

# Impact of environmental temperature on Atlantic cod *Gadus morhua* energy allocation to growth, condition and reproduction

M. J. Morgan\*, R. M. Rideout, E. B. Colbourne

Fisheries and Oceans Canada, St. John's, Newfoundland A1C 5X1, Canada

**ABSTRACT:** The effect of temperature on the allocation of energy to growth, condition and reproduction was examined in juvenile and adult Atlantic cod *Gadus morhua* inhabiting the southern Grand Bank off Newfoundland, Canada. The study period included both the warmest and coldest environmental conditions in the area over the past 60 yr. Temperature did not influence growth in length or weight, perhaps because growth at higher temperatures was limited by prey availability. Temperature significantly influenced both gutted body condition and liver condition (observed weight divided by predicted weight at length), but the effect was not consistent between the 2 measures of condition. Gutted body condition was highest at warm temperatures, whereas liver condition was highest at low temperatures. Measures of reproductive investment showed clear temperature effects. Fish matured earlier at both low and high temperatures than at intermediate temperatures. Fecundity of southern Grand Bank cod was highest at low temperatures, while the gonadosomatic index (GSI) was highest at warm temperatures. The lack of correlation with fecundity indicates that GSI may not be a good metric of reproductive investment but may be an indicator of how close fish are to spawning. The lower maturity and fecundity at intermediate temperatures could indicate a decrease in reproductive potential under these environmental conditions. Temperature throughout the entire year influenced fish condition, but only temperature during October to May affected reproductive investment. Most of the metrics were highly correlated between males and females, suggesting that both sexes make similar decisions about energy allocation over the observed temperature range.

**KEY WORDS:** Cod · Growth · Reproduction · Temperature

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

As with all consumers, the food energy assimilated by fish must be divided among the conflicting demands of survival (e.g. maintenance, activity, foraging), growth, and reproduction, all of which are important components of individual fitness. Because energy stores are finite, supporting growth and reproduction while still ensuring survival requires energetic trade-offs. Energy allocated to growth cannot be used for present reproduction, although current growth may enhance future reproduction through increased fecundity and egg/larval survival (Rijnsdorp 1994, Lambert et al. 2003). Energy allocated to reproduction may decrease survival, particularly if energy reserves are low (Lambert & Dutil 2000) and cannot be used for growth.

Decisions about how to allocate energy among these competing demands will to a large extent determine an individual's fitness.

The amount of surplus energy available to be allocated to growth and/or reproduction will be strongly influenced by the amount of food available for consumption. Greater food availability can lead to an increase in both growth and reproductive investment (Lambert & Dutil 2000, Rindorf et al. 2008). Temperature can also have a major impact and can interact with food availability. Metabolic processes are directly affected by temperature, and for each species there is an optimum temperature and food level that results in maximum growth. As food availability declines, the most efficient growth occurs at lower temperatures where requirements for maintenance are less because of a lower

\*Email: joanne.morgan@dfo-mpo.gc.ca

metabolic rate (Brett 1979). If temperature becomes too low, food consumption can decline, even as activity increases, with a resulting weight loss (Morgan 1992). Given sufficient food, growth will generally increase with temperature up to the species-specific optimum temperature for growth, after which growth will decline (Bjornsson & Steinarsson 2002). Temperature influences allocation to reproduction as well, with fish in warmer temperatures often maturing at a younger age and/or smaller size and producing more eggs compared to conspecifics in colder environments (Kjesbu et al. 1998, Morgan & Colbourne 1999, Yoneda & Wright 2005b). In addition, the type of food available can play a role in energy allocation (Rideout & Rose 2006).

The impact of a varying environment on energy allocation patterns may also differ between the sexes (Yoneda & Wright 2005a), since males and females do not always have the same energy allocation strategies. In particular, males often invest less energy into gonads than do females (Rijnsdorp & Ibelings 1989, Bromley et al. 2000), although they may invest more into behaviors associated with reproduction and mate choice. The smaller reproductive investment may be because less energy is required to produce sperm than eggs (Wootton 1990). There may also be differences in energy intake and growth between sexes (Rijnsdorp & Ibelings 1989, Swain & Morgan 2001).

