate between these stocks were minor compared with the effects of temperature.

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11 Conclusions with regards to Terms of Reference

11.1 TOR a) Develop models of growth in order to improve the quality of stock forecasting

11.1.1 Correlation models

Different models correlating growth with temperature and body size have been put forward. Although they do not necessarily explain the causal relationships they are important pointers to where interaction and relationships may be expected. i.e., besides being useful to improve prediction of growth *per se* they should form important elements in the considerations of where to put the effort in future data collection and establishment of bioenergetic models as well as other modelling approaches.

11.1.2 Bioenergetic models

An approach involving bioenergetic modelling is required to understand how e.g., temperature and food ration interact to influence growth. However, a prerequisite for bioenergetics modelling being a tool with sufficient power to explain growth variations in cod stocks is the establishment of a model where the swimming activity as well as the dynamics of lean soma, energy stores, and gonads enter as variables which depend on body size, food availability, photoperiod, and temperature. This implies, of course, that the model takes the internal regulation of energy allocation to the dependent variables into consideration. A mechanistic model, containing a number of state variables and rules for acquisition and allocation of energy, should be developed. It is suggested that four state variables are included:

length
lean soma
energy storage
gonads

The regulation of energy acquisition and allocation may be based on the following rules:

- A nutritional state index is used to provide feedback in the formulations for consumption and mortality, and for energy allocation: respiration, somatic growth, sexual maturity and spawning.
- Allocation of energy to gonadal development and respiration is treated as a daily demand function (demand of energy for gonadal development is modulated as a function of nutritional state).
- Allocation of energy between increment of length and body storage is controlled by the nutritional state index, as is depletion of energy from the different body parts.

(The use of other modelling approaches may be necessary in order to prepare the above rules - see the paragraph below). Further laboratory and field work will be needed to parameterise and validate the model. Among these, protocols for collecting biological data on research surveys should be reviewed in order to meet the data needs of the model as well as to ensure that they are appropriate for investigation of growth in general (see the other TORs).

Preliminary studies, which may give some general information about swimming activity levels and causes of growth limitation, should be performed on the basis of existing data:

Comparison of laboratory derived maximum consumption rates with consumption rates estimated from field data on stomach contents for selected stocks.

Calibration of activity levels in existing bioenergetic models by use of the above field estimates of food ration.

11.1.3 Other model approaches

A variety of different modelling approaches have been applied. Each of these has its own particular uses and limitations. A more complete approach to predicting individual growth may originate from the integration of life history models (e.g., maximising egg production over an individual lifetime), stochastic modelling of food acquisition and predator avoidance, bioenergetic models, and use of neural networks and genetic algorithms in models. However, progress is likely to be slow until more elaborated data sets on the growth, maturation, and environment of individual fish are available against which to develop and test the models. Several of the proposals and recommendations for further work address this need.

11.2 TOR b) Describe major sources of uncertainty in the prediction of growth rates and advise on further studies to reduce this uncertainty

11.2.1 Review of the main factors determining growth rates of cod:

Potential for growth is determined by:

- Genetic characteristics, although current information suggests that their impact on potential growth is small.
- Phenotypic factors, such as vertebra number and myotome counts, which are set by exposure to e.g., temperature, contaminants and irradiance, at particular stages in the early life, and maternal factors related to the physiological status of the spawning female.

Realized growth is determined by:

- Ambient temperature, i.e., the temperature actually experienced by the fish (see Section 4.2).
- Food availability, encounter rate and quality.
- Seasonal sensitivity to temperature and food (may be different for mature and immature fish).
- Other factors include irradiance, daylength, maturity, spawning season, oxygen availability, and contaminants.

11.2.2 What are the most important things to do to improve predictions of growth

1. Assemble data on weight, length and maturity from research vessel surveys for future use in modelling growth.
2. Review protocols for collecting biological data on research vessel surveys to ensure that they are appropriate for investigating growth.
3. Conduct further laboratory studies of relationships between growth, age, size, ration and temperature on wild and cultured fish to compare with results on reared individuals, and on fish from various stocks.
4. Maintain monitoring and forecasting programmes for environmental variables, especially temperature.
5. Develop methodology for estimating appropriate measures of mean temperature exposure and food exposure, including deployment of data storage tags, modelling of migrations in relation to spatially and temporally variable temperature and food distributions.
6. Incorporate probabilistic variability in weight at age into current forecast tools used in stock assessment.

11.3 ToR c) Assess the contribution of growth rate variability to the observed variability in stock biomass and stock forecasts

1. Variation in growth rate can contribute substantially to variability in stock biomass, especially in cold-water stocks. For example, the striking difference in the rate of recovery of the southern Gulf of St. Lawrence cod stock from collapses in the mid 1970s and early 1990s is partly attributable to a large difference in weight-at-age between the two periods.
2. Retrospective analyses of the effects of variation in growth on stock projections should be conducted for stocks and periods when growth rate is changing rapidly.
3. Variation in growth and condition can have a large impact on reproductive output and thus future stock biomass. Variation in the quality (e.g., condition and size composition) of spawner biomass needs to be considered in addition to its quantity. Indices that take this into account, such as total lipid energy of mature females, will provide a better measure of reproductive potential than spawner biomass.
4. Use of condition indices to improve prediction of reproductive output requires a knowledge of the seasonal cycle in condition. This seasonal cycle needs to be measured for additional stocks, especially fast-growing stocks.
5. Maturity ogives and weight at length/age should be updated annually to provide accurate measures of variation in spawning stock biomass and of growth rates.
6. Year class strength appears to be related to growth during early life history stages. Studies of larval and juvenile growth and size-at-age and their relation to size and abundance at adult stages are recommended to improve understanding of the effects of growth rate variability at early life history stages on future stock biomass.

11.4 ToR d) Recommend standard methods for comparing growth rates

We recommend quoting growth in terms of specific rates:

Specific Growth Rate (G) = $(\ln(W_{t2}) - \ln(W_{t1}))/(t2-t1)$, where W is either weight or length or some measure of size, and t is in days.

11.4.1 What is growth?

Changes in fish weight over time are a composite of changes in length and changes in weight at length. If the body mass of a fish may be considered as being made up of structural and reserve tissues then condition is essentially the ratio of reserve/structure. Structural material includes skeletal, nervous and essential organs. Reserve tissue can be metabolised in the event of starvation, and includes gonads in mature fish. Death may be considered to occur at some minimum ratio of reserve/structural mass. Body length may be considered as an index of structural mass.

The weight-at-age data available from eastern Atlantic assessments are usually based on commercial catch information and do not necessarily reflect size at age in the stocks. For western Atlantic stocks, weight at age is based on research vessel survey data. In addition, the assessment data are arithmetic mean values, derived in a variety of ways for different stocks. Attempting to model these data in relation to environmental information and compare these with results from laboratory experiments on individuals, without being fully aware of the limitations of these data, may be of dubious value.

Usually, weight data are derived values, based on measurements of length, and the application of a regression relationship between weight and length. Immediately, a component of the variability in weight at length has been eliminated from the derived data set. The expression of size at age in terms of arithmetic mean weights at age further distorts the variability, because neither length nor weight at age are necessarily normally distributed.

Ideally, a research exercise intended to expose the relationships between environment and stock effects on growth in the field should be founded on the basic observations of length, weight and age at the individual level. These could be derived from commercial catches or from research surveys.

Finally, changes in neither population mean length nor weight give unbiased estimates of growth rates. Size selective mortality causes bias as demonstrated for Southern Gulf of St. Lawrence (4T) cod. Back-calculation of individual growth histories from scales and otoliths is currently the only means of obtaining unbiased measures of growth of the survivors.

Potential estimates of condition include liver weight, RNA/DNA, protein content, lipid and water content.

11.4.2 Recommendations

A prelude to any future workshop in growth should be a concerted action to extract the basic length distributions, and individual data on length, age, weight and maturity from research vessel survey databases.

Back-calculation of individual growth histories from scales or otoliths should be developed as a method to obtain unbiased measures of the growth rates of survivors. Back-calculation studies are also a good method of investigating the intensity and direction of size-selective mortality.

The use of otolith isotopic ratios for assessing individual temperature histories should be developed to generate the data needed for modelling growth.

11.5 ToR e) Develop specific case studies which will be relevant to the advice of ICES

Work on incorporating growth into the assessment for Northeast Arctic cod was described. Models to forecast weight- and/or maturity-at-age from temperature and prey biomass (capelin) have been developed or are under development. Condition indices provide a dynamic index of growth that can be used to refine estimates of reproductive output. This work may lead to the development of biological reference points that incorporate variation in environmental and ecological factors, and management strategies that are sensitive to variation in growth and condition.

12 Recommendations

12.1 General

A standard method for describing growth rate is needed to facilitate comparative studies. The Workshop recommended describing growth in terms of specific growth rates:

$$G = (\ln W_{t2} - \ln W_{t1})/(t2\text{-}t1)$$

where W is a measure of size such as length or weight and t is time in days.

12.2 Recommendations for action by ICES

1. More research survey data on length, weight and maturity at age should be assembled as a prelude to further work on growth of cod. Data on size at age were assembled for most cod stocks and posted on the Workshop website in order to facilitate comparative analyses and the development of a single growth model for cod. For western Atlantic cod stocks, these data are from research survey catches, while the size at age data for most eastern Atlantic stocks are from commercial catch data. Size-at-age based on fishery catches depends on fishery characteristics (e.g., gear, seasonal timing) and may not accurately reflect variation in size-at-age within and among stocks.
2. Protocols for collecting biological data on research surveys should be reviewed to ensure that they are appropriate for investigating growth and documenting variation in weight-at-age.
3. Monitoring and forecasting programs for environmental variables, especially temperature, should be maintained.

12.3 Recommendations for further research

1. An approach involving bioenergetic modelling is required to understand how temperature and food ration interact to influence variation in cod growth. A mechanistic model, containing a number of state variables and rules for regulation of the acquisition and allocation of energy, should be developed. Further laboratory and fieldwork will be needed to parameterize and validate the model. Examples of additional research that should be undertaken to support this bioenergetic modelling are:

– to compare laboratory derived maximum consumption rates with consumption rates estimated from field data on stomach contents for selected stocks.

– to calibrate activity levels in existing bioenergetic models by use of the above field estimates of food consumption rates.

– to monitor seasonal cycles in condition and liver index in fast growing and slow growing stocks.

– to conduct further laboratory studies of relationships between growth, age, size, ration and temperature on wild and cultured fish to compare with results on reared individuals, and on fish from various stocks.

2. Backcalculation of individual growth histories from scales or otoliths should be undertaken for a number of stocks. A back-calculation study of the 4T cod stock indicated that changes in size-selective mortality were an important cause of changes in mean size-at-age for this stock. Similar studies should be undertaken for other stocks to determine whether variation in size-selective mortality is an important source of bias in other cases. Initial investigations should involve other slow-growing stocks (which recruit to the fishery over a prolonged period, when size selective fishing mortality is likely to occur). In addition to providing information on the effects of size selective mortality, back calculation studies provide measures of the growth trajectories of individual fish, which can be used in growth models and in tests of effects on growth.
3. Estimates of ambient temperature need to be further refined. Approaches that should be undertaken include:

– generating temperature time series from isotopic analyses of otoliths, if the signal-to-noise ratio can be shown to be adequate to produce meaningful results (e.g., problems with salinity).

– implementing a data storage tag program on a wider scale, in particular in the NW Atlantic.

4. Studies reported at the Workshop suggested a strong influence of size in the early life history stages on size and abundance at later stages, and further studies of growth and size at age during larval and pelagic juvenile stages and their relationship to temperature and year class strength should be undertaken.
5. Retrospective analyses of stock projections should be undertaken in stocks and periods when there have been rapid changes in growth rate. Probabilistic variability in weight at age should be incorporated into current forecast tools used in stock assessment.
6. Production analyses presented at the Workshop to examine effects of variation in growth on surplus production should be validated and extended.

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Appendix 2: Contributors who did not attend the Workshop

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Appendix 3: Agenda - Workshop on the Dynamics of Growth in Cod

8 May 2000

08:30–09:10	Welcome and Introduction

PRESENTATIONS AND DISCUSSION IN PLENARY

09:10–11:10	**Session on topic 1 - Factors explaining interannual variability**
09:10–09:20	Introduction by Doug Swain
09:20–09:30	K. Brander: Detecting the effects of environmental variability on growth and recruitment in cod *(Gadus morhua)* using a comparative approach
09:30–09:40	D. Swain *et al.*: Comparative analysis of effects of density and temperature on interannual variation in growth of cod in selected stocks
09:40–09:50	G. Ottersen *et al.*: Density-dependent growth in immature Arcto-Norwegian cod
09:50–10:00	E. Magnuson: Growth of cod on the Faroe Bank
10:00–10:20	Break
10:20–10:30	[D. Uzars: Feeding and growth variability in eastern Baltic cod.-cancelled]
10:30–10:40	J. D. Dutil: Cold water vs warm water cod stocks: what is driving growth and production?
10:40–11:10	Discussion and round up for the group work
11:10–11:55	**Session on topic 3 - Estimating “ambient” temperature**
11:10–11:15	Introduction by Geir Ottersen
11:15–11:25	M. Castonguay: Ambient temperatures and growth decline in northern Gulf of St. Lawrence cod
11:25–11.35	G. Ottersen *et al.*: Growth, distribution and abundance of Arcto-Norwegian cod in relation to ambient temperature
11:35–11:55	Discussion and round up for the group work
11:55–13:00	Lunch
13:00–13:35	**Session on topic 4 – Size selective fishing and back-calculation**
13:00–13:05	Introduction by Martin Castonguay
13:05–13:15	A. Sinclair *et al.*: Effects of size-selective mortality, density and temperature on size-at-age of southern Gulf of St. Lawrence cod
13:15–13:35	Discussion and round up for the group work
13:35–14:30	**Session on topic 5 – Effects of variation in growth on stock biomass**
13:35–13:40	Introduction by Keith Brander

13:40–13:50	A. Filin: Influence of fish growth rate in different age groups on state of commercial stock and its spawning part
13:50–14:00	N. Yaragina: Interannual variability in liver condition index of Northeast Arctic cod: forecasting potential
14:00–14:10	T. Marshall: Incorporating growth into the stock/recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential
14:10–14:30	Discussion and round up for the group work
14:30–14.50	Break
14:50–15:45	**Session on topic 6 – Environmental and density-dependent influence during early pelagic life and consequences of this on later size and abundance**
14:50–14:55	Introduction by Geir Ottersen
14:55–15:05	K. Brander and D. O’Brien: Predicting weight at age and recruitment of North Sea cod
15:05–15:15	H. Loeng and G. Ottersen: Covariability in early growth and year class strength of Barents Sea cod, haddock and herring: the environmental link
15:15–15:25	S. Skreslet: The influence of UVR and climate conditions on fish stocks: a case study of the Northeast Arctic cod (UVAC)
15:25–15:45	Discussion and round up for the group work
15:45–16:10	**Session on topics 2 and 7 – Single growth model covering all stocks**
15:45–15:50	Introduction by Keith Brander
15:50–16:00	B. Bjornsson: Growth potential of cod fed on maximum rations: effects of temperature and size
16:00–16:10	S. P. Despatie: Final temperature preferendum of Atlantic cod - effect of food ration
16:10–16:55	**Session on topics 2 and 7 – Bioenergetic models**
16:10–16:15	Introduction by Niels Andersen
16:15–16:25	N. Andersen: How may bioenergetics contribute to our understanding of the growth variations of cod?
16:25–16:35	M. Krohn: Does metabolic scope limit growth in cod?
16:35–16:55	Discussion and round up for group work on topics 2 and 7
16:55–17:30	**Session on topic 8 – Genetic variation of growth**
16:55–17:00	Introduction by Joe Brown
17:00–17:10	J. Brown: Inter-population differences in phenotypic response from common-garden experiments among four populations of Atlantic cod
17:10–17:30	Discussion and round up for group work
17:30–17:50	**Discussion of group work on topics May 9: participants in each group, meeting location for each group, etc.**

9 May 2000

Work on Topics

8:30–10:00 **Group work** in parallel on topic 6: Chair - Geir Ottersen
topics 1 and 4: Chair – Doug Swain
topic 7: Chair - Niels Andersen

10:00–11:30 **Group work** in parallel on topics 2 and 8: Chair – Keith Brander
topic 3: Chair - Geir Ottersen
topic 5: Chair – Jean-Denis Dutil

11:30–12:00 **Plenary session**: Overview of progress - reallocation of people and tasks among relevant groups

12:00–13:00 Lunch

13:00–14:00 **Final group work** on topics according to the conclusions from the preceding plenary session

14:00–16:30 **Presentation and discussion of group conclusions in plenary** (emphasis on the key issues for terms of references (TORs) (20 minutes on the average for each topic)

16:30–17:00 **Discussion of the group work May 10 on TOR's**

10 May 2000

Work on TORs

8:30–12:00 **Group work** in parallel

Group 1: Chair - Niels Andersen
a) Develop models of growth in order to improve the quality of stock forecasting.

Group 2: Chair - Geir Ottersen
b) Describe major sources of uncertainty in the prediction of growth rates and advise on further studies to reduce this uncertainty.
d) Recommend standard methods for comparing growth rates.

Group 3: Chair - Doug Swain
c) Assess the contribution of growth rate variability to the observed variability in stock biomass and stock forecasts.
e) Develop specific case studies which will be relevant to the advice of ICES.

12:00–13:00 Lunch

13:00–16:30 **Presentation and discussion of group reports in plenary**

13:00–14:00 Group 1

14:00–15:00 Group 2

15:00–15:30 Break

15:30–16:30 Group 3

16:30–17:30 **Closing discussion**

Appendix 4: Working Documents

Topic 1: Factors explaining interannual variability in growth

WD 1.1:	Detecting the effects of environmental variability on growth and recruitment in cod *(Gadus morhua)* using a comparative approach – K. Brander
WD 1.2	Comparative analysis of effects of density and temperature on interannual variation in growth of cod in selected stocks – D. P. Swain, A.F. Sinclair, M. Castonguay, G. A. Chouinard, K.F. Drinkwater, P. Fanning, and D. Clark
WD 1.3	Density-dependent growth and distribution patterns in immature Arcto-Norwegain cod – G. Ottersen, B. Bogstad, K. Helle, C. T. Marshall, K. Michalsen, and M. Pennington
WD 1.4	Growth of cod on the Faroe Bank – E. Magnuson
WD 1.5	Production analyses for cold-water and warm-water stocks and their use to predict surplus production – J.-D. Dutil, M. Castonguay, D. Gilbert, and D. Gascon

Topic 2: Single growth model covering all stocks

WD 2.1	Growth potential of cod (*Gadus morhua* L.) fed on maximum rations: effects of temperature and size – B. Bjornsson
WD 2.2	Final thermal preferendum of atlantic cod: effect of food ration – S.-P. Despatie, M. Castonguay, D. Chabot, and C. Audet

Topic 3: Estimating “ambient” temperature

WD 3.1	Ambient temperatures and growth decline of cod in northern Gulf of St. Lawrence – M. Castonguay, J.-D. Dutil, D. Gilbert, and D. Gascon
WD 3.2	Growth, distribution and abundance of Arcto-Norwegian cod in relation to ambient temperature – G. Ottersen, K. Michalsen and O. Nakken

Topic 4: Size-selective fishing and back-calculation

WD 4.1	The effects of size selective mortality, density and temperature on size at age of southern Gulf of St. Lawrence cod – A.F. Sinclair, J.M Hanson, D.P. Swain, G.A. Chouinard, L. Currie

Topic 5: Effects of variation in growth on stock biomass

WD 5.1	Modelling of the impact of cod growth rate variations on their stock status in dependence of food supply and temperature conditions – A. Filin
WD 5.2	Interannual variability in liver condition index of Northeast Arctic cod: forecasting potential – N. Yaragina
WD 5.3	Incorporating growth into the stock/recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential – C. T. Marshall, N. A. Yaragina, A. Dolgov, and B. Ådlandsvik

Topic 6: Environmental and density-dependent influence during early pelagic life and consequences of this on later size and abundance

WD 6.1	Predicting weight at age and recruitment of North Sea cod – K. Brander and D. O'Brien
WD 6.2	Covariability in early growth and year class strength of Barents Sea cod, haddock and herring: the environmental link – H. Loeng and G. Ottersen
WD 6.3	Growth of Atlantic cod and haddock larvae on Georges Bank: food-limited growth in fish larvae – L.J. Buckley, E.C. Caldarone and R.G. Lough
WD 6.4	The influence of UVR and climate conditions on fish stocks: a case study of the Northeast Arctic cod (UVAC) – S. Skreslet, C. Alonso, A. Borja, H.C. Eilertsen, G. Hansen, R. Meerkoetter, F. Saborido-Rey, J. Verdebout, T. Wyatt
WD 6.5	Predicting weight at age of southern Gulf cod from temperature conditions – D.P. Swain

Topic 7: Bioenergetic models

WD 7.1	Food consumption and activity of North Sea saithe (*Pollachius virens*) – N. G. Andersen
WD 7.2	Does metabolic scope limit growth rates of wild cod? – M. Krohn

Topic 8: Genetic variation for growth

WD 8.1	Inter-population differences in phenotypic response from common-garden experiments among four populations of Atlantic cod – J. A. Brown

Working Document 1.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Detecting the effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach

Keith Brander

Now published in Oceanologica Acta 4 (23) August 2000

Abstract

Data on growth and recruitment from ten stocks of cod are compared in order to describe the variability between years and areas and to examine the effects of temperature. Differences in growth rate are also shown for five haddock *(Melanogrammus aeglefinus)*, five saithe *(Pollachius virens)* and four whiting *(Merlangius merlangus)* stocks. Some of the inter-stock and inter-annual variability in growth rate can be related to temperature, as can inter-species variability at Faroe. Temperature during the first year has a strong influence on subsequent weight-at-age of cod in the North Sea and may account for much of the observed variability up to age six. The relationship between temperature and recruitment is weak for individual stocks of cod (with the exception of West Greenland), but when several stocks are looked at together a pattern emerges, in which recruitment is highest in the range 5–7°C. The problems of designing appropriate estimates of temperature for growth or recruitment studies are discussed in the light of recent work on fish distribution and behaviour.

