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GROWTH AND BIOENERGETICS OF NORTHERN COD (*GADUS MORHUA*)

by

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Abstract

Explaining the variability in growth rates of fish is critical to predicting the large fluctuations in biomass that characterize fish populations. Aside from directly affecting stock biomass, variability in size–at–age determines future production, because larger fish have larger growth increments and are more fecund. In northern cod, a 50% drop in weight–at–age in recent years was particularly concerning because it coincided with record low abundance. Although this drop was accompanied by low temperatures, bioenergetic analysis from the present work suggested that northern cod growth is not physiologically limited by cold water, but that temperature affects growth indirectly through prey supply. An analysis of cod stocks across the North Atlantic suggested that this indirect effect of temperature lies behind the temperature–growth relationships in other cod stocks, as well.

While weight–at–age of northern cod decreased across age–classes, analysis of size–specific growth rates indicated that growth has only decreased in the youngest age–classes, and that older age–classes are smaller because of environmental factors experienced at an earlier age. The observed pattern in growth was also consistent with the selective removal of larger fish of a given age by the fishery.

While growth represents a benefit, it comes at a physiological cost because tissue synthesis is energetically demanding. A comparison of the maximum rate of oxygen consumption of fed and unfed cod during exhaustive exercise indicated that oxygen supply for growth and digestion has priority over oxygen supply to the swimming muscles, and that aerobic capacity is limited by oxygen uptake by the tissues rather than by the gills.

In summary, growth rates of northern cod are correlated to temperature because of indirect effects such as prey supply, not because of physiological temperature limitation. Cod growth is most sensitive in early years, and this early growth is largely responsible for size later in life.

List of Abbreviations and Symbols

W_i = weight–at–age i;

G = size–specific growth rate

μ = swimming speed;

M_{O2} = oxygen consumption

AHI = apparent heat increment

SDA = specific dynamic action

CIL= cold intermediate layer

GSI= gonadosomatic index

ATP = adenosine triphophosphate

Q_{10} = temperature sensitivity coefficient

M_{O2} = oxygen consumption

M_{O2max} = maximum oxygen consumption

U_{crit} = critical swimming speed

SMR = standard metabolic rate

SEM = standard error of the mean

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Preface

Much of the material in Chapter one (Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua* L.). has been published in the Canadian Journal of Fisheries and Aquatic Sciences, vol 54:113–121 (1997). They have granted me permission to use this copyrighted material.

Much of the material in Chapter two (Declining weight–at–age in northern cod and the potential importance of the early years and size–selective fishing mortality) has been published in the NAFO Science Council Studies vol 29:43–50 (1997). They have granted me permission to use this copyrighted material.

Chapter three will be submitted to Reviews in Fish Biology and Fisheries, and Chapter four was submitted in July 1999 to the Journal of Experimental Biology.

Material from this thesis was presented at the following conferences and seminars:

Jan 1994. "Recent advances in cod bioenergetics: the OPEN experience." Canadian Conference for Fisheries Research (C.C.F.F.R.) in Saskatoon, Saskatchewan. Authors: Krohn, M.M and S.R. Kerr.

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General Introduction

The growth rates of organisms play a key ecological role. The growth rates and growth efficiencies (the proportion of consumed energy that goes into growth) of individuals within a trophic level, along with biomass, determine community trophic dynamics by affecting both grazing pressure and the supply of energy to potential predators. In recent years, the importance of an ecological context to understanding fish population dynamics has been increasingly recognized. While removal of fish by a fishery may often drive much of the variability in population biomass, the effect of abiotic and biotic factors on the variability in growth rates and recruitment of young fish can have a large impact on population biomass. Quantifying and determining the causes of variability in growth rates are critical in understanding the large fluctuations in fish population biomass and production.

Many abiotic and biotic factors have been found to affect growth rates of wild fish; among the most important are temperature, prey supply, density of conspecifics and competitors, oxygen concentration, salinity, pollutants, body size and size–selective fishing and predation. The growth rates of fish are highly plastic, they vary more than those of mammals, birds, reptiles and many amphibians (Weatherley 1972). This large variability in fish growth rates within species is apparent among populations, among years within a population and among individuals within a population at a given time. Among populations, indirect and direct affects of temperature can lead to enormous differences in size–at age. For example, Weatherley and Lake (1967) found a 27–fold range in weight at–age of trout from different

populations. Brander (1995) found a 12–fold range in weight–at–age among populations of Atlantic cod, for which 95% of the variability could be explained by differences in water temperature. As well as being important from an ecological perspective, this variability in size–at–age among populations of a given species is of great practical importance as it affects the productivity and potential yield of a fishery as well as its susceptibility to over–exploitation and the time frame of recovery.

To a somewhat lesser extent, growth rates vary among years within populations; weight–at–age can vary several fold among years (Brander 1995; Sinclair et al. 1995) affecting both the population biomass and fecundity. It is this temporal variability in size–at–age of northern cod (Atlantic cod off the east coast of Newfoundland) that is addressed in the current work, and was carried out partly in response to concerns over large decreases in size–at–age between 1979 and 1992 (northern cod of a given age weighed twice as much in 1979 as they did in 1992). These low sizes–at–age were particularly concerning because they coincided with record low population abundance, severe truncation of the age structure of the population, and unusually low indices for condition of the few remaining individuals. The observed declines in size–at–age may have been due to declines in water temperature, to declines in prey availability, to the selective removal of larger fish (of a given age) by the fishery, or very likely, to some combination of those factors. I address this question directly in chapter one. I quantify the relationships between northern cod growth rates and the independent variables bottom water temperature and prey supply, as well as the relationships between condition factor and these two

independent variables. Although correlative analyses can identify important relationships, they do not necessarily identify the mechanisms behind them. Temperature and ration interact to affect growth. Growth rates increase with temperature at high ration levels when the energy from high consumption rates can compensate for the higher costs associated with increased metabolic rates in warm water. When ration levels are low, growth rates decline with increasing temperature because the low consumption does not compensate for the increased metabolic rates at higher temperatures. In controlled conditions, for any given submaximal ration, an increase in temperature will result in a decrease in growth. However, in the wild, there is an added complexity because food supply may vary with temperature. Even when rations are well below maximal for a given temperature, an increase in temperature in the wild may lead to an increase in growth because food supply has also increased, if it has increased enough to more than compensate for the higher metabolic costs in the warmer water. Growth rates may therefore increase with temperature for two very different reasons. First, if the fish are feeding at maximal levels (and the maximum rate at which they can process food increases with temperature) growth rates will increase with an increase in temperature. Second, growth rates may also increase with temperature even if fish are feeding submaximally, if an increase in temperature is associated with a large increase in food supply. Bioenergetic modelling, which is based on biological mechanisms, can potentially help to identify the way in which temperature affects fish growth. I develop a bioenergetic model for northern cod, and use it to model maximal, or potential growth rates (growth rates associated with

maximum consumption rates which are physiologically limited by water temperature) for each year over the period for which the decline in weight–at–age was observed. These maximal growth rates, modelled as a function of the available temperatures for the given year, are then compared to realized growth rates for northern cod again for each year during that period. This comparison allows me to evaluate whether declines in growth associated with declines temperature were a result of physiological temperature limitation, or a result of reduced prey supply in colder water.

The decline in northern cod weight–at–age across age–classes is not necessarily an indication that growth rates decreased across age–classes. Size is an important determinant of growth rate. Larger fish have larger growth increments, although, proportional to their size, they grow more slowly. Size–specific growth rates (G) decrease with weight (W) according to the following allometric relationship:

(1) $G = a W^b$

Values for the weight exponent usually lie between –0.3 and –0.45 (Jobling 1993). Although larger fish have lower size–specific growth rates, they do have larger growth increments, so that differences in weight–at–age established early in life have the potential to be carried through the rest of a fish's life. Therefore, if a given age–class is small in a given year, even if the growth increment for that age–class is low, that group of fish may not have displayed low growth rates in the recent past, but may be small because of environmental conditions a number of years earlier. In chapter two, I identify, for northern cod between 1979 and 1993, in which age–classes size–specific growth rates decreased. Second, I quantify to what extent variability in weight–at–age

is determined from weight–at–age in previous years, as opposed to being determined by recently experienced environmental conditions. Lastly, I address whether the patterns in apparent size–specific growth rates are consistent with the possibility that selective removal of larger fish of a given age from the fishery has resulted in smaller weights–at–age.

There is an extensive literature identifying links between cold water and productivity of Atlantic cod stocks, largely examining temperature effects on recruitment and individual growth rates. Much of this research has been carried out by fisheries biologists interested in determining what role temperature, and cold water in particular, play in driving stock fluctuations. There is also a considerable body of physiological research examining how temperature and cold water affect individual fish, and individual Atlantic cod in particular, through their metabolic rates, muscle function, swimming performance, feeding capacity, growth rates, and survival. The relationship between temperature and growth is not straightforward, especially in the wild. It depends at once on the effect of temperature on the animals physiology, as well as the effect of temperature on food supply. As described earlier, I explore this dynamic in detail for northern cod in chapter one. In chapter three, by reviewing the literature, I review the relationship between temperature and growth rates both within other cod stocks and among all Atlantic cod stocks in the North Atlantic, as well as studies of Atlantic cod metabolism, feeding and growth, to investigate the reasons behind observed growth–temperature patterns. By identifying links between the fisheries and physiology literature I examine both how cold water affects Atlantic cod

and to what extent cold water is a threat to the productivity of wild cod populations.

In chapter four, I consider a shorter time scale when maximal performance (and therefore maximal metabolic rate) is not limited by the rate of energy supply, but by the rate of oxygen transport from the water to the tissues. Metabolic rate, measured by oxygen consumption of the fish, increases after feeding in response to the costs associated with absorption, digestion, and tissue synthesis, or growth. This increase in oxygen consumption is referred to either as apparent heat increment (AHI) or specific dynamic action (SDA). In cod, AHI has been found by several authors to increase oxygen consumption to half or more of its maximum (Saunders 1963, Soofiani and Hawkins 1982; Lyndon 1992, Blaikie and Kerr 1996). Given the high oxygen demands of digestion and growth, how do wild cod, and other fish species, cope with the concurrent oxygen demands of digestion, growth and swimming? There are three possibilities. First, a fish may sacrifice its rate of digestion and growth to allow oxygen supply to be directed to the swimming muscles to the same extent as in an unfed fish. Alternatively, digestion and growth may be a priority, and oxygen available for the swimming muscles may be reduced after a fish has fed. Third, the amount of oxygen available for digestion and growth may be independent of the oxygen available for swimming. In this third case, the maximum metabolic rate of swimming fish would be higher for fed than for unfed fish. In chapter four, I determine which strategy, or what combination of these strategies, is used by fish to cope with the concurrent demands of digestion, growth and locomotion.

It is not known the extent to which a fish's maximum aerobic metabolic rate, or

maximum rate of oxygen consumption, is limited by the rate of oxygen uptake from the water by the gills, by the capacity of the cardiovascular system to deliver oxygen to the tissues, or by the rate at which oxygen can be taken up and used by the tissues. Maximum oxygen consumption of a swimming fish would only depend on whether or not the fish is fed if the maximum rate of oxygen consumption is limited by the ability of the tissues to take up and use oxygen. If maximum oxygen consumption were limited by oxygen uptake at the gills, or by the capacity of the cardiovascular system to deliver oxygen, oxygen consumption would not be higher in fed than in unfed fish swimming maximally. In chapter four, I compare the maximum metabolic rates of fed and unfed fish during exhaustive swimming to determine whether aerobic capacity in cod is limited by the rate of oxygen uptake from the water and the ability of the cardiovascular system to supply oxygen to the tissues, or whether it is limited by the rate of oxygen uptake and use by the tissues.

Chapter 1

Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod.

Summary

Cod stocks of the northwest Atlantic have experienced steady decreases in growth rate since 1989 and in physiological condition since 1988. The declines have been attributed to various factors, including size–selective fishing pressure, anomalously low temperature fields and a decline in available prey. The precise balance of these factors is unknown. Simple correlation models were applied to determine that bottom water temperature and capelin (*Mallotus villosus*) biomass together explain 52% of the interannual variance in mean condition of 2J3K cod, and 23% of the interannual variance in 2J3KL mean cod growth rates. Bioenergetic models can potentially improve our understanding of the mechanisms behind these relationships because they allocate energy as a function of environmental variables such as water temperature and prey consumption. I developed a bioenergetic model for Atlantic cod to determine whether temperature could explain the observed decreases in growth rate of northern cod stocks. Model results suggest that the low growth rates of 2J3K northern cod observed in recent years are not due to physiological temperature limitation, while the growth rates of cod inhabiting cooler waters on the northern Grand banks (3L) may, at least in certain years, be temperature limited.

Introduction

Growth rates of northern cod (*Gadus morhua*) vary greatly among years and have exhibited a pronounced decrease over the last five years on the Labrador and northeast Newfoundland shelves. Although low growth rates have been seen in the past, they are a current concern because small size–at–age decreases the overall biomass of the stock and the surplus energy available for reproduction. Cod growth rates also vary spatially, growth rates being lower for cod in colder waters (Taylor 1958; May et al. 1965; Loeng 1989; Brander 1995).

Fish growth rates are influenced by both water temperature, which controls the rate at which food can be assimilated and metabolised, and by food supply, which may limit the consumption rates if prey densities are low. The low growth rates of northern cod in recent years may be due to declining water temperatures and/or to changes in capelin (*Mallotus villosus*) biomass or distribution, capelin being the major prey of northern cod (Lilly 1987).

When evaluating the effect of annual variability in ocean temperatures on growth rate, it is important to determine whether varying ocean temperatures do affect the thermal experience of cod. Cod are highly sensitive to slight differences in temperature (less than 0.3 °C) and may modify their thermal experience by adjusting their distribution (Rose et al. 1994; Claireaux et al. 1995). I therefore begin the analysis by examining the relationship between temperatures experienced by cod and ocean temperatures on the shelves over the last twelve years.

To evaluate the importance of temperature and food supply to northern cod

growth rates, correlations are examined among temperature, capelin biomass, cod growth and condition factor in three NAFO divisions (2J, 3K and 3L) on the Newfoundland and Labrador shelves (Fig.1.1) over the past fifteen years. The correlation analysis is an extension of that carried out by Bishop and Baird (1993). Although correlations can identify important relationships, they do not identify the mechanisms behind them. Bioenergetic modelling, however, is based on biological mechanism (growth equals energy intake minus energy expenditure) and can help to distinguish between the effects of temperature and prey supply on fish growth.

Kerr (1982) developed a bioenergetic model for Atlantic cod, which is updated here with newly available data on cod physiology. The updated bioenergetic model for Atlantic cod is applied to the northern cod stocks off the coast of Newfoundland and Labrador (NAFO divisions 2J3KL) to assess the potential physiological effects of temperature and food supply on growth. Potential growth (at maximum prey consumption) is modelled using shelf bottom temperatures from 1979–1993. Potential and realized growth for cod is compared over this period to determine when and where cod growth rates appear to have been physiologically limited by cold water or by food supply.

Materials and methods

Correlation analysis of temperature and growth

Temperature

The continental shelves off the east coast of Newfoundland and southern

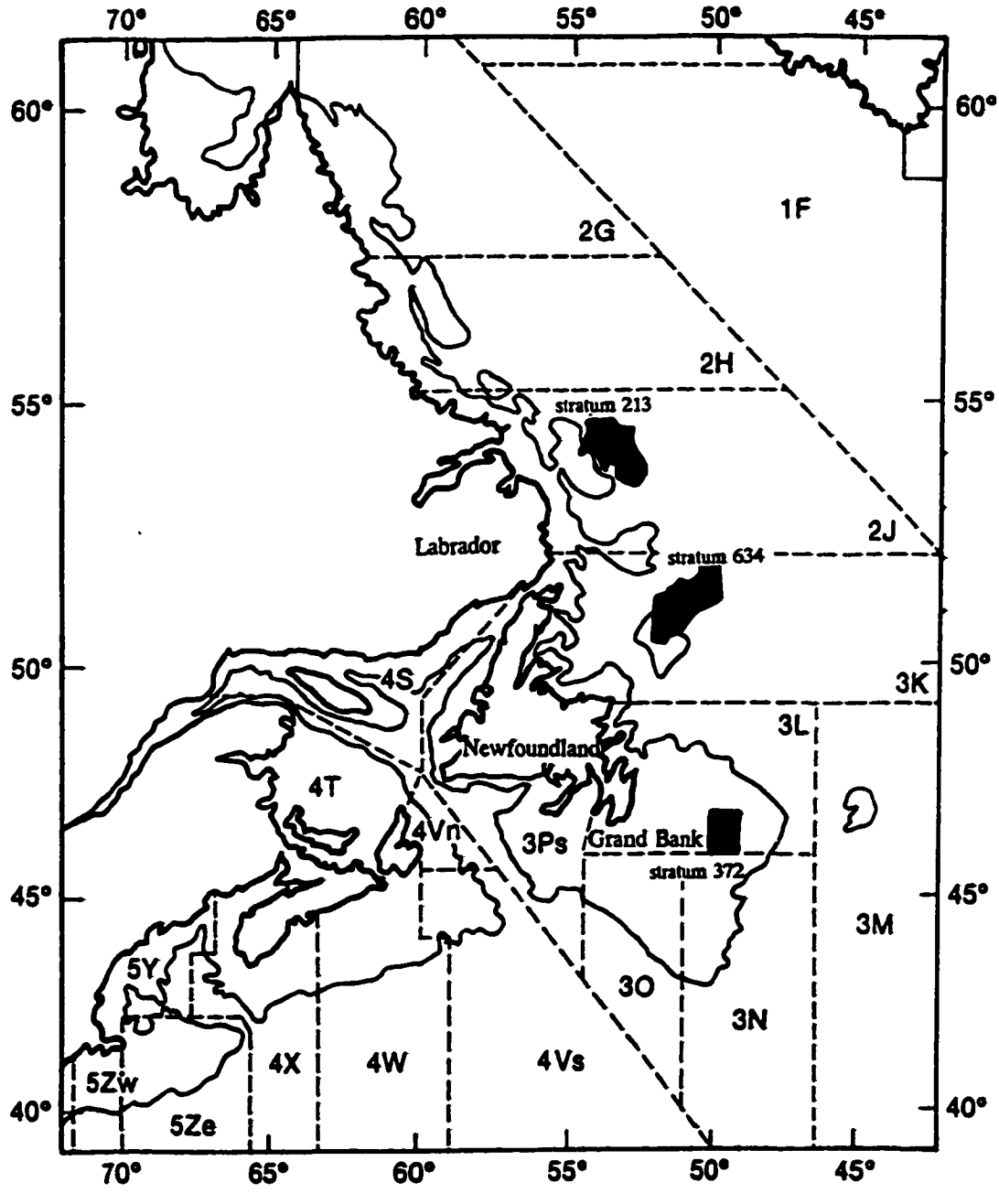


Fig. 1.1. Map of the Canadian east coast, locating NAFO Divisions 2J, 3K, and 3L, and the groundfish survey strata from which the chosen temperatures were taken.

Labrador are divided into three NAFO divisions, 2J, 3K and 3L from north to south (Fig. 1.1). For the groundfish survey, these divisions are subdivided according to depth contours into 137 strata. Autumn bottom shelf temperatures for the period 1977 to 1994 were taken from strata 213, 634, and 372 in NAFO divisions 2J, 3K, and 3L (Fig 1.1), respectively (Colbourne 1993; Colbourne unpubl. DFO, St.John's, NF.). Strata 213 and 634 encompass the area between the 200 and 300 m isobaths west of the shelf break in division 2J and 3K, respectively. Stratum 372 encompasses the area between the 57 and 92 m isobath in division 3L. These strata were chosen because they correspond to areas of high cod catches during the autumn survey (Lilly 1994).

The temperatures that cod experience ("cod temperatures") were taken from Rose et al. (1994), and are based on the temperatures at which the cod were trawled during the autumn groundfish survey from 1981 to 1992, and are weighted by catch rates.

Capelin biomass

Capelin biomass estimates were obtained from spring acoustic surveys (Carscadden 1992; Miller 1994; Miller 1995). For divisions 2J and 3K, a continuous time series was not available so Canadian and Soviet estimates were averaged for years in which they were both available, and one was used otherwise. For both the Soviet estimates (1977–1980, 1982–1987, 1990–1991) and Canadian estimates (1981, 1983–1987, 1990–1994), combined estimates of capelin biomass in divisions 2J and 3K were used. For the capelin biomass estimates in division 3L, Canadian estimates

for 3L specifically were used for the period 1982–1994.

Condition factor

Condition factors ([gutted weight (kg)/length^3 (cm)]·100) were calculated by Bishop and Baird (1993) from weight and length–at–age from the annual fall groundfish survey. Mean condition factor is a mean of all age–classes for each year, from 1977–1994 in 2J, 1978–1994 in 3K, and 1981–1994 in 3L.

Observed growth rates

Observed annual growth rates of northern cod in NAFO divisions 2J3KL were calculated from weight–at–age from the annual fall groundfish survey (Bishop et al. 1995). Growth rate of a given year–class in a given year (i) was determined from the difference in weight–at–age between consecutive years (W_i–W_{i-1}). For each year the year–class weighing closest to 1 kg was used, because that is the size for which the potential growth rates are modelled. In 2J and 3K 1 kg cod were between 4 and 6 years old and in 3L they were between 4 and 5 years old. Observed growth rates were normalized for a 1 kg fish by dividing growth rates (difference in weight–at–age) by the average of the weight of the fish at the beginning and end of the year ($(W_i-W_{i-1})/[(W_i+W_{i-1})/2]$). Weight–at–age available from the groundfish survey (Bishop et al. 1995) were used to calculated growth rates from 1979–1993 in 2J3K, and from 1981–1993 in 3L. Growth rates in 1994 were not included because sample sizes were extremely low from the groundfish survey (Bishop et al. 1995). Growth rates are

highly sensitive to small sample sizes because they are inferred from the difference in weight–at–age in two consecutive years, whereas condition factors are somewhat less sensitive because they are based on the relationship between length and weight of a single group of fish.

Correction for autocorrelation

A time series can not be assumed to be a set of independent values because the values are often correlated in time. Therefore the sample size (n) for growth, condition factor, temperature and capelin biomass time series were corrected for autocorrelation:

$$(1)\quad 1/n^{*} = 1/n + (2/n^{2}) + \sum_{i=1}^{n}[r(t_i)\cdot(n-i)]$$

The sample size n represents the number of observations (equal to the number of years for which the data were available) and the corrected sample size (n^{*}) is the reduced sample size to account for the autocorrelation. Autocorrelation at lag i [$r(t_i)$] is the correlation coefficient of the independent and dependent time series at a lag of i years. For multiple regressions, autocorrelation of the product of the dependent time series and each of the two independent variables was calculated, and the lesser of the two n^{*}'s was taken.

To correct for lack of independence among divisions, the number of observations from only one of two divisions was used if the dependent variables were correlated. All probabilities associated with the regression statistics were corrected for both autocorrelation and lack of independence among divisions.