Decisions about energy allocation directly affect survival and fitness and therefore should be selected to be

optimal in a particular environment. An individual's state (juvenile or adult) will affect the optimal allocation of energy, and in fact, these trade-offs with survival can determine the size and age at which maturation occurs (Roff 1983). Once they mature, individuals may gradually shift more energy to reproduction at the expense of growth (Jørgensen & Fiksen 2006). Under adverse conditions, adult fish may greatly reduce energy allocation to reproduction, resulting in skipped spawning (Rideout et al. 2005)

Here we explored the effect of varying temperature on energy allocation patterns for southern Grand Bank Atlantic cod *Gadus morhua*. This was once an important commercial stock that has become severely depleted due to over-exploitation (Morgan et al. 2007). Data span a 30 yr period that includes some of the coldest and warmest temperatures recorded in the area (Colbourne et al. 2005). We examined the effect of temperature on energy allocation through changes in patterns of growth, condition, and reproduction in this coldwater marine teleost, and we compared the energy allocation decisions made by males and females.

## MATERIALS AND METHODS

Data for these analyses came mainly from Canadian research vessel bottom trawl surveys of Northwest Atlantic Fisheries Organization (NAFO) Division 3N

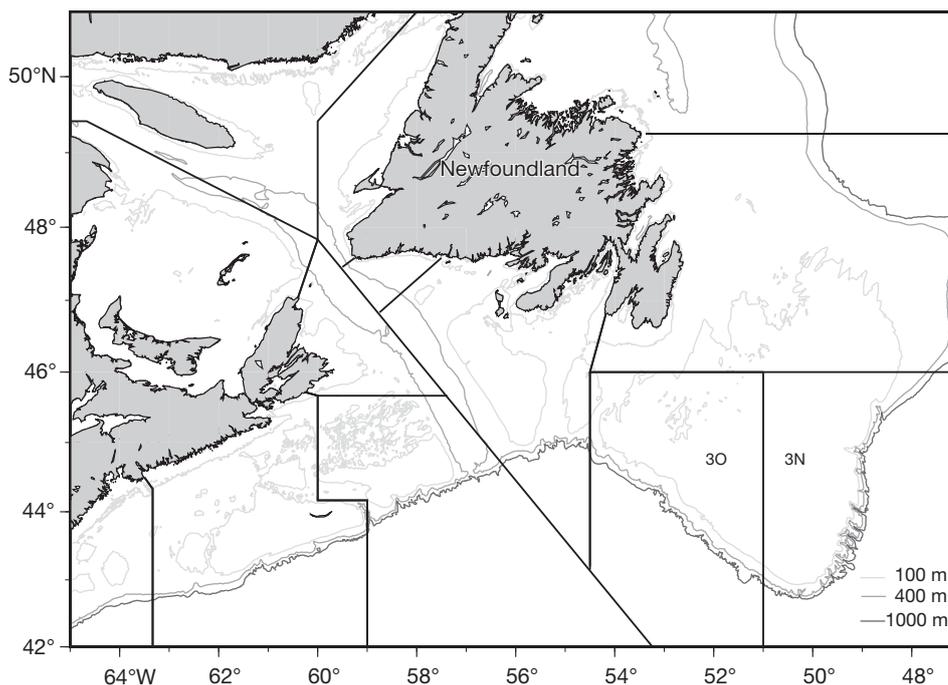


Fig. 1. Study area, showing the 2 Northwest Atlantic Fisheries Organization Divisions (3O and 3N) comprising the southern Grand Bank

and Division 3O (Fig. 1) from 1978 to 2008 (except 1983 and 2006). Surveys were conducted mainly in April and May using a stratified random survey design (Doubleday 1981). Cod on the southern Grand Bank spawn in spring, with a peak of spawning generally about mid-May (Myers et al. 1993), so that samples were taken from mainly juvenile and pre-spawning adult fish. All cod were measured for length and sex and were examined for maturity (Table 1). Cod were assigned to various maturity stages based on macroscopic examination of their gonads using the maturity classification of Templeman et al. (1978) originally developed for haddock and since adapted for most groundfish species in the Newfoundland region. Otoliths were extracted from a length-stratified sample for aging. For most of the fish that were collected for aging, the body weight had been measured, and for a subsample of these, the organ weights had been measured. All factors examined at age (mean length, weight, proportion mature) were calculated so as to correct for the bias introduced by length-stratified sampling (Morgan & Hoenig 1997).