Working Document 1.2

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Comparative analysis of effects of density and temperature on interannual variation in growth of cod in selected stocks

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Extended Abstract

Size-at-age of cod in many of the stocks in the Northwest Atlantic has changed dramatically over the past 25–30 years (e.g., Figure 1A). Suggested explanations for these apparent changes in cod growth include temperature-dependent growth, with faster growth when conditions are warmer (e.g., Campana *et al.,* 1995), density-dependent growth, with slower growth when abundance is high (e.g., Sinclair and Swain 1996), and size-selective fishing mortality (Hanson and Chouinard 1992). Different hypotheses have been emphasized for different stocks. The purpose of this paper is to simultaneously test two of these hypotheses, temperature-dependent and density-dependent growth, applying the same methods to several stocks, namely the southern Gulf of St. Lawrence stock, referred to here as the 4T stock; the northern Gulf of St. Lawrence or 3Pn4RS stock, the eastern Scotian Shelf or 4VsW stock; and the western Scotian Shelf or 4X stock.

To test for effects on growth, we used a modification of the three parameter von Bertalanffy model. Following Millar and Myers (1990), we let L_∞ depend on environmental conditions and abundance:

$$L_{yt} = L_{\infty_{y1}}(1-ae^{-k}) + \sum_{i=2}^{t}((L_{\infty_{yi}} - L_{y,i-1})(1-e^{-k})$$

where:

$$L_{\infty_{yi}} = L_{\infty_0} + d\,N_{yi} + t\,T_{yi}$$

where L_{yt} is the expected length-at-age t for year class y, and N_{yi} and T_{yi} are the abundance and temperature indices for year class y at age i. Using this approach, length-at-age is predicted by summing environmentally-dependent predicted growth increments to the observed age t. We fit the model to observed population mean lengths-at-age obtained from annual research surveys. Abundance estimates were $\log_e$ transformed and expressed as an anomaly from the longterm average. We used estimated abundance of cod aged j-1 to j+1 (N) to predict growth increments for age j cod. For the 4T stock, we used estimates of both cod-weighted or 'ambient' temperature during the feeding season (T_C) and available or 'environmental' temperature (T_E). For the other stocks, only indices of 'environmental' temperature were available. Examples of these indices are shown for the 4T stock in Figure 1.

Age alone accounted for only 58% of the variation (TSS – total sums of squares) in mean length of 4T cod. For this stock, effects of both temperature (a positive effect) and abundance (a negative effect) on mean length-at-age were highly significant. The single variable providing the most substantial improvement in model fit was T_C, accounting for an additional 22% of the TSS (compared to 10% for T_E and 13% for N). However, when N was already included in the model, addition of T_E resulted in greater model improvement (18% of TSS) than did addition of T_C (13% TSS). N may account for density-dependent changes in both food ration and T_C (4T cod tend to occupy colder temperatures at higher abundance levels (Swain and Kramer 1995)), while T_E may account for additional indirect effects of environmental conditions (e.g., length of the feeding season).

The explanatory variables that were closely associated with variation in length-at-age varied among cod stocks (Table 1). Both abundance and temperature conditions accounted for substantial amounts of the variation in length-at-age of 4T cod. Variation in the growth of 3Pn4RS and 4VsW cod was more closely associated with variation in temperature than with variation in abundance, though for 3Pn4RS cod even temperature accounted for only a small portion of the variation in length-at-age. For 4VsW cod, there was also a slight but significant effect of density on length-at-age. This effect was negative after accounting for the effect of temperature, but appeared to be positive if confounding with temperature was not taken into account (Figure 2). Growth of 4X cod appeared to be unrelated to variation in both abundance and temperature conditions. Age alone accounted for a much higher percent of the variation in the other stocks, especially the 4X stock, than in the 4T stock. In all significant cases, effects of abundance were negative and effects of temperature were positive after accounting for confounding between the two factors (Figure 2).

These differences between stocks in effects on growth may reflect differences in density and temperature conditions. Density-dependent growth may be strong in only the 4T stock because it is only in this stock that densities during the feeding season reach high enough levels to result in competition for resources. Mean catch rates in summer research surveys have reached much higher levels in the southern Gulf than in the other stock areas, and density-dependent changes in the distribution of 4T cod during their feeding season suggest that competition for resources does occur at high abundance levels in this stock (e.g., Swain 1999). Unlike the other stocks, growth of 4X cod was unrelated to temperature. The 4X stock occupies warmer waters than the other stocks, and the temperatures experienced by 4X cod may rarely be cold enough to limit growth.

For all stocks except 4X, strong patterns were evident in the residuals from the growth models. This suggests the operation of factors not accounted for by the models. Variation in the direction and extent of size selective fishing has a strong effect on variation in length-at-age of 4T cod (Sinclair *et al.*, WD 4.1). The strong pattern in residuals from the growth model for 4T cod is eliminated if an index of size selection is included in the model (Sinclair *et al.,* WD 4.1).

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Table 1. Tests of density-dependent (N) and temperature-dependent (T) growth for four cod stocks in the Gulf of St. Lawrence and on the Scotian Shelf. %TSS is the percent of the total sum of squares in mean length-at-age explained by a model or by the addition of terms to a model (improvement). T is a measure of environmental temperature (rather than ambient temperature).

	4T	3Pn4RS	4VsW	4X
%TSS				
Age	58.0	85.4	78.5	95.2
Age, N	70.7	86.9	81.0	95.2
Age, T	68.4	87.7	91.3	95.2
Age, N, T	88.5	87.7	91.5	95.2
Improvement (%TSS)				
N given Age	12.7	1.5	2.5	0.0
T given Age	10.4	2.3	12.7	0.0
N,T given Age	30.5	2.3	13.0	0.0
N given Age, T	20.1	0.0	0.3	0.0
T given Age, N	17.8	0.8	10.5	0.0
F-values				
N given age	65.211	12.542	19.589	0.150
T given age	49.295	20.061	217.255	0.583
NT given age	197.977	10.062	113.370	0.391
N given age,T	261.161	0.210	4.452	0.201
T given age,N	230.827	6.898	183.197	0.632
P-values				
N given age	<0.0001	0.0006	<0.0001	0.70
T given age	<0.0001	<0.0001	<0.0001	0.45
NT given age	<0.0001	0.0001	<0.0001	0.46
N given age,T	<0.0001	0.65	0.037	0.68
T given age,N	<0.0001	0.010	<0.0001	0.43

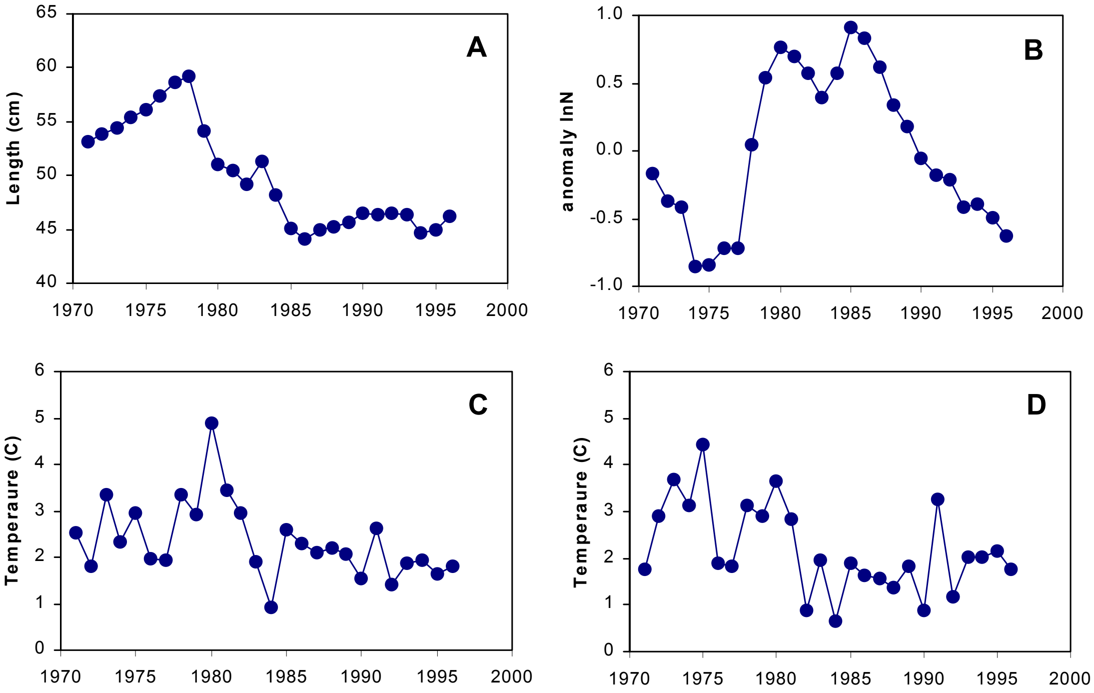

Figure 1. Examples of variation in length-at-age, abundance and temperature conditions for southern Gulf of St. Lawrence cod. A. Length-at-age 6 year; B. Abundance index for ages 5–7 years; C. Environmental temperature index; D. Average ambient temperature of 6-year-old cod in September.

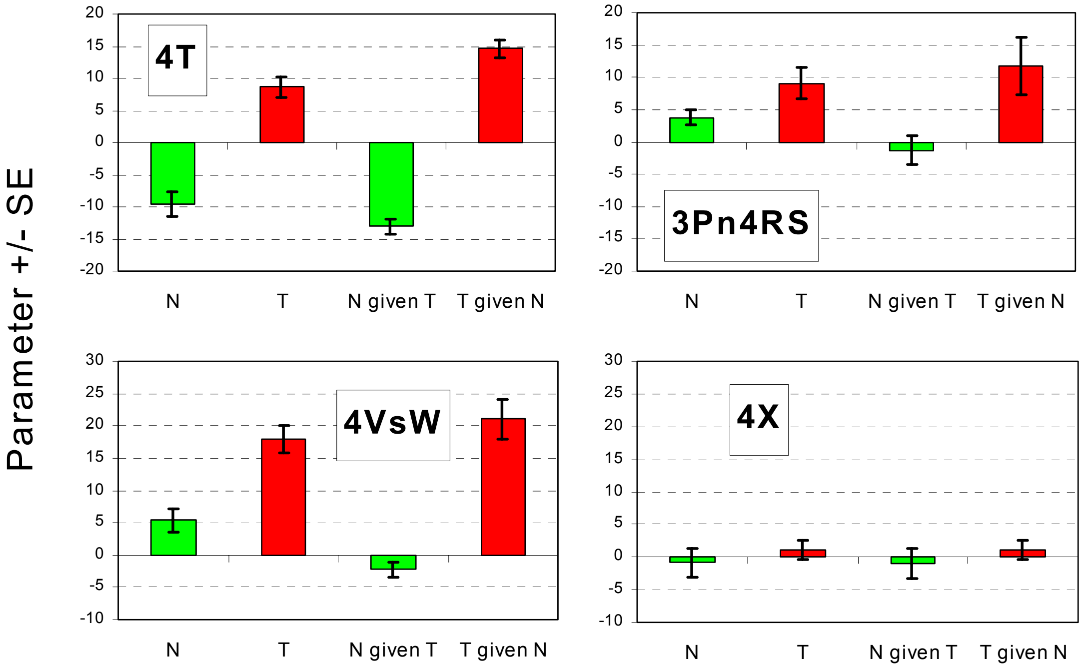

Figure 2. Effects of density (N) and environmental temperature (T) on length-at-age of cod in the Gulf of St. Lawrence (4T, 3Pn4RS) and on the Scotian Shelf (4VsW, 4X).

Working Document 1.3

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Density-Dependent Growth and Distribution Patterns in Immature Arcto-Norwegian Cod

Geir Ottersen, Bjarte Bogstad, Kristin Helle, C. Tara Marshall, Kathrine Michalsen, and Michael Pennington

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Extended Abstract

Density-dependent growth in fish populations has been reported since early in the 20th century (Backiel and Le Cren, 1967) and controlled experimental evidence has established that growth is often inversely related to stock density (Swingle and Smith, 1942). Further evidence for density-dependent growth in fishes has accumulated as stocks have become overexploited. Density-dependent growth has been shown for many heavily exploited marine fish stocks including cod, e.g., in the North Sea (Raitt, 1939; Houghton and Flatman, 1981; Daan *et al.*, 1990) and the north-west Atlantic (Ross and Almeida, 1986, Marshall and Frank, 1999).

For Arcto-norwegian cod in the Barents Sea (Figure 1), year-to-year variability in growth has been observed over a long period (Jakobsson, 1992; Nakken, 1994; Michalsen *et al.*, 1998). Several authors have suggested that this variability in growth is density-dependent (Ponomarenko, 1967; Rollefsen, 1953; Cushing and Horwood, 1977; Nilssen *et al.*, 1994). However, density-independet factors are also of importance, a number of earlier authors have observed larger mean lengths-at-age of Arcto-norwegian cod in warmer years than in colder, and proposed a positive relation between temperature and growth (Dementyeva and Mankevich, 1965; Nakken and Raknes, 1987; Loeng, 1989; Jørgensen, 1992; Michalsen *et al.*, 1998).

In the Barents Sea, the temperature decreases from west to east. Thus, the younger age groups, which during winter are mainly located in the eastern areas, inhabit waters of lower temperatures than the older ones found further west. This east-west gradient in age (or size) seems to be a general feature, regardless of interannual variability in temperature or abundance (Nakken and Raknes, 1987; Shevelev *et al.*, 1987; Ottersen *et al.*, 1998).

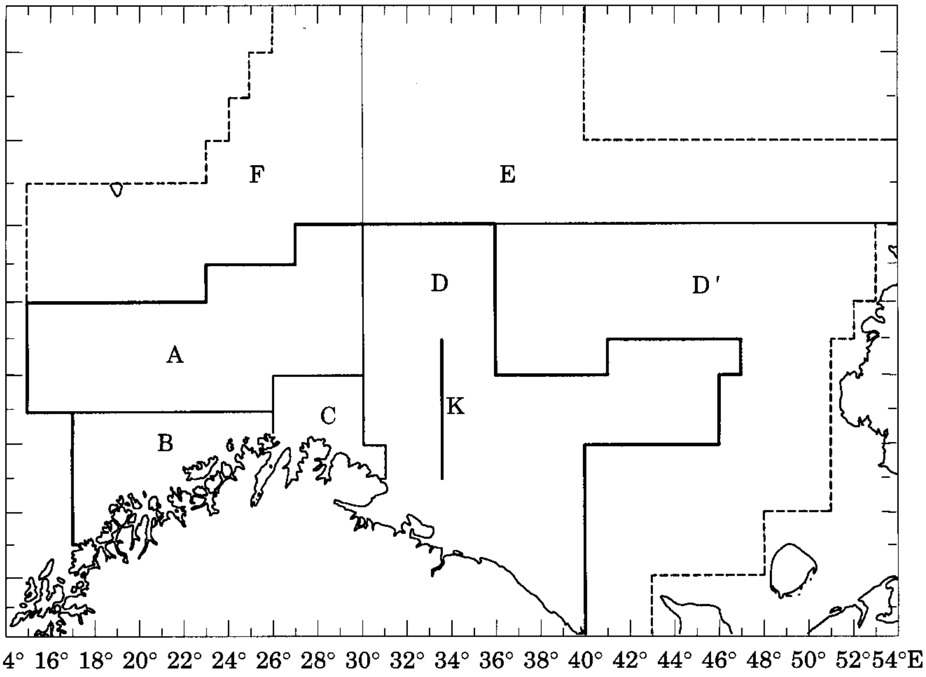

Figure 1. The Barents Sea, survey area with subareas framed. The fixed Kola section (K) is also indicated. This map is taken from Ottersen *et al.* (1998).

MacCall (1990) suggested that spatial variation in local density reflects gradients in resource availability: local density is highest when resources are abundant (prime or optimal habitat) and lowest where resources are scarce (marginal habitat). As abundance increases, optimal habitat becomes saturated causing the distributional area to expand and the local density of fish occupying marginal habitat to increase rapidly. This type of distributional response is referred to as density-dependent habitat selection (DDHS). DDHS has important implications for the analysis of interannual variation in size at age. If habitat that is marginal in the distributional sense is also associated with low growth rates, then density dependent growth could result from fish expanding into habitat that is suboptimal for growth when abundance is high and contracting into habitat that is optimal for growth when abundance is low (Daan *et al.*, 1990; Marshall and Frank, 1995; Toresen, 1990).

In the present paper we examine possible connections between abundance and mean length-at-age for immature Arcto-norwegian cod. Both relations within a cohort and inter-cohort density-dependent growth are studied. Assuming that population density is found to influence growth rate, the mechanism may be direct, through regulating local food availability. However, here we suggest that abundance effects growth through altering geographical distribution patterns.

We propose that lower growth rates during periods of high abundance is a result of a decrease in ambient temperature. This again is due to density-dependent mechanisms causing the geographic range of Arcto-norwegian cod to extend eastwards into colder water masses. Such a distributional response to fluctuations in abundance may be seen in the light of the theory of density-dependent habitat selection (DDHS; MacCall, 1990). Our hypothesis thus states that density-dependent growth is imposed on immature Arcto-norwegian cod by DDHS.

The data used in this study mainly originate from the combined bottom trawl and acoustic surveys conducted in the Barents Sea each February (Jakobsen *et al.*, 1997). The surveys followed a stratified random design until 1990, from 1991 onwards a stratified design. Until 1992, the area covered by the survey was limited to the ABCD area (Figure 1). While the number of trawl stations varied, the entire ABCD area was always reasonably well covered.

Mean lengths of Arcto-norwegian cod at ages 1–3 are negatively correlated with the total abundance of the cohort at the same and earlier stages. This result stands both when mean length is estimated for the whole Barents Sea and separately within regions. The opposing fluctuations are particularly clear for fish of age 2 (Figure 2).

Mean length of a year class may be affected also by the abundance of older conspecifics.

Length-at-age is significantly negatively correlated with the aggregated abundance of age groups 3–6. This is demonstrated for length-at-age 2 (Figure 3).

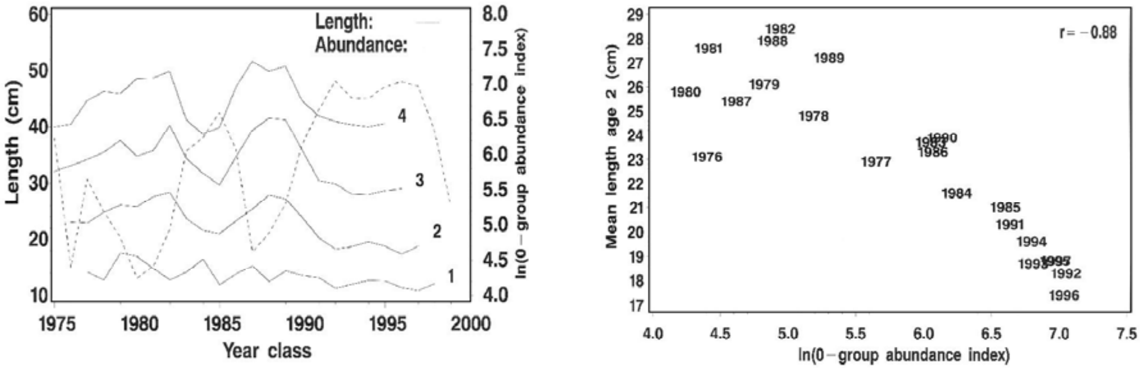

Figure 2. Left panel: Temporal development of length-at-age 1 to 4 (full lines) and abundance as 0-group (logtransformed, stipled line) of Arcto-norwegian cod from 1975 until 1999. Right panel: Scatter plot showing abundance as 0-group (logtransformed) versus mean length-at-age 2 for Arcto-norwegian cod 1977–1999. The Pearson correlation (r) is shown.

To examine the relations between abundance at age for the whole Barents Sea (in practice the ABCD region) and each separate area, we used relative abundances, i.e., the fraction of the total number of fish present in each area. This allows for examination of possible shifts in abundance between areas, and their connection to overall abundance, of this age group or for a larger part of the stock. The correlations among the relative abundances in different areas for fish at age 2, abundance in ABCD for age 2 and accumulated abundance within ABCD for ages 3 to 6, are given in Table 1

This study demonstrates that the mean length of 1–3 year old Arcto-norwegian cod tends to be small when the abundance of the same cohort is high. We furthermore show that small mean lengths at age are related to high abundance aggregated for age groups 3–6. These results indicate that growth of immature Arcto-norwegian cod is influenced by both intra- and intercohort density-dependence.

On limited rations, the temperature yielding the highest growth rate decreases as ration size decreases (Brett *et al.*, 1969; Elliott, 1975; Woiwode and Adelman, 1991). Therefore, if fish select the habitat that maximises their growth rate, preferred temperatures should decrease as food supply decreases (Elliott, 1975; Crowder and Magnusson, 1983; Swain and Kramer, 1995). If food supply is density-dependent, the proportion of the population occupying habitats of lower temperature should increase with population size (Swain and Kramer, 1995). The observed density-dependent spatial shifts could be taken as field support for this hypothesis.

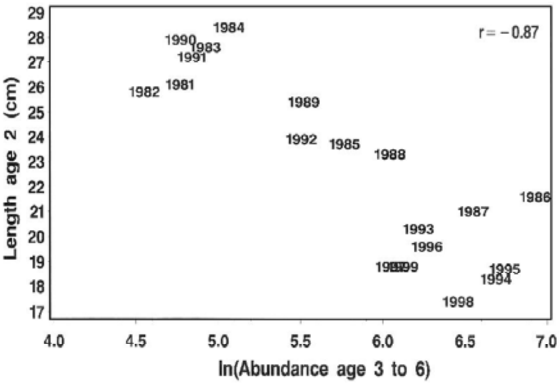

Figure 3. Abundance of age groups 3 to 6 vears length-at-age 2 for Arcto-norwegian cod from 1978 until 1999. The Pearson correlation (r) is shown.