Bioenergetic model

Potential growth rates

The bioenergetic model was used to estimate potential growth rates of cod, the rates at which they would grow at the observed temperatures if enough food was available for them to feed at maximum consumption rates. Potential growth, which represents an upper physiological limit to growth, was determined by subtracting the energy costs associated with activity (including standard metabolism), reproduction, heat increment (digestion and assimilation), and waste losses from the energy intake associated with maximum consumption rates, which are temperature–dependent. Potential growth from the model (in kilojoules) was converted to weight using an energetic coefficient of 3.95 $kJ \cdot g^{-1}$ wet weight, an average for cod derived from Edwards et al. (1972) and Daan (1975). Potential growth rates were modelled for cod weighing 1 kg (about 48 cm in length).

Activity metabolism

Activity metabolism was divided into two components, activity associated with feeding and with migration. Kerr (1982) coupled activity metabolism with ration level. Swimming speeds associated with feeding were modelled using an experimentally determined relationship from Björnsson (1993) between swimming speeds and consumption rates for cod feeding on live prey in a mesocosm. Because maximum consumption rates are temperature dependent and his experiments were carried out at a higher temperature (8°C), his consumption rates were converted from percent of maximum ([intake/maximum intake]·100) to meal size to obtain the following relationship between swimming speed (μ; $cm \cdot s^{-1}$) and meal size (M; g wet):

(2) $\mu = 9.79 + 0.307 \cdot M - 0.00131 \cdot M^2$

Based on maximum consumption rates at the observed temperatures, 48 cm cod swim throughout the day at an average speed ranging from 0.42 to 0.52 bodylengths$\cdot s^{-1}$, (or 20 to 25 cm$\cdot s^{-1}$) . These swimming speeds were converted to metabolic cost using the following relationship between swimming speed (μ; cm$\cdot s^{-1}$), temperature (T;°C) and oxygen consumption (M_{O2}; umol O_2 per min):

(3) $M_{O2} = 66.5\ e^{0.01\mu} + 3.48 \cdot T - 51.7$; $R^2 = 0.75$; $p<0.001$; $n = 122$

This relationship was determined using data from three studies (Nelson et al. 1994; Reidy et al. 1995; Y.Tang , Biology dept., Dalhousie University, Halifax, N.S. pers.comm.) in which Atlantic cod, weighing from 0.6 to 1.3 kg, were forced to swim in a tunnel respirometer at controlled speeds (10–60 cm$\cdot s^{-1}$) over a range of temperatures (2°C–15°C) (Fig 1.2). Oxygen consumption of each fish was normalized to that of a 1 kg fish using a mass exponent of 0.8 (Reidy et al. 1995). Oxygen consumption in this relationship includes oxygen consumed for standard metabolism. Standard metabolism at the different temperatures was estimated by extrapolating the oxygen consumption–swimming speed relationship (equation 3) to zero (Fry 1971). Oxygen consumption was converted to energy expenditure using the oxycalorific coefficient 13.56 J$\cdot$mg O_2^{-1} (Brett and Groves 1979).

Metabolic costs of forced swimming in a swim tunnel have been shown both theoretically (Webb 1991) and empirically (Boisclair and Tang 1993; Krohn and Boisclair 1994) to underestimate the costs of activity in free–swimming fish, which experience additional costs associated with turning and acceleration. The ratio of spontaneous swimming costs to forced swimming costs

Fig. 1.2. Oxygen consumption of 1 kg cod as a function of swimming speed ($cm \cdot s^{-1}$) and temperature (°C). ■ 2°C at 1, 20, 30, 40 $cm \cdot s^{-1}$ (Nelson et al. 1994); □ 5°C at 25, 30, 35, 40, 45, 50 $cm \cdot s^{-1}$ (Reidy et al. 1995); * 15°C at 15, 20, 30, 40, 50, 60 $cm \cdot s^{-1}$ (Tang unpubl.). Predicted oxygen consumption = $66\ e^{0.01\ speed} + 3.5\ temperature - 52$. $r^2 = 0.75$; $p < 0.01$.

(swimming cost ratio; SCR; excluding standard metabolism) has been found in the above studies to range from 3 to 14, the ratio being smaller for larger fish. Because no data were available for fish as large as 1 kg, a ratio of 1.4 was chosen, the highest value that would allow for a physiologically realistic potential growth rate; an SCR any higher than 1.4 did not guarantee that potential growth rate remained above the observed growth rate throughout the time series.

To estimate the costs associated with migration, the annual inshore–offshore cod migration was estimted to be approximately 770 km based on routes suggested by Rose (1993). During feeding migrations cod travel at approximately 20 $cm \cdot s^{-1}$ (G. Rose, unpubl., D.F.O., St.John's, NF) suggesting that they spend a total equivalent to 44 days a year swimming across the shelf (or 12% of their time). Metabolic costs associated with this migration velocity and distance were also converted to oxygen consumption using equation (3). Swimming costs during migration were not multiplied by a correction factor (SCR), based on the assumption that acceleration and turning costs are negligible for directed swimming associated with migration. Standard metabolism was subtracted because it had already been accounted for in estimating the activity costs associated with feeding. The modelled activity estimates, including standard metabolism and the metabolic costs associated with feeding activity and migration, fell between 2.1 and 3.0 times standard metabolism.

Apparent heat increment

Apparent heat increment (or specific dynamic action), the energy used for digesting and assimilating food, has recently been shown to depend on swimming speed (Blaikie and Kerr 1996). A relationship was developed between swimming

speed (μ; $cm \cdot s^{-1}$) and apparent heat increment (AHI; % energy intake) based on Blaikie and Kerr's values for AHI in cod fed capelin swimming at 20, 30, and 40 $cm \cdot s^{-1}$ in a swim tunnel, and Soofiani and Hawkins' (1982) values for AHI in resting cod fed a diet of fish and invertebrates.

(4) $AHI = 0.0005\,\mu^3 + 11$; $r^2=0.91$, $p<0.0001$; $n=16$

An AHI of 13% of energy intake was used, which was determined by weighting AHI according to the frequency distribution of swimming speeds of cod at their lowest activity level (Björnsson 1993). The assumption was made that cod are not highly mobile while digesting because, although physiologically possible, it is energetically expensive to simultaneously digest food and swim at high speeds. Little direct knowledge, however, is available for the interaction between activity level and digestion in the field. The interaction may well be important; according to equation (4), heat increment rises to 45% for a 50 cm cod swimming at 40 $cm \cdot s^{-1}$, a speed at which both feeding (Björnsson 1993) and migrating (G.Rose, unpubl.) cod have been observed to swim. Further investigation into the interaction between digestion, assimilation, and field activity levels would clearly be useful.

Maximum consumption rates

Maximum consumption rates for Atlantic cod were determined using feeding rates from Waiwood et al. (1991) over a range of 0.8 to 8°C. They found the amount of food consumed by a 1 kg cod fed to satiation once daily (C_{max}; grams) can be described as the maximum meal size (17.5 g) multiplied by the probability of feeding on a given day (P):

(5) $C_{max} = 17.5 \cdot P$

where (P) depends on temperature. P value was used from their results at 1 and 4 °C to obtain a relationship between C_{max} and temperature (T; °C):

(6) $P = 0.075 \cdot T + 0.468$

Maximum consumption was converted from wet weight to energy equivalents using an energy conversion factor of 4.66 $kJ \cdot g^{-1}$ for the food of North Sea cod 40–49 cm in length (Daan 1975). Braaten and Gokstat (1980) found that cod fed twice a day could eat, on average, 1.2 times more than cod fed once a day, and that consumption did not go up when cod were fed more often than twice a day. Consumption rates from Waiwood et al. were therefore multiplied by 1.2. Estimated maximum consumption rates were, on average across years, 4.8 times standard metabolism, in close agreement with Edwards et al. (1972) consumption rates for cod fed to satiation, which were, on average, 5.1 times standard metabolism. Maximum consumption from Waiwood et al. (1991) was used rather than from Edwards' et al. (1972) because the temperatures were not controlled in Edwards' et al. (1972) feeding experiments.

Waiwood et al.'s (1991) temperature range (1 to 4°C) covers 35 of the 46 temperatures observed during the three time series for the three divisions. Maximum consumption was extrapolated for the 11 coldest years.

Egestion and excretion

A constant value was chosen of 20 % of food intake for energetic losses through egestion and excretion, a value typical for piscivorous fish (Ursin 1979; Majkowski and Waiwood 1981; Hewett and Johnson 1992).

Reproductive losses

The fecundity of a mature 48 cm female cod was calculated using fecundity–length relationships from cod in the appropriate division, 2J3K or 3L (May 1967). The number of eggs (290 000 in 2J3K and 548 000 in 3L) was then multiplied by the energy content of a ripe cod egg, an average of 1.775 $J \cdot egg^{-1}$ found by Daan (1975) and 2.528 $J \cdot egg^{-1}$ found by Hislop and Bell (1987). Annual reproductive loss for female cod in 2J3K and 3L were estimated to be 624 and 867 $kj \cdot yr^{-1}$, or 16% and 23% of the energy content of their whole body.

The annual reproductive loss of a mature male cod was calculated from the gonadosomatic index of 5 yr old male cod (weighing approximately 1 kg) on the Grand Bank of Newfoundland (Trippel and Morgan 1994). The cod were believed to be a mix of spent and unspent individuals, so the upper limit of the gonadosomatic index (11%) was used, based on the assumption it would best represent the unspent individuals. The weight of the testes (110 g) was then multiplied by the energy content (3.83 $kJ \cdot g\ wet^{-1}$) of mature ripe male gonad in Pacific cod (*Gadus macrocephalus*) Smith et al. (1982). The energy content specifically for Atlantic cod testes is not available. Eliassen and Vahl's (1982) energy content for cod gonad (3.49 $kJ \cdot g^{-1}$; presumably based on both ovaries and testes), corresponds well with the energy content of the testes of Pacific cod. The annual male reproductive loss was estimated as 383 $kJ \cdot yr^{-1}$. Mature male and female reproductive loss was averaged and then multiplied by 50%, the proportion mature at 48 cm in length (Morgan et al. 1993).

Sensitivity analysis

To quantify the effects of parameter uncertainty on potential growth rates, a

sensitivity analysis was carried out both by quantifying the effect of the range in the parameters reported in the literature, and by varying the parameters systematically by ±10%. The model sensitivity (s) to a change in the parameter was calculated using the following formula:

(7) s = ((modelled growth after perturbation – modelled growth before perturbation) ·100) / modelled growth before perturbation.

The sensitivies for the temperature at which the effect of the perturbation was greatest were tabulated.

Results

Relationship between autumn shelf bottom temperatures and temperatures for autumn bottom trawled cod.

The mean temperatures at which cod were trawled in divisions 2J, 3K and 3L (T_{cod};°C;"cod temperatures") are significantly related to the autumn bottom shelf temperatures (T_{bottom};°C) in strata 213, 634, and 372, respectively, after correction for autocorrelation (T_{cod}= $1.0T_{bottom}$ + 0.19; r^2=0.61; $p<0.01$) (Fig. 1.3). The slope is not significantly different from 1, and the intercept is not significantly different from 0, indicating that the shelf temperatures chosen adequately represent the magnitude and interannual variability in the temperatures the cod experience and that cod are found in colder waters in colder years. If the three divisions are considered independently, cod temperatures and bottom shelf temperatures are not significantly correlated in division 3K. The range in temperatures was much smaller in 3K, and there is one anomalous year (1990), when the cod were found above 3°C and the mean bottom shelf temperature was only 1°C.

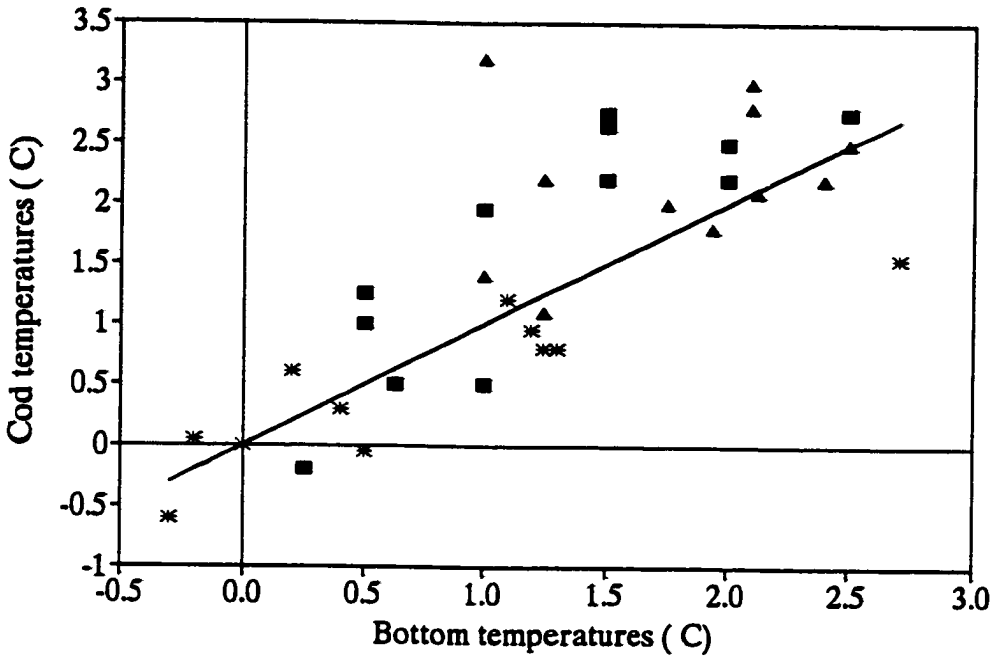


Fig. 1.3. Autumn bottom shelf temperature in Divisions 2J(■), 3K(▲), and 3L(*) versus temperature for autumn bottom trawled cod (weighted by catch) from 1981–1992. The line represents a 1:1 relationship. $r^2 = 0.61$; $p < 0.01$.

For most years only autumn temperatures were available, although there were seasonal groundfish surveys in 3L in 1985 (spring, summer, autumn and winter). The average temperature for cod weighted by catch over the four seasons in 1985 was 0.5 °C (G. Lilly unpubl. DFO, St.John's NF), whereas the temperature used from the autumn survey alone (stratum 372) was 0.4°C. This difference between annual and autumn temperature (0.1°C) represents less than 3% of the interannual range in 3L autumn bottom shelf temperatures in stratum 372 (−1.0 to 2.7°C). The extent to which autumn and annual temperatures are similar throughout the time series, however, is unknown.

Relationships between capelin biomass, temperature, growth and condition factor

Temperature and ln (capelin biomass) together explained 52% ($p<0.05$) of the interannual variability in mean cod condition factor in divisions 2J and 3K (Fig. 1.4), but were not significantly related to condition factor of 3L cod ($p>0.05$) (data not shown). Mean annual condition factors of 3L cod were less variable than are those in 2J and 3K, ranging from 0.74 – 0.79 in 3L, 0.64 – 0.84 in 2J, and 0.71 – 0.80 in 3K. Ln (capelin biomass) alone explained 35% of the variability in 2J3K condition factor ($p<0.05$).

Temperature and capelin biomass explained 23% of the variability in growth rates ($p<0.05$) when 2J, 3K, and 3L were included (Fig. 1.5). Temperature alone explained 56% of the variability in growth rates of 3L cod ($p<0.01$).

Condition factor and growth rates have both been low in 2J and 3K in recent years. Growth rates have been declining since 1979, and condition factors have been declining since 1988 (Fig. 1.6). Growth rate and condition factor for 1 kg

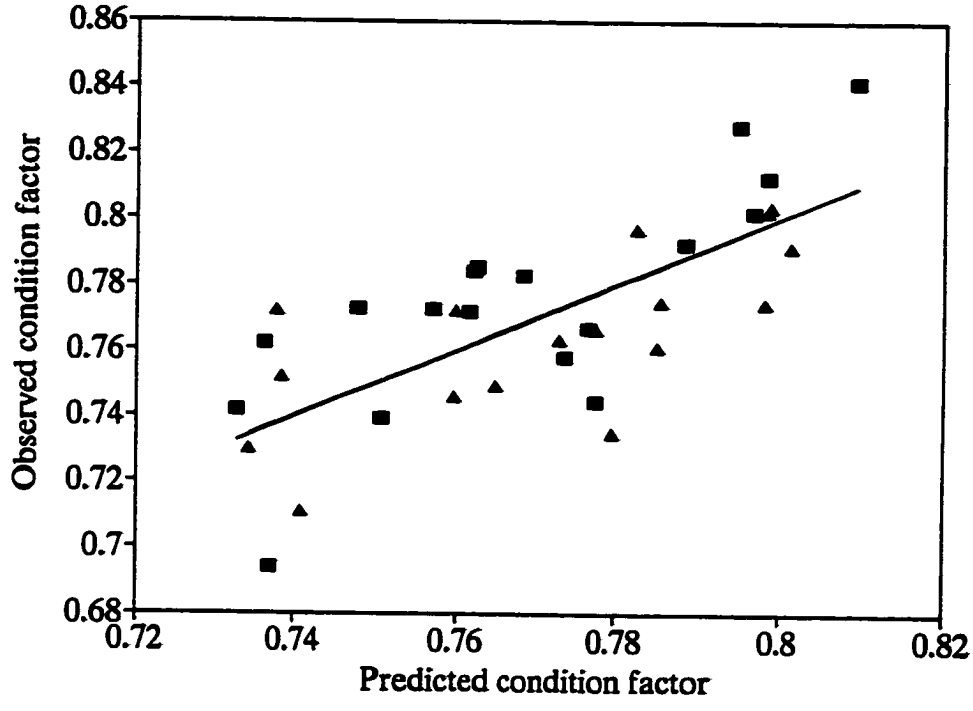


Fig. 1.4. Mean condition factor, for all age-classes of cod in Divisions 2J(■) (1977–1994) and 3K (▲) (1978–1994) (gutted weight·length^{-3}·100) as a function of ln [capelin biomass ('000 000 tons)) and temperature (°C). Predicted condition factor = 0.010 ln(capelin) + 0.16 temperature + 0.76. $r^2 = 0.52$; $p = 0.05$.

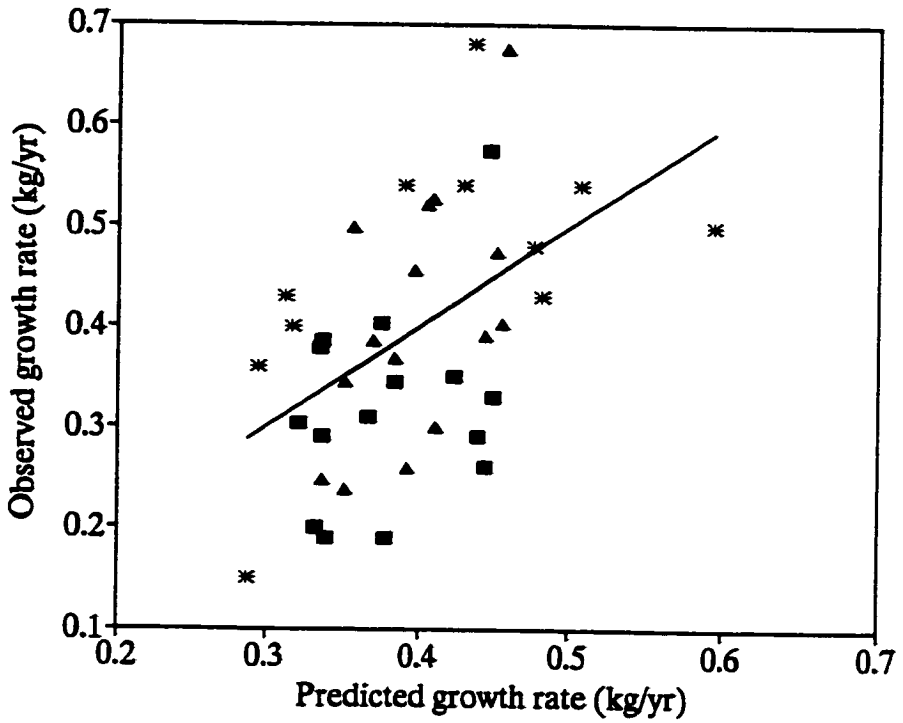


Fig. 1.5. Growth rate of 1 kg cod in 2J(■) (1979–1993), 3K(▲) (1979–1993), and 3L(*)(1981–1993) as a function of capelin biomass ('000 000 tons) and temperature (°C). Predicted growth = 0.035 capelin + 0.044 temp + 0.29. $r^2 = 0.23$; $p < 0.05$.

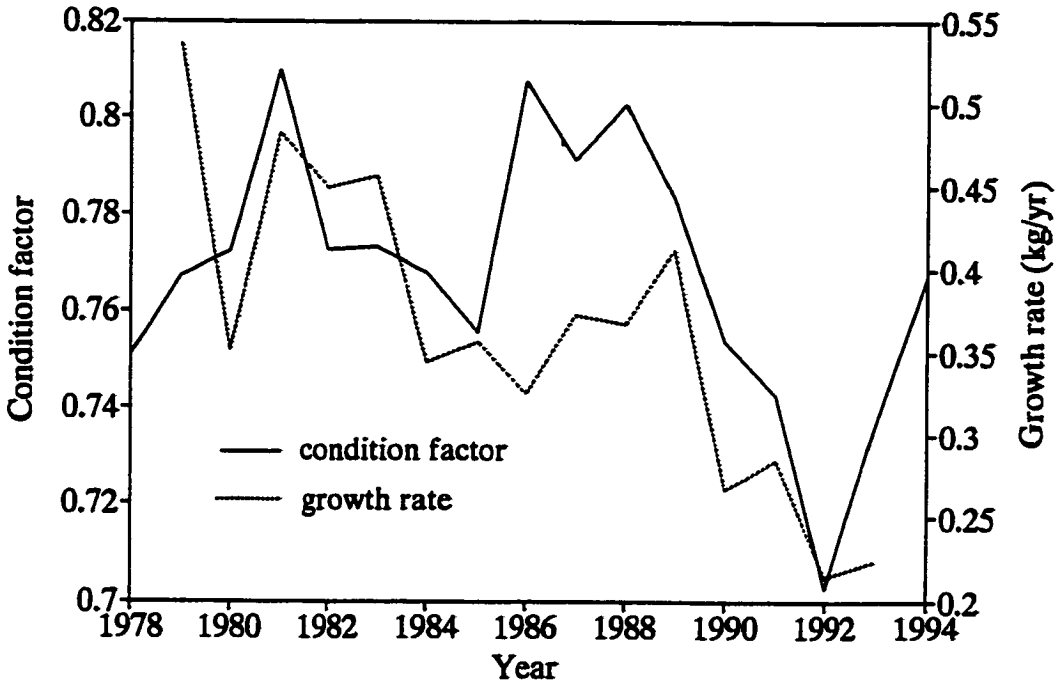


Fig. 1.6. Mean condition factor, for all age-classes of cod in Divisions 2J and 3K combined (gutted weight·length^{-3}·100) from 1978 to 1994, and mean annual growth rate of 1 kg cod in Divisions 2J and 3K from 1979 to 1993.

cod, however, were not significantly related over the time series ($p>0.05$). There is some indication that condition rose in 1994, however there were so few fish caught in the 1994 survey that the data must be interpreted cautiously (Bishop et al. 1995).