In 1990 and 1993 to 2005, ovaries were collected for fecundity analyses. Only ovaries that were ripening (i.e. had opaque oocytes) but showed no signs of spawning (i.e. clear oocytes) were included. This helped to ensure that all fish used in the fecundity analyses were at a similar stage of maturation and prevented fish that had already commenced spawning from being included, which would have led to an underestimation of fecundity. Upon removal, ovaries were immediately cut open and placed in jars of Gilson's fluid for 3 to 4 mo to digest the connective tissues that held the oocytes in place. First generation oocytes (i.e. those that would have been spawned in the current year) were separated from second generation (i.e. immature) oocytes and leftover connective tissue by rinsing through a series of sieves. The cleaned oocytes were stored in ethanol until counted. Oocytes were fractionated to a countable number using a modified whirling vessel (Wiborg 1951). Samples were counted manually under a stereomicroscope. Four subsamples were collected for counting from each pair of

ovaries, but the last 2 subsamples were only counted if the difference between the first 2 counts was greater than 5%. The mean oocyte count was adjusted to the total based on the proportion of the whole sample that was counted, to obtain the overall fecundity estimate.

The influence of temperature on cod energy allocation was investigated as described below. Since spawning peaks in May, a temperature series representing the entire year from the end of spawning in 1 year to spawning in the next was developed. Biological sampling primarily occurred just prior to spawning. To determine whether temperatures during different parts of the year may affect allocation decisions differently the year was also broken into 2 periods corresponding to a period of energy accumulation and a period of reproductive development. Atlantic cod are capital breeders using stored energy to support egg production (Jørgensen & Fiksen 2006). They accumulate this energy and complete most of their growth in a period of several months following spawning (Mello & Rose 2005). Oocytes generally start to ripen around October to November (Rideout 1999, Skjæraasen et al. 2009) and continue to develop throughout the winter. The main energy accumulation period was therefore defined as June to September, and the period for which energy is being allocated to reproductive processes was considered to be October to May. Historical oceanographic data for the Grand Bank region are available from archives at the Integrated Science Data Management (formally MEDS) directorate in Ottawa, Ontario (Canada). This data set was compiled from all sources; fisheries research and assessment surveys, oceanographic surveys, and opportunistic sampling. All available near-bottom temperature data from 1950 to 2008 were extracted from the database in the area on the top of the banks covering a depth range of 57 to 92 m and represents an area of 34 704 km<sup>2</sup> where historically a significant portion of the 3NO cod population was located. Temperature data collected throughout the 1950s used standard water sampling bottles fitted with reversing thermometers that measured temperature at selected depths including near-bottom. In the 1960s, bottle measurements were supplemented with mechanical bathythermograph (MBT) deployments, which provided a continuous depth-temperature profile to a water depth of 270 m. In the 1970s and early 1980s, temperature data were collected with expendable bathythermographs (XBTs), and in the late 1980s, these were replaced with conductivity-temperature-depth (CTD) profilers deployed either vertically during oceanographic surveys or as a trawl-mounted system on fisheries assessment surveys. The amount of data available varied from year to year, and not all months had observations in all years. For the 1983 spawning year, no observations were made in the October to

Table 1. *Gadus morhua*. Number of samples available for each sex, for each variable examined. na: not applicable

	Male	Female
Length	1388	1395
Age	1388	1395
Maturity	1388	1395
Body weight	848	827
Gonad weight	845	820
Fecundity	na	311

May period (October 1982 to May 1983). To produce an index of the temperature conditions in an entire year, a simple average of the monthly averages was calculated from June of year  $y - 1$  to May of year  $y$ . An anomaly for each year was produced by subtracting the average over the 1971 to 2000 period from the mean value calculated for each spawning year and is referred to as the annual anomaly. Similar anomalies were constructed for the period from June to September in year  $y - 1$  and for the period from October in year  $y - 1$  to May in year  $y$ .