That is, a density-dependent decrease in food availability should result in increased preference for habitats with lower density-independent costs, in this case lower temperatures. However, we are not able to determine whether the fish, when leaving high-density areas with low food availability, seek out areas with higher per capita food availability, or lower costs of food shortage.

Furthermore, while our results indicate easterly shifts in periods of high abundance, we are not able to rule out other causes for the apparent movement. Spatial variation in natural mortality, e.g., cannibalism, may shift the distribution without any active habitat selection being involved.

Table 1. Correlations among the relative abundances in different areas for fish at age 2, abundance within ABCD for age 2 and accumulated abundance within ABCD for ages 3 (all logarithmically transformed).

	Age 2 ABCD	Age 3–6 ABCD	Age 2 Fraction B	Age 2 Fraction C	Age 2 Fraction D
Age 2 Fraction A	-0.51 (0.03)	-0.44 (0.08)	0.58 (0.01)	0.72 (0.00)	-0.91 (0.00)
Age 2 Fraction B	-0.79 (0.00)	-0.40 (0.11)		0.65 (0.00)	-0.78 (0.00)
Age 2 Fraction C	-0.76 (0.00)	-0.50 (0.04)			-0.83 (0.00)
Age 2 Fraction D	0.67 (0.00)	0.42 (0.09)			

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Working Document 1.4

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Growth of cod on the Faroe Bank during the period 1983 to 2000

Eydfinn Magnussen

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Abstract

Bottom surveys have routinely been carried out on the Faroe Bank since 1983. Based on data from these bottom surveys, length and weight at age will be presented for the period 1983 to 2000. During this period the growth has fluctuated markedly. It was highest in 1985, it decreased gradually and was on a lowest level in 1989 It recovered during the period 1992 to 1996 and then is decreased again. For 1985, Bertalanffy growth equation for the length-at-age can be written as: $L(\text{age}) = 1386\ (1\text{-}e^{-0.246*\ \text{age}})$ and the weight-at-age: $W\ (\text{age}) = 27898\ (1\text{-}e^{-0.291*\ \text{age}})^3$. Based on this the average weight of a 5 years old cod in 1985 was 12.6 kg, 1989 the average weight was only 4.4 kg. For the Faroe Plateau cod, large fluctuations have also been found in the weight at age during the periods 1960 to present. In 1961 the average weight of a 7 years old cod was 7.1 kg while it in 1989 has decreased to 3.8 kg. After 1989 the weight increased again. This increase did not coincide with the variability in the see temperature. On the contrary, the annual average temperature tended to decrease during the recovery period in the early 1990s when the average weight at age increased with 62% during the period 1989 to 1995. Variability in food availability is a more convincing explanation for variability in the fish growth that particular period on the Faroe Plateau.

Working Document 1.5

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Production analyses for cold-water and warm-water stocks and their use to predict surplus production

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Extended Abstract

Introduction

Surplus and net production per capita became nil or negative in the mid-1980s in the northern Gulf of St. Lawrence (Dutil *et al.,* 1999). This situation was partly explained by a marked decline in growth production and is consistent with smaller sizes-at-age (Chouinard and Fréchet 1994) but also lower condition factor values during the same period (Lambert and Dutil 1997). The nutritional condition of cod in the Gulf of St. Lawrence varies markedly both seasonnally and annually (Lambert and Dutil 1997, Schwalme and Chouinard 1999) and this has been found to be associated with changes in swimming capacity (unpublished data), reproductive investment (Lambert *et al.,* 2000, Lambert and Dutil 2000) and risks of natural mortality (Dutil and Lambert 2000; and unpublished data). Positive slopes between size-at-age and temperature suggested faster growth rates at higher temperatures for northern Gulf cod, but correlations between size-at-age and temperature were not significant (Dutil *et al.*, 1999). Production analyses conducted for the northern Gulf of St. Lawrence were extended to other stocks. Growth production was assessed in order to determine its variability among and within stocks as a first step to measure its impact on the stock biomass.

Materials

Data used for virtual population analyses, i.e., natural and fishing mortalities, average size of fish of each age in the catch, numbers of fish of each age in the catch and in the population, were used to describe the temporal trends in stock production, following the method described in Dutil *et al.* (1999). Growth and surplus production were calculated and expressed on a per capita basis. Five different stocks covering a wide spectrum of sizes-at-age were examined using the data provided by ICES: Irish Sea, a fast-growing stock, Northeast Arctic and NAFO 4X, two stocks exhibiting intermediate growth rates, and the northern (NAFO 3Pn, 4RS) and southern (NAFO 4T, 4Vn) Gulf of St. Lawrence which are two slow-growing stocks. Temperatures for the northern Gulf of St. Lawrence are expressed as deviations from the long-term average for the cold intermediate layer (Dutil *et al.,* 1999). Temperatures for other stocks are those reported in Brander (1995).

Results

Surplus production on a per capita basis (SP) was greater for the Irish Sea cod stock than for the other stocks (Table 1). SP varied widely and ranged from 0.50 to 1.02 kg for Irish Sea cod, compared to a range of 0.09–0.84 kg for the Northeast Arctic cod and 0.21–0.57 kg for NAFO 4X cod. The southern and northern Gulf of St. Lawrence cod stocks had low SP values ranging from 0 to 0.47 and 0.30 kg, respectively. Differences in SP were associated with differences in growth production per capita (GP). Survivors produced on average 610 g in the Irish Sea, 420 g in the Northeast Arctic, 380 g in 4X, compared to only 140 and 150 g in the southern and northern Gulf of St. Lawrence.

Table 1. Growth (GP) and surplus production (SP) on a per capita basis for 5 different cod stocks and 3 time periods (in kg).

	< 1980		1981–1989		>1989	
	GP	SP	GP	SP	GP	SP
Irish Sea			0.69	0.80	0.59	0.79
Northeast Arctic			0.41	0.35	0.42	0.40
NAFO 4X			0.40	0.34	0.34	0.34
NAFO 4TVn	0.19	0.25	0.13	0.08	0.15	0.03
NAFO 3Pn4RS	0.21	0.22	0.17	0.10	0.10	0.05

In the northern Gulf of St. Lawrence, GP declined from the late 1970s through the 1980s and was lowest in the early 1990s when record low temperatures were also observed. Record low GP values on a per capita basis occurred in 1986 and in the period from 1990 to 1993 (Figure 1). These were the four coldest years of that period (Figure 2). While GP and temperature did not appear to be correlated when those four years were excluded from the analysis, cold temperatures were clearly associated with GP values less than 0.10 kg.

Mean GP of a stock increased with mean size of 3-year-old cod (Figure 3). Growth relative to size is expected to decrease as size increases. When GP was standardized for size however, GP did not appear to be larger in smaller 3-year-old fish than in larger 3-year-old fish. Relative growth seems in fact smaller in fish of a small size, i.e., in cold-water stocks This may have been due to smaller sizes being associated with lower temperatures (Figure 4).

Within stock, SP in year (t+1) was generally not correlated with GP from year (t) to year (t+1), suggesting that GP would not be a predictor of SP. There was a significant relationship however when several stocks were examined together (Figure 5).

Discussion

Production analyses revealed marked differences among stocks with a four-fold difference in GP among stocks. All stocks exhibited wide variations in GP among years, but a temporal pattern was present for both the northern and southern Gulf of St. Lawrence cod. The low SP values do not appear to be explained by GP alone although negative SP values were associated with record low GP values in both cold-water stocks. The late 1980s were characterized by colder than average temperatures in the northern Gulf of St. Lawrence. Only the coldest years were associated with low GP values for the stock, which is consistent with positive slopes between growth rate of 1 kg cod and temperature, and may explain why the correlations between size-at-age and temperature were not significant when corrected for autocorrelation (Dutil *et al.,* 1999). Cold water stocks exhibit growth rates which represent a larger fraction of the maximum rates achievable at cold temperatures than warm water stocks do at warm temperatures, but, overall, they appear to be more vulnerable to natural or man-made perturbations overall.

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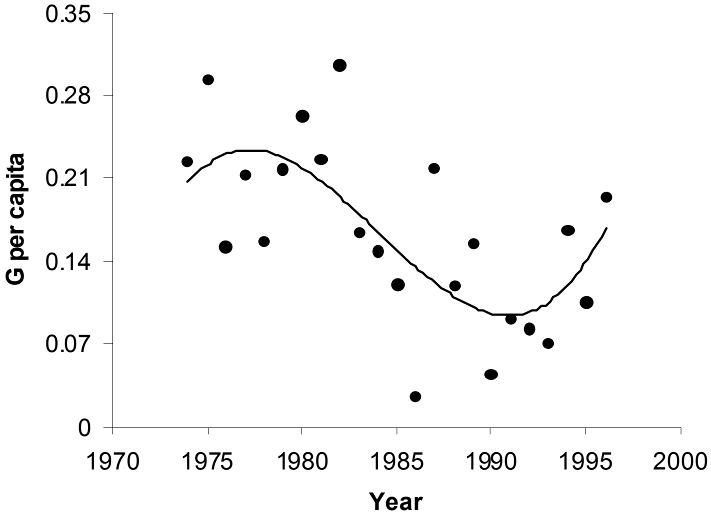

Figure 1. Growth production on a per capita basis of cod 3 years old and older in the northern Gulf of St. Lawrence for the period 1974–1996.

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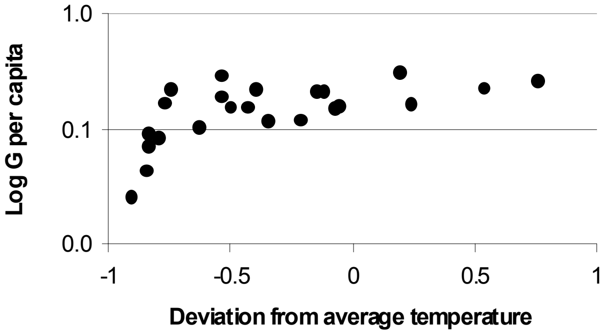

Figure 2. Growth production on a per capita basis of cod 3 years old and older in the northern Gulf of St. Lawrence and temperature anomaly for the cold intermediate layer.

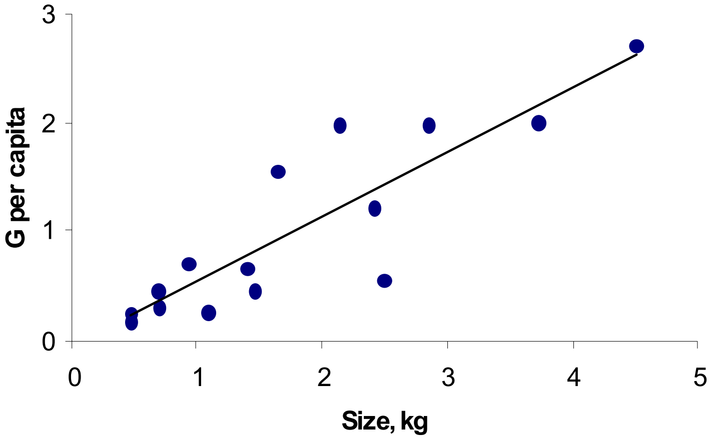

Figure 3. Growth production on a per capita basis and average size of 3-year-old fish in several stocks.

Fig. 4. Size-spec

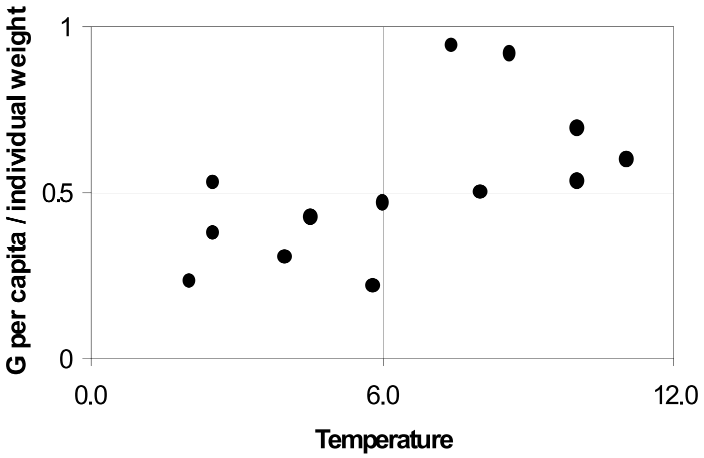

Figure 4. Size-specific growth production on a per capita basis and cod environment temperature for 3-year-old fish in several stocks.

Fig. 5. S

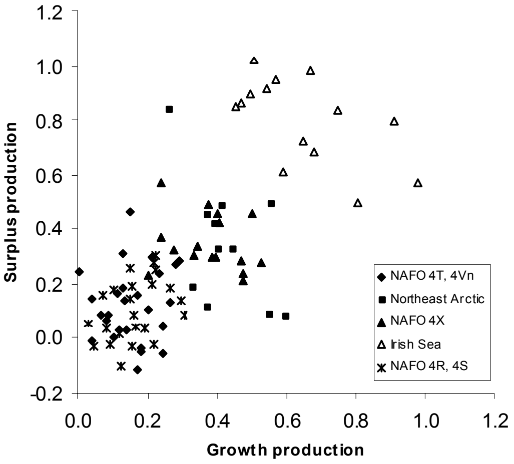

Figure 5. Surplus production in year t+1 and growth production of survivors from year t to year t+1 on a per capita basis for five different stocks.

Working Document 2.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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Growth potential of cod (*Gadus morhua* L.) fed on maximum rations: effects of temperature and size

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Extended Abstract

In the North Atlantic, there are several cod stocks which occupy different geographic areas with mean annual temperatures ranging between 2–11°C. The growth rates are affected by temperature, food availability and other factors, but it has been difficult to quantify their effects in population studies. Weight-at-age data from commercial catches are available for all major cod stocks, providing some indications about the year-to-year changes in growth rates but it is difficult to estimate the mean ambient temperatures of the fish stocks. The year-to-year changes in temperature of a given cod stock are small compared to the total range in temperature experienced by the different cod stocks and thus comparison between stocks may be useful in determining the effects of temperature on growth rate of cod. However, the effects of food availability, genetic differences and other factors are difficult to assess across stocks. An alternative approach to study the environmental effects on growth is to carry out laboratory experiments. In the present study data from several laboratory experiments were analysed with the aim of developing an empirical relationship useful in calculating food-unlimited growth rate of cod over a wide range in temperatures and fish sizes.

A linear relationship on a log-log scale was found between growth rate and weight of cod for any given temperature (Figure 1). Between 85–96% of the variation in growth rate could be explained by variation in fish size at a given temperature. The intercepts and slopes of these regressions were found to change linearly with temperature (intercept: $r^2=0.998$, $n=5$; slope: $r^2=0.946$, $n=5$). This allowed an empirical model to be developed to estimate growth rate (G) at maximum rations for any temperature (T) from 2 to16°C and weight (W) from 2 to 5000 g:

$$G=(0.701T-0.973)W^{(-0.026T-0.147)}$$

The model indicates that temperature has a much greater effect on the growth potential of juvenile (Figure 2A) than adult cod (Figure 2B). The model predicts that optimal temperature for growth of cod decreases with increased weight, from 14.5°C for 20 g fish to 6.0°C for 5000 g fish. It predicts that cod can grow maximally from 1 to 4000 g in 13.4, 5.8, 4.1, 2.9 and 4.8 years at 2, 3, 4, 8 and 16°C, respectively. The model also predicts that in three years 1 g cod can only grow to 28 g at 2°C compared to 1333 and 4301 g at 4 and 8°C, respectively. It is hoped that this estimate of the growth potential of cod may be useful when interpreting changes in growth rate in wild fish stocks as well as when estimating the feasibility of cod farming.

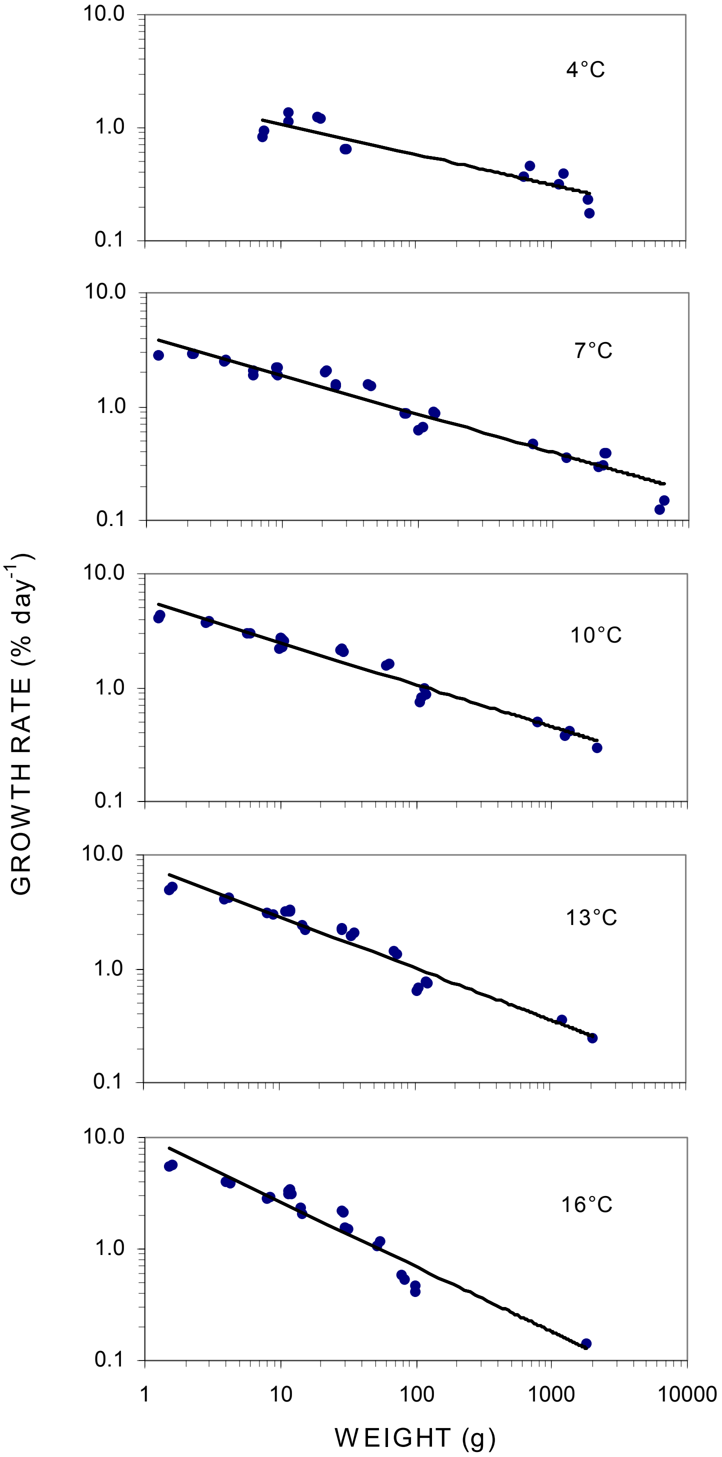

Figure 1. Growth rate of cod as a function of fish weight: a linear regression on a log-log scale for five different temperatures.

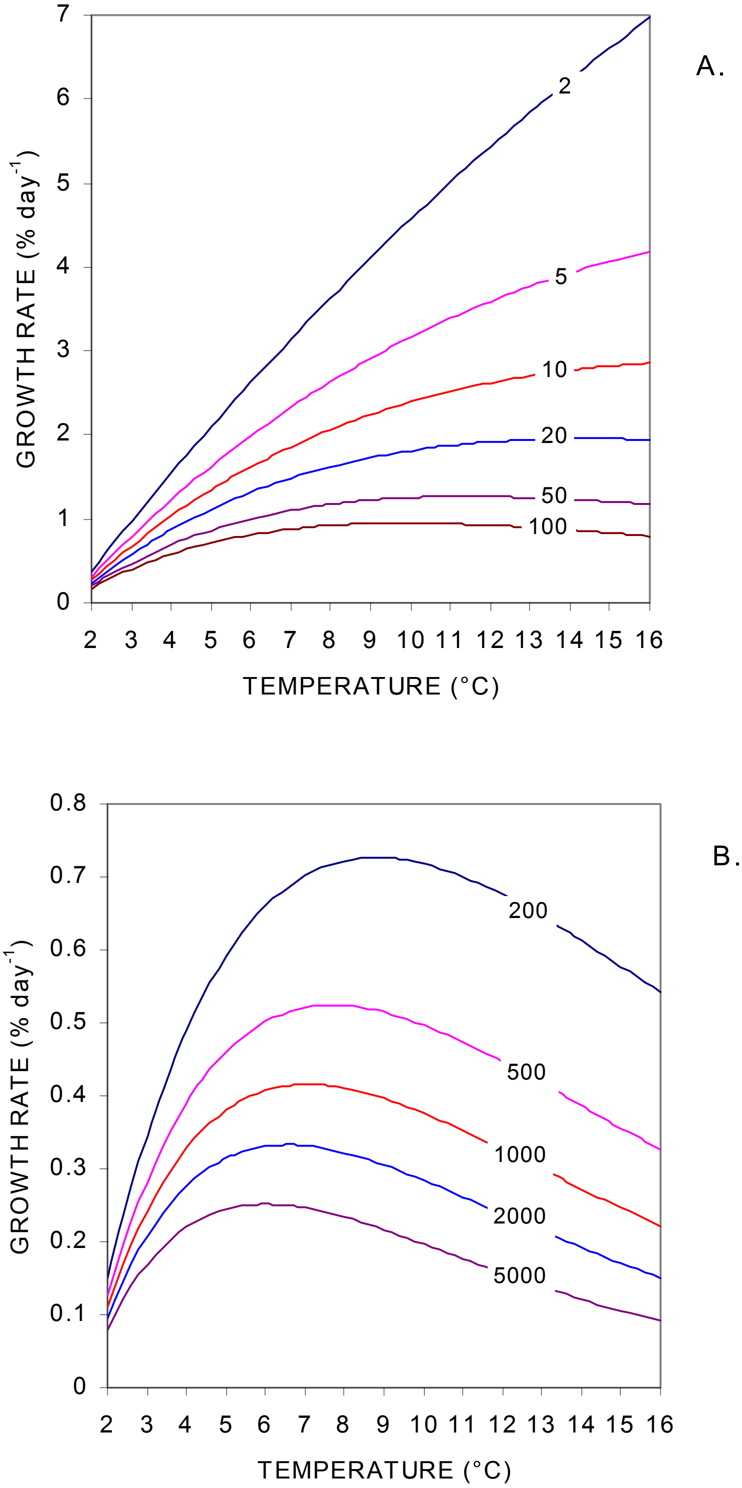

Figure 2. Growth rate of cod as a function of temperature for fish weight from 2–100 g (A) and 200–5000 g (B).