Potential and realized growth

Realized (or observed) growth falls well below potential growth (generated from the bioenergetic model) in both 2J and 3K (Fig. 1.7a and 1.7b) over the whole time series, from 1979 to 1993. Realized growth reaches, on average, 44 and 48% of potential growth in 2J and 3K, respectively. Differences in potential growth among years and divisions depend entirely on temperature inputs to the model, and the temperatures signals used for 2J and 3K (from strata 213 and 634, respectively) do not reflect as strong a decreasing trend as do the temperature signals from some other strata. The model was therefore run with the lowest observed temperatures across the shelf (Colbourne 1993) to obtain a lower limit for the potential growth rates. Since 1986 in 2J, and since 1988 in 3K, realized growth has not reached even these lower limits of potential growth. In 3L, however, realized growth closely follows potential growth over the time series (Fig.1.7c), realized growth reaching, on average, 70% of potential growth, suggesting that cod in 3L are growing close to the highest rate the temperature regime will allow in most years. Potential growth is lower in 3L than in 2J or 3K, directly reflecting the colder temperatures there. The mean temperatures observed over the time series are 1.6, 1.8, and 0.7 °C for 2J, 3K, and 3L, respectively.

Sensitivity analysis

The effect of a 10% perturbation was most pronounced for parameters

(a)

(b)

(c)

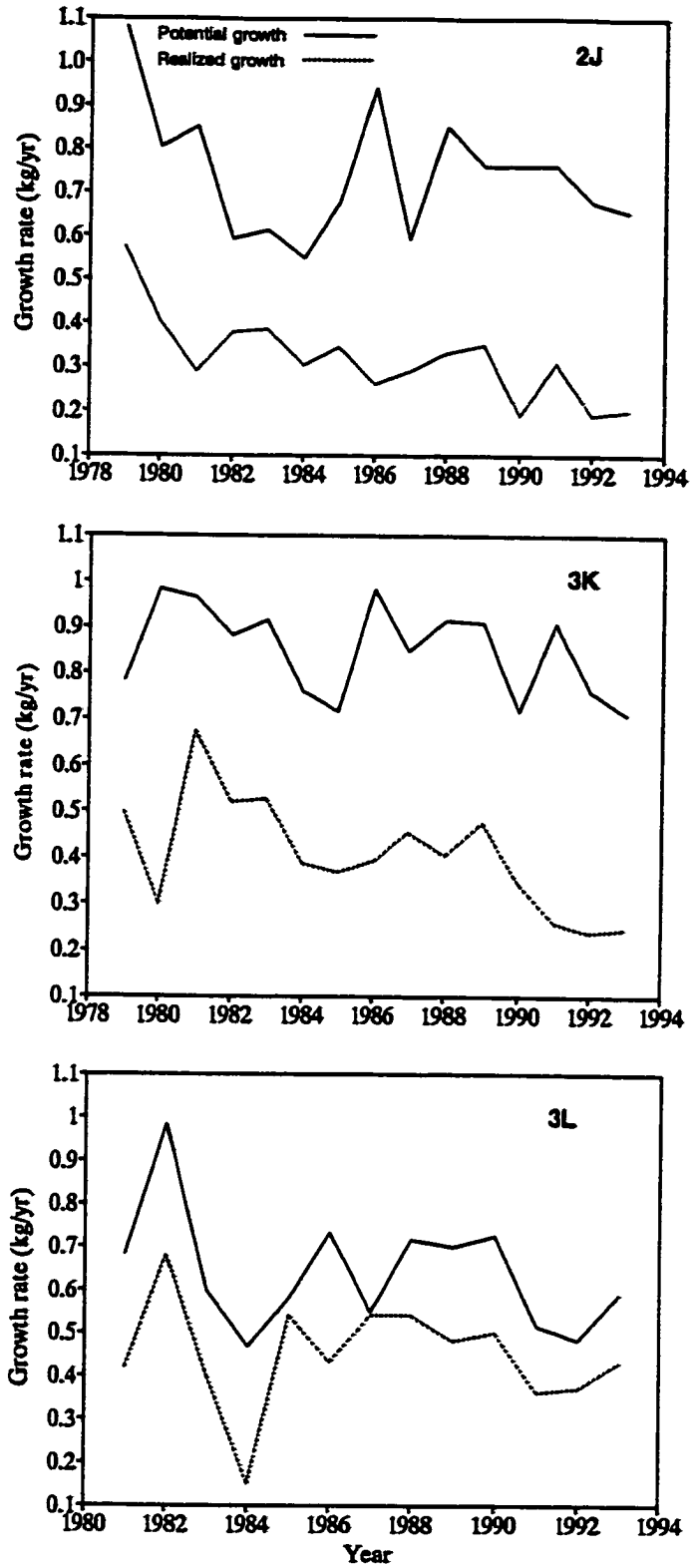


Fig. 1.7. Potential (modelled) and realized (observed) growth of 1 kg cod in a) 2J, b) 3K, and c) 3L.

associated with activity and consumption (Table 1.1). Perturbations of ±10% resulted in changes in sensitivities of over 25% for swimming speed, SCR, the speed coefficient and the constant for equation 3, and in sensitivities over 50% for maximum consumption and the energy content of the diet. Parameters associated with reproduction were the most robust with sensitivities of only 1 or 2% for a 10% perturbation.

Sensitivities to the total range of reported values from the literature incorporates both the sensitivity of the model to particular parameters and the degree to which the parameters are known. This analysis also highlights sensitivity of the model to parameters associated with activity and consumption, although the sensitivities of the model to activity parameters from the literature range are even higher (70–235%) than are the sensitivities to a 10% perturbation because the activity parameters are the least well known and activity costs in the field may be highly variable (Boisclair and Leggett 1989).

Discussion

Correlation analyses in the present study suggest that both temperature and capelin biomass are related to cod condition factor and cod growth rates on the Newfoundland and Labrador shelves. Capelin biomass is most important in the two northerly divisions (2J3K) for condition factor, whereas temperature is most important for growth rates in the colder waters of the most southerly division, 3L. Similarly, the bioenergetic analysis suggests that while food supply may be important in 2J3K, cod growth appears to be temperature–limited, at least in certain years, in 3L.

It is pertinent to note that condition factor and growth rates are not correlated

Table 1.1: Sensitivities of modelled growth to parameter perturbations

Variable	Value chosen	Literature range	Effect of range	Perturb. effect
Energy content of whole cod ($kJ \cdot g^{-1}$)	.95	3.85 (Daan 1975) 4.04 (Edwards et al. 1972)	±1%	±11%
Energy content ($kJ \cdot 1000\ eggs^{-1}$)	2.15	1.775 (Daan 1975) 2.528 (Hislop 1980)	±3%	±2%
Fecundity ('000 eggs)	290 548	272–290 (Pinhorn 1984) 403–548 (May 1967)	+2% +6%	±2% ±2%
Swimming speed ($cm \cdot s^{-1}$)	22	10 (Bjornsson 1994) 28 (Bjornsson 1994)	±235%	±27%
SCR (spontaneous/ forced swim cost)	1.4	1–2 (Boisclair and Tang 1994)	±107%	±25%
Speed coefficient for O_2 consumption relationship	66.5	53.5 (this study) 79.5	±70%	±31%
Temp. coeff. for MO_2 relationship	3.48	3.25 (this study) 3.71	±4%	±7%
Constant for MO_2 relationship	–51.7	–42.4 (this study) –61.0	±52%	±37%
Heat increment (% of consumption)	13	10 (Blaikie 13 and Kerr 1996)	–28%	±12%
Energy losses in egestion and excretion (%)	20	16 (Hewett and 26 Johnson 1992)	+37% –66%	±19%
Max.consumption (X standard)	4.8	4.2 (Waiwood et al. 1991) 5.1 (Edwards et al. 1972)	–81% +41%	±50%
Energy content of diet ($kJ \cdot g^{-1}$)	4.66	4 (Daan 1975) 5	–100% +54%	±60%
Male GSI (% of body weight)	11	6 (Trippel and 11 Morgan 1994)	+6%	±1%
Energy content of testes ($kJ \cdot g^{-1}$)	3.83	na	na	±1%

and that capelin biomass appears to explain variability in condition factor, while temperature appears to better explain variability in growth rates. I speculate that food supply may be more likely to affect condition because it determines the energy available for gonads and muscle production, while temperature may regulate the development of the whole animal including the growth of the skeleton, i.e. an increase in both length and weight.

The autumn bottom shelf temperatures and "cod temperatures" are calculated from data from the same surveys, with the shelf temperatures being based on temperatures in a single chosen stratum, and the "cod temperatures" being based on temperatures in all strata in the division, but weighted by catch. The two sets of temperature data are then not independent, but a strong one–to–one relation between them nevertheless suggests that the temperatures in the chosen strata adequately reflect the temperatures at which the cod were trawled in the greatest numbers and that, throughout the time series, in colder years cod did not move to warmer areas but did experience colder water.

Despite the recent coincident declines in growth rates, condition factor, and temperature in 2J3K, and despite the present finding that cod are not avoiding the cold water, the bioenergetic analysis suggests that the cold water in these two areas has not physiologically limited growth rates. The current bioenergetic analysis has several limitations. Most importantly, variability in temperature over the seasonal cycle is not accounted for. However, a comparison of autumn shelf temperatures and annual temperatures weighted by catch in 3L in 1985 suggests that the autumn bottom shelf

temperatures may index the temperature the cod experience throughout the year reasonably well.

The model also suffers the common problem of having to make parameter assumptions (Ney 1993), although less so than in the past because of the recent concentrated effort on understanding cod physiology. The sensitivity analysis highlights the model's sensitivity to consumption and activity parameters, and that the sensitivity to activity parameters is exacerbated by the extent to which they are unknown. Further research to constrain the range of swimming speeds, or more importantly costs, would clearly be very useful. Accordingly, the strength of the analysis is in evaluating the differences in the relative importance of food supply and temperature to growth in different areas, and not in the absolute magnitude of the potential growth rates.

The recent low growth rates and condition factors in 2J and 3K northern cod could be because of low prey supply or size-selective fishing pressure as has been observed in the southern Gulf of St. Lawrence cod (Hanson and Chouinard 1992). It is also possible that temperature, even if it has not physiologically limited growth rates, has reduced growth rates indirectly by reducing prey availability. In cold years the cross sectional area of the cold intermediate layer (CIL) is larger (Colbourne et al. 1994). Cod generally avoid penetrating the CIL, although they may briefly swim up into it in search of capelin, which are generally distributed in colder waters than are cod (Rose and Leggett 1989). In colder years the larger CIL may hamper the cod's ability to prey on capelin, resulting in lower feeding and growth rates. Scatter plots

(Shelton and Lilly 1995) and time series (de Cardenas 1994) of CIL and cod growth rates in 2J3KL suggest that in cold years cod may feed less, even if they are not physiologically limited by their temperature–dependent maximum consumption rates. According to preliminary results (Lilly 1994), cod feeding on capelin was low from 1990–1992 in 2J, although the same was not true in 3K.

Unlike cod growth in divisions 2J and 3K, cod growth in 3L does appear, in some years, to be physiologically limited by temperature. Cod in 3L experience colder temperatures than cod in 2J or 3K and are growing, and presumably eating, as much as expected at the temperatures that are available to them. Cod in 3L therefore have lower potential growth rates, and need less food to attain them. The absence of a decline in condition factor in cod in 3L compared to cod in 2J3K (Bishop and Baird 1993) could be explained by the possibility that cod in 3L are not food limited.

In summary, the present results suggest that cod growth rates are physiologically limited by cold temperatures on the northern Grand Banks, while prey supply and availability are more likely to be limiting growth rates on the northeast Newfoundland and Labrador shelves.

Chapter 2

Declining weight-at-age in northern cod and the potential importance of the early years and size-selective fishing mortality.

Summary

Weight–at–age of northern cod declined between 1979 and 1993 for all age classes, with the greatest reduction in size–specific growth evident at ages 3, 4, and 5. The extent to which the declining weights at these young ages have been responsible for smaller weights in older age classes is determined. On average, 68 % of the decline in weight of 4–to 8–year–olds was attributable to a decline in weight at–age in previous years. Differences in weight–at–age among cohorts suggests that cohorts that are small early in life tend to remain small, suggesting that size in early years greatly influences future production. These findings suggest that the environment for growth may have worsened specifically for these young ages, highlighting the importance of studying what is affecting growth processes in the early years. Furthermore these results point to the possibility that size–selective fishing on the 3–to 5–year–olds may have played an important role in the decline in weight–at–age.

Introduction

Fish growth rates exhibit a high degree of plasticity depending largely on temperature and food availability. Weight–at–age of Atlantic cod can vary up to 12–fold among stocks (Brander 1995) and up to 2–to 3–fold among years within a given stock (Sinclair et al. 1995). These variations in growth rate affect current production as well as future production because larger fish are more fecund. Weight–at–age of northern cod (*Gadus morhua*) has been declining over the last 15 years on the Labrador and northeast and Newfoundland shelves (Div. 2J and 3K) (Bishop et al. 1995). On average, a cod of a given age in 1979 weighed almost twice as much as a cod of the same age in 1993 (Fig.2.1). In the more southerly division (Div. 3L), on the northern Grand Banks, weight–at–age has not declined, therefore 3L weights–at–age were not included in the analysis.

The low weights–at–age in Div. 2J and 3K are not unprecedented; they were also low through the early and mid 1970's. However, these low weights–at–age were particularly concerning because they were concurrent with very low stock biomass. This decline in weight–at–age coincides with declines in temperature. Water temperature and capelin biomass are correlated with both northern cod condition factor and northern cod growth (Millar and Myers 1990; Bishop and Baird 1993; de Cardenas 1994; Shelton and Lilly, 1995; Chapter 1) and temperature is correlated with size–at–age of cod on the Scotian shelf (Campana et al. 1995).

For the same size–specific growth rate, smaller fish have smaller growth increments; therefore, smaller growth increments in a given year may not indicate

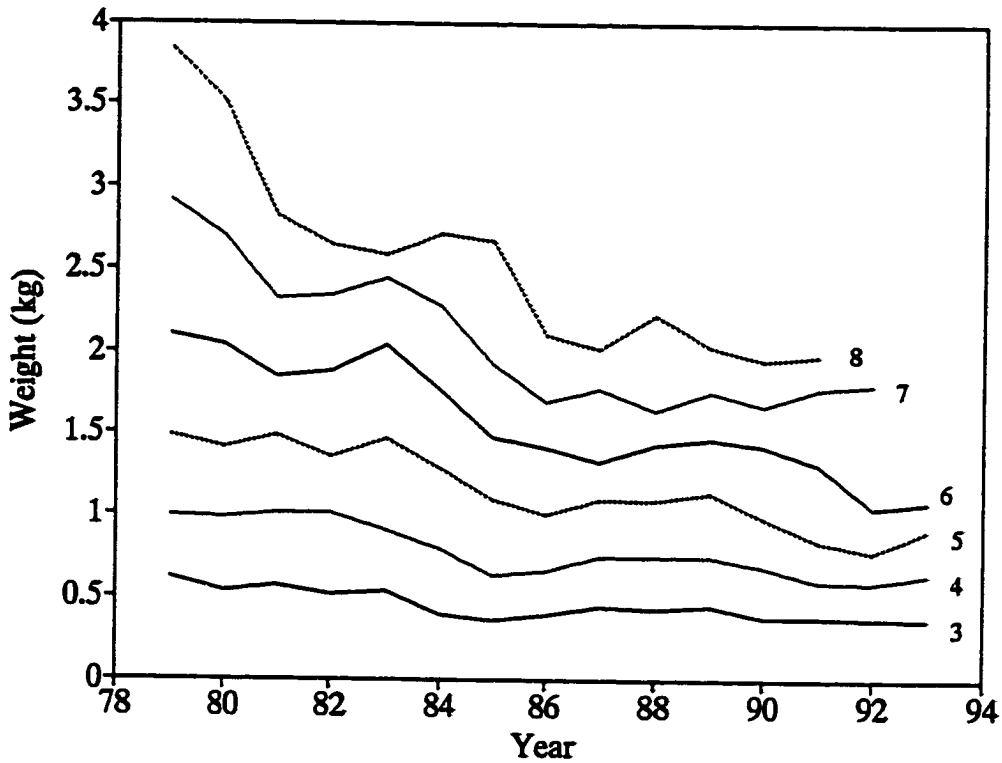


Fig. 2.1. Time series of weight–at–age of 2J3K cod (3 to 8 year–olds).

slower size–specific growth, but may be due to smaller size at the beginning of that year. This chapter addresses whether weight–at–age of northern cod on the Labrador and northeast Newfoundland shelves has declined across age classes because of decreased size–specific growth rate in all the age classes, or has a decrease in size–specific growth been restricted to young ages and the smaller size carries on through to the older age classes? Identifying the ages for which specific growth rate has declined may help point to the reasons for the decline in weight–at–age.

During this same period, fishing mortality increased (Baird et al 1992; Myers et al. 1997). It is therefore possible that some of the reduction in weight–at–age was not due to reduced growth rates at all but was due to the selective removal of larger fish by the fishery. For age classes that are not fully recruited to the fishing gear, the slower growers of a given age class have a higher chance of escaping through the nets. Because growth rates are measured as differences in weight–at–age of the same cohort in two different years, an increase in size selective fishing pressure could make growth rates appear to increase or decrease depending on which age–classes are most affected. Reduced weight–at–age may be expected to persist through the older age classes even if size selection is limited to the first few age classes that are recruited to the fishing gear, because for the same size–specific growth rate, smaller fish grow by smaller increments.

The goal in this paper is to identify in which age classes size–specific growth has decreased the most, and to establish whether these are the same age classes that experience the greatest size–selective fishing mortality. By tracking the cohorts it is

also possible to determine to what extent decreases in weight–at–age of cod early in life lead to the observed decrease in weight–at–age later in life.

Materials and methods

General approach

After identifying the age classes in which size–specific growth rates declined to the greatest extent,

(1) the proportion of variance in weight–at–age that can be explained by weight–at–age of the corresponding cohorts in previous years was determined

(2) the difference in weight–at–age among cohorts was examined to determine whether differences in weight–at–age track through the life of a given cohort.

(3) the proportion of the decline in weight–at–age of older age classes that can be attributed to weight–at–age in previous years was assessed using a simulation model

Weight–at–age and size–specific growth

Mean annual weight–at–ages from the annual autumn groundfish surveys, as reported by Bishop et al. 1995, were used for the analysis. They calculated weight–at–age from length–at–age using the same length–weight relationship in all years. The annual changes in weight–at–age therefore directly reflect changes in length, not weight.

Mean weight–at–age and size–specific growth rates were averaged for Div. 2J

and Div. 3K. Size-specific growth (G) was estimated using weight-at-age (W(1) and W(2); in kg) in two consecutive years (t(1) and t(2); in days):

$$G = ([\ln W(2) - \ln W(1)] / [t(2) - t(1)]) \times 100 \quad (1)$$

The analyses were limited to the period 1979 to 1993 (the period over which the recent decline in weight-at-age was observed) and age classes 3 to 8. The analyses included weight-at-age of northern cod in Div. 2J and 3K, but not 3L where weight-at-age has not declined. Weights-at-age of the 7- and 8-year-olds in 1992 and 1993 were eliminated from the analyses because of low sample sizes (see Table 20 and 21 Bishop et al. 1995).

Corrected size-specific growth rate

Because size-specific growth decreases with increasing weight (Jobling 1983), size-specific growth was corrected for weight. This correction allowed for a comparison of size-specific growth of cod among years for cod of the same age but different weights. Size-specific growth was corrected by dividing it by $0.1021 \cdot \text{weight}^{-0.441}$. The weight exponent was taken from Jobling (1983), and the slope was calculated by fitting the size-specific growth rates with the weight exponent of -0.441. The exponent calculated in this study for the size-specific growth rates was not used (as described below) because it was high compared to other estimates (see Jobling 1983 and 1993 for reviews). The exponent calculated from the present data may be an overestimate because of size-selective mortality in some or all age-classes.

Relative weights–at–age

To include weight–at–age of age 3 to age 8 cod in the same analyses, weight–at–age was corrected for age. Relative weights–at–age were calculated by dividing weight–at–age for a given age class in a given year by the mean weight–at–age of the age class over the period 1979 to 1993. For example, if the weight at age 3 in 1979 was 0.65 kg, and the mean weight of age 3 cod over the period 1979 to 1993 was 0.5 kg, the relative weight of age 3 in 1979 would be 1.3. Each age class, therefore, had a mean relative weight–at–age equal to 1.

Detrended weight–at–age

The weights–at–age were detrended, or corrected for "year", to remove environmental effects that could be confounded with cohort effects. The mean was taken of the relative weight–at–age of all age classes in a given year, and then divided each relative weight–at–age by the mean for the year. For example, if the mean relative weight of all age classes in 1979 was 1.4 kg (i.e., if in 1979 across age classes, cod were 40% larger than average), then the weight–at–age for each age class in 1979 was divided by 1.4.

Differences in weights–at–age among cohorts

To determine whether differences in weight–at–age persist through cohorts, a bootstrapping program was used to compare relative weights–at–age among cohorts (for details see Krohn and Boisclair 1994).

Proportion of the decline in weight–at–age due to the decline in weight–at–age of the same cohorts in previous years.

Simulations were run to determine the proportion of the decline in weight–at–age of older age classes that could be due simply to smaller weights at an earlier age, specifically at age 3, 4 and 5. For all pairs of years over which there was a reduction in weight–at–age in a given age class, the expected difference in growth from the earlier observed weights of the same two cohorts at age 3, 4 and 5 were simulated. Size–specific growth rates were used from the appropriate division, 2J or 3K (Fig. 2.2; and see below). The expected decline (from the two modelled weights–at–age) was divided by the observed decline in the two weights–at–age to obtain a proportion of the observed reduction in weights–at–age that, given equal growth rates, could have been due solely to smaller weights at age 3, 4, or 5.

To simulate appropriate growth rates for cod in the 2J3K area, size–specific growth (G) was modelled as an function of weight (W(2)) Fig. 2.2:

(2) $G = a \cdot W(2)^b$

Modelled growth was used as a function of weight at the end of the growth interval (W(2)) rather than at the beginning (W(1)) to avoid creating a spurious negative correlation between size–specific growth ([ln W(2) – ln W(1)] / [t(2) – t(1)]) x 100) and initial weight (W1), because size–specific growth decreases with weight. Age 3 through age 12 cod were included to extend the weight range.

For the simulation of growth rates starting from observed weights–at–age, the weight exponent directly from the survey data was used rather than the exponent from

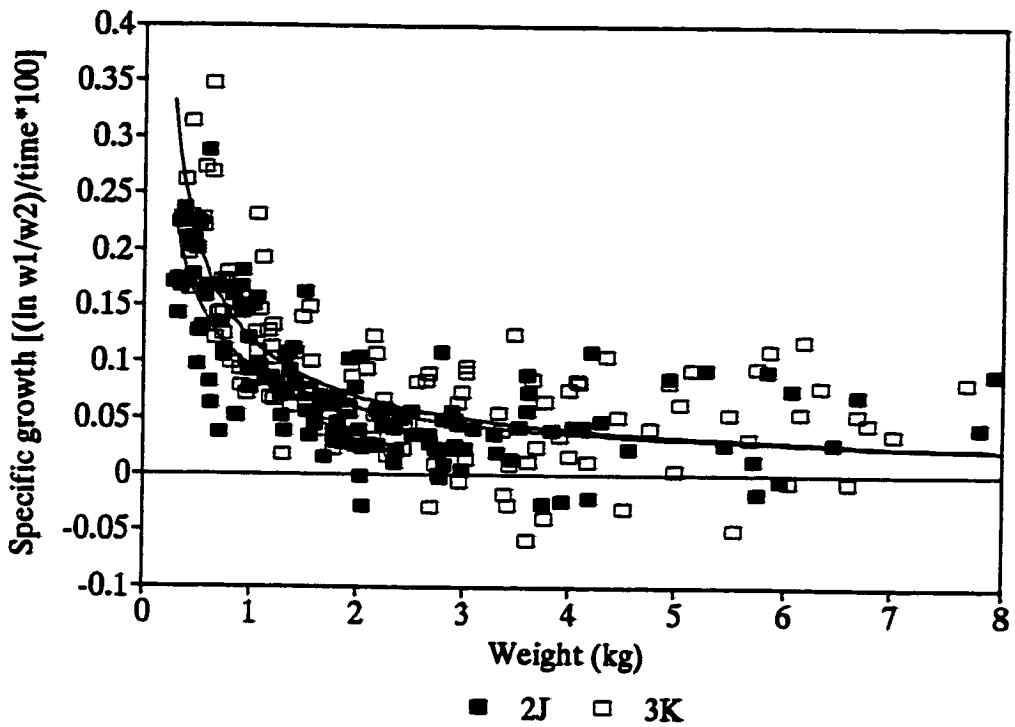


Fig. 2.2. Size-specific growth rates of 2J and 3K cod as a function of weight. 2J growth = 0.096* weight$^{-0.70}$; r^2 = 0.56; p< 0.001. 3K growth = 0.120* weight$^{-0.80}$; r^2 = 0.63; p< 0.001.