Mean length at age was calculated by sex for each year. To control for the presence of varying age ranges in the data, only ages 3 to 10 were used. Length increments were calculated from mean length at Age  $a - 1$  in year  $y - 1$  to length at Age  $a$  in year  $y$ . To examine the effect of temperature on length increments they were first modeled as a function of age

$$\ln(\Delta L_{a,y}) = \tau + \beta_a + \varepsilon \quad (1)$$

where  $\Delta L_{a,y}$  is the length increment for a cohort at Age  $a$  in year  $y$ ,  $\tau$  is the intercept,  $\beta_a$  is the age effect, and  $\varepsilon$  is the normally distributed error. For females, the residuals from this fitted model were then tested for a significant effect of temperature using a generalized linear model (GLM). For males, there was no significant effect of age on length increment, so analyses were conducted on the log of the length increments directly using the same GLM with the same temperature bins. Preliminary analyses indicated that the effect of temperature on most of the biological variables was nonlinear. Therefore, temperature was binned into 'low,' 'intermediate,' and 'high' by dividing the temperature anomalies so that one-third of the data fell into each bin. Other aggregations of the data were also examined, but the results were not affected.

Mean gutted weight at age was also calculated by sex for each year, using Ages 3 to 10. Weight increments were calculated as described for length above. To examine the effect of temperature on weight increments, they were first modeled as a function of age:

$$\ln(\Delta W_{a,y}) = \tau + \beta_a + \varepsilon \quad (2)$$

where  $\Delta W_{a,y}$  is the weight increment for a cohort at Age  $a$  in year  $y$ ,  $\tau$  is the intercept,  $\beta_a$  is the age effect, and  $\varepsilon$  is the normally distributed error. For both sexes, there was a significant effect of age on weight increment. The residuals from this fitted model were then tested for a significant effect of temperature using a GLM with temperature as a class variable and temperature binned into low, intermediate, and high as described above.

Relative condition indices were used to explore changes in condition over time. For gutted condition, only fish >20 cm fork length were used because of low

reliability in the weight measurements below this size as a result of the precision of the balances. Relative  $K$  for gutted condition ( $Kr$ ) was calculated as:  $Kr = W/\hat{W}$ , where  $\hat{W}$  is the predicted body weight from a length–weight relationship. The form of the length–weight relationship was  $\log(W) = \text{intercept} + \log(L)$ . Separate regressions were carried out for each sex. Data for all years combined were used in the regressions. To calculate  $Kr$  for an individual fish, its gutted body weight was divided by the gutted body weight predicted by the length–weight regression for a cod of that length and sex. For liver weight, only fish  $\geq 30$  cm in fork length were used because the balances lacked the precision to weigh small organs. There was a pattern in the residuals of the linear regression of  $\log$  (liver weight) against  $\log$  (length). A model of the form  $\log(LW) = \text{intercept} + \log(L) + [\log(L)]^2$  was fit to the data, where  $LW$  is liver weight. This model resulted in a significant fit for both males and females and minimized patterns in the residuals. The results of these models were used to produce an index of liver condition,  $LKr = LW/L\hat{W}$ , where  $L\hat{W}$  is the predicted liver weight from the length–liver weight relationship. The effect of temperature on these condition indices was modeled using GLMs with gamma error and an identity link function. Again temperature was binned into low, intermediate, and high.

Proportion mature at age was modeled by sex and cohort using GLMs with a binomial error and a logit link function. For these analyses, data from surveys from 1972 to 2008 were used. The effect of temperature was analyzed by examining the effect on the estimated proportion mature at Age 5. The estimated proportion mature at this age for both males and females was >0 but <1 for the entire time series. For each cohort, the average annual temperature anomaly up to the age of 5 was calculated by averaging the temperature occupied in each year from 0 to 5. The average temperature anomaly up to Age 5 was binned into high, intermediate, and low as above, and its effect on proportion mature at Age 5 was tested with a GLM with an identity link and gamma error.

The gonadosomatic index (GSI) was calculated for each individual as the weight of the gonad divided by the gutted weight of the fish. Only fish that were maturing to spawn in the present year but that had not yet started spawning were included. The effect of temperature on GSI was modeled using GLMs with gamma error and an identity link function with temperature binned into low, medium, and high.