Working Document 2.2

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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Final Thermal Preferendum of Atlantic Cod: Effect of Food Ration

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Abstract

The spatial distribution of Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence changed substantially between the 1970s and 1980s. It was proposed that fish occupied different temperatures in the Gulf depending on food availability as influenced by their abundance. To evaluate one key aspect of this hypothesis, we determined the final thermal preferendum of Atlantic cod in relation to food ration. After 6 to 15 weeks of conditioning to one of three predetermined rations, 72 fish 40 to 50 cm long were left three at a time to behaviourally thermoregulate in a horizontal thermal gradient for 45 h. The food rations produced significant differences among condition indicators of the three groups. A small but significant difference (ANOVA, $P < 0.05$) in final thermal preferendum was found between fish fed at intermediate and low rations. After omitting data from the first three weeks of the experiment, which showed signs of interaction (ration*week) indicating that ANOVA assumptions were not fulfilled, the difference between high and low rations became significant (high 6.52°C; intermediate 6.36°C; low 4.02°C). These findings partly support the hypothesis for changes in distribution of southern Gulf of St. Lawrence Atlantic cod since fish in this study thermoregulated differently depending on the availability of food. Fish with negative growth rate and poor condition tended to select colder water. However, the absence of significant difference between high and intermediate rations suggests that Atlantic cod need to be in poor condition before their temperature preference is decreased. The final thermal preferenda reported here are slightly warmer than average temperatures occupied in the wild during the test season but are well below the value commonly accepted for the species (13.5°C). This discrepancy may stem in part from inter-population differences as well as ontogeny.

Working Document 3.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Ambient temperatures and growth decline of cod in northern Gulf of St. Lawrence

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Abstract

Temperature and food rations are the two primary factors driving growth in fishes. Growth models need to incorporate representative measures of ambient temperatures experienced by the fish during the growth season to account adequately for environmental variability. Research surveys provide snapshots of ambient temperatures which may or may not represent an adequate integrated measurement. On the basis of winter and summer research surveys in the northern Gulf of St. Lawrence, we found no evidence that cod mean ambient temperature changed with the recent cooling of the Gulf (see Figures 4 and 8 of Castonguay *et al.,* 1999). There was a simultaneous decline among a temperature index (anomaly in the cold intermediate layer), a distribution index (median latitudinal distribution in winter, which was more to the south), and a growth index (standardized lengths-at-age for ages 4, 6, and 8) (see Figure 3 of Dutil *et al.,* 1999). Once accounting for autocorrelation, the correlation between the temperature and the distribution indices was significant as well as the correlation between the distribution and the growth indices. However the correlation between the temperature and the growth indices was not significant, which suggests that the coherence between temperature and growth occurred through distribution changes. Another line of evidence suggests that growth variations were not directly related to temperature: relationships between various temperature indices and size-at-age were not significant once accounting for autocorrelation (see Table 1 of Dutil *et al.,* 1999).

Together, these data suggest that (1) cod responded to the cooling by changing their distribution and migration patterns to remain within a zone of preferred temperatures, and that (2) this distribution change resulted in the growth and condition decline. We propose a food limitation hypothesis (reduction of feeding season duration and quality) to account for the decline of northern Gulf cod growth from the mid 1980s to the mid 1990s (Castonguay *et al.,* 1999; Dutil *et al.,* 1999). Hence, in this stock, the growth and condition declines seem to have been related to food availability and/or quality, and ambient temperatures do not appear to have been the key variable driving changes in growth, although we recognize that interannual changes in ambient temperatures may have occurred at times other than January or August that the surveys would not have detected.

Several lines of work are being pursued to examine further this food-limitation hypothesis:

- Data storage tag study, which provide a long-term continuous record of ambient temperatures to validate ambient temperatures from research surveys.
- Compare seasonality of fall cooling and of fall condition with indices of spatial distribution.
- Application of seasonal Ecopath-type trophic models to assess impact of a physically-driven change in spatial distribution on energy available to cod.
- Laboratory examination of interactions between temperature, thermal preferendum, and growth.

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Working Document 3.2

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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Growth, Distribution and Abundance of Arcto-Norwegian Cod in Relation to Ambient Temperature

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Extended Abstract

Since fish often inhabit regions of relatively large horizontal temperature gradients they may, depending on their movements, experience temperature variations, which are quite different from those, measured in any geographically fixed point. When studying the effect of temperature on growth the temperature of interest is that actually experienced by the fish, their ambient temperature. Ambient temperature may be defined as a fish density weighted temperature mean estimated by the following equation:

$$T_{amb} = \frac{\int \left[\rho(x,y,z,t) \quad T(x,y,z,t) \right] dxdydzdt}{\int \rho(x,y,z,t) dxdydzdt}$$

where $\rho(x, y, z, t)$ is fish density at position (x, y, z) and time t, $T(x, y, z, t)$ the corresponding temperature, and the integration is done, separately for each age group, over the whole distribution volume of the fish and the time period in question (Ottersen *et al.*, 1998).

For Arcto-norwegian cod in the Barents Sea and Svalbard waters (Figure 1), annual mean temperatures range from 6–8ºC at the spawning grounds along the west coast of Norway (Aure and Østensen, 1993) down to 0 or even –1ºC along the Polar front in the northern and north-eastern parts where the fish feed during summer and autumn (Mehl *et al.*, 1985; Woodhead and Woodhead, 1965). Cod is in this region mainly found at depths below 100 metres (Korsbrekke *et al.*, 1995) where seasonal variations at fixed locations are rather small, 1–3ºC (Ottersen and Ådlandsvik, 1993). This indicates that the inter-annual variation in temperature experienced by the cod may be more dependent on year-to-year differences in distribution patterns than on temperature fluctuations at any given fixed location.

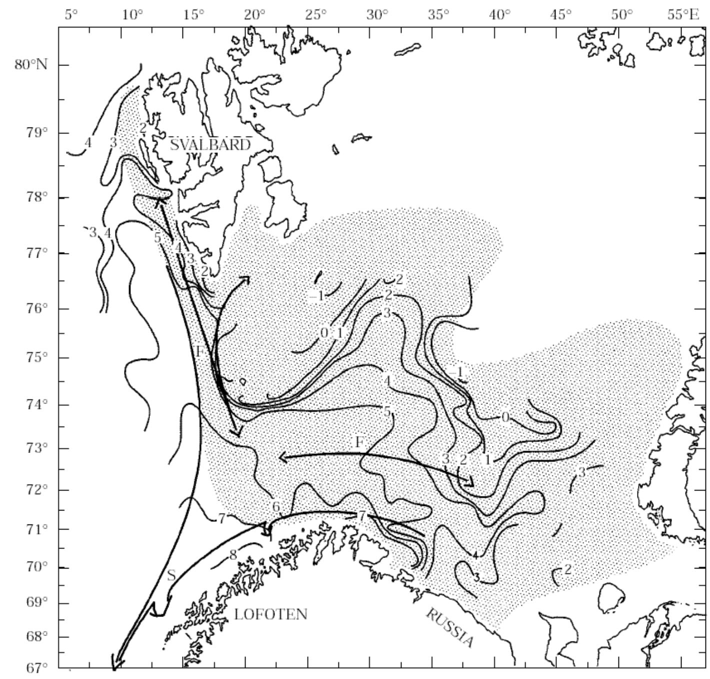

Figure 1. The Barents Sea with the area of distribution of north-east Arctic cod and isotherms (°C) at 100m depth. Feeding areas (hatched), seasonal feeding migrations (F) and spawning migrations (S) are indicated (see Mehl, 1991). Temperature distribution is for August 1995 (ICES, 1996). This map is taken from Ottersen *et al.* (1998).

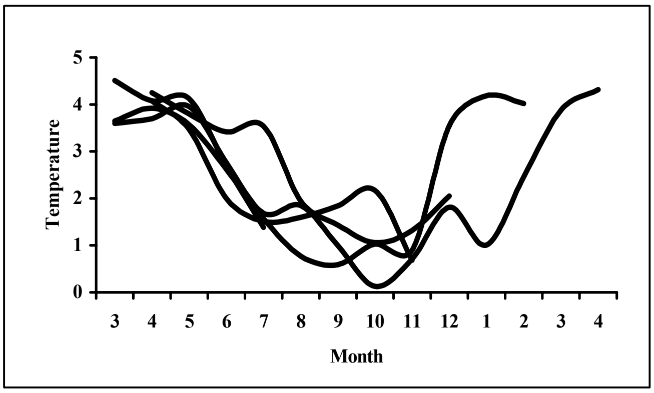

Figure 2. Seasonal variability in ambient temperature of Arcto-Norwegian cod as measured by data storage tags. Smoothed means of measurements done every two hours are shown.

Here, ambient winter temperatures for Arcto-norwegian cod were calculated from survey data by age (1–7) and year (1988–1995) and compared with variations in growth, distribution and abundance. Inter-annual variability in ambient winter temperature was higher than in the fixed Kola-section. Mean individual growth rate was highest for year classes experiencing high temperatures. Mean lengths at age increased with increasing lifetime accumulated ambient winter temperature. Older fish were found in higher temperatures, further west. Increased abundance of young cod is associated with an extension of the distribution area towards east and north, into colder water (Nakken *et al.*, 1987; Ottersen *et al.*, 1998; Michalsen *et al.*, 1998).

Due to the seasonal migration patterns of cod, the actual annual means of ambient temperature are lower than the values from February alone, more so with increasing age. In order to get more precise estimates of the effect of temperature on growth of cod, ambient temperature should be known also for other seasons. One approach is to apply electronic data-storage tags, which measure depth and temperature in the surroundings of the individual fish (Figure 2). While the number of tags returned still is to small for the mean values to be reliable estimates for the whole population or age group, we show examples of temperature histories that support our expectations from migration patterns.

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Working Document 4.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

The Effects of Size Selective Mortality, Density and Temperature on Size at Age of Southern Gulf of St. Lawrence Cod

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Introduction

Size at age of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence, Canada, has varied considerably since 1971 (Figure 1, data from Chouinard *et al.,* 1999). Many factors affect population mean length-at-age and three commonly proposed explanations for interannual variability include: effects of changes in environment on growth, most notably temperature; density-dependent effects on growth; and the consequences of size selective fishing. Previous work on the effects of these three mechanisms on size at age of this and other fish stocks have generally focused on one mechanism making it difficult to determine the relative importance of alternatives. In this paper, we have considered all three mechanisms and have attempted to rank their importance. We begin with an analysis of size-selective mortality of the adult population using direct evidence from back-calculated length-at-age. Indices of size selection were developed for inclusion in growth analyses. We use both non-linear and linear models to test the effects size selection, population density, and temperature on mean length-at-age.

Methods

Data on mean length-at-age of cod in the southern Gulf of St. Lawrence were obtained from stratified random bottom trawl surveys conducted annually in September, 1971–1998 (Hurlbut and Clay 1990). Otoliths (sagita) were collected on a length-stratified basis from each research tow for age determination. The original otolith collection of age 3–11 fish was sub-sampled for back-calculations. A total of 13,008 otoliths were successfully read as part of the study.

The otoliths were either manually broken (1971–1982) or resin embedded and sectioned (1983–1998). Ages were determined by counting the number of hyaline zones on the otolith cross section. The distance from the nucleus of the otolith to the outside edge of each hyaline zone along the longest axis of the cross section was recorded for back-calculations. This edge was assumed to correspond with the end of the winter slow-growth period which occurs in April.

Individual fish lengths at age were back-calculated using the biological intercept procedure described by (Campana 1990). The biological intercept is the position on the otolith radius/fish length plane at which the relationship between the 2 variables becomes linear. We estimated the biological intercept from non-parametric density plots (Anon., 1994) of otolith radius/fish length for the cohorts sampled at all ages used in the study. The density plot shows a characteristic v-shape due to the fact that faster growing fish have proportionately smaller otoliths (Figure 2). The biological intercept for back-calculations was estimated by determining the intersection point of 2 lines drawn along the upper and lower limits of the outermost contour of the density plot. This contour enclosed approximately 90% of the observations. We chose a biological intercept of 0.44 mm otolith radius, 2.44 cm fish length.

Additional otolith measurements were made for age 0, 1, and 2 fish from the 1987 year class to verify this choice of biological intercept. These additional points are shown in Figure 2. 90% of these measurements fell within the biological intercept arc, thus supporting the estimation.

Our test for size selective mortality was to compare, within year classes, the mean back-calculated lengths at age among successive ages of capture. We used pairs of ages that were 3 years apart, i.e., 3 and 6, 4 and 7, 5 and 8, 6 and 9, 7 and 10, 8 and 11. The back-calculated length at the annulus corresponding to the younger of the two ages in the pair was the basis for the tests. Separate analysis of variance of the following form was used for each age group.

$$L'_{i,t,y} = \beta_0 + \beta_1 \mathbf{Y} + \beta_2 \mathbf{I(Y)} + \varepsilon$$

where $L'_{i,t,y}$ is the back-calculated length-at-age i of a fish caught in year t of year class y

Y = a matrix of 0 and 1 that designates year class
I = a matrix of 0 and 1 that designates age of capture.

The age of capture was i for the younger age in the pair and i+3 for the older age. The year of capture was i+y for the younger age in the pair and i+y+3 for the older age.

The parameter vector β_2 and the associated standard error vector was used to test the null hypothesis of no difference in back-calculated lengths at age.

Two indices of size selection were calculated for use in growth modelling. A cumulative size selection index was defined as the year class specific difference in the population mean back-calculated length-at-age 3 between the year of capture and when the fish were age 3. A negative value indicates that smaller, and thus slower growing, age 3 fish had a higher survival rate than larger fish. We would expect that the growth parameter associated with this index to have a positive sign.

An annual size selection index was determined as the difference between the population mean back-calculated length-at-age i-1 calculated from fish caught in year i+y and those caught in year i+y-1. Negative values indicate that the fish surviving to year i+y were smaller at age i-1 than were fish surviving to age i+y-1. We reasoned that, in such cases, the annual growth increment measured by population means would be less than if the index was zero, all other things remaining equal. We would expect the growth parameter associated with this index to have a positive sign.

Our main objective in the growth analysis was to quantify the effects of size selective mortality, temperature, and population density on length-at-age of southern Gulf of St. Lawrence cod. The size selection indices are described above. The index of population density ($N_{i,y}$) was taken as the survey estimates of mean numbers per tow at age and year. The density variables were z-score standardized for each age to equalize the scale of measurement. The mean bottom temperature index (V_t) was calculated as the stratified mean of the tow-by-tow temperature measurements. The occupied temperature index ($T_{i,y}$) was calculated as the catch weighted stratified mean temperature by age and year.

The von Bertlanfy growth equation has been commonly used to model growth of fish. While it is possible linearize the equations, there are inherent problems when analysing annual means because the observations are used as both dependent and independent variables. But, this is not the case if growth increment data are taken from individual fish. Thus, we have applied a non-linear analysis to annual mean lengths at age and a linear analysis of back-calculated growth increment data.

We followed a hierarchical model selection process. Models including all possible combinations of effects were run and the residual sums of squares (RSS) were recorded. For each effect in each model, the sum of squared residuals explained by adding that effect in a model including the other effects was calculated (Type III sums of squares). The intent was to find the most parsimonious model which had the lowest overall residual sum of squares and in which each parameter was statistically significant based on Type III sums of squares.

Millar and Myers (1990) investigated three non-linear formulations of the von Bertlanfy equation which incorporated environmental effects, 1) a reversible effect on the growth constant (k), 2) a reversible effect on the terminal length (L_∞) and 3) an irreversible effect on L_∞. We found formulation 2 provided the best treatment of our data in terms of stability of solutions and overall percent variance explained.

The procedure for the non-linear estimation was as follows. For each cohort in the analysis, we first estimated the length-at-age 2 as:

$$\hat{L}_{2,y} = (L_\infty + \beta_4 L'_{3,3+y,y})(1 - e^{-k(2-t_0)})$$

where $L'_{3,3+y,y}$ was used as an indicator of variability in growth in the initial years of the year classes's existence. For ages 3–11, the lengths at age are estimated by summing the estimated length at the previous age and the predicted length increment.

$$\hat{L}_{i,y} = \hat{L}_{i-1,y} + (L_\infty - \hat{L}_{i-1,y} + \beta_4 L'_{3,i+y,y}$$
$$+ \beta_5 S'_{i,y} + \beta_6 N_{i,y} + \beta_7 T_{i+y} + \beta_8 V_{i,y})(1 - e^{-k})$$

The equation shows all the explanatory variables ($L'_{3,i+y,y}$, $S'_{3,i+y,y}$, $N_{i,y}$, T_{i+y}, $V_{i,y}$). Note that for ages 3–11, the cumulative size selection factor reduces to the back-calculated length-at-age 3 for fish caught at age i of year class y. The model parameters were estimated by minimising the squared differences between observed and predicted mean lengths at age using Proc NLIN of SAS. The relative importance of each explanatory variable was determined by calculating the marginal reduction in squared residuals associated with each variable in all possible 1, 2, 3, 4, and 5 parameter models.

A linear analysis of back-calculated growth increments was also used to test for the effects of size selective mortality, temperature and density on length-at-age. The growth increments of individual fish were back-calculated between the last and second last annuli. The von Bertlanfy growth equation may be rearranged (Gulland 1983, p. 91) to represent this increment as:

$$D'_{i,i+y,y} = L'_{i,i+y,y} - L'_{i-1,i+y,y} = (L_\infty - L'_{i-1,i+y,y})(1 - e^{-k})$$

Additional explanatory variables (E) may be added in a manner that affects L_∞, similar to the non-linear analysis.

$$D'_{i,i+y,y} = (L_\infty - L'_{i-1,i+y,y} + \beta_1 E)(1 - e^{-k})$$

Let $\beta_3 = 1 - e^{-k}$

Then:

$$D'_{i,i+y,y} = \beta_3 L_\infty - \beta_3 L'_{i-1,i+y,y} + \beta_3 \beta_1 E$$

Then the linear regression, including all explanatory variables, becomes:

$$D'_{i,i+y,y} = \beta_0 + \beta_1 L'_{i-1,i+y,y} + \beta_2 L'_{3,3+y,y} + \beta_4 C'_{i,y} + \beta_6 N_{i-1,y} + \beta_7 T_{i+y-1} + \beta_8 V_{i-1,y}$$

Note the subscripts for the environmental effects N, T, and V are for one year before the sampled fish were captured. This is because the growth increment being measured occurred between April and March, and therefore the relevant growing season was in the year previous to capture. Note also that the annual size selection index was not included in the analysis of growth increments. This is because growth increment data were obtained from individual fish, not from annual means.

Results

The analysis of variance tests for size selective mortality are summarised in Table 1. The main effects were all highly significant. The estimated differences in back-calculated lengths at a common age for different pairs of ages indicate that there has been a significant change in the pattern of size selection (Figure 3). During the early to mid-1970s the back-calculated lengths at age from the older fish were greater than those obtained from younger fish, suggesting that there was selection (in the evolutionary sense) for fast growth during this time. This trend was evident for all ages. The pattern was reversed during the 1980s and early 1990s. For the age groups 3 and 6, 4 and 7, 5 and 8, 6 and 9, there was a tendency for the back-calculated lengths at age obtained from older fish to be less than those obtained from younger fish. The largest differences occurred in the late 1980s and early 1990s for ages 3 and 6, 5 and 8, 6 and 9. The differences were reduced at the end of the time series. This pattern corresponds with the trend in commercial fishing mortality where there was a large increase in the late 1980s until the fishery was closed and then a decline following the closure. However, there was no evidence of size selective mortality on the oldest age groups during the 1980s and 1990s.

The residual sums of squares (RSS) and sums of squares explained by the addition of each variable to all possible 1, 2, 3, 4, and 5 parameter non-linear growth models indicate that size selective mortality was the dominant effect on mean length-at-age (Table 2). For the 1 parameter models, the lowest RSS was obtained with a model that included the direct size selection index. Models with only cumulative size selection or occupied temperature also had relatively low RSS. The poorest fits were obtained with models with population density and bottom temperature. For the 2 parameter models, the lowest RSS was for a model with direct size selection and occupied temperature. Other 2 parameter models with low RSS included cumulative size selection and direct size selection, direct size selection and population density, and cumulative size selection and population density. The lowest RSS for a 3 parameter model was obtained with direct size selection, cumulative size selection, and population density. The second lowest RSS was for a model with direct size selection, population density and mean bottom temperature. Two of the 4 parameter models had almost the same RSS. Both included direct size selection, cumulative size selection, and population density. The 5 parameter model was justified by the reduction in sums of squares. The parameter estimates for the preferred model are given below.

$$\hat{L}_{2,y} = (25.28 + 2.151\, L'_{3,3+y,y})(1 - e^{-0.0976(2+1.680)})$$

$$\hat{L}_{i,y} = \hat{L}_{i-1,y} + (25.28 - \hat{L}_{i-1,y} + 2.151\, L'_{3,i+y,y} + 9.108\, S'_{i,y} - 5.757 N_{i,y} + 2.167\, T_{i+y} + 3.261\, V_{i,y})(1 - e^{-0.0976})$$

The relative influence of the 5 variables on predicted size at age in the non-linear analysis was determined by multiplying the variable standard deviation by the parameter estimate. The influence, in relative order, was direct size selection (19.9), population density (5.9), cumulative size selection (5.8), occupied temperature (2.2), and bottom temperature (0.8).