Jobling 1983. As mentioned previously, the exponent calculated from the survey data include any effects of size-selective mortality, effects that need to be included in the modelled weights-at-age so they can be compared to the observed weights-at-age.

Results

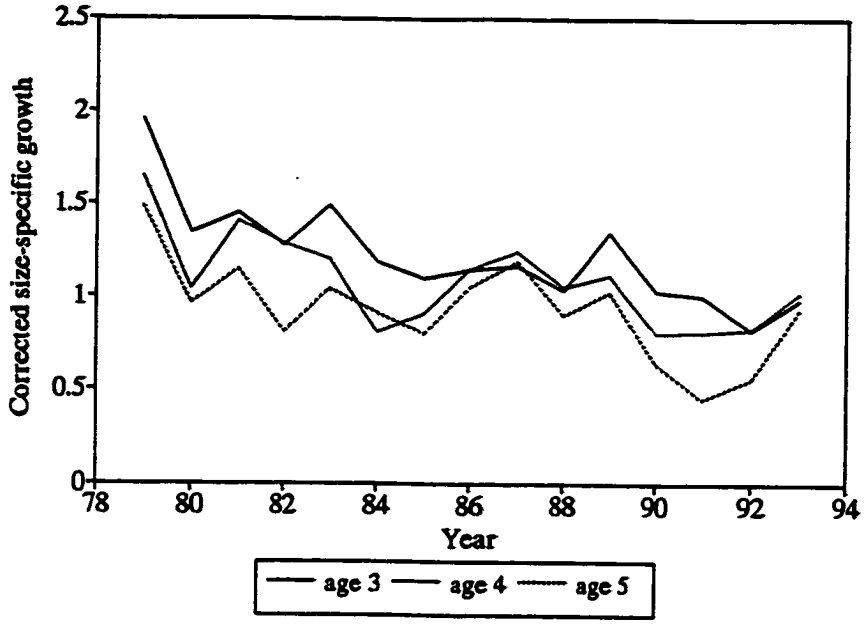
Size-specific growth rates

Size-specific growth rates declined significantly for 3, 4 and 5 year-olds ($p < 0.0005$, 0.01, 0.02, respectively), the first three years that cod are recruited to the fishery (Fig.2.3a; Table 2.1). Size-specific growth rates did not decline significantly for the 6-, 7- and 8-year-olds (Fig. 2.3b;Table 2.1). Growth rates are estimated from changes in weight between consecutive years, so the more pronounced decline in growth rate for the 3-year-olds represents a large decrease in the difference in weight-at-age of 2- and 3-year-olds through time or, more specifically, reflects a decrease in the weight at age 3 relative to a more stable weight at age 2. It is possible, however, that weight at age 2 has also decreased but that the sampling gear only catches the largest 2-year-olds. Therefore, size-specific growth rate declined sometime before age 3, not necessarily between age 2 and 3.

Relationship between weight-at-age of the same cohort in two consecutive years

To quantify the importance of size in one year on size of the same fish in the following year, relative weights-at-age in year X were regressed against relative

(a)



(b)

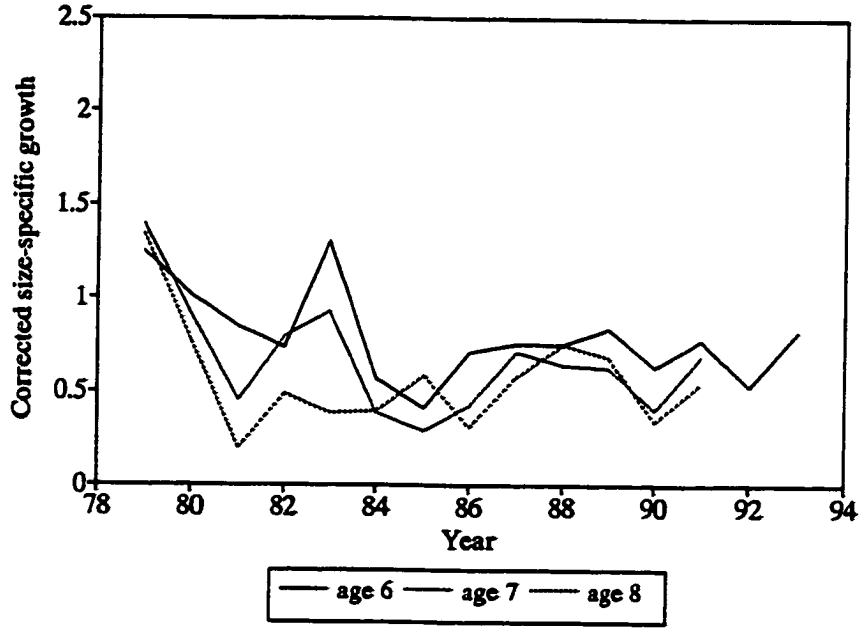


Fig. 2.3. (a) Time series of corrected size-specific growth rates of 2J3K cod (3 to 5 year-olds).
(b) Time series of corrected size-specific growth rates of 2J3K cod (6 to 8 year-olds).

Table 2.1: Regression coefficients for the change in size–specific growth rate from 1979 to 1993.

age	r^2	p	n
3	.62	<0.001	15
4	.43	<0.01	15
5	.39	<0.02	15
6	.23	>0.05	15
7	.24	>0.05	13
8	.08	>0.05	13

weights–at–age of the same cohort in year X + 1, and found that 70% of the among–year variability in weight–at–age can be explained by weight in the previous year, suggesting that once fish are small, they stay small (Fig. 2.4). This relationship was weaker, but was still significant with the detrended relative weights–at–age ($r^2 = 0.35$, $p < 0.001$, Fig. 2.5).

Differences in weights–at–age among cohorts

Relative weights–at–age differed significantly among cohorts; the largest–bodied cohorts being as much as 84% larger than the smallest ones in Div. 2J ($p < 0.001$; Fig. 2.6), and 50% bigger in Div. 3K ($p < 0.001$; Fig. 2.7) with the earlier cohorts being larger than the more recent ones. After detrending the weights–at–age, the range in relative weights among cohorts was greatly reduced, but the differences in relative weights among cohorts were significant ($p < 0.004$; and $p < 0.02$ in Div. 2J (Fig. 2.8) and 3K (Fig. 2.9), respectively). Therefore, even after removing most of the variability in weights–at–age among cohorts, cohort effects were still detectable in both divisions.

Proportion of the decline in weight–at–age due to the decline in weight at ages 3–5.

According to the simulations, the decline in weight at age 3, 4, and 5 explained, on average across age classes, 67%, 65% and 75 % of the declines in weight–at–age in the older age classes.

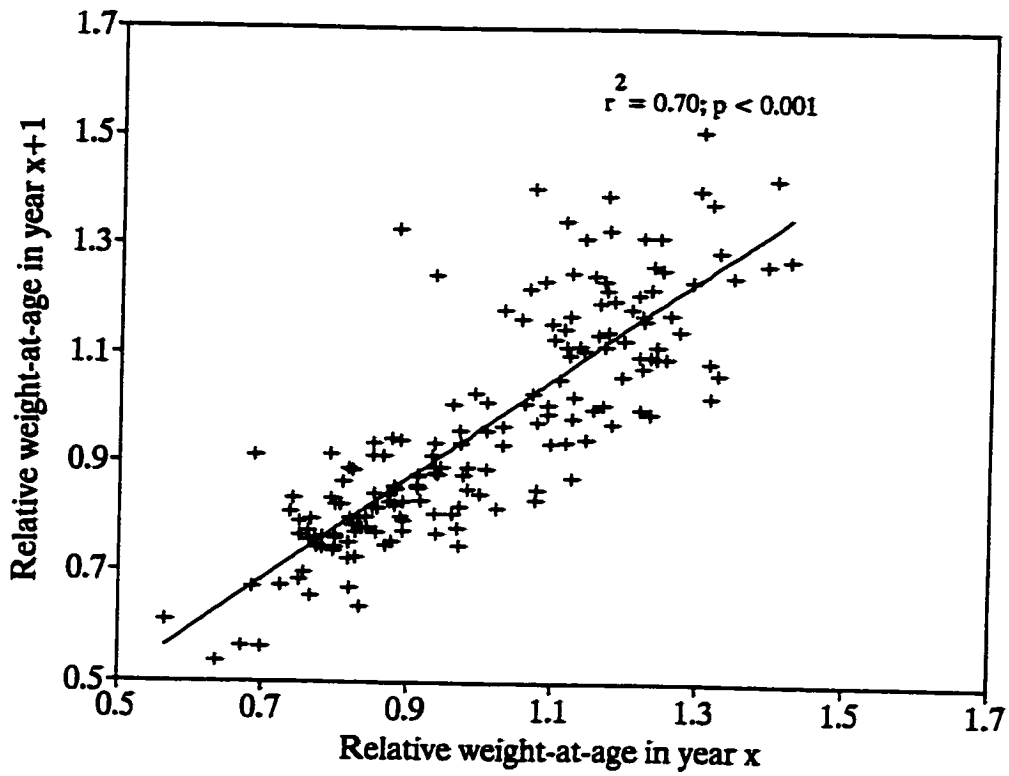


Fig. 2.4. Effect of weight–at–age of 2J3K cod on weight–at–age in the following year

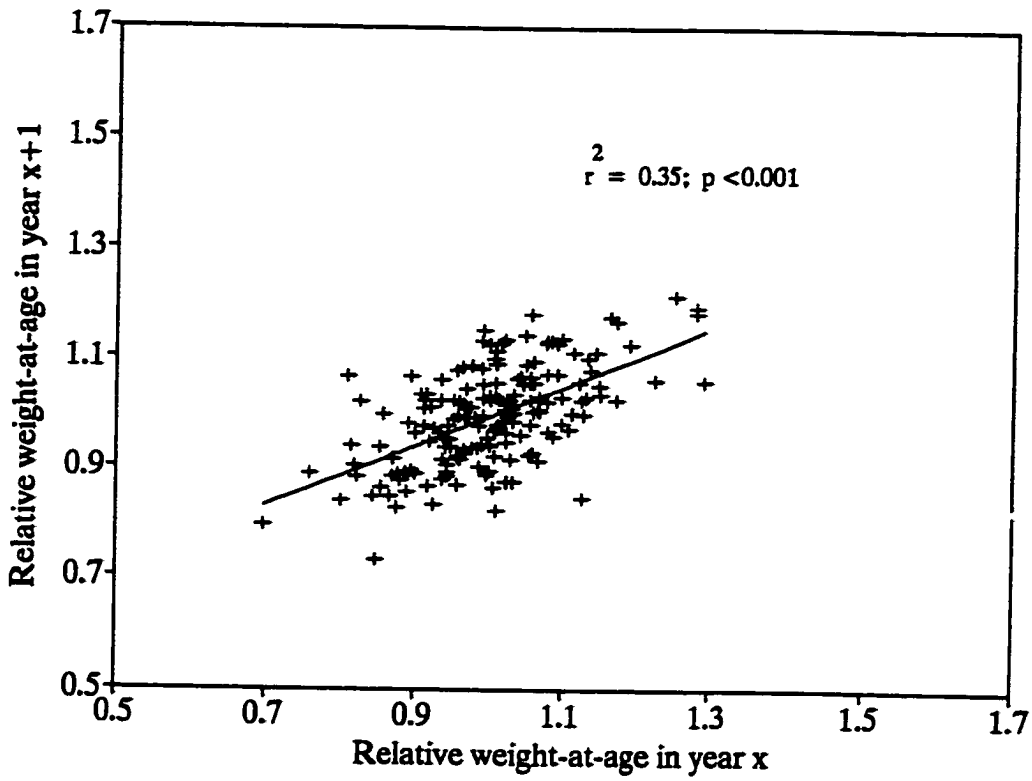


Fig. 2.5. Effect of weight–at–age of 2J3K cod on weight–at–age in the following year, detrended for annual environmental effects.

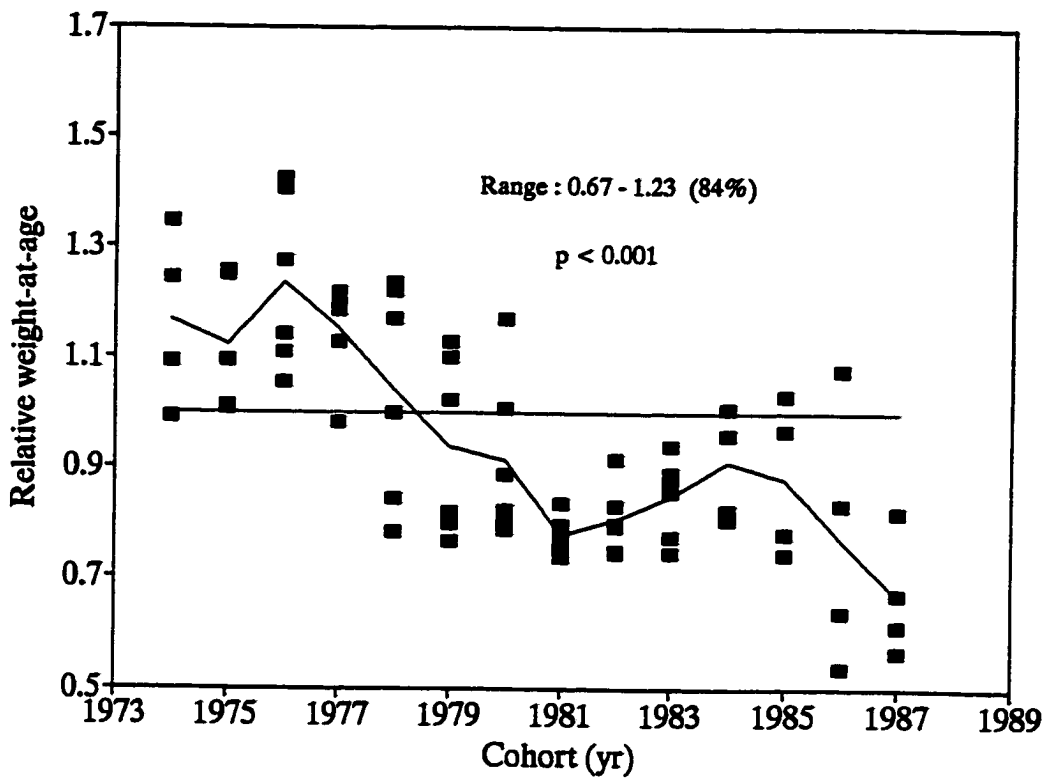


Fig. 2.6. Relative weight–at–age of cohorts (3–8 year–old cod in division 2J).

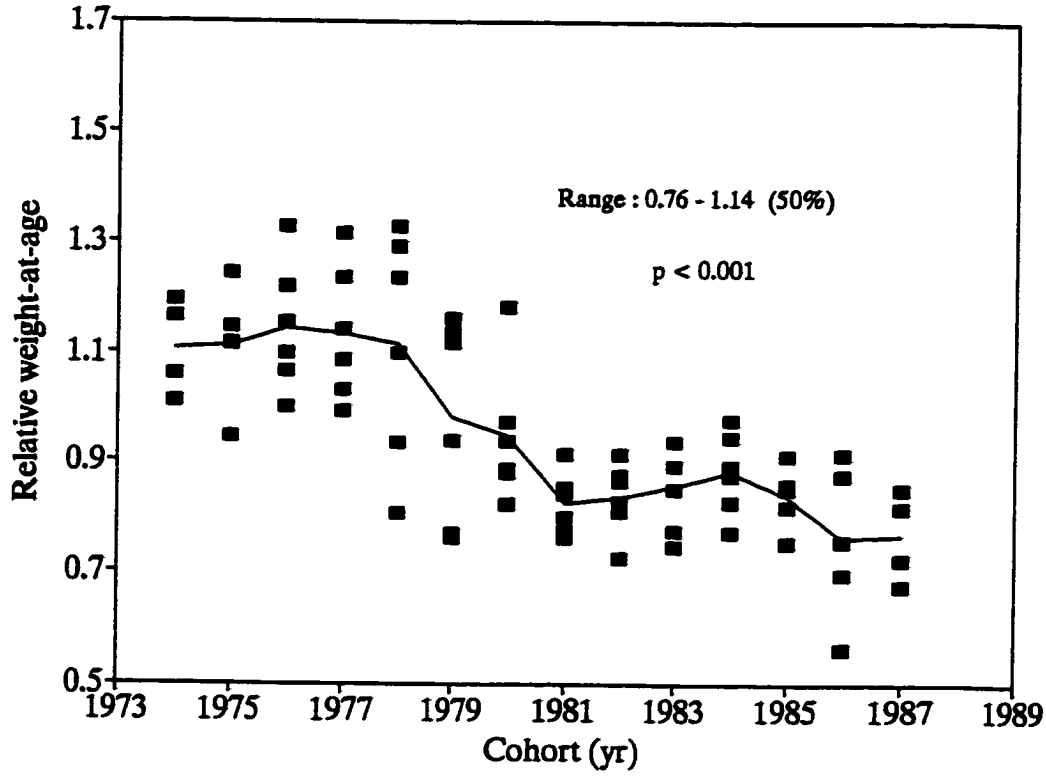


Fig. 2.7. Relative weight–at–age of cohorts (3–8 year–old cod in division K).

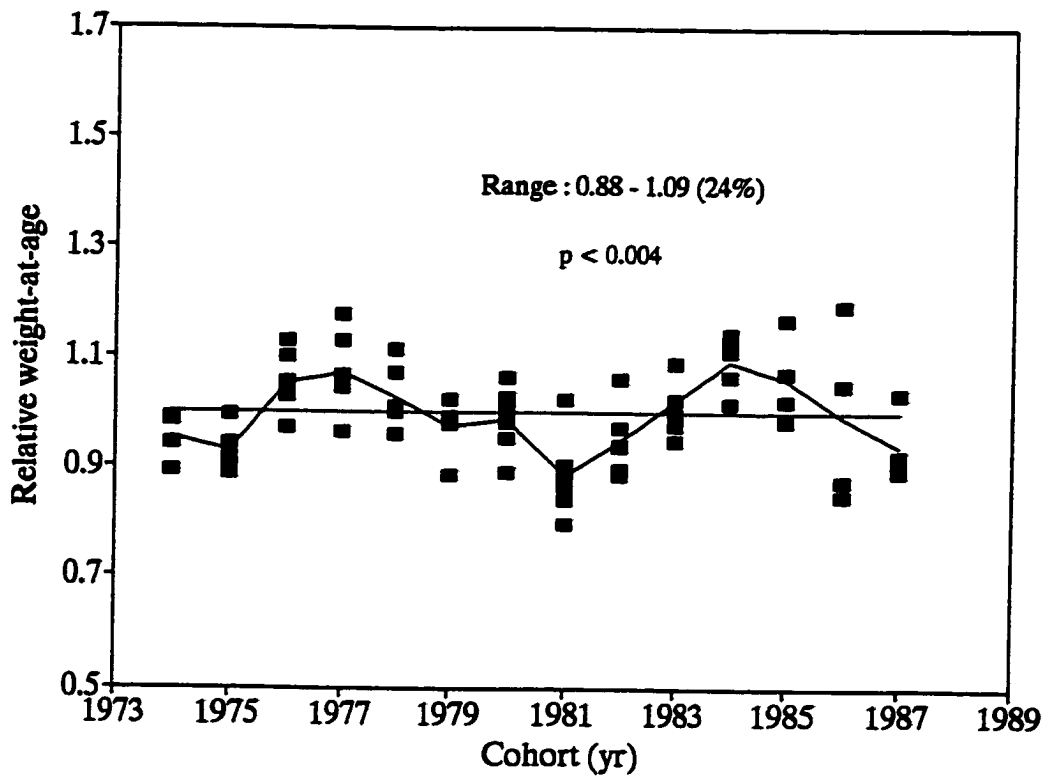


Fig. 2.8. Relative weight–at–age of cohorts, detrended for annual environmental effects. (3–8 year–old cod in division 2J).

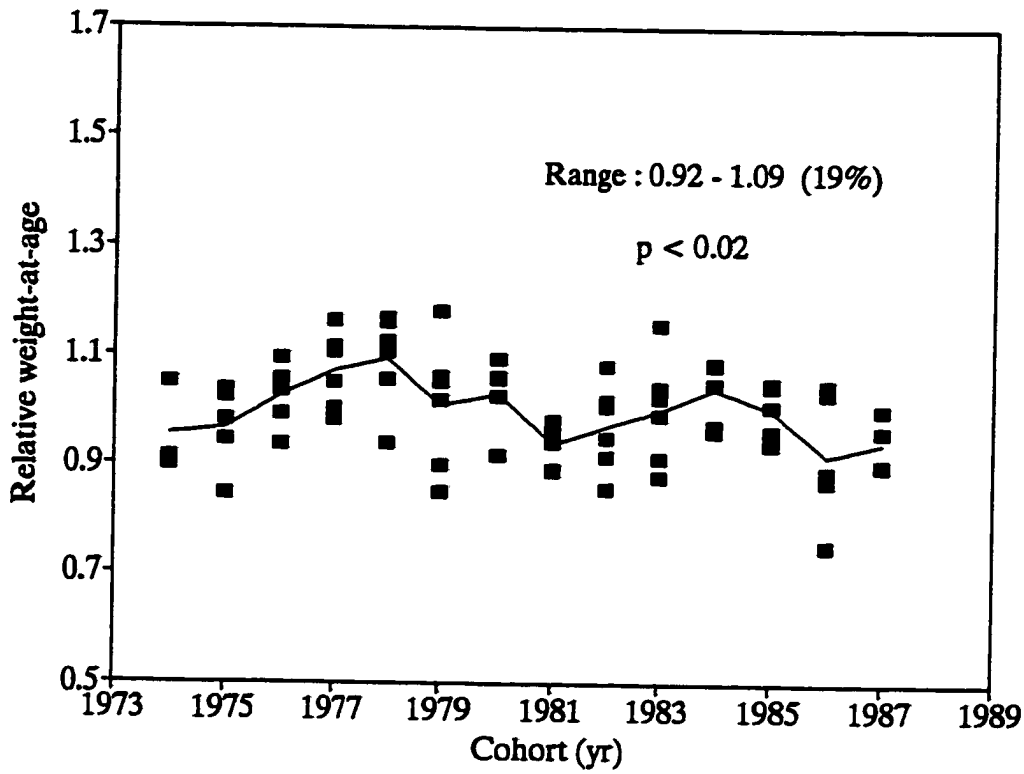


Fig. 2.9. Relative weight–at–age of cohorts, detrended for annual environmental effects. (3–8 year–old cod in division K).