Relative fecundity was calculated as the number of eggs  $g^{-1}$  of gutted weight. The effect of temperature on relative fecundity was modeled using a GLM with gamma error and an identity link function. Again temperature was binned into low, medium, and high.

Measures of growth and reproductive investment were compared between males and females using correlation analyses. The model fits for the various growth and reproductive factors examined were compared for the 3 temperature series (annual anomaly, June to September period, and October to May period) using Akaike information criteria (AIC) for models where there was a significant temperature affect.

## RESULTS

The average annual bottom temperature calculated over a reproductive year in the Divisions 3NO area ranged from 0 to 3°C over the 1950 to 2008 period. Over the period for which we have biological data (1978 to 2008), the average ranged from 0 to 2.8°C, and the annual anomaly ranged from 1°C below to 1.7°C above the long-term average (Fig. 2). The average temperature over the June to September period from 1978 to 2008 ranged from 0.2 to 3.0°C, with an anomaly that ranged from 1°C below to 1.8°C above the long-term average. For the October to May period, the average ranged from -0.2 to 2.9°C, with an anomaly ranging from 1°C below average to 2.1°C above average.

There was substantial interannual variability in measures of growth, condition, and reproduction for both males and females (Figs. 3 & 4). However, some temporal patterns are evident. Growth in length showed some decline from the early 1980s to the early 1990s and subsequently increased during the late 1990s. Growth in weight also declined until the mid-1990s, after which there was little trend. Body and liver condition generally increased from 1978 to 1982. This was followed by a period of decline, especially in body condition, which

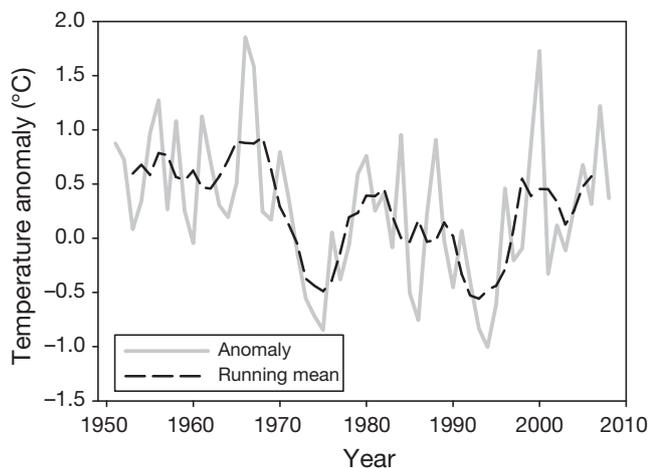


Fig. 2. Bottom temperature anomaly (°C) for the southern Grand Bank area (gray solid line) and 5 yr running mean of the anomaly (black broken line). The anomalies are relative to the average temperature during each year from 1971 to 2000, calculated from June of year  $y - 1$  to May of year  $y$

lasted until the mid-1990s. Condition has increased since then. Both males and females showed a trend to maturation at a younger age with estimated proportion mature at Age 5 increasing from less than 0.2 to 0.7 for females and 0.9 for males. GSI was more variable but was generally low for both sexes from the mid-1980s to the mid-1990s and increased thereafter, with a peak for both sexes in 1999. For females, relative fecundity was low from 1996 to 2004, a period when GSI reached its peak. Growth, condition, and reproductive factors were highly positively correlated between males and females, with correlation coefficients ranging from 0.5 to 0.9. The only exceptions were the residuals from the weight increment model, which were not significantly correlated between the sexes.

Temperature had little effect on growth in length or weight in either males or females (Fig. 5). For males, there was no significant effect of temperature on the log length increment ( $F_{2,152} = 1.85$ ). There was a significant effect of temperature on the residuals from the model of weight increment ( $F_{2,166} = 4.3$ ,  $p < 0.02$ ), but temperature accounted for very little of the variation, with  $r^2 = 0.05$ . For females, there was no significant effect of temperature on the residuals from the model of length increment ( $F_{2,142} = 1.05$ ) or on the residuals from the model of weight increment ( $F_{2,154} = 2.10$ ). Dividing the temperature series into June to September and October to May led to similar results, with no significant effect of temperature in either period on growth in length for males (June–September  $F_{2,152} = 0.1$ ; October–May  $F_{2,152} = 1.6$ ) or females (June–September  $F_{2,142} = 0.4$ ; October–May  $F_{2,142} = 0.9$ ). Growth in weight was significantly affected by temperature from October to May for males ( $F_{2,161} = 4.7$ ,  $p < 0.05$ ) and from June to September for females ( $F_{2,149} = 4.9$ ,  $p < 0.01$ ) but in both cases very little of the variation was accounted for, with  $r^2 = 0.06$ .