If one followed a similar hierarchical model forming process, but ignored the size selection variables, one would accept a model including population density, occupied temperature, and bottom temperature. The lowest RSS for a 1 parameter model was obtained with occupied temperature. For a 2 parameter model, the lowest RSS was for a model including population density and bottom temperature. For the 3 parameter model including all 3 variables, each parameter estimate was statistically significant. However, the RSS for this model (2036) was considerably higher than that obtained from the 3 parameter model including direct size selection, cumulative size selection, and population density (866).

The most parsimonious linear model was obtained using the cumulative size selection and population density variables (Table 3). All of the 1 parameter models were statistically significant at the 0.05 level. The lowest RSS was obtained with a model including cumulative size selection, and the remaining variables produced successively higher RSS in the order of population density, temperature occupied, and bottom temperature. For the 2-parameter models, 4 produced statistically significant parameter estimates for both parameters. The lowest RSS was obtained for the model with cumulative size selection and population density. The bottom temperature parameter was not statistically significant in models containing cumulative size selection and temperature occupied. The lowest RSS for a 3-parameter model was obtained with the cumulative size selection, population density, and temperature occupied variables. However, the occupied temperature parameter was not statistically significant. In the 4-parameter model, neither temperature parameter was significant. The parameter estimates for the preferred model are given below.

$$D'_{i,i+y,y} = 3.51 - 0.128\, L'_{i-1,i+y,y}$$
$$+\, 0.271\, L'_{3,3+y,y} + 0.316\, C'_{i,y} - 0.455\, N_{i-1,y}$$

If one followed a similar hierarchical model-forming process, but ignoring the cumulative size selection variable, one would accept a model including population density, occupied temperature, and bottom temperature. The lowest RSS for a 1-parameter model was obtained with population density. For a 2-parameter model, the lowest RSS was for a model including population density and occupied temperature. For the 3-parameter model including all variables, each parameter estimate was statistically significant. However, the RSS for this model (276) was considerably higher than that obtained from the 2 parameter model including cumulative size selection and population density (181).

Summary

There has been significant variation in size selective mortality of this cod stock. During the early 1970s, there was a tendency for larger individuals to have better survival than smaller animals, indicating selection (in the evolutionary sense) for large size at age. During the 1980s and early 1990s, the reverse seemed to be the case when smaller individuals had higher survival rates.

The growth analyses indicated that size selective mortality was the dominant effect on changes in size at age. After size selection, it appears that population density was the next most important effect. This was followed by temperature. It should also be noted that temperature occupied might interact with population density given evidence for density dependent habitat selection for this stock (Swain and Kramer 1995). That is to say, when population density is high, the stock distribution expands into marginal areas, and in the southern Gulf of St. Lawrence these are areas of relatively low temperature.

The change in direction of size selection could have resulted from a combination of fishery regulations (mesh size) and environmental conditions. Fishing mortality in the southern Gulf of St. Lawrence cod fishery is dome shaped with respect to length (Sinclair 1998). As a result, fishing mortality is highest at intermediate sizes. During the 1970s the regulated mesh size was relatively low, population density was low, and ambient and occupied temperatures were relatively high. It is possible that these conditions meant that the fastest growing cod grew through the length range most vulnerable to fishing relatively quickly while the slower growing individuals remained in the vulnerable length range. The net result was higher survival of faster growing fish. The regulated mesh size was higher in the 1980s than in the 1970s thus moving the vulnerable length range to higher lengths. Population density was higher, at least in the early and mid-1980s, and temperatures were lower. As a result, some of the slowest growing fish may not have become fully recruited to the fishery while the faster growing fish remained vulnerable to fishing for a longer period of time. This would reduce mean lengths at age.

Fishing was the likely source of this size selective mortality. The strongest selection for slow growing fish occurred during the late 1980s and early 1990s when the overall fishing mortality was extremely high. The indices of size selection became neutral following the fishery closure.

Failure to consider size selective mortality can lead to incorrect conclusions about the role of environmental factors in determining growth. Population density appeared to be the dominant environmental effect on growth in models that did not include indices of size selective mortality. Given the apparent importance of size selective mortality in determining size at age of this cod stock and the relative ease with which indices of size selection can be created from archival otolith collections, it would be prudent to investigate its importance for other stocks before drawing firm conclusions about the relative importance of environmental effects on growth.

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Table 1. Summary statistics from ANOVA of back-calculated lengths at age. The last 2 columns give the F values for the main effects. All are highly significant (p<0.0001).

Ages	Year classes	N	R^2	Y (df=24)	I(Y) (df=25)
3 and 6	1968–92	3249	0.32	43.48	19.39
4 and 7	1967–91	3087	0.36	62.35	9.48
5 and 8	1966–90	2887	0.54	123.59	13.30
6 and 9	1965–89	2685	0.56	135.16	6.80
7 and 10	1964–88	2240	0.57	115.02	6.01
8 and 11	1963–87	1755	0.58	85.58	8.67

Table 2. Residual sums of squares (RSS) and sums of squares explained by the addition of specific variables for all 1, 2, 3, 4, and 5 parameter non-linear growth models. The variables are cumulative size selection (c), direct size selection (s), population density (n), occupied temperature (t), and mean bottom temperature (v). The "*" designates the lowest sum of squares for the respective number of parameters.

Model	RSS	Sum of Squares Explained by This Variable				
Base	6174	c	s	n	t	v
1 Parameter						
c	2713	3461				
s *	2302		3872			
n	4165			2009		
t	2778				3396	
v	4584					1590
2 Parameters						
cs	1561	741	1152			
cn	1623	2542		1090		
ct	1962	816			751	
cv	2689	1895				24
sn	1572		2593	730		
st *	1405		1373		897	
sv	2101		2483			201
nt	2469			309	1696	
nv	2184			2400		1981
tv	2735				1849	43
3 Parameters						
ctv	1842	893			847	120
cnv	1537	647		1152		86
cnt	1458	1011		504	165	
csn *	866	706	757	695		
cst	1156	249	806		405	
csv	1557	544	1132			4
snt	1174		1295	231	398	
snv	999		1185	1102		573
stv	1401		1334		700	4
ntv	2036			699	148	433
4 Parameters						
csnt	790	384	668	366	76	
csnv *	789	210	748	768		77
cntv	1448	588		394	89	10
sntv	968		1068	433	31	206
5 Parameters						
csntv *	766	202	682	23	23	24

Table 3. Residual sums of squares (RSS) and sums of squares explained by the addition of specific variables for all 1, 2, 3, and 4 parameter linear growth models. The variables are cumulative size selection (c), population density (n), occupied temperature (t), and mean bottom temperature (v). The "*" designates the lowest sum of squares for the respective number of parameters. Bold type indicates variables that were statistically significant at the 0.05 level.

Model	RSS	SS Explained by This Variable			
Base	383	c	n	t	v
1 Parameter					
c *	224	**159**			
n	313		**70**		
t	325			**58**	
v	364				**20**
2 Parameters					
cn *	181	**132**	**43**		
ct	215	**110**		**8.9**	
cv	223	**141**			2
nt	284		**42**	**30**	
nv	283		**81**		**30**
tv	325			**39**	0
3 Parameters					
ctv	206	**119**		**16**	**9**
cnv *	181	**102**	**42**		0
cnt	179	**104**	**36**	2	
ntv	276		**49**	**7**	**7**
4 Parameters					
cntv	179	**97**	**28**	2	1

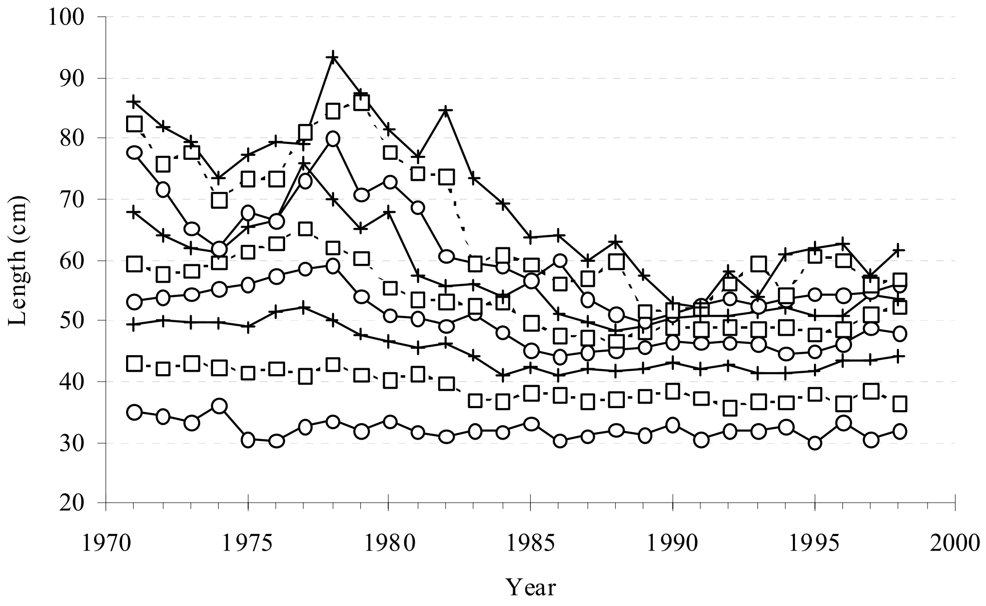

Figure 1. Mean length-at-age 3–11 for southern Gulf of St. Lawrence cod (1971–1998) estimated from annual bottom-trawl surveys. The age lines are labelled alternatively with circles squares and crosses beginning with age 3.

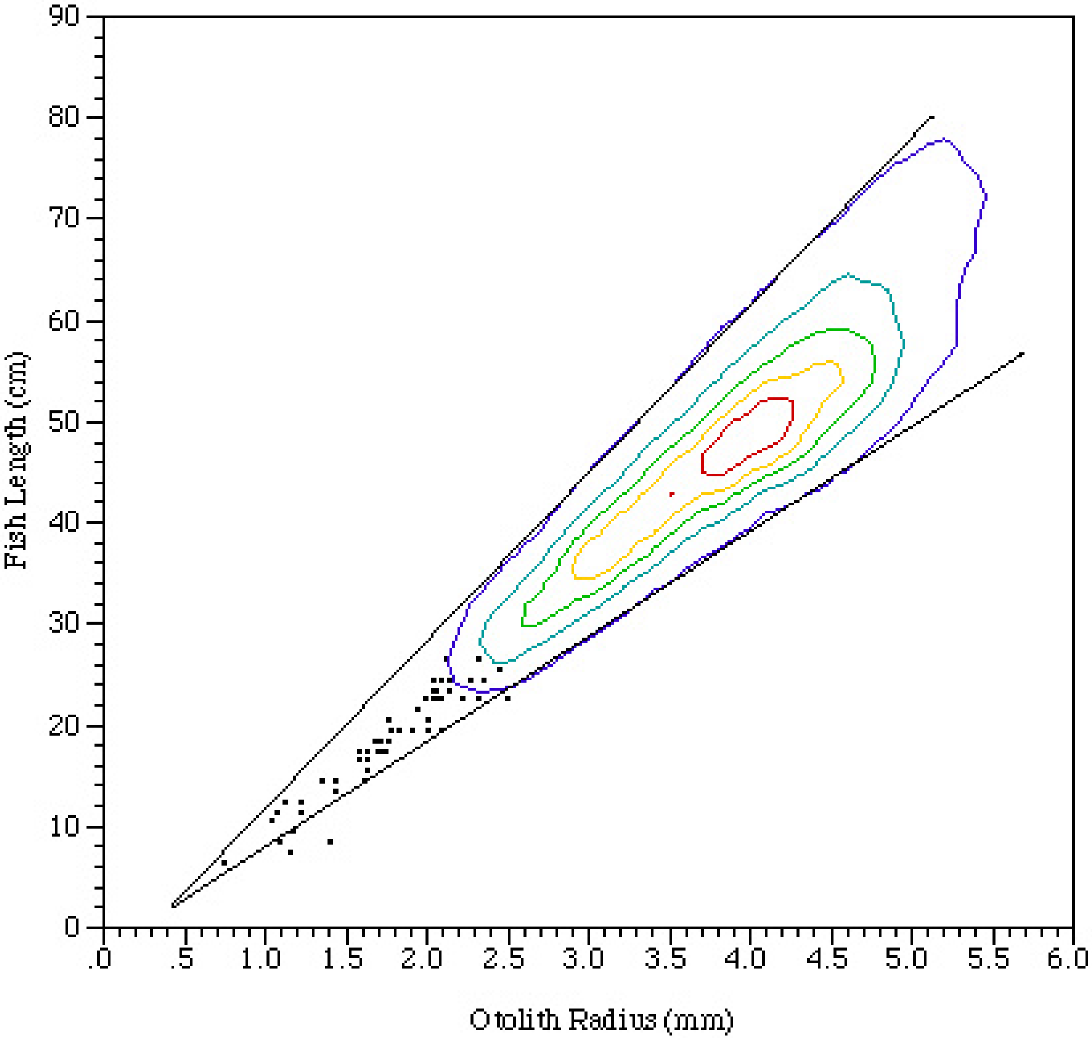

Figure 2. Summary of the approach used to calculate and confirm the biological intercept used in back-calculations. The contour lines are a non-parametric density plot of otolith radius vs. fish length for age 3–11 fish from the 1968–1987 year classes, the year classes sampled over the same age range. The outermost contour contains approximately 90% of the data. The biological intercept was defined as the apex of an arc, which contained the outermost contour. The individual data points are for ages 0, 1, and 2 fish of the 1987-year class, and these were not used to draw the density plot. That 90% of these measurements fall within the biological intercept arc supports its choice for back-calculation.

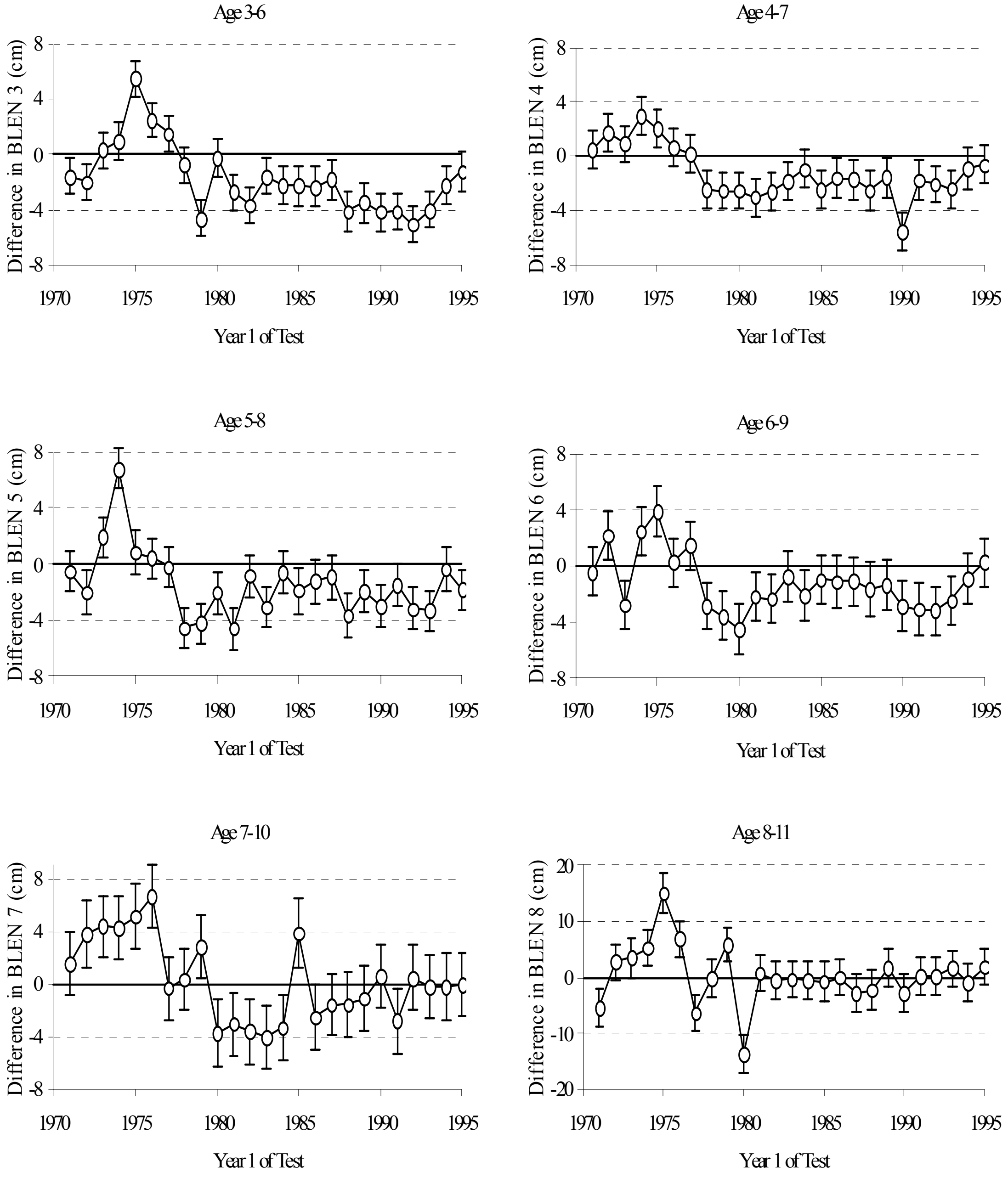

Figure 3. Within year class differences in mean back-calculated lengths at a common age but from fish caught three years apart. The label on each panel gives the ages of capture. The differences are calculated as the mean of the older fish less the mean of the younger fish. All panels have a common x-axis, which is the year in which the younger age group was caught. Back-calculations assumed a biological intercept of 0.44 mm otolith radius and 2.44 cm fish length.

Working Document 5.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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Modelling of the Impact of Northeast Arctic Cod Growth Rate Variations on their Stock Status in Dependence on Food Supply and Temperature Conditions

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Extended Abstract

The Northeast Arctic cod is characterised by the considerable year-to-year variations of growth rate. In different years, the mean weight of cod at the same age can differ more than 3 times. This is necessary to be taken into consideration when substantiating the cod fishery management strategy. Harvest control rules for the cod stock in the Barents Sea are based on the established fishing mortality coefficient, however TAC is calculated in units of biomass. Besides, the value of the spawning biomass serves as the only one biological reference point reflecting the stock status when determining the fishing mortality coefficient according to the scheme of precautionary approach developed within ICES.

To analyse the impact of the cod growth rate to their stock status and potentialities of fishery we have developed a STRAFICOD model (STRAtegy FIshing of COD). The cod growth rate in the model is calculated on the basis of rations and depends on the three factors as follows: food supply, abundance of the cod population and water temperature.

To characterise water heat content in the Barents Sea, data on the mean annual water temperature at the depth of 150–200 m in the “Kola Section” were employed. To adjust the model, rations calculated using the data on cod stomach content as the base were taken.

The concept basis of the model is developed on the assumptions as follows:

- the proportion of a prey in the predator’s ration reflects the proportion of biomass of this prey population to the overall biomass of all prey species to the predator in the sea;
- the maximum, the possible limit of the predator’s ration, is dependent on the weight of its body and temperature of the environment;
- coefficient of the proportion between the predator’s real and maximum rations is a function of biomass of the available food;.
- biomass of the food available to the predator in the form of a particular type of a prey is determined by the total biomass of the prey, its food suitability for the predator and coefficient of food competitiveness of the predator when consuming this prey;
- coefficient of the cohort intraspecific food competitiveness reflects the relative rate of the overall consumption of prey by individuals of the age group under study compared to the other predators and is proportional to the abundance of cohort, the mean value of rations of its individuals and their portion in the ration of the prey under study;
- growth of cod is a function of the body weight and value of the ration expressed in units of energy.

The model includes two species: cod as an object of fishery, and capelin as a food item of cod. The cod stock in the model is divided by age groups, from age 3 to 15, and by mature and immature individuals. Capelin are divided just into age groups: age 1–5. The model is not structured spatially. All the calculations in the model related to cod are done on the cohort basis. The time step of the calculations in the model is 1 year.

Input data for the model are as follows:

for the initial year:

a) biomass of the total cod stock by the beginning of the year;
b) age composition of cod stock by the beginning of the year;
c) mean weight of one individual of cod by age groups by the beginning of the year;

for the modelling period:

a) recruitment (abundance of cod at age 3)
b) mean weight of one individual of two-year-old cod by the beginning of the year;
c) ogives of maturation;
d) cod exploitation pattern;
e) total biomass and age composition of capelin population;

f) mean annual water temperature.

Calculations in the model are performed in the following order:

1) Calculation of composition of cod rations (a proportion of capelin and “other food” in the ration).
2) Calculation of the size of cod rations:
3) Calculation of the mean weight of one individual of cod by age groups.
4) Calculation of cod fishing mortality coefficients.
5) Calculation of the total stock biomass.
6) Calculation of the spawning stock biomass:
7) Calculations of the annual catch.

Results of the modelling analysis shows that capelin stock have considerable impact on the status of both as total as spawning stocks of cod in the Barents Sea and it influence depends on the temperature conditions and age composition of cod stock.

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Working Document 5.2

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Interannual variability in liver condition index of Northeast Arctic cod: forecasting potential

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Abstract

Temporal variation in the liver condition index (LCI) of five length classes of Northeast Arctic cod was described and compared to the abundance and availability of capelin and herring in the Barents Sea. Large and rapid interannual variations in LCI occurred which were synchronous across length classes.

For all length classes the annual mean LCI was non-linearly related to capelin stock biomass such that LCI decreased rapidly when capelin stock biomass was below one million t. LCI and the frequency of occurrence of capelin in cod stomachs were positively associated. Neither the abundance of juvenile herring in the Barents Sea nor the frequency of occurrence of herring in cod stomachs were positively correlated with LCI. However, a significant, inverse relationship between the frequency of occurrence of capelin in cod stomachs and total stock biomass of herring was observed suggesting that herring influence LCI of cod via predation on capelin.