Discussion

These analyses point to the importance of the decline in size–specific growth rate of young fish, 5 years old or less. They have experienced the greatest decline in growth rate, and this small size has propagated through the older age classes. The 6– to 8–year–olds did not experience a significant decline in size–specific growth, but were smaller because they were smaller at an earlier age.

To establish whether an increase in size–selective fishing mortality at young ages could be responsible for small sizes in older age classes, it is important to determine whether cohorts that are small early in life remain small through their lives. Differences in weight–at–age among cohorts may, however, not reflect cohort differences *per se*; for example, cohorts in recent years may be much smaller than cohorts 15 years ago, not because of anything inherent in the cohort, but because of a concomitant change in the environment over the same period. It was, therefore, necessary to detrend the weights–at–age to remove environmental effects that could be confounded with cohort effects. One can partition the influences on growth into two categories; one category that includes environmental influences, which vary annually (such as food supply or temperature) and a second that includes cohort effects, most importantly the size of the fish at the beginning of the year. To remove annual environmental effects that act on all age classes at once, weight–at–age was deternded, or corrected weight–at–age for year. The correction for annual environmental effects corrects only for those annual effects that act across the age–classes.

Weight–at–age in a given year had a strong effect on weight–at–age of the same cohort in the very next year, both before and after weight–at–age was detrended, suggesting that small–bodied cohorts in one year are still small the next year. This implies that the most important determinant of weight–at–age is weight–at–age in the previous year. By tracking the relative weight–at–age of cohorts through their lives, one can see that this effect of weight–at–age in one year on weight–at–age in the next year does translate into significant differences in relative weight–at–age among whole cohorts, both before and after detrending the data for annual environmental effects. Detrending the weight–at–age gives a conservative estimate of the effect of weight in a given year on weight in following years. It is not possible to separate the effects of environment and cohorts and, in detrending data to remove the effects of annual environmental conditions, most the range in the weights–at–age and possibly much of the cohort weight effect was removed.

Given the importance of weight–at–age on future growth, what proportion of the observed decline in weight–at–age in older ages can be attributed to a decline in weight at age 3, 4 and 5, the ages which experienced the decline in size–specific growth? The simulations suggest that, on average, 68% of the observed declines in weight–at–age can be attributed to reduced weight at age 3, 4, and 5. A mean of 100% across the age classes would have suggested that all of the reduction in weight–at–age of older age classes could have been explained entirely by reduced weight at age 5 or earlier, and that after age 5, cod have not experienced reduced growth rates but are smaller only because of smaller initial sizes. The mean of 68% suggests that

lower weight at age 5 and earlier is not entirely responsible for the decline in weight–at–age in later age classes. The size–specific growth rates themselves may have also declined somewhat, but it does suggest that most of the decline in weight–at–age may be a direct result of smaller sizes at or before age 3 to 5.

Significant decreases in size–specific growth rate are limited to 3– to 5–year–old cod, but these decreases in size–specific growth rate carry through the cohorts leading to decreases in size through all age classes. These results suggest first, that, in the early years, growth of cod and other species may be more sensitive to environmental influences, and therefore point to the potential utility of examining the age classes separately to identify important environmental influences. Second, these results highlight the possibility that size–selective fishing mortality may play an important role in weight–at–age. The decline in weight–at–age of age classes that are not fully recruited to the fishery may not be due to reduced growth rate, but may be due to the selective removal of the largest fish of a given age by the fishery (Hutchings 1996; Shelton 1996). Hanson and Chouinard (1992) found that the Atlantic cod fishery in the Gulf of St. Lawrence selectively removed the largest or fastest growing 3– and 4–year–olds during the earlier period they studied, 1971–1976. During the later period, 1984–1989, after increases in mesh size and in boat power, the fishery consistently removed the largest 3– to 8–year olds. It therefore seems likely that there could also have been size–selection against large 3– to 5–year–old northern cod. The mean length–at–age of 8 year–olds in the Southern Gulf of St Lawrence during that period was 48 cm (Hanson and Chouinard 1992), which is

comparable to the mean length–at–age of the 5–year–olds (51 cm; Bishop et al. 1995) in divisions 2J and 3K over the studied period, 1979–1993.

To cause a decline in weight–at–age 3 to 5 through time, fishing mortality on 3–5–year–olds would have had to be strong enough to result in the observed effect , and would have had to increase over this period. Fishing mortality on 7– to 9–year–old cod did increase steadily over this period (Baird et al. 1992) but it is not clear whether fishing mortality also increased on the younger age classes. According to the fishing mortality estimated from Virtual Population Analysis, fishing mortality on age 3 fish did not increase between 1978 and 1991 (see Table 45 in Baird et al 1992). However, according to survey–based estimates of mortality, juvenile (age 3) mortality did increase with adult mortality in northern cod during this same period (Myers et al. 1997). Even if juvenile mortality did increase, it remains to be determined whether size–selection and fishing mortality was high enough to explain the observed decreases in weight–at–age.

If size–selective fishing were a key factor in the decline in weight at age 3 to 5, the simulations would have underestimated the potential effect of size–selective fishing on weight–at–age for two reasons. First, if smaller fish have inherently lower size–specific growth rates, removing the largest fish would involve removing the fastest growers. Second, size–selective fishing does not only act on the 3– to 5–year–olds; Hanson and Chouinard (1992) found that size–selection continued on the older age classes. Therefore, observed weight–at–age of older age classes may be lower than was simulated from weight at age three to age five partly due to lower size–specific

growth rates of the remaining fish, and partly to continued size-selection on the older age classes. To establish whether size-selective fishing mortality was strong enough to have resulted in the observed decreases in weight-at-age, one would need to simulate the effect of size-selection given the selectivity of the types of fishing gear used, the fishing mortality, and the change in size frequency of the population.

In the longer term, size-selective fishing could cause a reduction in the inherent growth rate of the upcoming generations. To confirm that size-selective fishing has an effect on gene frequencies associated with growth rate, both the selection differential (the change in weight-at-age distribution) and the heritability of growth rate would have to be quantified. There is certainly a heritable component to fish growth rate (Basic and Gall 1983; Gjedrem 1983; Hoerstgen-Schwark 1993; Tave 1994). Heritabilities of fish growth rates have only been quantified in captive fish, however, and are therefore likely to be overestimated. Heritabilities in the wild have been found to be lower than in controlled environments because of reduced environmental heterogeneity compared to the field (Simons and Roff 1994). The estimation of heritability of growth rates in the wild, and therefore the evolutionary effect of size-selective fishing on growth rate, would require large-scale fishing experiments such as the one proposed by McAllister et al. (1992).

In summary, at least 68% percent of the decline in weight-at-age of northern cod can be attributed to a decline in weight at age 5 or earlier. This finding highlights both the importance of studying what is affecting growth processes at these young ages and the possibility that size-selective fishing may have played an important role

in the decline in weight-at-age.

Chapter 3

Is cold water a problem for Atlantic cod? Effects of low temperature on Atlantic cod feeding, growth, swimming performance and survival.

Introduction

Atlantic cod (*Gadus morhua*) is a cold water species, residing in waters with annual mean temperatures between 1 (northern Grand Bank; Colbourne et al.1994) and 11°C (Celtic Sea; Brander 1995). Productivity of cod stocks is thought to be adversely affected by cold years, particularly in the stocks at the colder end of the range (Brander 1994, 1995; Taggart et al. 1994; Mann and Drinkwater 1994; Sætersdal and Loeng 1987; Garrod and Schumacher 1994; Loeng 1989; deYoung and Rose 1993; Nilssen et al. 1994; Ellertsen et al. 1989; Malmberg and Blindheim 1994; Lear and Parsons 1993). Cold temperatures affect all species, and much research has been carried out within the broader context of cold water effects on fish. I focus on Atlantic cod because of the attention directed at explaining Atlantic cod stock fluctuations in recent years and because of the relatively large amount of laboratory research available on Atlantic cod. The effects of cold water on Atlantic cod ecology and physiology have received much attention in an effort to understand how anomalously cold years may adversely affect production of cod stocks. People have addressed the question both by studying temperature effects on individuals, in particular by examining effects of low temperature on cod metabolism, feeding, growth, swimming performance, and mortality, and by studying temperature effects on populations, in particular by analyzing the effect of cold temperatures on stock–recruitment relationships and on population growth rates. These studies are scattered through the fisheries literature, making it difficult to establish links between them. My purpose is to review the evidence for cold water effects on Atlantic cod at these

different levels in order to establish how much we know about physiological effects on individuals and to determine whether these physiological effects are strong enough to be detected in ecological studies at the level of populations. This synthesis is intended to determine how much we know about the links between cold water and cod productivity and to highlight the gaps in our knowledge.

Because temperature affects the rates of all biochemical reactions, it affects the rates of both energy-producing pathways (ATP supply) and energy-consuming pathways (ATP demand). Therefore, in ectotherms, the rates of movement, digestion, and tissue synthesis depend on the temperature of the surrounding water. And because temperature affects the strength of covalent bonds, it also affects the structural stability of molecules and cellular membrane function. Temperature extremes can therefore lead to the breakdown of membrane transport, and can kill the fish. Subzero temperatures can also kill a fish by freezing tissues or by disrupting membranes with ice crystals.

I will address three principal routes by which low temperatures might directly affect an individual fish. First, low temperature affects swimming performance either by limiting the energy available for swimming, or by limiting the power generated by muscle. Reduced maximum speeds might lead to reduced success in prey capture or predator avoidance, particularly if the prey or predators are better adapted to swimming at cold temperatures. Evidence will be reviewed for a decrease in Atlantic cod swimming performance at low temperatures.

Second, low temperatures can limit growth in the wild by limiting the rate at which food can be digested and absorbed. Does the maximum rate of processing food

limit consumption and growth in the wild? Or, conversely, are consumption rates and growth rates limited by the availability of food? This question will be addressed by reviewing temperature and growth relationships both within and among Atlantic cod stocks.

Third, how likely are Atlantic cod to die directly from the cold? It has been suggested that natural mortality of Atlantic cod may increase in very cold years for both prerecruit (Valerio et al. 1992; NAFO 1992) and adult cod (Woodhead and Woodhead 1964; NAFO 1992; Lear and Parsons 1993). I will examine whether mortality from cold water could possibly be an important contributor to stock fluctuations.

The most important environmental effects on fish stocks may be at the prerecruit stage, when mortality is extremely high (Serchuk 1994). Cold temperatures can directly reduce the survival of young fish by freezing them or by otherwise interfering with physiological function. Or, cold temperatures can indirectly reduce the survival of young fish by causing a decrease in their food supply, possibly through changes in plankton production or changes in the time and location of hatching relative to peaks in plankton production, or by increased advection of larvae out of their optimal habitat. I will review evidence that cold years are associated with low recruitment of Atlantic cod.

Metabolic rate

Because temperature determines the state of activation of molecules in the

metabolic network of reactions, it operates as a controlling factor (Fry 1947). From thermodynamic considerations, a roughly 2– to 3– fold increase in reaction rates is expected over a 10°C increase in temperature (Hazel 1993; Randall et al. 1997). A cold–acclimated fish has acquired the ability to function at a faster rate at low temperatures, and so demonstrates much less of a change in metabolism, and other rate processes, for a given decrease in temperature than one would expect based purely on thermodynamic considerations. How much, then, does low water temperature affect metabolism of Atlantic cod?

For fish, and all ectotherms, the ambient temperature sets upper and lower bounds to metabolic performance. A given temperature demands a minimum metabolic rate for maintenance of the tissues (standard metabolism) and permits a maximum rate, conditions permitting (active metabolism) (Fry 1971). The difference between the minimum and maximum metabolism defines the metabolic scope for activity, the amount of energy the fish has available at any one time for swimming, digesting, building tissues and other activities. The scope is lowest at the coldest and warmest temperatures within the temperature range the fish can tolerate (the "thermal zone of tolerance"; Fry 1947), and is highest at some midpoint. If, at the cold end of the temperatures cod experience, metabolic scope is greatly reduced, we might expect to see lower maximum swimming speeds, lower maximum consumption rates, and lower growth rates.

To examine the relationship between metabolic scope and temperature all available data were assembled for standard and active metabolic rates of acclimated

Atlantic cod from the literature (Table 3.1). First, relationships were fitted between metabolic rate and temperature across studies (Fig 3.1), and second, temperature sensitivities of metabolic rate were calculated within studies for which metabolism was measured at more than one acclimation temperature (Table 3.1). Only those studies for which at least 5 animals were used at a given temperature are included in Fig. 3.1. As a result, two studies (Soofiani and Hawkins 1982; Soofiani and Priede 1985) were omitted from Fig. 3.1. in which 2–3 individuals were used per temperature. Their values for standard metabolism were very similar to those in the studies with higher sample sizes. However, trends in active metabolic rate, metabolic scope, swimming performance and temperature sensitivity were inconsistent with other studies.

Fish, and cod in particular, can exhibit among–population differences in metabolic rate (Nelson et al. 1994). Therefore, for the fitted relationships between temperature and metabolism (Fig. 3.1), only those studies using Atlantic cod from the Scotian shelf were included. As well, the same experimental facilities were used in six of the eight studies of Scotian shelf cod.

Both standard and active metabolism of Scotian shelf cod are well correlated with temperature (r^2=0.95, $p<0.001$ and r^2=0.98, $p<0.001$ respectively). They both increase with temperature, with scope (active – standard metabolism) appearing to be somewhat lower at low temperatures (Fig. 3.1). This trend is more clearly seen within studies, where scope is consistently lowest at the lowest temperature (Table 3.1).

The sensitivity of a physiological process or rate to temperature change can be quantified using Q_{10}, an index that represents the change in the rate over a 10°C

Table 3.1. Standard and active metabolism of Atlantic cod (corrected to 1 kg) from the Scotian shelf and from several stocks in the Northeast Atlantic. The numbers in brackets are the Q_{10} values relative to the lowest temperature in the experiment.

Temperature (°C)	Standard metabolism ($umolO_2 \cdot kg^{-1} \cdot hr^{-1}$)	Active metabolism ($umolO_2 \cdot kg^{-1} \cdot hr^{-1}$)	Metabolic scope ($umolO_2 \cdot kg^{-1} \cdot hr^{-1}$)	Stock	Reference
2	18	57	39	Scotian shelf	Nelson et al. 1994
15	50 (2.2)	108 (1.6)	58 (1.4)	Scotian shelf	Tang unpubl.
5		74		Scotian shelf	Tang et al. 1994
5		76		Scotian shelf	Reidy et al. 1995
5	22	80	58	Scotian shelf	Krohn unpubl.
5	22	72	51	Scotian shelf	Webber et al.
10	35 (2.5)	97 (1.8)	62 (1.5)		1998
5	22			Scotian shelf	Saunders 1963
10	34 (2.4)				
15	42 (1.9)				
12	38			North Sea	Edwards 1972
5	19	72	53	Kattegat	Schurmann &
10	27 (2.0)	99 (1.9)	72 (1.8)		Steffensen 1997
15	31 (1.6)	104 (1.5)	73 (1.4)		
7	28*	77	49	West Scotland	Soofiani &
10	39* (1.6)	91 (1.2)	52 (1.1)		Hawkins 1982
15	45* (1.8)	144 (2.2)	99 (2.4)		
18	45* (1.6)	137 (1.7)	92 (1.8)		
10	38	70	32	West Scotland	Soofiani & Priede
15	48 (1.6)	118 (2.8)	70 (4.8)		1985
4	24	58	34	West Greenland	Bushnell et al. 1994

*As reported in Soofiani and Priede 1985

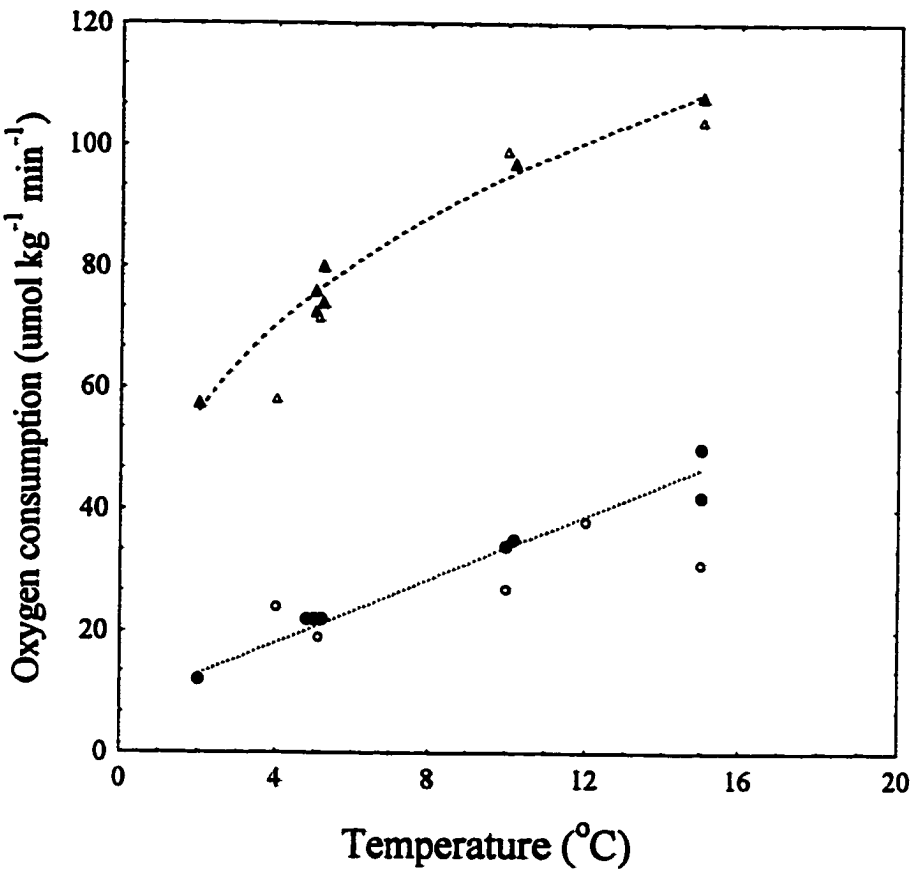


Fig. 3.1. Standard and active metabolic rates of Atlantic cod as a function of temperature. Standard (dotted line) and active (dashed line) metabolic rates are fitted to Scotian shelf cod only. (Standard metabolic rate = 2.60 temp + 7.72, $r^2 = 0.95$; active metabolic rate = 44.81 $temp^{326}$, $r^2 = 0.98$). Circles represent standard metabolic rate, triangles represent active metabolic rate, filled symbols represent data for Scotian shelf cod and open symbols represent data for Northeast Atlantic cod.

change in temperature. Q_{10} is calculated using the following formula:

(1) $$Q_{10} = (k_2/k_1)^{10/(t2-t1)};$$

where k_1 and k_2 are rate constants at temperatures t1 and t2, respectively (Randall et al. 1997). The expected 2 to 3 –fold increase in reaction rates over a 10°C increase in temperature then corresponds to a Q_{10} of 2 to 3. Again, focusing on the studies with a minimum of 5 animals, scope decreases with declining temperatures to a similar but lesser extent than does active metabolism (Q_{10}=1.3 to 1.8 and Q_{10} =1.5 to 1.9 respectively), because standard metabolism decreases with declining temperature as well (Q_{10} = 1.6 to 3) (Table 3.1). Cod standard and active metabolic rate decline with declining temperature to a very similar extent as they do other species (Q_{10} 1.6–2.0; Fry and Hochachka 1970). A drop in temperature of 1°C, then, may reduce the energy a cod would have available for swimming and processing food by 4 to 8%.

Unfortunately, because of the difficulties in maintaining very cold temperatures, very little is known about Atlantic cod metabolism below 2°C. Cod metabolism may well be more sensitive to temperature changes at the low end of their thermal range. Some of the coldest stocks, for example northern cod on the northern Grand Bank, spend much of the year below 2°C. In fact it is not uncommon to find northern cod at temperatures as low as –1.4 °C (Thompson 1943, Wroblewski et al. 1994, Lilly 1994). As temperatures drop further from habitat temperatures, thermal sensitivity increases (Guderley and Blier 1988). Arctic cod (*Boreogadus saida*), even though they live at subzero temperatures most of the year show a high sensitivity to changes in temperature (Q_{10} = 6.7 to 7.1) between –0.5 and 2.7°C (Hop and Graham 1995).

Swimming performance

Swimming performance at any given temperature may be limited either by ATP production (energy supply to the tissues), or by the amount of ATP that can be used by the muscles to power swimming. Both the ATP supply and the potential power output of muscle fibers are lower in cold water (Guderley and Blier 1988). Aerobic ATP supply is lower in cold water in large part because maximum rate of oxygen transport from the gills to the muscle fibres declines with temperature. The associated reduction in maximal oxygen consumption with temperature is reflected in the decline in metabolic rate discussed above. The power output of muscle fibers is determined by both the force generated by each contraction and the speed at which the muscle contracts, and both decline with temperature (Wardle 1980; Rome et al. 1984; Rome and Sosnicki 1990). The extent to which these declines in both ATP supply and muscle power output result in reduced swimming performance will be discussed below.

Maximum sustainable speeds

Maximal sustainable swimming speed, a measure of aerobic swimming performance, is limited both by oxygen delivery to the swimming muscles and by reduced power output of the red, or aerobic muscle (Guderley and Blier 1988). Red muscle fibers are recruited first, followed by white (anaerobic) fibers. Because fish in cold water generate less force in individual red fibers than do fish in warmer water, they must recruit more red fibers for a given speed (Rome et al. 1984; Rome et al.

1990). The maximum sustainable swimming speed is the speed at which all red fibers have been recruited. To reach higher speeds, or burst speeds, white fibers must be recruited. The speed at which all red fibers have been recruited to provide propulsion is therefore lower in cold water, reducing maximum sustainable speeds (Rome et al. 1984).

During a process of acclimation, fish can increase their maximum sustainable speeds in cold water by increasing the power generated by the individual muscle fibers (that is by undergoing biochemical modifications that increase the force generated by individual fibers or the maximum rate of muscle contraction) or by increasing the number of fibers. Cyprinids do both (Johnston et al. 1990); however, non-cyprinids appear to show little or no compensation after acclimation for force produced by individual fibers or for maximum rate of contraction. Both cyprinid and non-cyprinid species have been shown to increase the muscle power output at low temperatures by increasing the number of red fibers during cold-acclimation (e.g. goldfish, Johnston and Lucking 1978 and Sidell 1980; striped bass, Jones and Sidell 1982). This increased number of red fibers after cold-acclimation raises the swimming speed at which the white fibers need to be recruited in cold water, and therefore raises the maximum sustainable speeds.