There was a significant effect of annual temperature on body condition (Fig. 5) for both males ( $\chi^2 = 14.9$ ,  $df = 2$ ,  $p < 0.001$ ) and females ( $\chi^2 = 36.6$ ,  $df = 2$ ,  $p < 0.00001$ ). Temperatures from June to September (males  $\chi^2 = 37.91$ ,  $df = 2$ ,  $p < 0.0001$ ; females  $\chi^2 = 38.8$ ,  $df = 2$ ,  $p < 0.0001$ ) and October to May (males  $\chi^2 = 10.5$ ,  $df = 2$ ,  $p < 0.01$ ; females  $\chi^2 = 35.6$ ,  $df = 2$ ,  $p < 0.0001$ ) also had a significant effect on body condition for both males and females. AIC showed very little difference in model fit for the 3 temperature series for either sex, with the maximum difference in AIC being  $< 1\%$ , even though the  $\chi^2$  for the June to September period for males was much greater than for the other 2 time periods. For both sexes, body condition was greater at higher and intermediate than at low temperatures for all 3 temperature series. There was no significant effect of temperature on liver condition (Fig. 5) for males (annual  $\chi^2 = 1.7$ ; June–September  $\chi^2 = 2.2$ ; October–May  $\chi^2 = 2.3$ ). For females, however, liver con-