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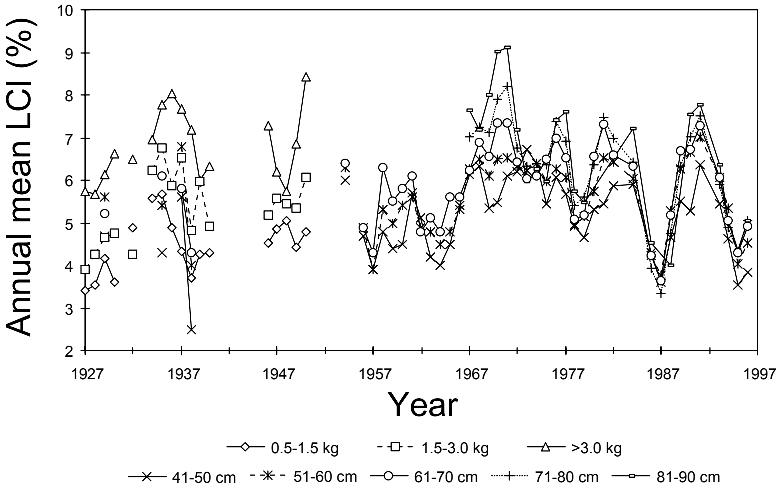
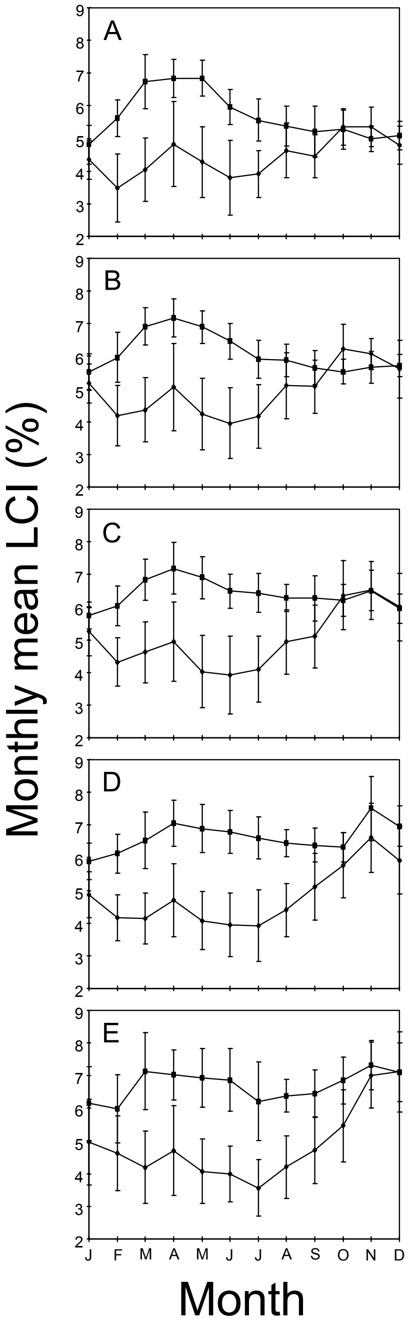


Time series of annual mean liver condition indices (LCI) (%) of Northeast Arctic cod. Capelin biomass was known to be below 1 million tons from 1985–1989 and from 1993–1996.



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

Working Document 5.3

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Incorporating growth into the stock/recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential

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Abstract

Correlation and simulation analyses have previously suggested that for the Northeast Arctic cod stock the total lipid energy (TLE, units of kilojoules) contained in the livers of mature females is proportional to total egg production and exhibits a similar dynamic response to varying food abundance. Thus, TLE is a more sensitive index of reproductive potential and, as such, a potential correlate of recruitment. The TLE was estimated for a fifty one-year time period (1946–1996) using several historical databases for NA cod. The formula used to estimate TLE amplified the effect of growth variation by including year-specific values of proportion mature and weight at length which were predicted from food abundance (capelin biomass) and observed values of the liver condition index. The temporal trend in TLE differed from that of spawner biomass (Figure 1) and suggests that the reproductive potential of the NA stock has been in decline since the mid-1970s The relationship between TLE and recruitment differed from the indeterminate relationship between spawner biomass and recruitment in several important respects: (1) there was a statistically significant, positive relationship between TLE and recruitment; (2) the dynamic range in TLE was comparable to that in recruitment; and (3) the relationship was linear which challenges the traditional view of a density-dependent stock/recruit relationship. Residual variation in the relationship between TLE and recruitment was significantly correlated with mean temperature at the Kola hydrographic section. We conclude that spawner biomass is an insensitive measure of reproductive potential because it responds to variation in spawner quantity but fails to incorporate the effect variation in condition has on reproductive potential. Reconstructing the stock/recruit relationship using more sensitive measures of reproductive potential is the necessary first step in resolving environmental and ecological effects on recruitment.

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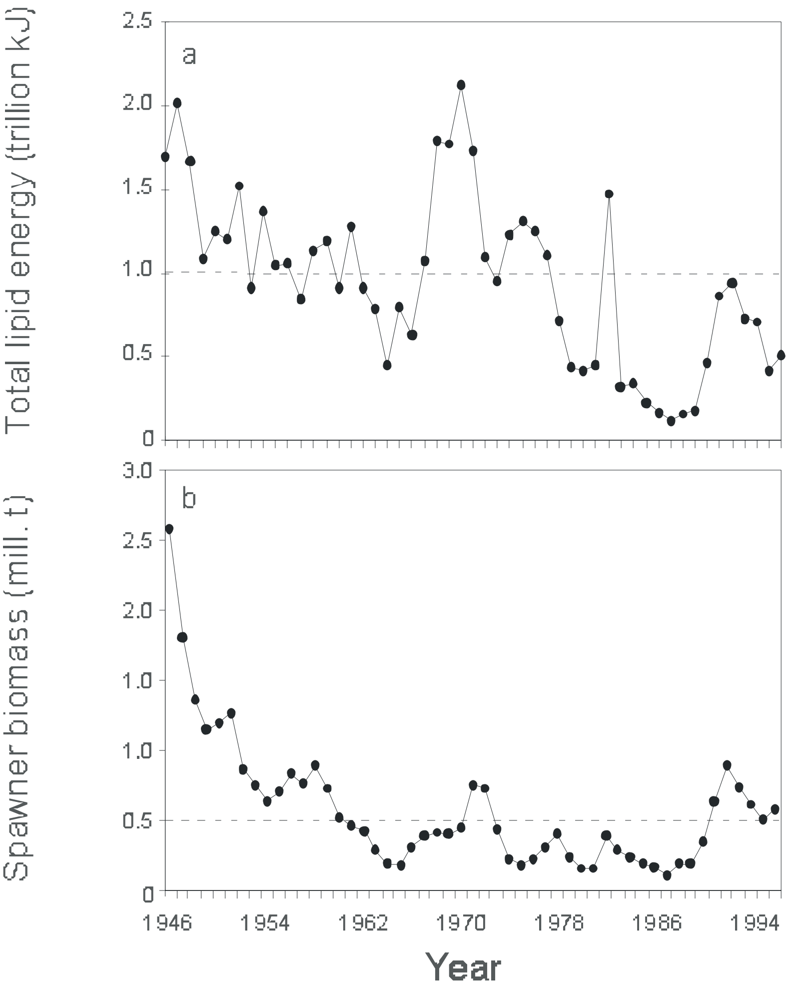

Figure 1. (A) Time series of total lipid energy. Dashed horizontal line indicates a level of 1 trillion kJ. (B) Time series of spawner biomass. Dashed horizontal line indicates a level of 500,000 t.

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Temperature data may provide additional information for predicting weight at age and recruitment of North Sea cod

Keith Brander and David O'Brien

Extended Abstract

One of the aims of the Cod and Climate Change programme is to provide additional information about the environment, which may be relevant to fisheries assessment. A workshop on cod growth, planned for next year, will bring together and evaluate existing studies and also carry out new analyses of the causes of variability in growth between and within stocks. Preparations for this workshop are in hand (C.Res.1999 attached) and the following material is part of the preparation. It is being presented to the WGNSSK because feedback and a dialogue will help to ensure that the growth workshop is well informed about the interests and requirements for assessments and also because some of the material may already be relevant to WGNSSK. The presentation has been kept very short in recognition of the time pressure under which WGNSSK unfortunately has to work, but more detail can be provided on request.

Temperature and growth of North Sea cod

1. Material and methods:

The data on stock weight at age of North Sea cod are taken from the 1998 WG report. Market sampling gives a biased estimate of the weight at age 1 (and possibly 2?) for North Sea cod because the fish in this size range are partially exploited (selected) and there are changes in mesh size and in minimum landing size (whether for legal or commercial reasons).

The data on bottom temperature are from the ICES oceanographic database and are annual means of the deviations for each 1^o*1^o rectangle for each month. A weighted mean was also calculated, using the annual distribution patterns of cod, by age, from the IBTS. Because the pattern of temperature variability is highly correlated over the whole North Sea (Dippner, 1997), there is very little difference between the weighted and unweighted means. Since there are no IBTS data for most of the years being analysed here, the unweighted mean was used.

2. Results:

Trends in weight at ages 1 to 4 since 1960 are shown in Figure 1, together with the deviation in bottom temperature during the year in which they were spawned. It appears that temperature during the year in which they were spawned determines 30% or more of the subsequent variability in weight at age. The trends in weight at ages 1 and 2 do not match the temperature trend as well as is the case for ages 3 and 4, but are still statistically significant. The correlation matrix is given in Table 1 and the regression coefficients in Table 2 with their respective plots in Figure 2. The fitted regressions up to age 6 can be used to forecast (or now-cast in the case of 1999) the weights at age up to five years ahead and these forecasts are given in Table 3.

3. Discussion:

Weight at age (x+1) equals weight at age (x) times the specific growth rate. Very large differences in weight at age are known to arise during the first year of life. An extreme example is the mean weight of cod larvae in the Barents Sea, which differed by a factor of more than three between 1987 and 1990 (normalised to 31 August, Loeng *et al.,* 1995) and correlated well with temperature. Even if there is variability in subsequent specific growth rates, such large differences in "initial" weight at age will persist through to later life, hence providing a likely explanation for the correlations presented above. The poorer fit with age 1 and 2 cod in the North Sea is surprising, but could be due to bias in the market sample based estimates for these ages.

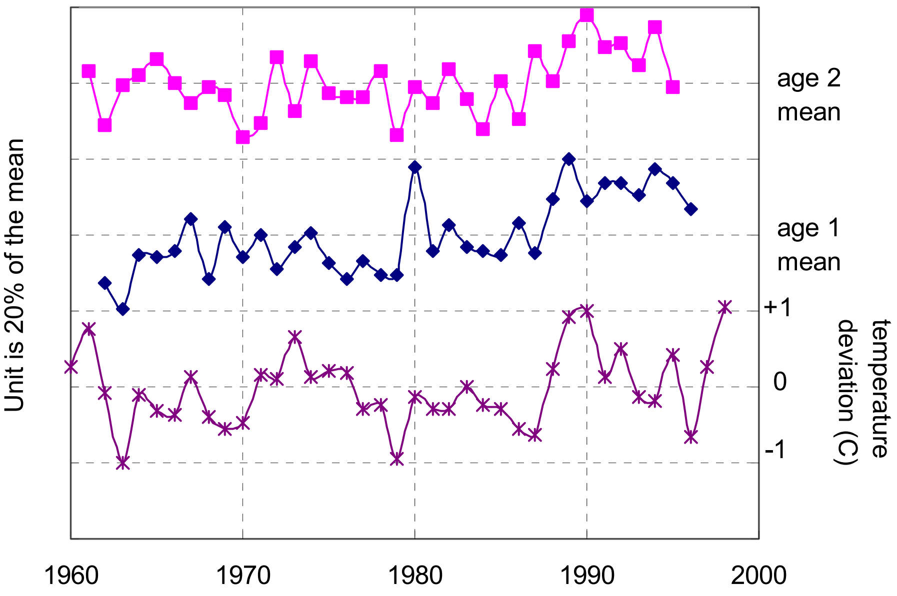
An alternative explanation of variability in North Sea cod weight at age is provided by Cook et al (in press), who relate it to stock biomass (density dependence). Their correlation is at least as good as the one presented here, but it depends on estimates of stock biomass since 1991 and is therefore very sensitive to the outcome of the most recent assessment. The correlation with temperature does not depend on which period of years is included.

Temperature and recruitment of North Sea cod

Several authors have pointed out the relationship between temperature and recruitment for North Sea cod (Dickson *et al.*, 1973, Svendsen 1995, Dippner 1997, Planque and Fredou in press, Brander in press). The processes linking temperature and recruitment are not yet evident and therefore it is difficult to select the most appropriate measure of temperature (and other linked potentially linked variables, such as food for larvae). Also recruitment is unlikely to be determined by a single process. Not surprisingly therefore, the coefficients of determination in the existing relationships are generally fairly low and the predictions are probably only useful as a rough early indicator. Since temperature data have in the past not been needed very urgently, we do not have much North Sea data for 1999. If temperature (or other environmental factors) are to be used for recruitment forecasting then they will have to be made available more rapidly in future.

Figure 3 shows the time series of recruitment of North Sea cod together with the annual mean deviation in bottom temperature for the North Sea and the NAO (winter index). Both give statistically significant correlations ($R^2 = 0.2$; $p < 0.001$) and could be used as a preliminary indication of recruitment.

Perhaps a more important reason for looking closely at the evidence that environmental factors influence recruitment concerns the consequences for interpreting the stock recruit relationship, when deciding on reference points for management strategies. The period of high recruitment of cod (and other gadoid species) during the 1960s and 1970s was almost certainly influenced by the environment during that period, of which the low winter NAO values are one indicator.



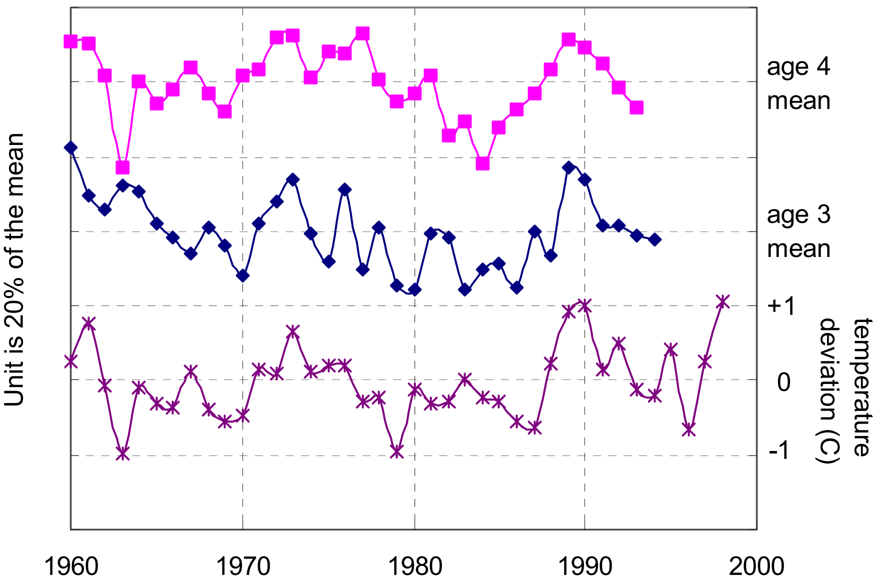


Figure 1. Deviations from the mean weight at age and mean bottom temperature for North Sea cod. The top panel shows ages 1 and 2; the bottom panel shows ages 3 and 4. The horizontal dashed lines correspond to 20% deviations from the mean weight.

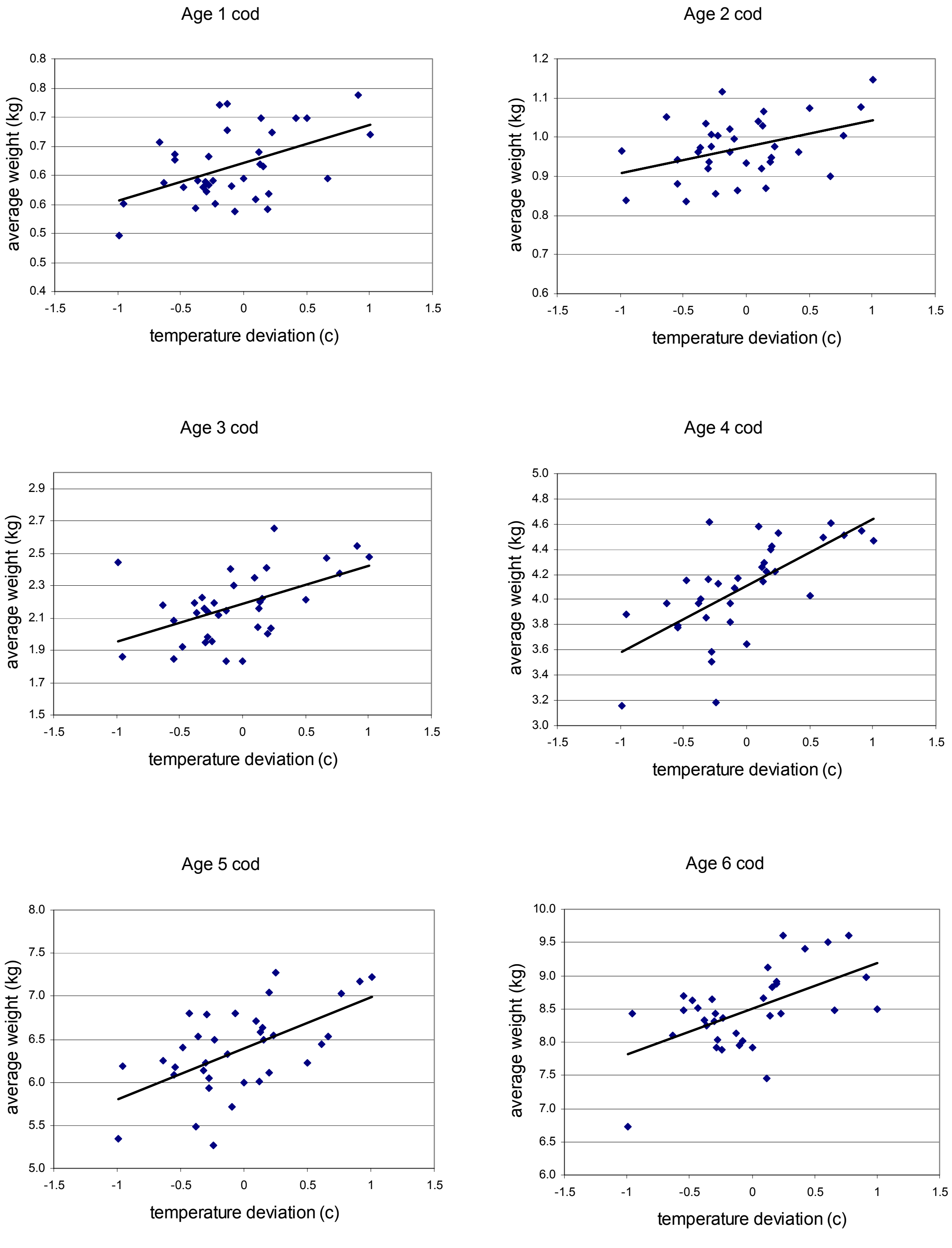


Figure 2. Plots of mean weight of cod ages 1 through 4 as a function of deviations from mean bottom temperature. Relevant statistics are given in Tables 1 and 2.

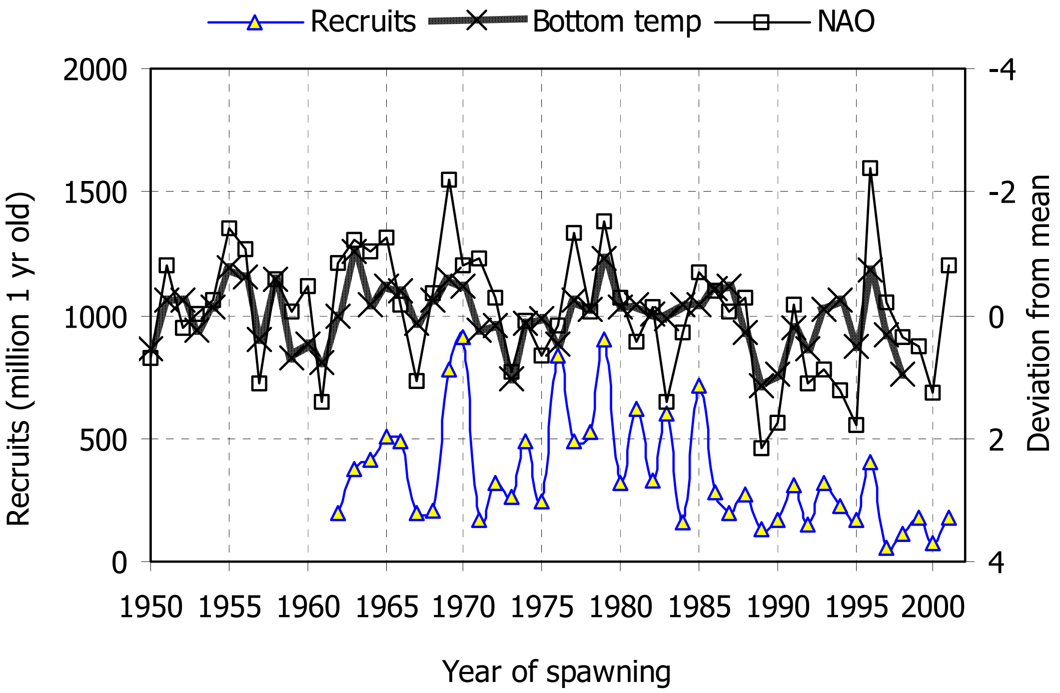


Figure 3. Cod recruitment plotted with deviations from bottom temperature and the North Atlantic Oscillation (NAO) index. The right hand scale for bottom temperature and NAO is inverted.