Although increased number of red fibers increases maximal power output of red muscle in cold-acclimated fish relative to fish acutely exposed to cold temperatures, maximal power output in cold acclimated fish is not as high as in fish in warmer water. That is, fish, and seemingly all other ectotherms, do not show perfect

temperature compensation for power generation (Bennett 1990). Therefore, although cold acclimation raises maximum sustainable speeds in cold water, compensation is not complete. Even after acclimation, maximum sustainable speeds decline with temperature (e.g. goldfish (Fry 1971), coho salmon (Griffiths and Alderdice 1972), striped bass (Sisson and Sidell 1987), carp (Johnston 1993); northern squawfish (Kolok and Farrell 1994), rainbow trout (Keen and Farrell 1994) and sea lamprey (Holmes and Linn 1994) and see Beamish (1978), Guderley and Blier (1988), and Bennett (1990) for reviews).

Cold–acclimated fish can also exhibit higher aerobic capacity of the swimming muscle (Johnston and Dunn 1987; Guderley 1990), enabling them to meet the extra energy demand associated with the increased ability for power generation they acquire during acclimation. However, as was shown earlier (Table 3.1 and Figure 3.1), even after cold acclimation, active metabolic rate and metabolic scope in Atlantic cod and other fishes is not as high as in warmer water.

With a decrease in metabolic scope with declining temperature in Atlantic cod, as well as a decrease in power generation and maximum sustainable speeds found in other species, one might expect a decline in maximum sustainable speeds of Atlantic cod with a decline in temperature. According to the available studies for Atlantic cod, maximum sustainable speeds of acclimated cod decline to a similar extent as other species studied; the Q_{10} for critical swimming speed (a measure of maximum sustainable speed) ranges from 1.1 to 1.7 (Table 2). This translates into a 1 to 7% change in speed per degree.

Table 3.2. Critical swimming speeds of Atlantic cod. Corrected critical swimming speeds are corrected for length to a standard length of 50 $cm \cdot s^{-1}$. Q_{10} values (relative to the lowest temperature in the experiment) are presented in brackets.

Temperature (°C)	Length (cm)	Critical swimming speed ($bl \cdot s^{-1}$)	Corrected critical swimming speed ($bl \cdot s^{-1}$)	Stock	References
2	48.8	1.04	1.02	Scotian shelf	Nelson et al. 1994
15	46.7	1.20	1.15 (1.1)	Scotian shelf	Tang unpublished
5	49.5	.99	.98	Scotian shelf	Reidy et al. 1994
2	30	1.40	.98		Bishop,Webber,
5	30	1.67	1.13 (1.6)	Northern cod	Reidy and Krohn
10	30	1.66	1.20 (1.3)	(Newfoundland)	unpublished
10	27.5	1.95	1.34	West Scotland	Soofiani and
15	27.5	1.44	0.99 (.55)		Priede (1985)
5	31	1.60	1.18	West Scotland	Schurmann and
10	32	1.70	1.28 (1.2)		Steffensen (1997)
15	33	1.90	1.46 (1.2)		
5	36	2.29	1.86	Scotian shelf	Beamish (1966)
8	36	2.71	2.23 (1.8)		
.8	44	1.2	1.1	Northern cod	He (1991)

The use of Q_{10}'s as an index of temperature sensitivity is usually limited to rate processes, and is most commonly used for biochemical rates of reaction (such as rates of enzyme activity or metabolic rate) and for muscle contraction speeds and muscle power output. Less commonly, Q_{10} is used an index of temperature sensitivity of swimming speed (Webb 1978; Fuiman 1986; Videler and Wardle 1991; Keen and Farrell 1994; Gibson and Johnston 1995). I have also chosen to use Q_{10} for this purpose, but it should be pointed out that one can not compare Q_{10}'s of two different processes if they are not linearly related to one an other because the index is sensitive to dimension. Because swimming speed is not linearly related to oxygen consumption, one would not expect equivalent Q_{10} 's for swimming speeds and metabolic rate for a given level of temperature sensitivity. Similarly, because power output of muscle and swimming speed are not linearly related, one would not expect equivalent Q_{10}'s for muscle power output and swimming speed (see Webb 1978), even if they exhibited equivalent sensitivites to temperature. The expected Q_{10} of 2 to 3 would therefore not apply across all physiological processes (metabolism, locomotion, growth) as has been suggested (Randall et al. 1997); in fact Q_{10} for growth using change in weight through time would be a cubic function of Q_{10} for growth using change in length through time. When comparing Q_{10}'s for two different sources the temperature range must also be considered, because the Q_{10} of a given physiological processes depends on the temperature range being considered (Randall et al. 1997).

Although one cannot compare Q_{10}'s for swimming speed to Q_{10}'s for metabolic rate, the available studies suggest that maximum sustainable speeds are only

moderately compromised cold water over the temperature range for which they have been studied. However, the ecological implications of a 7% decline in speed with each 1°C drop in temperature are unknown, and may be considerable. The moderate reduction in maximum sustainable speeds with declining temperature in Atlantic cod, as in other fishes, is due to a combination of lower metabolic scope, reduced muscle contraction speeds and to reduced force generation of the muscle fibers. Again, it is likely that thermal sensitivity of Atlantic cod swimming performance increases as they get further from their preferred temperatures, temperatures at which swimming performance has not yet been examined. He (1991) measured Atlantic cod swimming performance at less than 1°C, and found that they could sustain over 1 bodylength·s^{-1}. However, because the cod were not swum over a range of temperatures, the level of temperature sensitivity at this low temperature can not be established, and comparisons of swimming performance among studies can be misleading.

Burst swimming

Anaerobic or burst swimming in fish is also reduced in cold water, because reduced contraction speeds and force production of the white muscle fibers result in a decline in power output of the white muscle (Lannergren 1978; Bennett 1984). Q_{10}s for the twitch contraction time of isolated white muscle falls between 1.8 and 2 (Wardle 1980; Videler and Wardle 1991; Inoue et al. 1993) or when measured from recorded speeds during burst swimming (Webb 1978; Batty et al. 1991; Weatherhead and Robertson 1992; Batty et al. 1993; Gibson and Johnson 1995). Wardle (1980)

examined the effect of temperature (2 – 15°C) on burst speeds of Atlantic cod, as estimated using muscle contraction times and stride length, and found a Q_{10} of 2, comparable to the other species cited above (contraction time and swimming speed are linearly related). Unfortunately, burst swimming of Atlantic cod has not yet been measured at temperatures below 2°C.

Q_{10}s for burst swimming (1.8–2) appear to be somewhat higher than for maximum sustained speeds, or aerobic swimming speeds, which tend to be somewhat less than 1.3 in Atlantic cod as well as in the other species studied, suggesting that burst swimming may be more sensitive to declines in temperature than is sustained swimming. A direct comparison is not possible, however, because acclimation times and temperature ranges differ among studies.

Both sustained (Griffiths and Alderdice 1972) and burst swimming (Webb 1978, Wardle 1980, Weatherhead and Robertson 1992 and Inoue et al. 1993) show increased sensitivity to temperature at the low end of the range of thermal tolerance, highlighting the need to study cod swimming performance at zero and subzero temperatures.

Feeding and Growth

Consumption and growth in the laboratory

Digestion in fish, like swimming performance, also slows in cold water (Jobling 1993). Temperature drives both the rate at which ATP is made available for digestion, and the rates at which ATP is used to break down food, to absorb nutrients

into the bloodstream and to incorporate the nutrients into the tissues. As with swimming performance, temperature may limit the rate of digestion by reducing aerobic energy supply, as well as by directly limiting the rates of the biochemical reactions using ATP, or ATP demand. Limits to oxygen transport from the gills to the tissues limit the aerobic ATP supply, and this transport may be limited either by oxygen uptake by the gills from the water, by the capacity of the cardiovascular system to transport oxygen to the tissues, or by oxygen uptake at the tissues themselves. The assumption of a fixed metabolic scope for both physical activity and digestion is that both of these processes are limited by oxygen uptake at the gills or by the cardiovascular system or both, but not by oxygen supply and uptake at the tissue level. This assumption does not hold for the Burmese python where maximum metabolic rate is 7–fold higher during digestion than during peak physical activity (Secor and Diamond 1997), and does not appear to hold for Atlantic cod either. Maximum oxygen consumption has been found to be higher for Atlantic cod that are digesting while swimming than for unfed cod during peak physical activity (Blaikie and Kerr 1996; Krohn et al. unpublished results). Reidy et al. (1994) also found that the maximum oxygen consumption of Atlantic cod during peak physical activity depended on the swimming protocol. These activity–dependent or variable maximum metabolic rates suggest that limits to oxygen demand or supply at the tissues may be limiting the maximum rates at which ectotherms can digest and move around, particularly at cold temperatures when the oxygen concentration of water is highest. They also suggest that upper limits to metabolic rate and full metabolic scope can not

necessarily be determined by exercising unfed animals.

Regardless of the exact limitations to digestion in cold water, it is clear that digestion is slower in cold water in fish in general, as well as in Atlantic cod in particular. Evacuation rate (of food in the gut) in Atlantic cod at 2°C was found to be one third the rate of that at 10°C (or a 5% drop in rate per°C at the low end of the temperature range, Tyler 1970), and was found to show similar temperature sensitivity between 5 and 15°C (Jobling 1982). In two laboratory studies in which Atlantic cod were fed to satiation, consumption rates were reduced in cold water; on average cod were 70% as likely to eat a meal on a given day at 1 than at 4°C (or a 12% drop per°C at the low end of the temperature range; Waiwood et al. 1991) and juvenile cod ate 63% as much at 0.6 as at 4.5°C (also a 12 % drop per°C at the low end of the temperature range Brown et al. 1989). Similarly, Jobling's (1988) empirical model of food intake predicts that cod will eat 68% as much at 3 as at 7°C, with a drop of 10% per°C at the low end of the temperature range.

Because growth rate depends on consumption rate, one might expect growth rate to show a similar level of sensitivity to temperature. The sensitivity of growth to temperature, however, is more variable, because growth is a small fraction of the total energy budget and depends on how much energy is left over once energy has been allocated to all other functions. When fish are fed at maximum consumption rates, their growth increases with temperature up to an optimal temperature. However, the level of sensitivity of growth to temperature will depend on how consumption and metabolic rate scale with temperature. Jobling (1988), combining a number of

laboratory studies, found that growth rate of Atlantic cod fed to satiation was 6–fold higher at 11 than at 3°C , or decreased by 20 to 25% per°C at the low end of the temperature range.

Although the growth rate of satiated fish is lower in cold water, the opposite is true for fish that are feeding at a submaximal level. Given equal rations, a fish in colder water will grow faster than a fish in warmer water, because metabolic costs increase with temperature (Hawkins et al. 1985; Brandt 1993). Unless cod are fed to satiation, or at least are able to feed more in warmer water, one would not expect a positive relationship between temperature and growth.

Consumption and growth in nature

Temperature, then, can physiologically limit consumption rates of cod fed to satiation, but temperature may not limit consumption rates in nature. At the temperatures available to them, are cod eating as much as they can, or is their feeding (and therefore growth) limited by the amount of prey available to them?

Studies of both stomach fullness and growth rates of cod stocks across the North Atlantic, as well as relationships between growth and food availability, suggest that, at least for the most part, cod stocks are not feeding at or even close to maximum levels at the temperatures available to them. That is, their growth appears to be limited by food supply, not by temperature. According to relationships between weight–at–age and capelin biomass, growth rates of Icelandic cod appear to be food limited (Steinarsson and Stefansson 1991 and 1996; Malmberg and Blindheim 1994; de

Cardenas 1994). Northeast Arctic cod growth is also related to capelin biomass (Jørgensen 1992), and the stomach contents and growth rates of the Balsfjord population of northeast Arctic cod also suggest that growth rates are limited by food availability and not temperature (Jobling 1982). Cod off the West coast of Scotland, in Loch Torridon, grow at submaximal rates, suggesting food is limiting (Hawkins et al. 1985).

Similar results have been found in the northwest Atlantic. Northern Cod on the northeast Newfoundland and Labrador shelves grow below their potential growth rates, given the temperatures available to them (Chapter). Stomach fullness indices in this same area were found to be higher in colder water (−1.5 to 0°C) than in warmer water (2 to 3.5°C) (Lilly 1994). At least in the warmer water, then, these cod could be eating more at the temperatures available to them. In this same study, cod in larger catches had emptier stomachs than those in the small catches, also suggesting that feeding was limited by prey availability and not temperature. The condition factors of northern cod on the northeast Newfoundland and Labrador shelves appear to be correlated to capelin biomass (Bishop and Baird 1993; Chapter 1), also suggesting that prey is limiting growth. Although northern cod on the northern Grand Bank grow much closer to their potential growth rates than do northern cod on the northeast Newfoundland and Labrador shelves (Chapter 1), stomach contents suggest that cod on the northern Grand Bank are food limited over much of the year, even in unusually cold years (Lilly, unpublished data). On the western Scotian Shelf, larval cod growth was found to be strongly correlated to zooplankton biomass, and not to temperature

(Suthers and Frank 1989). Kohler (1964) concluded that temperature differences were not great enough to explain interannual differences in growth of cod in the western Gulf of St Lawrence, and that growth must therefore be limited by prey supply. George's Bank cod have much lower stomach fullness indices than do cod in the North Sea, and cod on the Newfoundland and Scotian shelves (Serchuk et al. 1994) suggesting that George's Bank cod could eat more prey if it were available.

According to an ICES (1992) cross-stock comparison of Atlantic cod feeding habits, stomach fullness of Atlantic cod is inversely correlated to temperature across the North Atlantic, presumably because gut evacuation rates are higher in warm water. These results suggest that, at least for the warmer stocks, cod could be eating more than they are at the temperatures available to them, and therefore that stocks in colder water are growing closer to their potential than are stocks in warmer water. This same negative relationship between stomach fullness and temperature was found among years within stocks for Newfoundland and Icelandic cod, but not for cod from the Barents sea.

If cod are not eating at maximal rations, and if cod feeding at submaximal rations grow more quickly in colder water, why would we expect growth rate of wild stocks to increase rather than decrease with water temperature? Positive temperature/growth relationships have been found in Atlantic cod both across stocks (Taylor 1958; Campana 1995; Brander 1994; 1995) and among years within stocks (Loeng 1989; Millar and Myers 1990; de Cardenas 1994; Brander 1995; Shelton and Lilly 1995; Shelton et al. 1999; Chapter 1). Brander's 1994 and 1995 analyses include

17 Atlantic cod stocks and average annual temperatures that range over 10°C. Growth rates from 0 to 4 years old over the 10°C temperature range vary by 13–fold, that is they drop by 22% per 1°C, or as described by Brander, they increase by 29% per 1°C increase in temperature. This strong effect of temperature on growth rate ($r^2 = 95$; $p<0.001$) is surprising given that, according to the studies reviewed above, the growth rates of at least 7 of the 17 stocks do not appear to be physiologically limited by temperature. If Atlantic cod stocks are not directly temperature limited, then the reason for the strong temperature–growth relationships must be an indirect one. Warmer waters must be more productive and supply more food; enough food to more than compensate for the higher metabolic costs of life in warmer water, although not enough to allow cod to fully take advantage of their higher maximum consumption rates.

Consumption rates are either temperature or food limited at any one time. However, for some proportion of the year, cod may be physiologically able to eat more food than is available to them, while at other times they may be eating as much as they can process at the temperatures available to them. It is likely that over the time scale of a year, fish are not eating as much as they possibly can, but that for shorter periods of hours, days or even for a season, they may not be limited by food availability. The same variability is expected on a spatial scale, where cod in one area may be feeding on a school of capelin and have full stomachs , while cod nearby may be feeding at much lower levels. Lilly (1994) found that northern cod located in high density aggregations had, on average, less capelin in their stomachs than cod found at

low densities, and that cod at low densities may be feeding to satiation, whereas cod at higher densities appear to be food limited.

Mortality

Temperature not only affects fish by determining the rates of biochemical reactions, it also has a structural affect. As mentioned earlier cold temperatures can potentially be fatal to fish either by causing structural changes to molecules that lead to a breakdown in physiological processes, for example in cellular membrane transport, or, if temperatures are low enough, they can kill a fish by freezing the blood or tissues. Northern cod are frequently found in waters where there is a potential risk of freezing. However, juvenile and adult cod produce antifreeze in their blood lowering the temperature at which ice crystals form and thereby allowing them to inhabit waters that would otherwise cause them to freeze. In the absence of antifreeze proteins, Atlantic cod blood freezes at -0.7°C (Fletcher et al. 1982). Antifreeze prevents the blood of adult northern cod from freezing down to -1.2°C (Fletcher et al. 1987; Kao and Fletcher 1988); however they are still at a potential risk of freezing because cod are frequently found in colder waters (as low as -1.6°C (Thompson 1943), -1.5°C (Wroblewski et al. 1994), and -1.4°C (Lilly 1994)). Juveniles are freeze resistant down to -1.5°C (Kao and Fletcher 1988; Goddard et al. 1992), and are therefore well protected under most circumstances, although extreme low temperatures (-1.8°C) and ice crystals mixing in shallow water could cause mortalities (Goddard

and Fletcher 1994).

In adult northern cod, antifreeze begins to be produced in detectable quantities at 0°C (Fletcher et al. 1987) compared to 2 or 3°C for juveniles (Goddard et al. 1992). Adults are therefore at a greater risk of freezing than are juveniles if temperatures drop abruptly before they have produced sufficient antifreeze (Goddard and Fletcher 1994). Even in warmer stocks, cod may die from cold shock independent of freezing if they are trapped in cold water to which they are not acclimated, for instance if they are trapped in bays with no warm deep passage to higher temperatures offshore (Templeman 1964, Templeman and Fleming 1964).

There are a few anecdotal accounts of dead cod being found in association with cold water, (reviewed by Templeman 1964, Templeman and Fleming 1964, Woodhead and Woodhead 1964, and Harden Jones and Scholes 1974, and recent accounts are discussed by Lilly et al. 1999). However, the scarcity of such reports (Templeman and Fleming 1964) and the observed resistance of cod to low temperatures suggest it is unlikely that adult or juvenile mortality in cold water is often high enough to be an important factor in cod stock fluctuations. It has been suggested that natural mortality of adult and/or juvenile cod from ecological factors, presumably low temperatures, may have played an important role in the recent Atlantic stock collapses (NAFO 1992; Lear and Parsons 1993). This suspicion, however, was not borne out by subsequent analyses (Myers and Cadigan 1995).

Cod eggs and larvae do not produce antifreeze proteins but depend on external tissues that prevent them from freezing (Valerio et al. 1992) . Valerio et al. (1992)

found that cod eggs can survive down to −4 °C, and therefore have no risk of freezing, while cod larvae can freeze below −1.3°C, a temperature not uncommon in the surface waters off the coast of Newfoundland and Labrador as late as April. They concluded that in unusually cold years, when ice cover coincides with larval development, the risk of larval freezing may be significant. However, it is not clear whether larval mortality from cold water is high enough to influence stock fluctuations.

Recruitment

One out of a million spawned cod eggs typically survive to the first year (Serchuk et al. 1994), so any small change in this high mortality during egg and larval and post larval stages has a potentially strong effect on recruitment (Sissenwine 1984). Recruitment variability can be very high; for example, recruitment varies 14–fold among years in Northern cod (Taggart et al. 1994), 4–fold in the Gulf of St–Lawrence cod (Chouinard and Fréchet et al. 1994) and in North Sea cod (Hislop 1984 et al. 1994) and 16–fold in Arctic cod (Nilssen et al. 1994), although recruitment can vary even more in other gadoids (Hislop 1984). Fluctuations in spawning stock biomass are believed to be largely responsible for variability in recruitment of Atlantic cod as well as in recruitment of other marine fish (Myers and Barrowman 1996). Annual differences in environmental conditions are believed to cause much of the remaining variability in recruitment. Koslow et al. (1987) and Myers et. al (1995a, 1995b) found synchronous changes in year–class strength among cod stocks in the Northwest

Atlantic, suggesting that large scale (up to 500 km) biological and/or climatic features influence cod recruitment.

The effects of cold water on recruitment could be direct if temperatures drop below the freezing point of the cod larvae or juveniles, or if temperatures drop quickly below those to which the fish are acclimated. Cold temperatures can indirectly affect recruitment by delaying zooplankton blooms, which could cause starvation for larvae at the onset of feeding (Ellertsen 1989). It has also been suggested that cold temperatures may slow larval development and increase their risk of predation (Ellertsen et al. 1989; Mann and Drinkwater 1994), or lead to changes in the distribution of spawning adults that may cause larvae to hatch in unfavourable locations (deYoung and Rose 1993).

Temperature–recruitment relationships have been examined in many cod stocks, and recruitment has been found to be low in cold years in three stocks: northern cod (NAFO 1992; DeYoung and Rose 1993), Southern Grand Bank cod (NAFO 1992), Barents Sea (or Northeast Arctic cod) (Cushing 1982; Loeng 1989; Ellertsen 1989; Nilssen 1994; Ottersen et al. 1994) and West Greenland Cod (Hansen and Buch 1986), although in none of these three stocks were the relationships strong across the temperature range. Three separate analyses of northern cod (Koslow 1987; Myers et al. 1992; Hutchings and Myers 1994a), one analysis of Southern Grand Bank cod (Koslow et al. 1987), and one analysis of West Greenland cod (Koslow et al. 1987) have found recruitment to be independent of temperature. Cod recruitment has also been found to be unrelated to temperature in the Gulf of St Lawrence (Chouinard and

Fréchet 1994), on the Scotian shelf (Koslow et al. 1987), on George Bank (Serchuk et al. 1994), and in Icelandic waters (Astthorsson et al. 1994). Myers (1998), in a review of environment–recruitment correlations for a wide range of species, found that out of eleven temperature–Atlantic cod recruitment correlations that were reexamined with new data or analyses, nine did not hold out. Out of the two populations that did show consistent relationships, one was positive (Barents Sea, as discussed above) and one was negative (Gulf of Maine; Sutcliffe et al. 1977; Drinkwater and Myers 1987). Consistent with his findings for other species, Myers (1998) found the temperature–correlations that held up upon reexamination were on populations at the northern or southern extremes of the species range. Similarly, Planque and Cox (1998) report that positive recruitment–temperature relationships for Atlantic cod are found in northern waters while negative relationships are found in southern waters.

In summary, although lower recruitment in cold years has been found in four different cod stocks, separate analyses have found a lack of a temperature–recruitment relationship in three of them. The temperature–recruitment relationships that have been found are not strong throughout the temperature range, and are non–existent in the five other cod stocks that have been examined.

This difficulty in identifying consistent relationships between environmental and recruitment indices is not unique to Atlantic cod and temperature. Many authors have addressed the problem of environment–recruitment relationships (see Walters and Collie 1988, Tyler 1992, Mann and Drinkwater 1994, and Myers 1988; for reviews).

The question is not only whether environmental variability influences larval and juvenile survival, but also whether the important environmental variables can be identified, and whether their influence can be analyzed and used to predict the size of year–classes not yet recruited to the fishery. It remains uncertain to what extent environmental variability affects recruitment relative to the extent spawning stock biomass affects recruitment. Scepticism abounds; environment–recruitment relationships that have been identified have largely failed the test of time, and are therefore not reliably predictive (Myers 1998). The strength of a year–class depends on survival rates at different life–history stages, each of which may depend on a different environmental variable, and even within a life–stage the dominant environmental variable influencing survival can change with time. The chances of detecting spurious relationships between environmental and recruitment signals are high because many of the signals are strongly autocorrelated and because many more correlations are examined than are reported. For both these reasons significance levels are inflated for those correlations that are found.