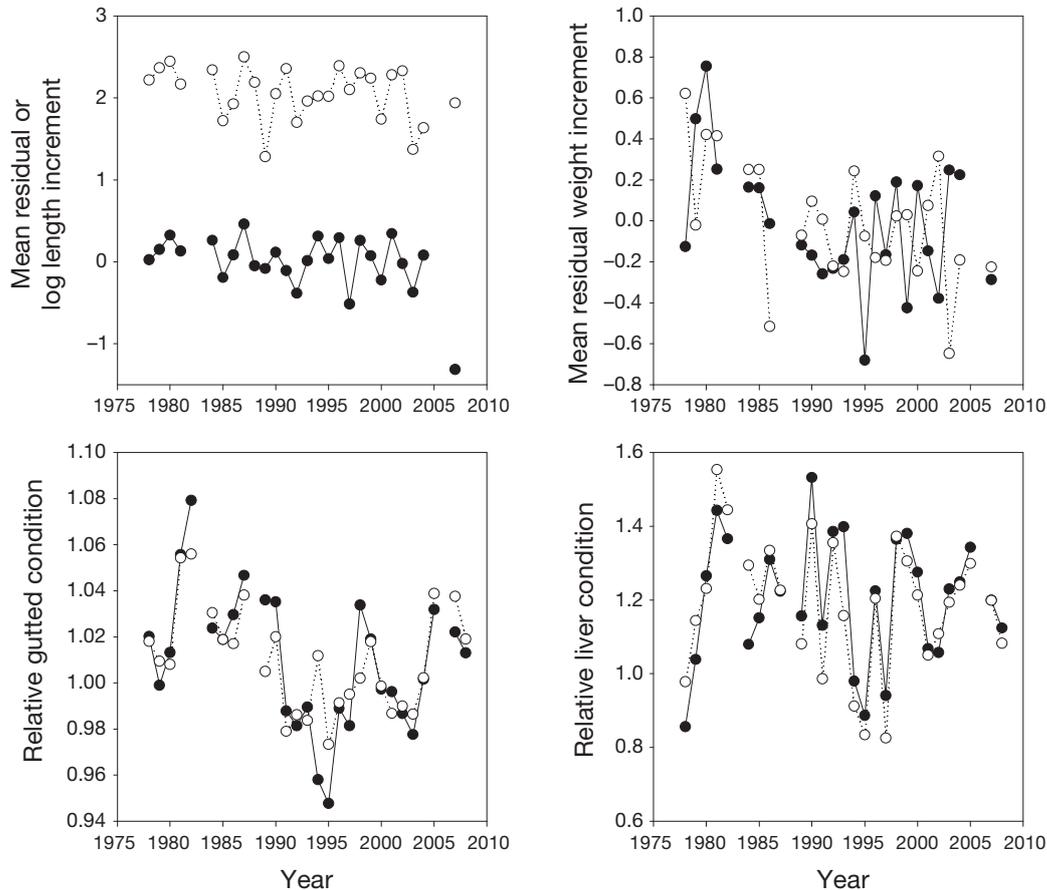


Fig. 3. *Gadus morhua*. Time series of growth (length and weight increment) and condition (relative gutted somatic condition and relative liver condition) variables available for (●) female and (○) male southern Grand Bank cod. See 'Materials and methods' for details of the calculation of the factors

dition was significantly greater (annual  $\chi^2 = 11.6$ ,  $df = 2$ ,  $p < 0.005$ ; June–September  $\chi^2 = 13.8$ ,  $df = 2$ ,  $p < 0.005$ ; October–May  $\chi^2 = 12.7$ ,  $df = 2$ ,  $p < 0.005$ ) at low temperatures than at intermediate or high temperatures. AIC indicated very little difference in model fit among the 3 temperature series.

Proportion mature at Age 5 was not affected by temperature in males (annual  $\chi^2 = 2.0$ ; June–September  $\chi^2 = 0.6$ ; October–May  $\chi^2 = 2.0$ ). For females, there was a significant effect of temperature over the whole year ( $\chi^2 = 6.9$ ,  $df = 2$ ,  $p < 0.05$ , Fig. 6) and over the October to May period ( $\chi^2 = 6.9$ ,  $df = 2$ ,  $p < 0.05$ ) but not over the June to September period ( $\chi^2 = 3.2$ ). Proportion of females mature at Age 5 was significantly greater at high than at intermediate temperatures, and the difference between low and intermediate temperatures approached significance. AIC indicated no difference in model fit between the 2 temperature series that produced a significant effect on proportion mature at Age 5 in females.

There was a significant effect of annual temperature on GSI for males ( $\chi^2 = 22.5$ ,  $df = 2$ ,  $p < 0.0001$ ) and for

temperature over the October to May period ( $\chi^2 = 18.3$ ,  $df = 2$ ,  $p < 0.0001$ ) but not for temperatures over the June to September period ( $\chi^2 = 4.6$ ). The same result was found for females, with a significant effect of annual temperature ( $\chi^2 = 20.2$ ,  $df = 2$ ,  $p < 0.0001$ , Fig. 6) and temperature over the October to May period ( $\chi^2 = 20.3$ ,  $df = 2$ ,  $p < 0.0001$ ) but not for June to September temperatures ( $\chi^2 = 3.1$ ). GSI at high temperature was significantly greater than at intermediate or low temperature. AIC indicated little difference between model fits for either males or females.

Relative fecundity was significantly affected by annual temperature ( $\chi^2 = 7.6$ ,  $df = 2$ ,  $p < 0.03$ ) as well as by temperature over the October to May period ( $\chi^2 = 6.2$ ,  $df = 2$ ,  $p < 0.05$ ) but not by temperatures from June to September ( $\chi^2 = 3.7$ ). Fecundity was significantly greater at low temperatures than at intermediate temperatures. Relative fecundity did not differ significantly between high and intermediate temperatures (Fig. 6). AIC indicated little difference in model fit between the annual and October to May temperature series.