Table 1. Correlation matrix for mean weights at age and bottom temperature deviations.

Age	1	2	3	4	5	6	7	Bottom T dev
1	-	-	-	-	-	-	-	-
2	0.484	1.000	-	-	-	-	-	-
3	-0.048	0.455	1.000	-	-	-	-	-
4	0.188	0.212	0.415	1.000	-	-	-	-
5	0.339	0.330	0.455	0.790	1.000	-	-	-
6	0.259	0.157	0.268	0.660	0.659	1.000	-	-
7	-0.013	0.105	0.105	0.230	0.146	0.278	1.000	-
Bottom T dev	0.485	0.405	0.508	0.669	0.579	0.556	0.001	1.000

Table 2. Statistics for mean weight at age regressed on bottom temperature deviation during age 0.

Statistics	r^2	n	Significance	Slope	SE	Intercept	SE
Age 1	0.2122	35	0.0031	0.0649	0.0204	0.6207	0.0094
Age 2	0.1385	35	0.0159	0.0669	0.0263	0.9755	0.0122
Age 3	0.2360	35	0.0018	0.2338	0.0689	2.1866	0.0318
Age 4	0.4303	35	0.0000	0.5322	0.1030	4.1103	0.0486
Age 5	0.3151	35	0.0003	0.5949	0.1458	6.3984	0.0695
Age 6	0.2881	35	0.0005	0.6868	0.1788	8.5038	0.0848
Age 7	-0.0303	35	0.9971	0.0010	0.2693	10.1262	0.1293

Table 3. Predicted mean weights at age and upper (U95%) and lower (L95%) 95% confidence limits for North Sea cod. All values are in units of kg.

Year		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
1999	L95%	0.433	0.908	1.494	3.815	5.924	8.105	8.540
	estimate	0.690	0.993	2.031	4.334	6.283	8.417	10.127
	U95%	0.947	1.078	2.568	4.852	6.643	8.729	11.713
2000	L95%	-	0.709	2.031	2.942	5.914	7.935	9.657
	estimate	-	1.047	2.247	3.756	6.648	8.371	10.126
	U95%	-	1.384	2.462	4.569	7.382	8.807	10.595
2001	L95%	-	-	1.581	3.920	4.850	7.903	9.473
	estimate	-	-	2.435	4.247	6.002	8.792	10.126
	U95%	-	-	3.289	4.574	7.154	9.681	10.779
2002	L95%	-	-	-	3.383	6.088	6.651	8.796
	estimate	-	-	-	4.676	6.551	8.046	10.127
	U95%	-	-	-	5.970	7.014	9.441	11.458
2003	L95%	-	-	-	-	5.199	8.120	8.038
	estimate	-	-	-	-	7.031	8.681	10.125
	U95%	-	-	-	-	8.863	9.242	12.213
2004	L95%	-	-	-	-	-	7.016	9.286
	estimate	-	-	-	-	-	9.234	10.126
	U95%	-	-	-	-	-	11.452	10.967
2005	L95%	-	-	-	-	-	-	9.287
	estimate	-	-	-	-	-	-	10.127
	U95%	-	-	-	-	-	-	13.446

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Covariability in Early Growth and Year class Strength Of Barents Sea Cod, Haddock and Herring: the Environmental Link

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Extended Abstract[*]

The concept that size-specific growth and mortality rates interact to determine survivorship in fish populations has long been a foundation of fisheries theory (Gulland, 1965; Cushing, 1974; Ware, 1975; Campana, 1996). Simply stated, the theory predicts that survival of a cohort is directly related to growth rates during the pre-recruit period (Anderson, 1988). A rapid growth rate through the larval and juvenile stages is thought to increase the probability of survival due to an enhanced ability to feed and avoid predators (Rice *et al.*, 1993; Cushing and Horwood, 1994). While widely accepted, field evidence supporting the hypothesis for marine fishes has been elusive (Campana, 1996).

In this paper, the connection between size and year class strength at the early stages is examined for the commercially important Barents Sea stocks of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*). Data on number, length and geographical distribution of these stocks have been collected annually in the Barents Sea and adjacent waters since the mid 1960s during the International 0-group surveys in late August / early September. Data are taken from the survey reports, e.g., ICES (1996a). Virtual population analysis (VPA) estimates of year class abundance at age 3, based on commercial catch data, were used (ICES, 1996b, 1996c). Annual mean temperatures for the 0–200 m depth range were derived from the Russian hydrographic section off the Kola peninsula (Bochkov, 1982; Tereshchenko, 1996).

Figure 1 provides an update of the mean length of 0-group cod, haddock, and herring given by Loeng *et al.* (1995). Temporal development of cod length as 0-group shows a clear synchrony with abundance as 0-group and age 3 as well as annual mean sea temperature along the Kola section (Figure 2). However, in some years the discrepancies between the four variables are considerable, particularly during 1965–1967.

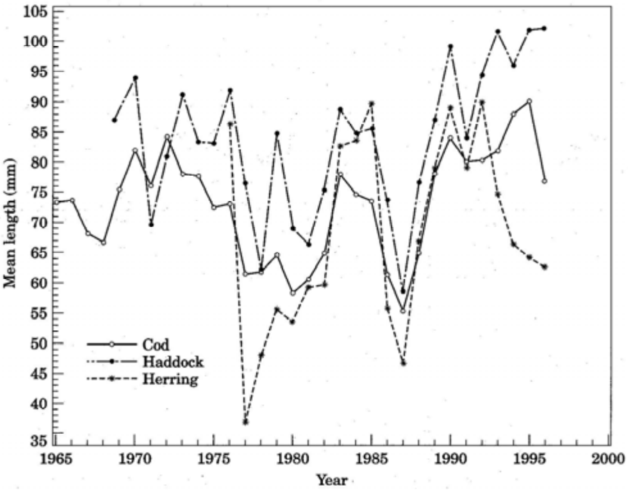

Figure 1. Mean length of 0-group cod, haddock and herring in August-September, 1965–1996.

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[*] The full paper can be found in ICES Journal of Marine Science:
G. Ottersen, and H. Loeng, 2000. Covariability in early growth and year class strength of Barents Sea cod, haddock and herring: The environmental link. ICES Journal of Marine Science. 57(2): 339-348.

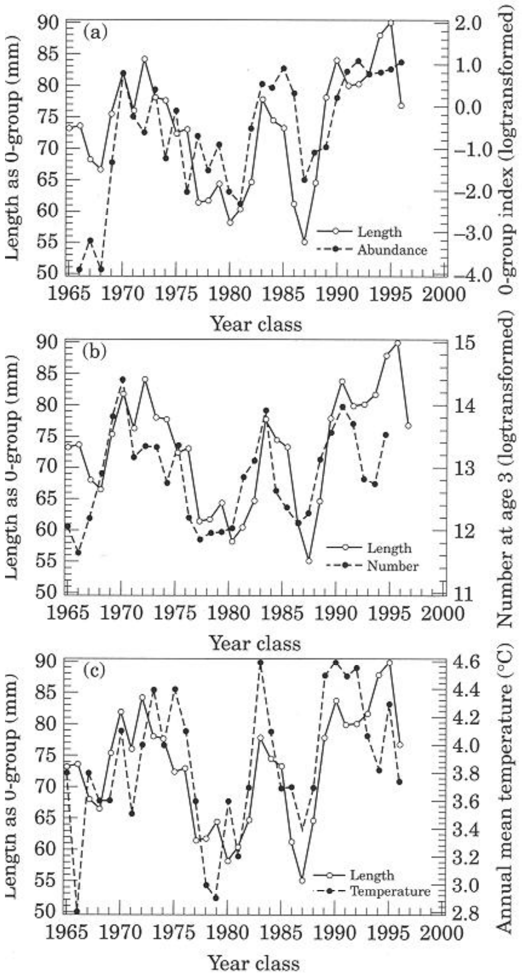

Figure 2. Temporal development in length of 0-group cod in comparison with (a) abundance as 0-group, (b) abundance at age 3, and (c) annual mean temperature in the Kola section.

Temperature influences growth and survival at the early life stages in several different manners (Figure 3); it affects the development rate of the fish larvae directly, but also indirectly through regulating the production of prey.

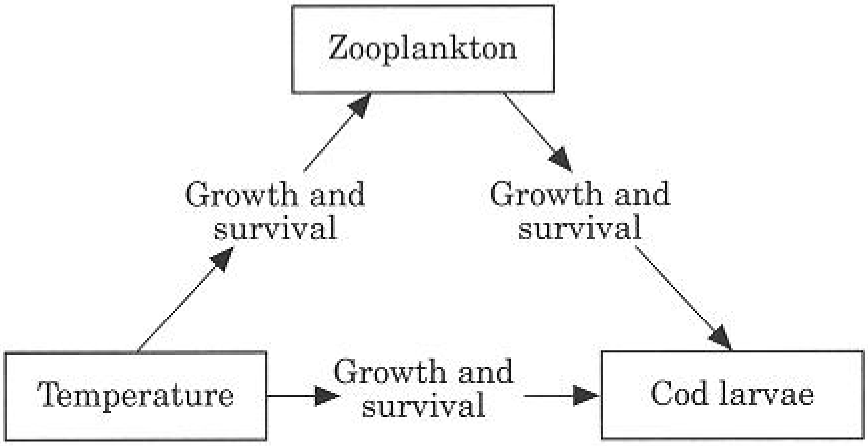

Figure 3. Mechanisms linking temperature to growth and survival.

Nesterova (1990) showed that zooplankton biomass in the Norwegian and Barents Seas is generally larger when temperature is high. High food availability for larval and juvenile fish results in higher growth rates and greater survival through the vulnerable stages when year class strength is determined. Temperature also affects the development rate of the fish larvae directly and, consequently, the duration of the high-mortality and vulnerable stages decreases with higher temperature (Ottersen and Sundby, 1995; Ottersen, 1996).

Our empirical results based on field data for Barents Sea cod, haddock and herring generally support the established theory of a positive connection between growth and survival during early life stages for marine fish (Gulland, 1965; Cushing, 1974; Andersson, 1988; Meekan and Fortier, 1996**)**. They also confirm the hypothesis of Houde (1989; 1990) that the larvae of species inhabiting a cold environment should be more exposed to environmental fluctuations than species that inhabit warmer waters due to longer development times.

Interannual variability in the temperature conditions is concluded to be the underlying cause of the covariability between growth and year class strength. We hypothesize that for stocks at the high latitude end of the overall range of the species the environmental signal tends to over-ride density-dependent effects on growth.

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Growth of Atlantic cod and haddock larvae on Georges Bank: food-limited growth in fish larvae

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Abstract

As part of the US GLOBEC Northwest Atlantic Georges Bank Program and earlier programs we have examined the processes affecting growth, survival and retention of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. This effort was concentrated in the months of April and May when larvae are most abundant on the southern flank, with more limited sampling in March. After first feeding recent growth of both species increased rapidly with larval size to about 100 µg dry weight. Through the remainder of the larval period growth was unrelated to larval size. Growth rates in both species were greatest in May at temperatures close to 7°C, yielding a dome-shaped relationship with temperature. Maximum growth rates observed on Georges Bank were 0.15 d^{-1}. In contrast, growth rates of well-fed cod larvae in the laboratory increased with temperature to at least 13 or 14°C with specific growth rates as high as 0.25 d^{-1} (Otterlei *et al.,* 1999). On Georges Bank, temperature may limit growth of both species below 7°C. The observed decline in growth at temperatures above the 7°C optimum is compelling evidence that larval growth was food limited at higher temperatures on Georges Bank. Earlier studies have indicated that larvae are too dilute to impact production of their planktonic prey and that it is the concentration or availability of prey rather than the total prey biomass that is limiting.

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ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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European Commission Contract N^o EVK3-CT-1999–00012

UVAC the Influence of UVR and Climate Conditions on Fish Stocks: A Case Study of the Northeast Arctic Cod

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Extended Abstract

A comprehensive understanding of the causal chains of natural impact factors is essential for a sustainable exploitation of wild fish stocks in the future. This will be even more relevant if global change (enhanced greenhouse effect, ozone depletion) and its impact on marine ecosystems will come true as expected by the scientific community.

The main objective of UVAC is to investigate the impact of solar ultra-violet radiation (UVR) on the stock of Northeast Arctic cod (*Gadus morhua*), in its spawning habitats at the Lofoten Islands, north Norway This relation will be investigated as part of a more comprehensive impact system, including both other geophysical factors such as climate, and planktonic species that are important for the cod stock.

In experiments with artificial exposure to UV-B, eggs of both cod and the planktonic copepod *Calanus finmarchicus* have been found to be vulnerable to radiation (Kouwenberg *et al.*, 1999a, b). In the sea, UVR larger than 1% of the surface intensity occurs to about 10 m depth, which is the depth range where radiation may be harmful to organisms.

Cod eggs are buoyant in seawater and tend to float at the very surface in calm weather. In general, egg mortality has not yet been seriously regarded as a factor that has a major impact on year class formation in cod. However, UVR could hypothetically be of importance to the year class strength in periods when the spawning stock biomass is low.

The eggs of *C. finmarchicus* sink and tend to accumulate below the upper 10 m depth range. However, mixing by wind and tide probably keeps the copepod's eggs in suspension and brings a fraction in contact with harmful UVR near the surface. Considering also that wave formation increases the radiation across the sea's surface in high latitudes where the solar inclination is low, eggs of both copepod and cod may be affected even deeper in the sea.

Copepods including *C. finmarchicus* are known to perform diel vertical migration and spend the daytime in deeper water than at night (Maucline 1998). At the Lofoten Islands in May, Ellertsen *et al.* (1989) have observed that the nauplii of *C. finmarchicus* may migrate from 30 m depth at noon to the surface at night. However, initial UVAC field work in Lofoten documented that during some conditions, and for reasons that are at present unexplained, a majority of both *C. finmarchicus* females and NIII-VI may occur at the surface or very close to it at noon, even in bright sunshine (Figures 1 and 2).

If the copepod females presented in Figure 1 were actually producing eggs, UVR could hypothetically influence their egg production rate, the viability of their eggs, or the ovulation of subsequent egg batches.

The *nauplii* that were observed close to the surface (Figure 2) occurred in a concentration that might attract feeding cod larvae and cause them to be exposed to UVR. If this may occur, one day's exposure to high UVR levels possibly imposes retarded growth or mortality in larval cod.

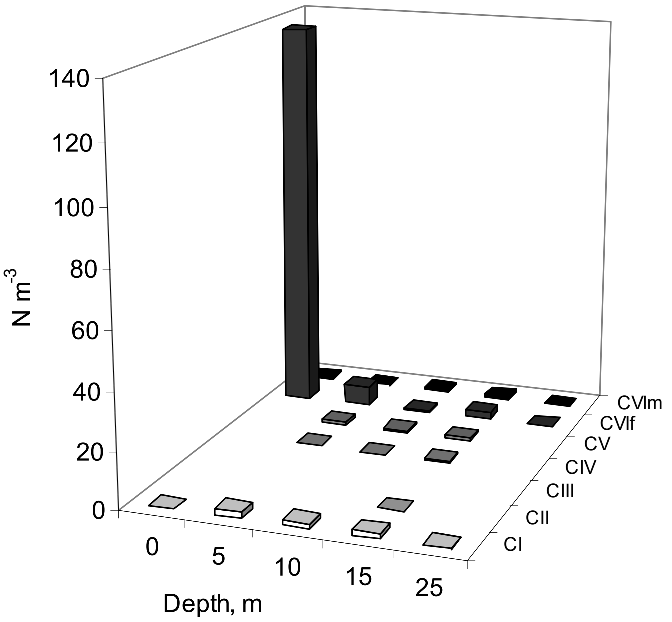

Figure. 1. Depth distribution of *C. finmarchicus* copepodites sampled by Clarke-Bumpus closing nets at Henningsvær, Lofoten Islands 24 March 2000, at noon in bright sunshine (Skreslet and Olsen, unpublished).

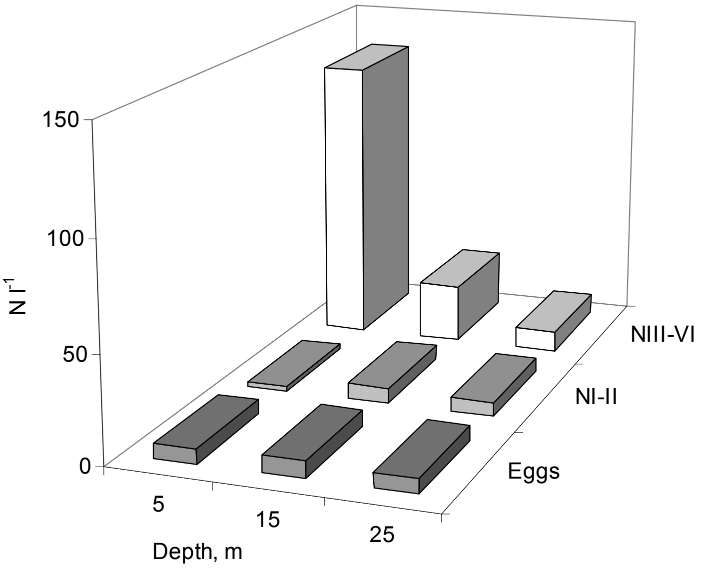

Figure. 2. Average concentration of *C. finmarchicus* eggs and nauplii collected in 3x2 liter water samples at Henningsvær, Lofoten Islands 14 April 2000, at noon in bright sunshine (Skreslet and Olsen, unpublished).

The UVAC project is still in its initial phase. Fieldwork in 2000 is devoted to testing of methods and techniques that will be fully exploited in 2001. The field experiments and the laboratory designs address biological features and processes that may potentially cause changes in the recruitment of young fish to the Northeast Arctic cod stock. That may either occur by the direct effects of UVR as a density independent factor on the viability of cod eggs and larvae, or its indirect effect on density dependent relationships between juvenile cod and the production, survival and growth of their prey.

In hypothetical terms, UVR may potentially affect cod growth in several ways:

Lethal effects on cod eggs and larvae may directly decrease the size of a year class, and indirectly generate a growth bonus for surviving individuals.

Sublethal effects may harm the function of organs and reduce individual growth.

Effects that reduce survival and growth of food organisms may affect feeding and growth of juvenile cod.

The sum of the potential effects can possibly be discerned by the study of stock parameters. Therefore, the project will perform time-series analyses on annual cod landing records and Norwegian 0-group indices on the biological side, and records of local climate conditions, regional climate indices and total ozone/UVR records on the geophysical side. If possible, the analyses will separate the impact of climate from that of UVR.

High-resolution maps of the relevant UVR parameters from 1987 to 2000 will be constructed for the Vestfjord area. They will be based on satellite data of total ozone (mainly TOMS and ERS-2 GOME data) and cloud coverage/optical depth (NOAA/AVHRR and Meteosat data) and calculated with state-of-the-art radiative transfer models. The calculated seasonal and interannual variation in UVR will be related to abundance estimates of *C. finmarchicus* that over-wintered close to the Lofoten Islands in the same period. One rationale for this is to observe UVR variability in a habitat where *C. finmarchicus* spawn during summer and relate it to the size of the subsequent wintering stock of the copepod. Another is to address the hypothesis that the copepod wintering stock size and the UVR effects on the Lofoten organismic system in concert may force the variability in the O-group cod index.

The time-series investigations will be supported by field and laboratory experiments and studies that will cover the whole scope of biological and geophysical factors assumed to play a role in the UVR – cod interaction.

The combined results of the above work will be used to develop modelling tools (short-term process modelling and long-term modelling), which can reproduce past (observed) cod stock variation and eventually predict variability in the future.

The project will hopefully enlighten the influence of a potentially important natural variable on marine ecosystems. Integration of UVR impact processes into fish stock size modelling tools have the potential to improve these tools, both in terms of uncertainty reduction and long-term applicability of such tools, which is of importance for a future sustainable fishery management.

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Working Document 6.5[1]

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Predicting weight at age of southern Gulf cod from temperature conditions in their first year

D. P. Swain

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Strong positive correlations have been found between weights of North Sea cod at ages 1 to 6 yr and the deviation in bottom temperature during the year in which they were spawned (Brander and O'Brien WD 6.1). In this working paper, I test for similar correlations in the southern Gulf of St. Lawrence cod stock.

Material and Methods

Weights at age come from bottom-trawl surveys conducted in the southern Gulf of St. Lawrence each September since 1960. (Spatial coverage was incomplete in surveys conducted prior to 1971, but results are similar omitting the earlier years). Two indices of temperature conditions were used: 1) the CIL (Cold Intermediate Layer) mean minimum temperature extrapolated to July 15; and 2) the mean spring and early summer air temperature at the Magdalen Islands. The CIL temperature index is from Gilbert and Pettigrew (1997). It is based on all available data collected between May 1 and September 30. The CIL covers the bottom over most of the Magdalen Shallows. The air temperature index was used as a proxy for temperature conditions in surface waters. It was the average of mean monthly temperatures for May, June and July.

Results

Mean weights at age varied widely for the 1952–1994 year classes of cod (Figure 1). Weights at age were strongly correlated between ages within year classes (Table 1). Temperature conditions also varied widely over the 1952–1994 period (Figure 2). There was no correlation between weight at age of cod and CIL temperatures in the summer of the year they were spawned (Table 2). Spring and summer air temperatures at age 0 were negatively correlated with weights at subsequent ages (Table 2). These negative correlations were quite strong for ages 3–5.

Discussion

The strong positive relationship seen in North Sea cod between temperature conditions in their first year and weights at subsequent ages was not apparent for southern Gulf of St. Lawrence cod. Indeed, air temperatures during their first spring and summer were *negatively* correlated with weights at subsequent ages for southern Gulf cod. Variation in size at age of southern Gulf cod appears to be strongly influenced by size selective mortality and density dependent growth (Sinclair *et al.*, this Workshop). For this stock, these factors appear to exert a stronger effect on variation in size at age than temperature conditions during early life history stages. It is possible that confounding with these other factors obscured any effect of early temperature conditions on later weight at age of southern Gulf cod.