It is not difficult to hypothesize mechanisms linking physical processes with survival rates, but it is difficult to establish them (Walters and Collie 1988). Several authors have explored possible mechanisms that might lie behind temperature–recruitment relationships in Atlantic cod. In the Northeast Arctic, where cold water seems most clearly associated with weak year–classes of Atlantic cod, Ellertsen et al. (1989) have examined how annual differences in temperature might affect larval cod survival through the timing of cod spawning relative to the timing of the bloom of the

copepod *Calanus*, the dominant prey of larval Northeast Arctic cod. They found that *Calanus* peaked much later in cold years, but that the timing of cod spawning did not depend on temperature. Their findings suggest that, because larval cod hatch much before the *Calanus* peak in cold years, survival of larval cod may be low because of starvation.

Brander and Hurley (1992) examined the relationship between the timing of cod spawning and the timing of plankton production among areas on the Scotian shelf, and found that they are well matched; both cod spawning and plankton production are progressively later from the southwest to the northeast Scotian shelf. Brander and Hurley (1992) suggest the timing of cod spawning in a given area is adapted to an average timing of plankton production in that area but cod are not adapted to adjust the timing of spawning according to the year to year variability in the plankton peak. Myers et al. (1993) also came to the conclusion that spawning dates do not vary with the timing of the plankton peaks. However, because they did not find a tight match between the timing of the plankton peak and cod spawning among areas, they suggest that annual differences in timing of the peak are not likely to strongly affect cod recruitment. Note, however, that the data used in these studies were aggregated over relatively large spatial scales; these results do not preclude the possibility that the timing of plankton production and cod spawning were well matched for localized cohorts, and that those cohorts may have overwhelmingly determined year-class strengths.

Hutchings and Myers (1994b) looked directly at the interannual variability in spawning time and found that cod on the Grand Banks spawned later in cold years, but on the St Pierre Bank, cod actually spawned earlier in the coldest years, or years when bank temperatures were low. Their explanation for this difference was that, on the St Pierre Bank, cod delayed their spring migration in the years that bank temperatures were low, staying longer in the warmer continental slope waters off the shelf before migrating across the colder waters on the bank to spawn. They suggest that in St Pierre cod, gonads develop more quickly in cold years because the cod have resided longer in warmer slope waters. They concluded that water temperature controls cod spawning time physiologically (gonad development is slowed in cold water) and that the timing of cod spawning is not an adaptive response to match the phytoplankton peak. Delayed spawning in cold water has also been observed in Atlantic cod in the laboratory (Kjesbu 1994), where a 1°C drop in temperature delayed spawning by about 8–10 days.

According to Hutchings and Myers (1994b), the timing of northern cod spawning is affected by temperature, but it does not appear to be an adaptation to match interannual differences in the plankton peak. Their interpretation agrees with those of Ellertsen et al. (1989), Brander and Hurley (1992), and Myers et al. (1993) that cod spawning is not matched year to year to the plankton peak. However, whether stronger mismatches occur in cold years and whether such mismatches do lead to recruitment failures is unclear.

De Young and Rose (1993) concluded that recruitment failures in northern cod

are associated with cold years, and attributed these failures to changes in spawning stock distribution. Their analysis and that of Rose et al. 1994 indicated that in cold years cod have a more southerly distribution, and they proposed that, when cod spawn in the south, larval retention within the production system is poorer than when they spawn in the north. However, not all analyses have consistently shown that cod in cold years do have a more southerly distribution (Lilly 1994; Hutchings and Myers 1994a; Hutchings 1996).

Although recruitment is possibly an important means by which cold water can influence cod production, and much effort has been directed at examining the relationship between temperature and recruitment in many cod stocks, there is surprisingly little consensus about how or even whether recruitment is adversely affected by cold temperatures. Given the number of relationships that have been examined, it does not appear that there is a strong effect of annual temperature variations on year-class strength, at least not an effect that is identifiable at the spatial scale of the whole stock. It is possible that a strong relationship exists at smaller spatial scales; that is that temperature in a given water mass strongly affects the survival of larva in that water mass. It would, however be difficult to detect such a relationship, let alone use it to explain past year-class failures or to predict the strength of upcoming ones.

Relationship between productivity and temperature among stocks

Because differences in productivity (as indexed by individual growth rates,

age–at–maturity, or population growth rates) and temperature are greater among cod stocks than among years within a single cod stock, the relationships between temperature and productivity are easier to detect and to model among stocks than among years (Brander 1995). Brander (1994, 1995) and Myers (1996) have looked at productivity as a function of temperature across cod stocks, and both showed clearly that stocks in warmer waters are more productive. These relationships between productivity and temperature among stocks, however, do not necessarily apply among years within a given stock. Temperature–growth relationships have been found within stocks, where differences in seasonal temperatures vary generally by less than 2 °C and weight–at–age varies less than 3–fold. They are, however, not as strong as Brander's among–stock relationship where there is a 10°C range in temperature, and weight–at–age varies 13–fold.

Myers (1996) found a strong among–stock relationship between the maximum population growth rates of Atlantic cod and temperature and attributes this strong relationship to the faster growth and earlier maturity of cod in warmer stocks. In the early–maturing stocks, more eggs are produced for a given stock biomass, increasing the population growth rate 5 to 6 fold over the 11°C temperature range. There is no indication, however, that age–at–maturity varies from year to year in response to temperature (O'Brien 1990). Age–at–maturity does vary from year to year, and has declined in many Atlantic cod stocks in recent years. This decline, however, is not likely temperature–related. It is more likely a density–dependent response to low stock sizes (O'Brien 1990), or a result of selection for faster maturing fish due to the loss of

older age–classes from increased fishing mortality.

Given that cod stocks are less productive in colder areas, would we necessarily expect stocks to be less productive in colder years? Atlantic cod from the coldest stocks grow more slowly, mature later and have a slower intrinsic population growth rate. One might expect these cold water populations (e.g. Newfoundland, Labrador, Gulf of St Lawrence, and Greenland) to be more vulnerable in anomalously cold years, because they are further from their optimal temperatures, and because their longer generation times would cause a slow recovery from a series of weak year–classes. There is evidence that warmer and colder stocks do not show the same response to a given environmental change. Garde and Schumacher (1994) found that New England and Northeast Arctic/Iceland landings were negatively correlated over a 60 year time series, and suggested the negative relationship could be attributed to Atlantic–wide environmental changes that might have opposite effects in southern and northern stocks. As discussed earlier, the direction and strength of relationships between temperature and cod recruitment depend on the distribution of the stock (Myers 1998; Planque and Fox 1998). Zwanenberg (unpubl. data; Bedford Institute of Oceanography, Box 1006, Dartmouth, N.S. Canada, B2Y 4A2) examined the temperature selectivity of Atlantic cod across the northwest Atlantic, and found that cod in the coldest areas preferentially selected warmer temperatures, while cod in the warmest areas preferentially selected cooler temperatures. Cod only displayed this temperature selectivity at temperature extremes; between 1 and 10°C there was no difference between the distribution of ambient temperatures and temperatures at which

cod were located. Although cold years have been clearly shown to compromise growth rates of Atlantic cod in some stocks, cold years may actually be beneficial to productivity in some of the warmer stocks.

Summary

Although it has been shown in several studies that the metabolic scope of Atlantic cod decreases with temperature down to at least 2°C, and that this decrease is associated with moderately reduced aerobic swimming performance and a strong decline in maximum consumption rates, reduced metabolic scope in cold water does not appear to be a limiting factor over much of the year for stock production of Atlantic cod. Stomach contents, growth rates, and relationships of growth and capelin biomass suggest that feeding and growth of Atlantic cod in nature are limited by food availability and not physiological rate, at least over the time scale of a season or a year. Growth, both among stocks and within stocks, is nevertheless highly sensitive to ambient temperatures, most likely because food availability is higher in warmer water. Growth rate is even more sensitive to temperature than is consumption because small changes in consumption can result in very large changes in growth rate.

It is possible that growth of Atlantic cod may be reduced in cold water in part because they are less successful at catching prey. Cold water affects cod sustained swimming performance only moderately but, perhaps more importantly for prey capture or predator avoidance, burst swimming speeds of Atlantic cod may be more sensitive to temperature change, varying 2–fold over 10°C . Capelin, the major prey of

cod in both the northwest and northeast Atlantic, occupy colder waters than do Atlantic cod. Capelin may therefore be better adapted to swimming in cold water, and may be harder for cod to catch the colder it gets.

Cold water may also have an important effect on productivity through survival. It does not seem likely that cold water is an important contributor to juvenile or adult mortality, but it is much less clear what role it plays in larval mortality. Low recruitment has been shown to coincide with low temperatures in a number of analyses of Northeast Arctic cod, but in other stocks there is very little consistent evidence of a clear trend with temperature, or even of a tendency for low recruitment at low temperatures. Unfortunately, recruitment is the component of productivity about which we know the least, and is potentially the most important component of stock productivity, directly affecting the number of individuals in a population. The number of individuals recruited from one year-class in a given cod population can vary up to 16-fold (Nilssen et al. 1994), whereas the weight-at-age in one population typically varies by 3-fold or less (Krohn et al. 1997).

As with all commercially important species, much effort is directed toward understanding the driving forces behind cod stock fluctuations, particularly in recent years with the large number of cod stock collapses in the northwest Atlantic. Fishing pressure undoubtably has an overwhelming influence on these fluctuations, particularly with respect to the stock collapses (Hutchings and Myers 1994). However, cold temperatures, although not to the extent of causing a stock collapse, are also believed to be detrimental to cod stock productivity. According to this examination of the

studies addressing cold water and Atlantic cod, this widely–held belief is supported by empirical evidence. It is clear that cod stocks in colder waters are less productive, with growth rates varying 13–fold with temperature and population growth rate varying 5 to 6–fold with temperature. In colder years, within a given stock, cod productivity is also lower with weights–at age varying up to 3–fold with temperature, although it is not clear how much of a role cold water plays in the substantial interannual variability in cod recruitment.

Chapter 4

Effect of feeding on maximum rate of oxygen consumption and maximum sustainable swimming speed in Atlantic cod.

Summary

Oxygen consumption (M_{O2}) and maximum sustainable swimming speed were measured in fed and unfed Atlantic cod (*Gadus morhua* L.) swum to exhaustion in a swim-tunnel/respirometer. Maximum metabolic rate (M_{O2max}) was 18% higher in fed than in unfed cod, which is equivalent to a 25% increase in metabolic scope. This difference suggests that M_{O2max} in fish is not limited exclusively by the rate of oxygen uptake by the gills or by cardiac output, but may be limited by the rate of oxygen uptake by the tissues as well. Because of the higher M_{O2max} in fed cod, maximum sustainable swimming speed, measured as critical swimming speed (U_{crit}), was only moderately lower (9%) in fed than in unfed cod. Apparent heat increment (AHI), measured as the absolute increase in M_{O2} after feeding, was equal to standard metabolic rate (SMR), such post-prandial M_{O2} was 2 X SMR, or 0.5 X M_{O2max}. AHI was constant across swimming speeds (it was not reduced even at U_{crit}), suggesting that once a fish starts digesting a large meal, digestion cannot be slowed in order to maintain a high level of swimming performance.

Introduction

Aerobic metabolic scope, the difference between an animal's maximum sustainable metabolic rate and the minimum metabolic rate it needs to maintain its tissues, is the amount of energy an animal has available at any one time to fuel all of its activities, including swimming, digesting, and tissue building. Over a short time scale (seconds to minutes) an animal can expend energy at a higher rate by relying on anaerobic metabolism, but this oxygen "debt" must be repaid. Extensive investigations of the upper limits to aerobic metabolism, carried out primarily on unfed animals, have revealed much about how the various components responsible for oxygen transport from the air or water to the tissues both adjust to the high demand for oxygen delivery at maximal activity levels (e.g. Kiceniuk and Jones 1977; Wood and Perry 1985; Taylor et al. 1987), and how they may limit oxygen transport, or maximum rates of oxygen consumption (M_{O2max}) (Mitchell and Blomquist 1971; Kiceniuk and Jones 1977; Taylor and Weibel 1981; Hoppeler et al. 1987; Wagner 1995; Bassett and Howley 1997; Suarez 1998; Hoppeler and Weibel 1998).

What is less well understood is how an animal allocates its energetic resources when it is both fed and active, as is often the case in nature. The energetic cost associated with processing a meal is referred to as apparent heat increment (AHI) or standard dynamic action (SDA), and includes costs associated with ingestion, digestion, absorption and, perhaps most importantly, assimilation into tissue (Jobling 1981; Jobling 1983; Beamish and Trippel 1990). AHI can be very high. The Burmese python is an extreme example: its metabolic rate during digestion can be up to 44

times its minimum or standard metabolic rate (SMR) (Secor and Diamond 1997). It is not well-understood how animals in general, and fish in particular, cope with the concurrent costs of digestion and activity. One possibility is that well-fed animals may maintain a high activity level in the face of high digestive costs by sustaining a higher M_{O2max} relative to unfed animals. Alternatively, digestion and activity may act as conflicting demands; in well-fed active animals either maximum activity level or the rate of digestion may be compromised. These possibilities are not mutually exclusive and, because animals exhibit a wide range of metabolic strategies, some being much more active than others, and some feeding more continuously and some sporadically, the answer may well be different for different animals.

The question has only been addressed directly for rainbow trout, in which activity level (maximum sustained swimming speed) was found to be compromised in fed compared to unfed fish (Aslop and Wood 1997). Aslop and Wood also found that energy allocated toward digestion is not compromised; energy is not directed away from digestion towards the swimming musculature as speeds approach maximum. Third, they found equal M_{O2max} in unfed and fed trout swimming maximally, that is that fed trout do not have any additional metabolic capacities.

In this chapter, I address the question of how Atlantic cod, a less active fish than rainbow trout, deal with the concurrent metabolic demands of digestion and activity. Atlantic cod have less than half the metabolic scope of rainbow trout and other salmonids, and may therefore be under additional metabolic constraints. Priede (1985) suggested that because Atlantic cod experience a high cost of digestion relative

to their scope, fed cod may have greatly reduced or even no swimming capabilities. There is, however, some indication that the M_{O2max} of cod that are both fed and swimming may be above maximum sustained metabolism of unfed swimming cod (Soofiani and Priede 1985; Blaikie and Kerr 1996), unlike the case for rainbow trout. An increased metabolic capacity of fed cod might allow them to maintain a high activity level despite the large metabolic demands of digestion, and would suggest that M_{O2max} is not necessarily limited by the ability of the gills to take up oxygen but can also be limited by the ability of the tissues to consume it.

The objectives in this chapter are to determine first, whether fed Atlantic cod have an increased metabolic capacity (M_{O2max}) relative to unfed cod, second, whether feeding reduces their maximum sustainable swimming speed (measured as critical swimming speed, or U_{crit}), and third, whether energy they allocate toward digestion declines with swimming speed.

Materials and methods

Experimental animals

Atlantic cod were caught in Eastern Passage, Nova Scotia in the fall of 1995 and in Shad bay, Nova Scotia, in the fall of 1998. They were maintained in ambient and temperature controlled seawater (5 to 10°C) in holding tanks at Dalhousie University until one month prior to the experiments at which time they were acclimated to a fixed tempaerture of 5°C. They were fed mackerel and squid twice per week prior to the experiments. Mean mass and length of the 5 cod used for the

experiment were 2.64 kg (1.3 to 3.7 kg) and 66 cm (58 to 72 cm), respectively.

Swimming and feeding metabolism

Swimming and feeding trials were carried out in a "Brett style" swim tunnel respirometer at 5°C. During the measurements the 89 l respirometer was run as a closed system with a 1.2 x 0.2 m straight section for the fish to swim in. The respirometer is described in detail in Webber and O'Dor (1986) and in Webber et al. (1998). Water temperature was computer controlled within 0.05°C. Oxygen concentration of the water was measured in a parallel external circuit to control for flow over the two probes (Endeco/YSI pulsed oxygen probes). Oxygen concentration of the water was measured once every 5 min. The external circuit had its own temperature control and was also used to calibrate the oxygen system at 71% and 100% saturation every day. Biological oxygen demand (BOD) was measured before putting each fish in the respirometer and after taking it out. BOD averaged 0.10 $umol \cdot l^{-1} \cdot min^{-1}$.

Each fish was put in the respirometer one to two weeks prior to the swim trials. During this time the fish was swum at 75 to 85% of their U_{crit} for six hours a day and at 50 to 60% of U_{crit} for the remainder of the day. During this period the fish became accustomed to feeding in the respirometer. At the end of the training period the fish were fed *ad libitum* and oxygen consumption (M_{O2}) of the resting fish was tracked for 48 hours to determine the time to peak AHI. A computer-controlled solenoid valve automatically stopped and started water flow to the respirometer,

allowing M_{O2} of the fish to be measured around the clock. Time to peak AHI varied from 20 to 30 hours after feeding. AHI remained at this high level during the remainder of the 48 hours. Rations averaged 6.7% (4 to 10%) body mass. Although the fish were fed *ad libitum* in the respirometer, they will be referred to being "well–fed" rather than satiated because they were only fed a single meal and, because, based on personal observations of cod feeding in large mesocosms, they are capable of eating more (>10% body mass).

Unfed fish were not fed for seven days prior to the U_{crit} protocol, while fed fish were fed 20 to 30 hours before the U_{crit} protocol, depending on the time to peak AHI of the individual fish in the feeding trials described above. Fish were swum at 30 $cm \cdot s^{-1}$ for one hour before any measurements were taken. After measuring oxygen consumption at 30 $cm \cdot s^{-1}$ for 0.5 h, the speed was increased by 10 $cm \cdot s^{-1}$ every hour. M_{O2} was measured for the first 35 to 40 min and then the respirometer was flushed with air–saturated water for 20 to 25 min. Fish were considered exhausted once they could not maintain their speed for at least 30 s after lowering and raising the speed in the respirometer. Prior to exhaustion, fish assumed a burst and glide form of swimming indicating that they were no longer able to maintain the speed using red aerobic muscle and were depending on white anaerobic muscle for propulsion. If oxygen measurements had not yet stabilized, the speed was lowered to the highest speed the fish could maintain to allow for an estimation of M_{O2max}. This method was chosen to estimate M_{O2max} rather than extrapolating M_{O2} at their U_{crit} using the M_{O2} *versus* swimming speed relationships because it resulted in higher M_{O2max} values.

M_{O2max} was calculated using maximum oxygen consumption within a 15 min period. Oxygen concentration of the water never dropped below 80% saturation. A total of 10 paired (fed and unfed) swimming trials were carried out on 5 fish.

U_{crit} was determined for each fish using the following formula (Brett 1964):

$$U_{crit} = U + I(T/t),$$

where U is the swimming speed prior to the speed at which the fish exhausted, I is the speed increment, and t is the time swum at each speed and T is the time swum at the final speed before exhaustion.

Following the unfed U_{crit} trials, M_{O2} of the resting fish was measured for a minimum of 15 hours to provide an estimate of SMR after full recovery from anaerobic debt. SMR was estimated from the lowest M_{O2} that was maintained for at least one hour.

Swimming speeds were corrected for blocking effects using the cross-sectional area of each fish (Webb 1974). This resulted, on average, in a 30% increase in swimming speed. Oxygen consumption was standardized to a 1 kg fish using a mass exponent of 0.8 determined by Saunders (1963).

Analysis

Because the same individuals were used for the fed and unfed swimming trials, paired (dependent) t-tests were performed to compare fed and unfed U_{crit} and $M_{O2\,max}$. To test for differences in M_{O2} between fed and unfed fish across speeds, and to test for differences in energy allocated to digestion among speeds, a repeated measures

ANOVA was used. If the repeated measures ANOVA was significant, post–hoc comparisons were performed to identify which treatments were significantly different. Data are presented as mean ± standard error.

Results

M_{O2max} was 18.1% higher for fed than for unfed fish (95.34 ±1.28 and 80.73±0.80 umol·kg^{-1}·min^{-1}, respectively) ($p < 0.0001$; Table 4.1 and Fig. 4.1). Metabolic scope, the difference between M_{O2max} and SMR, was 75.33 and 60.72 umol·kg^{-1}·min^{-1}, or 3.76 and 3.03 X SMR, for fed and unfed fish, respectively. Increased M_{O2max} of fed fish resulted in a 25% increase in scope. M_{O2max} was 4.00 and 4.76 X SMR for fed and unfed fish respectively.

U_{crit} was 9.4% lower for fed (63.80±0.74 cm·s^{-1}) than for unfed (70.35±0.80 cm·s^{-1}) fish ($p < 0.0003$; Table 4.1 and Fig.4.2). These speeds are equivalent to 0.98±0.01 and 1.08±0.01 bodylengths·s^{-1} for fed and unfed fish, respectively.

Post–prandial M_{O2} (M_{O2} 20 to 30 hours after feeding) was 40.03±3.22 umol·kg^{-1}·min^{-1} or 2 X SMR (20.01±0.91 umol·kg^{-1}·min^{-1}) or almost exactly half of M_{O2max} for unfed fish.

Oxygen consumption (umol·kg^{-1}·min^{-1}) increased significantly with swimming speed (cm·s^{-1}) for both fed and unfed fish ($37.7 \cdot 3.92^{speed/10}$; $r^2 = 0.64$; $n = 45$; $p < 0.001$ and $20.3 \cdot 5.83^{speed/10}$; $r^2 = 0.83$; $n = 45$; $p < 0.001$, respectively).

For all speeds during the U_{crit} protocol, M_{O2} of fed fish was consistently higher

Table 4.1. Critical swimming speed (U_{crit}) and maximum oxygen consumption (M_{O2max}) of fed and unfed Atlantic cod.

Fish #	length (cm)	weight (kg)	U_{crit} unfed ($cm \cdot s^{-1}$)	U_{crit} fed ($cm \cdot s^{-1}$)	M_{O2max} unfed ($umol \cdot kg^{-1} \cdot min^{-1}$)	M_{O2max} fed ($umol \cdot kg^{-1} \cdot min^{-1}$)
1	67	2.90	72.56	68.67	78.86	83.56
2	69	3.00	81.50	75.54	74.67	87.16
3	58	1.27	67.97	60.10	93.60	119.36
	58	1.27	59.88	57.30	79.84	97.84
4	64	2.37	65.48	64.84	71.01	86.97
	64	2.37	68.48	56.28	78.52	86.02
	64	2.37	64.84	55.43	74.34	98.37
	64	2.37	68.48	58.64	79.83	85.89
5	72	3.66	77.01	70.64	87.46	103.07
	72	3.66	77.26	70.52	89.16	105.14
mean	65.2	2.52	70.35	63.80	80.73	95.34
±SE	±1.6	±0.26	±0.80	±0.74	±0.80	±1.28

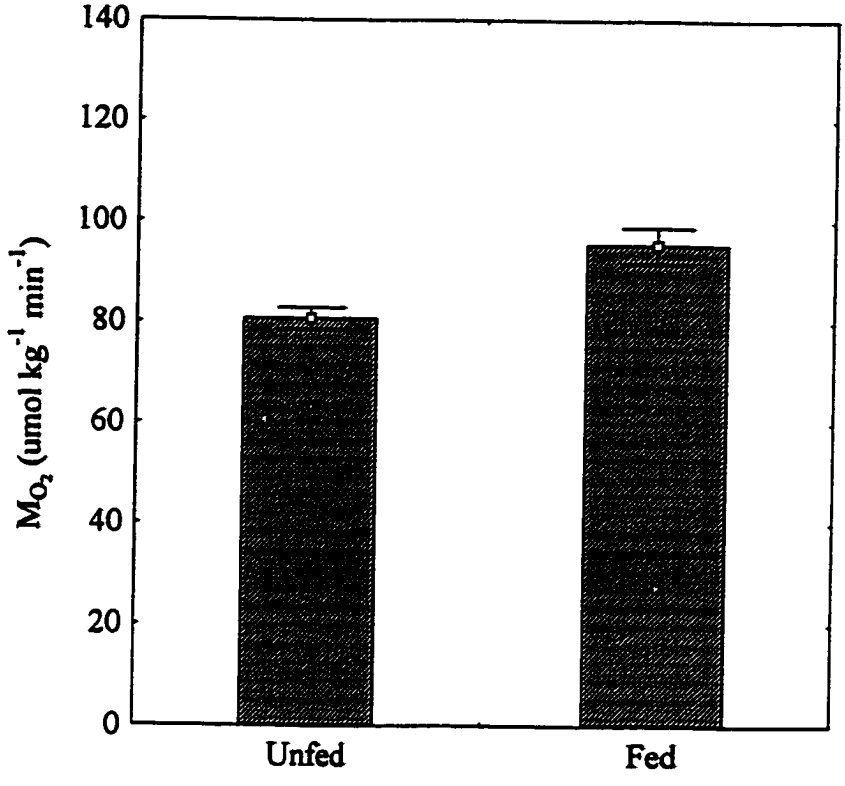


Fig. 4.1. Maximum oxygen consumption (M_{O2max}) of fed and unfed fish. Values are expressed as means±SEM (n=10). Mean M_{O2max} of fed fish is significantly higher than unfed fish ($p < 0.0001$).