References

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[1] Working Document 6.5 posted on Website but not presented at Workshop.

Table 1. Correlation matrix for mean weight at age of southern Gulf of St. Lawrence cod. Weights are from bottom trawl surveys conducted from 1960–1998. Correlations are between ages within year classes.

Age	3	4	5	6	7
3					
4	0.778				
5	0.755	0.890			
6	0.716	0.843	0.960		
7	0.762	0.794	0.914	0.952	
8	0.707	0.725	0.840	0.895	0.952

Table 2. Correlations between mean weight at age of southern Gulf of St. Lawrence cod and indices of temperature conditions in the year they were spawned. CIL = Cold Intermediate Layer index, mean water temperature minimum in the southern Gulf extrapolated to July 15; MAT = mean spring and summer air temperature at the Magdalen Islands.

Age	3	4	5	6	7	8
CIL	0.083	0.045	-0.032	0.022	0.048	0.044
MAT	*-0.400*	***-0.481***	*-0.350*	-0.308	-0.236	-0.204

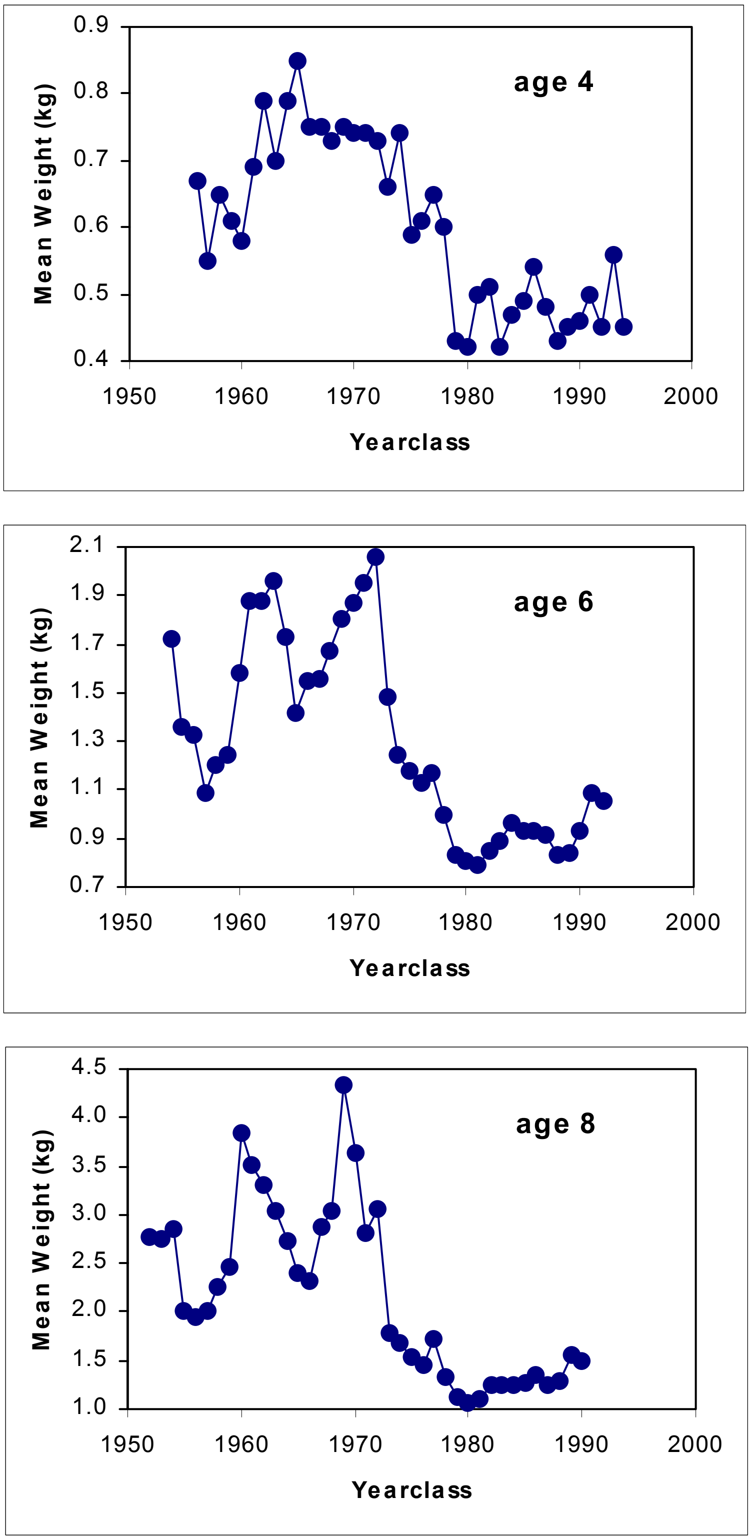
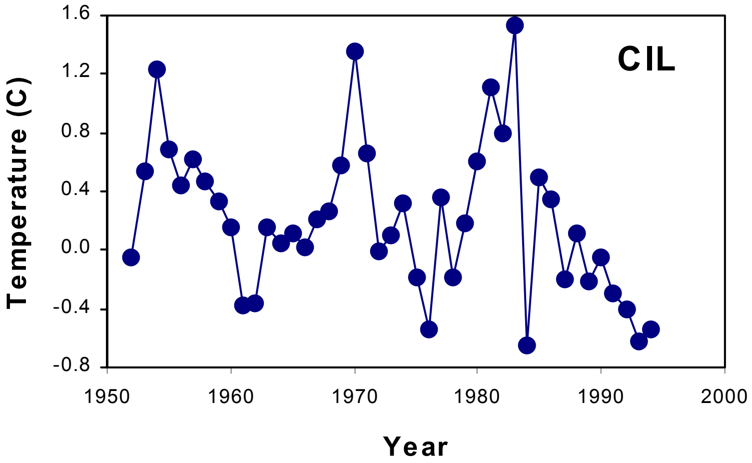


Figure 1. Mean weight at age of southern Gulf of St. Lawrence cod from September bottom-trawl surveys.



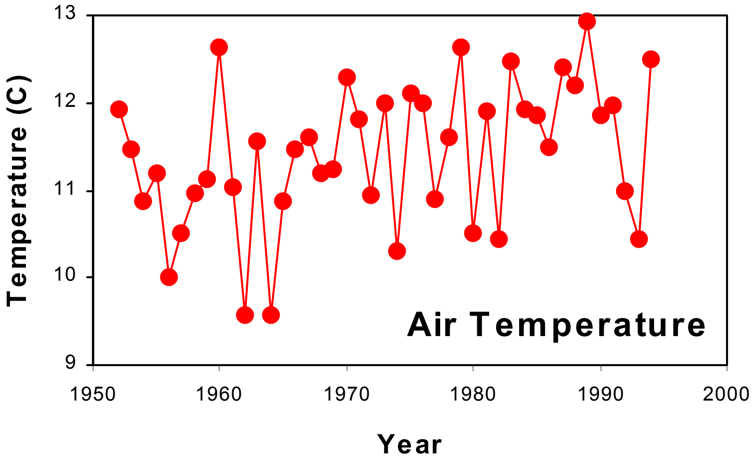


Figure 2. Temperature conditions in the southern Gulf of St. Lawrence. CIL = mean CIL minimum temperatures extrapolated to 15 July (from Gilbert and Pettigrew 1997); Air Temperature = mean monthly air temperatures (May, June, July) at the Magdalen Islands.

Working Document 7.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Food consumption and activity of North Sea saithe (*Pollachius virens*)

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Extended Abstract

A recently accomplished EU project contracted by research institutes from Spain, Portugal, Norway, Germany, Scotland, and Denmark aimed at producing valid estimates of food consumption rates of major predatory fish in the North Sea and the South-European Atlantic. Two approaches were applied. *The gastric evacuation method* combines field data on the amount of stomach content in a predator with information about the relationship between gastric evacuation rate and amount of stomach content. *The food conversion (bioenergetic) method* combines field data on the growth and costs of living of a predator with information about the food conversion efficiency. Both approaches were applied on North Sea saithe, which together with grey gurnard were 'the Danish species' in the project. The work on saithe may serve as an example of an approach for evaluating roughly food limitations and activity levels of a predatory gadoid.

The gastric evacuation method

The change of stomach content during time as a function of food intake and gastric evacuation may be described by:

$$dS/dt = C - \rho S^{\alpha} \text{ g h}^{-1}$$

where S is total weight of the stomach content, t is the time, C is the consumption rate, and ρ and α are the parameters in a power model describing gastric evacuation. We have no consistent information about the meal sizes ingested in the field. It is therefore crucial that the evacuation model describes gastric evacuation independently of meal size, i.e., evacuation depends on the instantaneous amount of stomach contents only. It was demonstrated that the square root version of the model (a α value of around 0.5) possesses this ability for a variety of predators and preys. Temperature, body size, and prey energy density affected the rate constant ρ and a universal set of parameter values appeared to be applicable to the different predatory gadoids:

$$\rho = 0.00132\, L^{1.44}\, e^{0.078\,T}\, E_d^{-0.875} \text{ g}^{0.5} \text{ h}^{-1}$$

where L is the total length (cm) of the gadoid, T is the ambient temperature (°C), and E_d is the energy density of the stomach content (kJ g^{-1} wet weight). Over time and population the average consumption rate can then be estimated by:

$$C_{\text{avg}} = \text{avg}\,[\, \rho S^{0.5}\,] \text{ g h}^{-1}$$

where S is the total stomach content of a saithe stomach sampled in the field and avg denotes a more elaborate average from the stratified sampling design applied by ICES.

Stomach content data

The results from the International ICES stomach-sampling project in 1991 were applied to estimation of the quarterly food rations by age class of saithe. Data on the relative prey compositions and average weight of stomach content were obtained from Tables of aggregated data in the Database Report of the Stomach Sampling Project 1991 and from material delivered by John Hislop (SOAEFD, Scotland) and Niels Daan (RIVO, Netherlands). The size class distributions of the main fish prey were extracted from the 1991 stomach database by Morten Vinther (DIFRES, Denmark). All ICES stomach data on saithe are pooled into predator length groups. In that case the calculations of food ration become more complicated and some bias will inevitably be introduced because $\text{avg}\,[\,\rho\, S^{0.5}\,] \neq \text{avg}\,[\,\rho\,]\,(\text{avg}\,[\,S\,])^{0.5}$ - even though a factor correcting for $\text{avg}\,[\,S^{0.5}\,]$ being $\neq (\text{avg}\,[\,S\,])^{0.5}$ was applied - because the prey composition and energy density of the content in the individual stomachs (affecting the value of ρ) is not generally similar to the average prey composition and energy density of the pooled stomach contents. The above-mentioned correction factor was estimated from two data sets on stomach contents from individual saithe sampled in 1996 and 1997 with the Research Vessel Dana.

The main prey was sampled on a quarterly basis, and the energy density determined by size class. The main prey of most of the major predators in the North Sea were covered by the project.

Ambient temperature

Catch rates of saithe in numbers per hour of trawling by age group and trawling depths were acquired from

ICES' IBTS database for quarters 1–4 in 1991. The arithmetic average from all hauls within a statistical rectangle were calculated for catches of saithe by age and quarter. The average catch depth was obtained in the same way. The average temperature at average catch depth by statistical rectangle and quarter was calculated from data obtained using a hydrographic model for the North Sea (Pohlmann, 1996). The average temperature experienced by saithe at age class and quarter was then calculated as a weighted average according to the average catch rate by statistical rectangle.

The estimated food ration by age class expressed as feeding level (see below) appears from Figure 2.

The food conversion (bioenergetic) method

The daily increment of somatic energy of a fish is described as

$$G_s = (1 - \alpha)\, \beta\, C - M_{st} - M_a - G_g =$$
$$\kappa f\, C_{max} - M_{st} - M_a - G_g$$

where C is the food (energy) consumption rate [the feeding level f ($0 \leq f \leq 1$) multiplied by the maximum consumption rate C_{max}], β is the absorbed part of the consumed food, α is the total costs associated with processing of the consumed food, $(1 - \alpha)\, \beta$ is the net conversion efficiency κ, M_{st} is the standard metabolism, M_a is the swimming activity costs, and G_g is the increment in gonadal energy. The gonadal production is set to zero in juvenile fish and is put into a cyclic function in adults. The increment in gonadal energy is described by an exponential function from onset of gonadal growth and until spawning, and the total gonadal energy is released instantaneously around the middle of the spawning season.

Maximum ration and net conversion efficiency

C_{max} was measured as a function of temperature and body size in the laboratory, and the net conversion efficiency κ was estimated from laboratory data on somatic energy increment as a function of temperature, body size, and food ration. The net conversion efficiency is depicted as a function of body size and feeding level in Figure 1.

Somatic growth and gonadal costs

The quarterly lengths of saithe by age class were estimated as weighted average values, based upon data on the number of saithe caught per hour fishing in ICES areas III and IV (the Database Report of the Stomach Sampling Project 1991). Quarterly power functions relating saithe weight to length were obtained from unpublished Scottish data on commercial catches from the North Sea. Saithe intended for determination of energy densities were sampled quarterly by the research vessel *Dana* and by Norwegian research vessels.

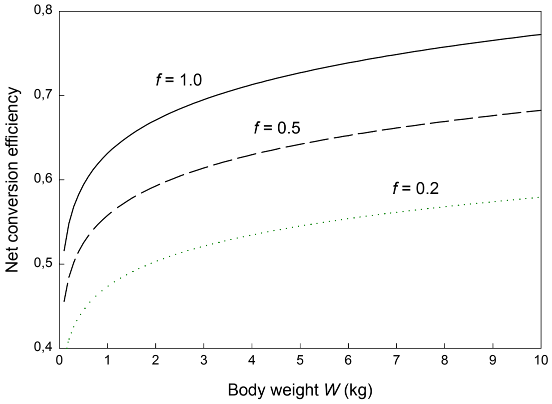

Figure 1. Net conversion efficiencies in saithe fed Norway pout. Effects of body size and feeding level.

The total gonadal energy produced by a female by age class was obtained by multiplication of the fecundity with the maturity index and the energy content of an egg (all available as literature values). The gonadal production of males was considered similar to that of females.

Standard metabolism and swimming costs

The standard metabolism was determined as a function of temperature and body size. The swimming costs were estimated by combining diurnal field measurements of swimming speeds with laboratory measurements of the oxygen consumption of fish forced to swim at various constant speeds. Swimming speeds in the field were calculated from sequentially recorded 3-D positions of individual saithe using split-beam hydro-acoustics. The measurements discriminated against schooling fish and are suspected to favour the more active, presumably foraging, specimens. The bioenergetic model was, therefore, calibrated to North Sea saithe by tuning the costs of locomotion to food rations obtained independently of bioenergetics by the gastric evacuation method. Results from the output of the runs of the bioenergetic model for the different age classes of saithe are shown in Figure 2, where allocation of the net energy ($\kappa f\, C_{max}$) is depicted. An activity multiplier $m_a = (M_a + M_{st})/\, M_{st}$ of 2–3 (increases with the age of saithe) can be calculated from these results. This is very much in accordance with literature values for active, predatory fish. The food ration by age class expressed relative to C_{max} by the feeding level f is shown in Figure 2. The feeding level ranges from less than 0.6 to somewhat above 1.0 for age classes 3–8 - i.e., younger saithe may be food limited.

Under the assumption that schooling saithe move around at optimum cruising speed (other findings on saithe in the literature) it could be calculated that approximately 5% of the time were spent on chasing prey (the activity levels measured by hydro-acoustics). This finding comes close to an assessment of how often the saithe eat as judged from examination of stomach content data, which were collected on a diurnal basis at the cruises where the activity measurements were performed.

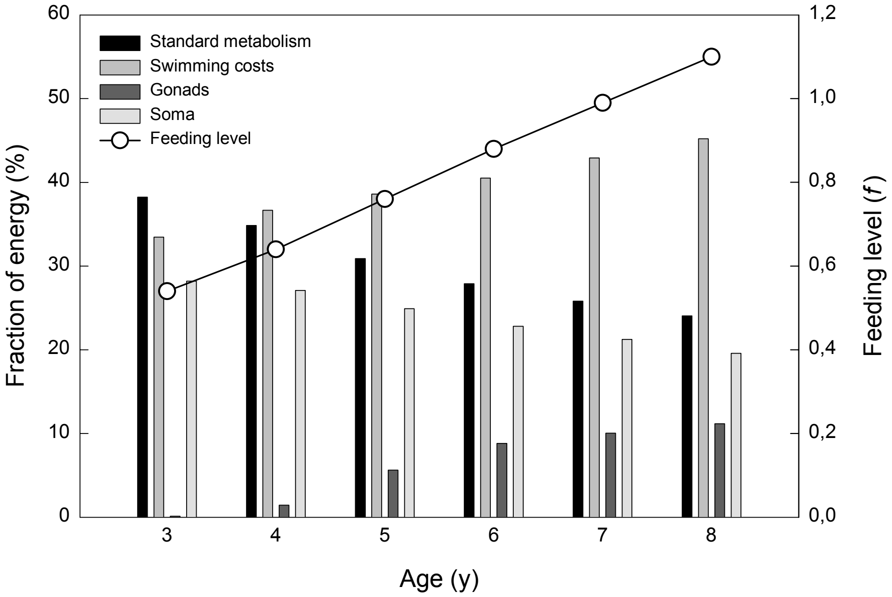

Figure 2. Feeding level and allocation of net energy in North Sea saithe by age class.

Working Document 7.2

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
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Does metabolic scope limit growth rates of wild cod?

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Abstract

1) Metabolic scope of Atlantic cod is lower at cold temperatures, and this decrease in scope in cold-water results in decreased consumption rates, swimming performance, and potential growth rates in the lab.
2) However, a survey of the literature suggests that the relationship between metabolic capacity and temperature is not responsible for the strong positive relationships between growth and temperature within or among wild populations of Atlantic cod. Most cod stocks are feeding well below their maximum consumption rates, and therefore do not appear to be physiologically limited by their temperature-dependent metabolic capacity, at least over much of the year.
3) Two separate bioenergetic analyses have suggested that one or more of the colder Newfoundland stocks may be growing close to their maximum potential growth rates. However, an examination of stomach fullness indices give some indication that even in these colder Newfoundland stocks food limitation may characterize much of the year.
4) The relationship between temperature and growth is complex. Temperature and consumption rates interact, such that growth increases with temperature if rations are maximal, and decreases with temperature at fixed submaximal rations, because of increasing metabolic demands at high temperatures.
5) Because of this interaction, we would not necessarily expect to find positive relationships between growth and temperature within and among stocks if cod are feeding well below their maximum consumption rates, i.e., when they are not limited by metabolic scope, but by food supply. The positive relationships between growth and temperature within and among stocks must be indirect, due possibly to higher food availability (and/or accessibility) in warmer waters. Food availability might increase with temperature enough to more than compensate for increased metabolic demands in warmer water, but not enough to allow cod to take full advantage of their increased metabolic capacity.

Additional points raised during the Workshop:

6) The positive relationships between growth and temperature may have a physiological basis, even if they are not directly limited by metabolic capacity. Warmer temperatures may stimulate higher levels of feeding activity than colder temperatures.
7) The positive relationships between growth and temperature among stocks may also reflect differences in the length of the feeding season. Cod in the warmer stocks may feed during a larger proportion of the year.
8) In a number of stocks, at certain times of the year, even when food appears to be available, cod may not feed or may feed very little (i.e., they choose not to eat). This suggests that feeding is not necessarily always limited by either temperature or food supply but at times may be under the control of more subtle seasonal influences on appetite.

Working Document 8.1

ICES/GLOBEC Workshop on the Dynamics of Growth in Cod
Dartmouth, Canada 8–10 May 2000

Inter-population differences in phenotypic response from common-garden experiments among four populations of Atlantic cod

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Abstract

Geographically separated cod (*Gadus morhua*) stocks in the northwest Atlantic exhibit life history variation, and have been shown to differ genetically. The genetic and environmental contributions to phenotypic differences however have not yet been measured. In one set of experiments we used common environment experiments to evaluate the importance of temperature to the observed growth variation between Grand Banks (GB) and Gulf of Maine (GOM) cod stocks. Larvae from the GB grew faster than GOM larvae at both temperatures tested. Growth rates of juveniles were not different, but GB juveniles had higher food conversion efficiencies than those from the GOM. The results indicate that faster growth of GOM cod in the wild is not due to a higher genetic capacity for growth rate in these fish. The findings support the theory of counter gradient variation in growth rates, and molecular studies on population differentiation in cod.

In a second set of experiments we were again interested in determining the genetic and environmental contribution towards phenotypic variation among cod populations and we expanded our study to four populations. We compared the growth performance of populations of laboratory reared (Grand Banks, GB and Gulf of Maine, GOM) and wild caught (Fortune Bay, FB and Bonavista Bay, BB; Newfoundland) juvenile cod under common environments. Populations in each group responded similarly to temperature change in specific growth rates, food conversion efficiencies, condition factors, liver water content, and muscle water content. However, GOM cod had higher condition factors, and showed differences from GB cod in phenotypic plasticity of hepatosomatic index to temperature. These differences were not present in a different population comparison between FB and BB cod. All populations had higher growth rates and food conversion efficiencies at warmer temperatures, and exhibited compensatory growth when temperature was increased. The results suggest genetic differences between GB and GOM cod, but similarity between FB and BB cod.

As part of the above studies we were also interested in looking at antifreeze protein production. Many fishes produce antifreeze proteins or glycoproteins (AF(G)Ps) in the blood to provide freeze resistance in cold seawater. Cod from colder environments generally produce more AFGPs than those in warmer areas, however the genetic and environmental contribution to this variation has not been determined. Using juveniles from the above experiments and four populations, GB, GOM, FB, and BB we looked for differences in AFGP production. Antifreeze glycoprotein levels were similar in GB-GOM and FB-BB cod, suggesting little variation between the populations in each group. The results indicate that high temperatures associated with the production of hatchery-reared fish does not negatively affect the ability to produce AFGPs. In addition, young cod from as far south as the Gulf of Maine are capable of producing AFGPs at levels similar to those from the northeast coast of Newfoundland.