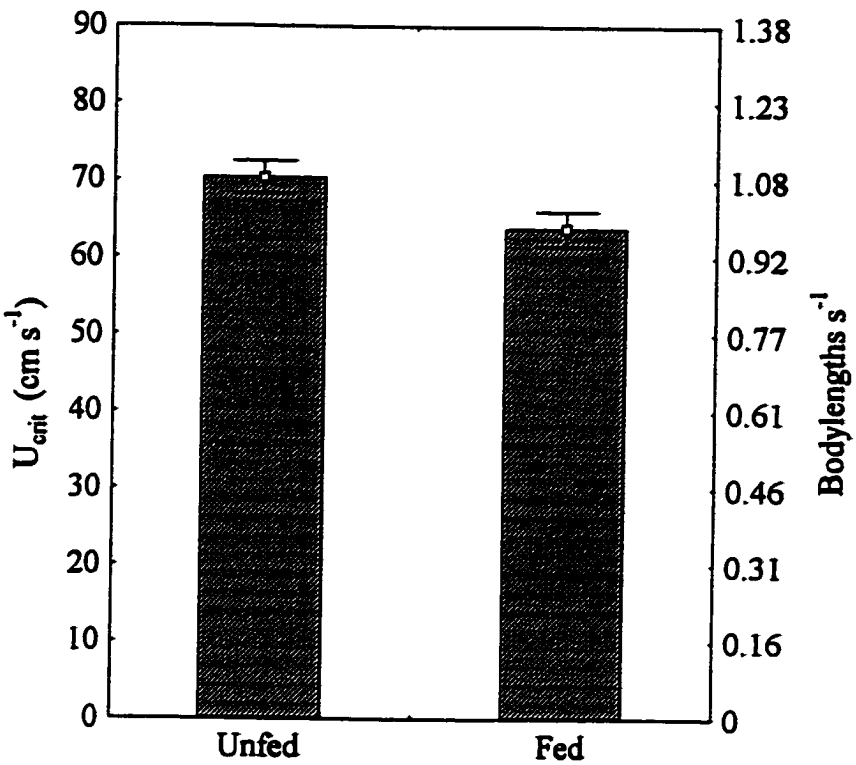


Fig. 4.2. Critical swimming speed (U_{crit}) of fed and unfed fish. Values are expressed as means±SEM (n=10). Mean U_{crit} of fed fish is significantly lower than that of unfed fish ($p < 0.0003$).

than that of unfed fish ($p < 0.0001$) (Fig.4.3). The interaction between swimming speed and feeding status (fed vs unfed) in the repeated measures ANOVA was not significant ($p=0.08$), but the low p value suggested that elevation in M_{O2} due to feeding (AHI) may not be entirely consistent across speeds. AHI was isolated at each speed by subtracting the M_{O2} of an unfed fish from the M_{O2} of the same fish, but fed, at the same speed (Fig 4.4). To estimate AHI at fed M_{O2max} for each fish, an interpolated value for M_{O2} was subtracted from the M_{O2} of the same fish unfed at the speed at which fed M_{O2max} was measured. A repeated measures ANOVA was performed on these AHI estimates across speeds. When all speeds were included, from resting to the speeds at which fed M_{O2max} was measured, AHI was not significantly different across speeds but the p value again was low ($p=0.08$). Post-hoc comparisons determined that AHI at the corrected speed of 39 $cm \cdot s^{-1}$ (or uncorrected speed of 30 $cm \cdot s^{-1}$) was significantly different (lower) than for all other speeds $p<0.05$, but that no other comparisons were significantly different ($p>0.49$).

Because 39 $cm \cdot s^{-1}$ was the first and lowest speed at which M_{O2} was measured during the U_{crit} protocol, M_{O2} values at this first speed were more variable than the others. There was sometimes (in six out of twenty trials) little or no increase in M_{O2} between the first and second speed. The apparent lower AHI at 39 $cm \cdot s^{-1}$ may therefore be an artifact of the experimental protocol. AHI varied very little among the other five speeds, ranging from 19 to 21 $umol \cdot kg^{-1} \cdot min^{-1}$.

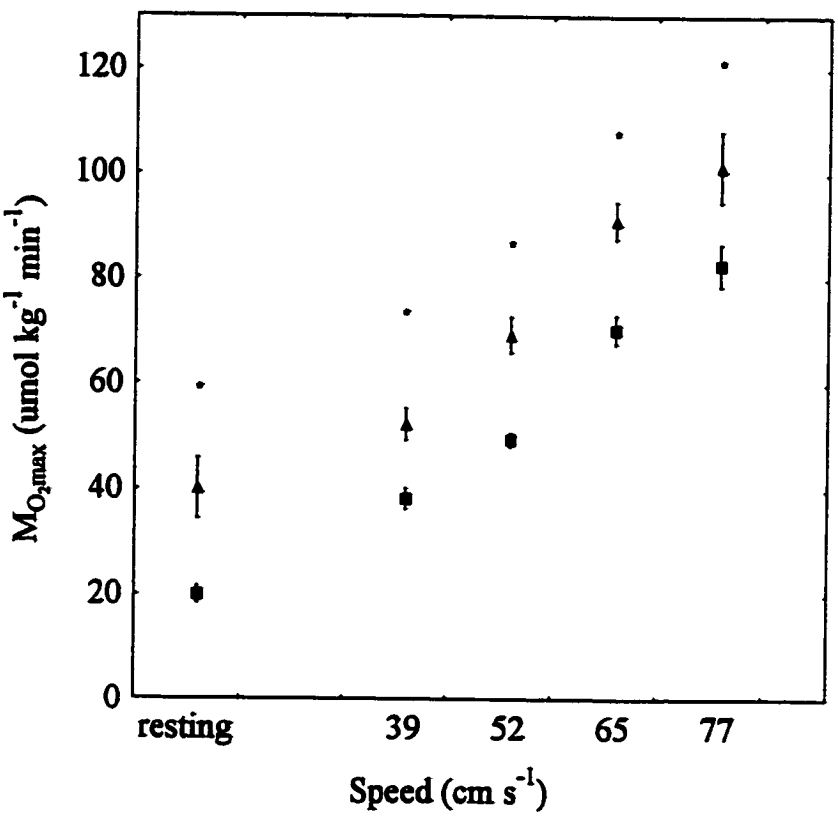


Fig. 4.3. Oxygen consumption (M_{O2}) of fed (triangles) and unfed (squares) fish resting and swimming at mean corrected swimming speeds of 39, 52, 65, and 77 cm·s^{-1} (or uncorrected swimming speeds of 30, 40, 50 and 60 cm·s^{-1}). Values are expressed as means ± SEM (n=10). * $p < 0.0005$.

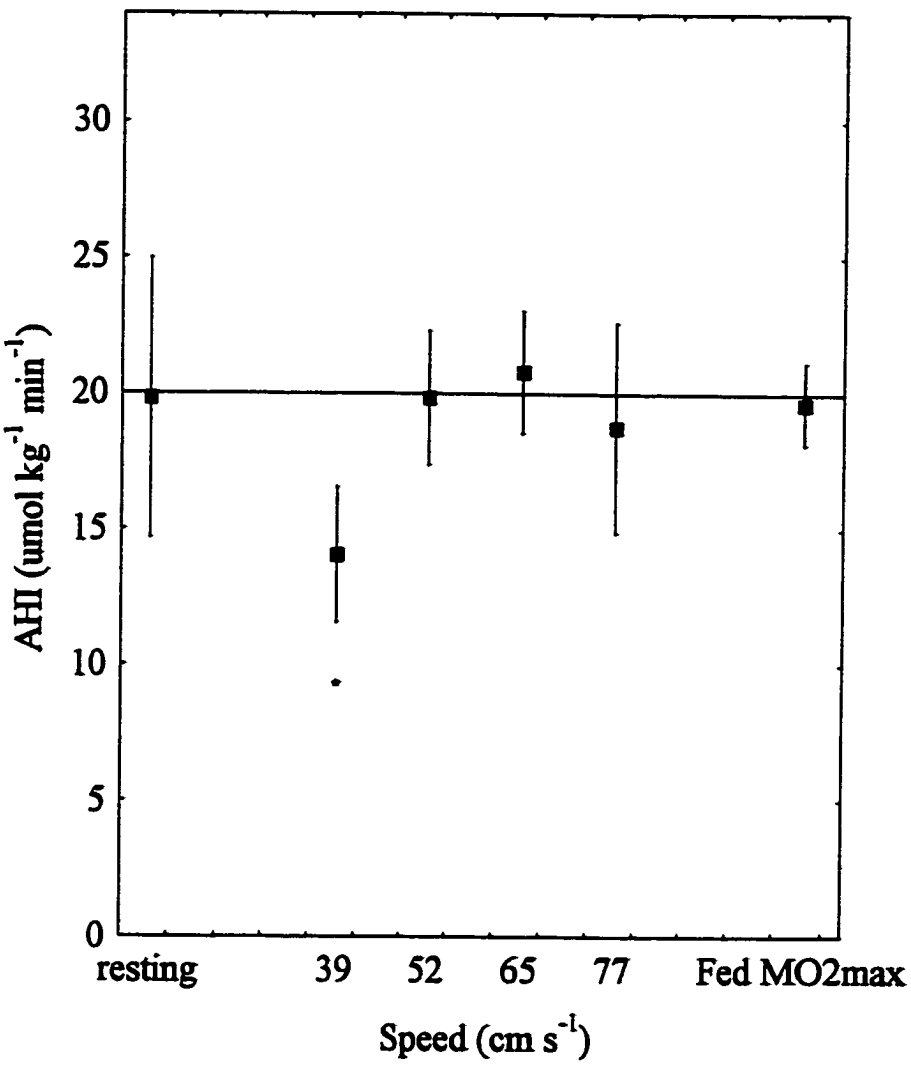


Fig. 4.4. Energy allocated toward digestion (AHI) while resting and swimming at mean corrected swimming speeds of 39, 52, 65, and 77 $cm \cdot s^{-1}$ (or uncorrected speeds of 30, 40, 50 and 60 $cm \cdot s^{-1}$) and at the speed at which M_{O2max} of fed fish was measured . Values are expressed as means ± SEM (n=10). * significantly different from the other 5 speeds, $p<0.05$.

Discussion

Maximum rate of oxygen consumption

Our results indicate that Atlantic cod can buffer the effect of digesting a large meal on maximum activity level by increasing their maximum metabolic rate (M_{O2max}) by 18%, which is equivalent to a 25% increase in metabolic scope. This is the first time a significant increase in M_{O2max} associated with feeding has been reported for either fish or mammals, but a large increase has been observed in the Burmese python, whose M_{O2} during digestion is 7–fold higher than during exercise (Secor and Diamond 1997). The present results clearly support two studies (Soofiani and Priede 1985; Blaikie and Kerr 1996), both on Atlantic cod, which suggest that fed animals may have a higher M_{O2max} than unfed animals. Neither of these studies tested the question directly, but inferred a possible difference by comparing metabolic rates of fed and unfed animals from two separate experiments.

Rainbow trout is the only other fish species for which the interaction of feeding and maximal exercise has been closely examined (Aslop and Wood 1997). Unlike Atlantic cod in the present study, satiated and unfed rainbow trout swimming maximally exhibited equivalent levels of M_{O2max}. It is perhaps not surprising that the more powerful aerobic muscle of a highly active salmonid species is able to take fuller advantage of the maximum rate of oxygen consumption than is the less active Atlantic cod. A strict species comparison, however, is not warranted as the two species were at very different developmental stages; the mass of mature wild–caught Atlantic cod in this study were 2 to 3 orders of magnitude higher than the juvenile hatchery–raised

rainbow trout studied by Aslop and Wood. The cod were also swum in water 10°C cooler than were the rainbow trout, where oxygen supply may be less limiting.

Consistent with the present findings, models based on cardiovascular work, swimming performance and respiration rates of tuna predict that they do not use their full aerobic capacity at maximum sustainable swimming speeds (Korsmeyer et al. 1996; Korsmeyer et al. 1997). The authors suggest that this oxygen reserve may allow for other metabolic processes such as digestion and repayment of oxygen debt to continue even at maximum sustainable swimming speeds.

It is generally thought that oxygen supply to the tissues, and not oxygen demand of the tissues, limits maximal endurance performance and associated M_{O2max} (e.g. Wagner 1995; Bassett and Howley 1997). The more relevant question is whether aerobic performance is limited by oxygen uptake by the lungs or gills, or whether it is limited by oxygen transport to the tissues, or both. In the mammalian literature, the concept of symmorphosis, proposed by Taylor and Weibel (1981) predicts that the limits of oxygen flux at all steps in the respiratory system are matched to each other, such that no one step limits M_{O2max}. Subsequent research has not only supported this prediction, but has suggested that a change in the capacity of any one step will alter M_{O2max}, in the same way that resistors in series control electrical current (Wagner 1995; Wagner et al. 1997; Hoppeler and Weibel 1998). Although this perspective was developed for mammals, it is also helpful for thinking about limits to M_{O2max} in other organisms. In fish and other aquatic poikilotherms, however, one would not expect a tight coupling between maximal oxygen uptake by the gills and maximal oxygen

supply to the mitochondria. While both oxygen uptake and delivery to the tissues are considered to be limiting factors in determining aerobic swimming performance in fish (Wood and Perry 1985), the relative importance of each one may depend on ambient conditions. For example, M_{O2} of a fish in hypoxic or warm water is likely to be limited to a greater extent by oxygen uptake at the gills than by oxygen supply to the tissues (Priede 1985).

The difference in M_{O2max} between fed and unfed cod suggests that when unfed fish, and possibly fed fish, are at their maximum activity levels, M_{O2} is not necessarily limited by uptake at the gills but can, at least in Atlantic cod, be limited by oxygen uptake by the tissues. The added oxygen consumption of the visceral tissues in the fed cod to that of the maximally active skeletal muscles led to an increase in M_{O2max}. The importance of oxygen supply to the tissues in limiting M_{O2max} can also be seen from the difference in M_{O2max} between Atlantic cod swum to exhaustion in an aerobic swimming protocol and cod swum to exhaustion in a chase, or primarily anaerobic protocol (Reidy et al. 1994). M_{O2max} of cod swum to exhaustion in a chase protocol, using white muscle, was 38% higher than the M_{O2max} of a fish swum to exhaustion in a sustainable swimming protocol, presumably using primarily red aerobic muscle. White "anaerobic" muscle makes up the bulk of the swimming musculature and has substantial aerobic capacity as well. Use of this white muscle tissue in the chase protocol (Reidy et al. 1994) increased M_{O2max} above the M_{O2max} achieved in the sustainable swimming protocol to a greater extent than did AHI costs in the present study, suggesting the even the fed cod swimming at maximum sustainable speeds in

the present study may not have been at their true M_{O2max}. Perhaps true M_{O2max} can only be reached when most or all of the tissues are maximally active, for example in a satiated fish being chased when it is producing gametes and spawning.

As discussed earlier, M_{O2max} is not necessarily limited by one step in the respiratory chain. An increased capacity in any one step may lead to a small increase in flux across all steps (Wagner 1995; Wagner et al. 1997; Hoppeler and Weibel 1998; Suarez 1998). Although I have concluded that M_{O2max} in Atlantic cod was limited by supply of oxygen to the tissues, this does not preclude the possibility that oxygen uptake at the gills was also a limiting factor. In unfed cod, the extent to which the oxygen content of the venous blood was lowered was likely due largely to the activity of red muscle. The gills may have been extracting as much oxygen from the water as possible given the difference in oxygen concentration of the venous blood and the water. If increased metabolism of the digestive tissues of fed fish increased oxygen extraction from the blood, oxygen content of mixed venous blood was probably lowered to a greater extent, allowing the gills to extract more oxygen from the water.

Critical swimming speed (Ucrit)

Despite a constant allocation of energy toward digestion at all swimming speeds, feeding only reduced U_{crit} to a minor extent because of the increased metabolic scope of the fed fish. Using M_{O2}– swimming speed relationships, it was estimated that, were it not for the increased metabolic scope of the fed fish, U_{crit} would have decreased in response to feeding by 27% rather than by less than 10%.

Priede (1985) suggested that fully satiated cod use such a large proportion of their metabolic scope for digestion that they may have greatly reduced, or even no swimming ability depending on whether or not digestion takes precedence over activity. Although this was not tested directly, (the cod in this study were likely close to, but not fully satiated), the present results suggest it is unlikely that satiated cod are unable to swim. As Priede proposed, digestion does take precedence over activity. Nevertheless, the well–fed cod (6.7% body mass) in this study maintained a swimming speed of almost 1 bodylength·s^{-1}, less than a 10% decrease relative to unfed cod. The effect of feeding on swimming ability in Atlantic cod is minor partly because their scope is at least 25% higher when fed than unfed (possibly even more if they are more fully satiated), and partly because AHI does not use up the whole metabolic scope (AHI was only 2X SMR, or 0.5 M_{O2max}).

Energy allocated toward digestion

Atlantic cod exercised maximally did not divert energy away from digestion; AHI was not reduced even at maximum sustainable swimming speeds. A constant AHI independent of swimming speeds has also been found in smallmouth bass (Beamish 1974) and rainbow trout (Aslop and Wood 1997). The fixed AHI at all speeds is consistent with the independence of evacuation rate on swimming speed found in Atlantic cod (Tyler 1977), with the independence of the duration of AHI on swimming speed in smallmouth bass (Beamish 1974) and, conveniently, with the implicit assumption in bioenergetic models that AHI duration and magnitude are

independent of swimming speed. The apparent lack of ability to reduce energy allocated to digestion is also consistent with Claireaux et al.'s (in press) observations of Atlantic cod regurgitating food when oxygen concentration of the water dropped below a critical level. There is a discrepancy, however, between the present results and those of Blaikie and Kerr (1996), who found that AHI increased with swimming speed in Atlantic cod. This discrepancy may be explained in part by the absence of an increase in M_{O2} with swimming speed in their unfed fish which is noted in their discussion (estimates of unfed swimming cost were used to isolate AHI effect in swimming fish).

As discussed by Aslop and Wood (1997), the irreducible cost of digestion suggests that the increased blood flow to visceral tissues in response to feeding is not redirected to the muscles during exercise. Nevertheless, the limited effect of feeding on maximum swimming speeds in cod suggests that blood flow to the red muscle may not be greatly reduced during digestion and, therefore, that total cardiac output may also be higher in fed than in unfed fish at maximum swimming speeds. Cardiac output immediately following feeding in Atlantic cod has been found to be higher than in unfed cod swimming at close to maximum sustainable speeds (Webber 1999). This high cardiac output was not maintained during the course of digestion, and cardiac output was not measured on cod that were both fed and active.

The priority of blood flow in fed active fish has not been investigated. It is clear that an inactive fish, upon feeding, can redirect blood flow from the muscles to the digestive system (Axelsson et al. 1989; Axelsson and Fritsche 1991), and that an

active unfed animal can redirect blood flow to the muscles at the expense of blood flow to the digestive system (Randall and Daxboeck 1982; Newmann et al 1983; Thorarensen et al. 1993). However, even for unfed active fish the findings are not entirely consistent. When unfed rainbow trout were swum at the maximum speed they could maintain without recruiting any anaerobic fibers, the 27–fold increase in blood flow to the aerobic muscle was supplied entirely by an increase in cardiac output; there was no associated drop in blood flow to the intestine (Wilson and Eggington 1994).

The combined effects of feeding and exercise on the distribution of blood flow has been investigated for several mammalian species. Consistent with the findings from this study, mammalian studies have shown that, after a meal, blood flow to digestive organs is maintained during exercise in humans (Eriksen and Waaler 1994), in dogs (Fronek and Fronek 1970) and in baboons (Vatner 1978). Other studies have shown that blood flow to digestive organs is lower in active compared to a resting humans (Qamar and Reed 1987 and Perko et al. 1998). The differences among these studies are likely due to a combination of differences in exercise intensity, differences in which arteries were studied, and real differences among species (Perko et al. 1998). While studies of blood flow distribution in fed active fish are needed (Aslop and Wood 1997), it is possible they will also differ among species and experimental protocols.

This increase in M_{O2} after feeding in resting and swimming cod to be 2 X SMR, consistent with Saunders' (1963) estimates of post prandial M_{O2} in satiated

Atlantic cod (1.6 X routine metabolic rate), with Lyndon et al.'s (1992) estimates of post prandial M_{O2} in Atlantic cod fed 6% body mass (1.5 X routine) and with the post prandial M_{O2} found in other fish species as well (see Jobling 1981 for a review). However Soofiani and Hawkins (1982) found M_{O2} for fed resting Atlantic cod was equal to or greater than M_{O2max} for unfed swimming fish. The cod in their study fed at a much greater rate than did the cod in the present study. They were fed four meals of 4 to 5% body mass in dried pellets two days apart, which in wet weight is equivalent to over 20% body mass. The high post–prandial M_{O2} relative to maximum swimming M_{O2} they found may have been due to this high caloric diet. Alternatively, because the post–prandial M_{O2} and the maximum swimming M_{O2} were determined in separate experiments, differences in methodology may have complicated the comparison.

Synopsis

These results show, for the first time, that M_{O2max} can be significantly higher (18%) in fed than in unfed fish. This increase in M_{O2max} buffers the effect of feeding on aerobic swimming performance, such that well–fed cod only experience a minor reduction in U_{crit} relative to unfed cod. This higher MO_{2max} of fed fish, along with the higher M_{O2max} found in chased fish (Reidy et al. 1995), suggests that, depending on the species and the ambient conditions, "true" M_{O2max} may only be reached when many tissues are maximally active. The results from this study also suggest, consistent with those of Aslop and Wood (1997) and Beamish (1974), that once a fish starts digesting

a large meal, digestion can not be stopped in order to maintain swimming performance.

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