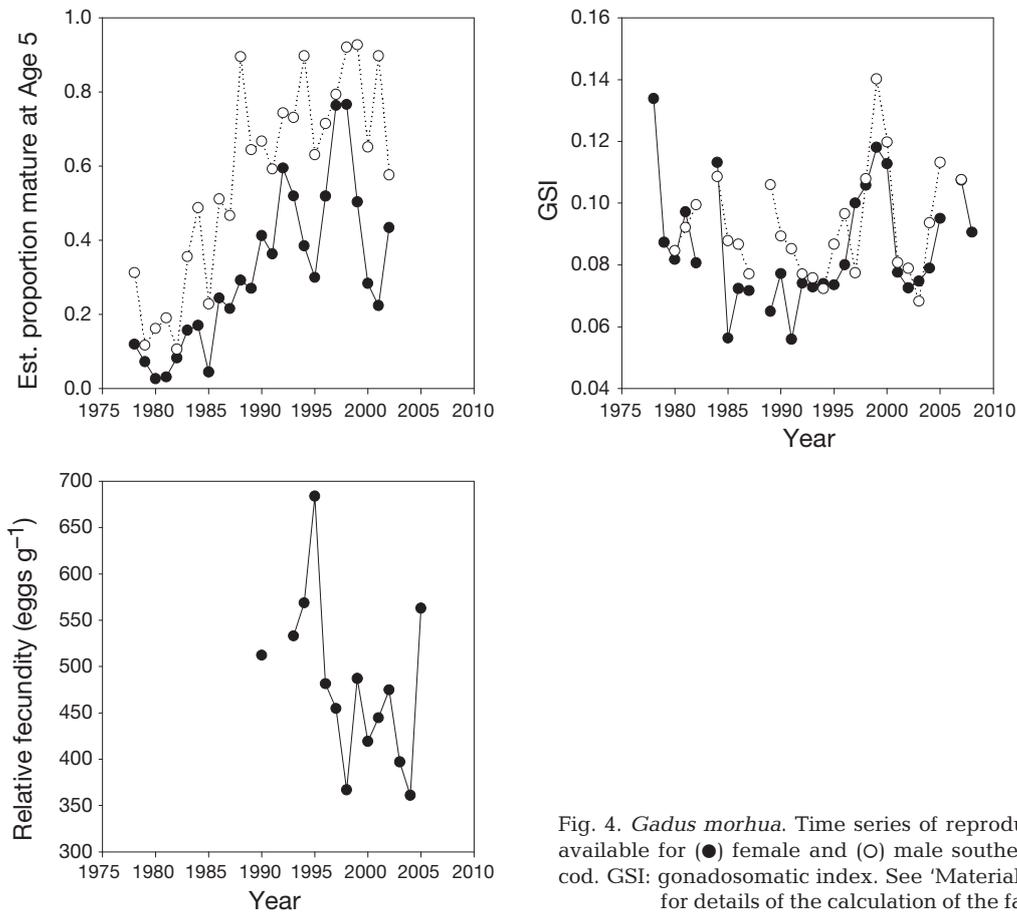


Fig. 4. *Gadus morhua*. Time series of reproductive variables available for (●) female and (○) male southern Grand Bank cod. GSI: gonadosomatic index. See 'Materials and methods' for details of the calculation of the factors

## DISCUSSION

The impact of temperature on metabolic processes (Brett 1979, Claireaux et al. 1995) means it can potentially affect decisions about the allocation of energy between growth, reproduction, and reserves or condition. In this study, interannual variation in growth in terms of length and weight was observed but could not be explained by temperature. Instead, temperature appeared to influence fish condition and reproductive investment. This indicates that for cod on the southern Grand Bank, temperature affects decisions about allocation of energy to reserves and reproduction but that temperature is not an important factor driving variation in growth, at least within the range of temperatures observed during the 30 yr period covered by this study.

The average temperatures for a reproductive year on the southern Grand Bank ranged from 0 to 2.8°C. This range of temperatures may be low compared to some other populations of cod (Neat & Righton 2007) and might help explain the lack of response in growth. However, even small changes in temperature can be important to fish since they are capable of detecting

and reacting to temperature differences as small as 0.1°C (Steffel et al. 1976). Cod have been shown to differentiate between and avoid temperatures varying by <0.5°C (Claireaux et al. 1995, Goddard et al. 1997). A change in temperature from 2 to 3°C can produce a 25% change in growth in cod (Bjornsson & Steinarsson 2002).

The lack of a temperature effect on growth may be surprising given that many studies have found such an effect for cod, with increased temperature leading to increased growth (Jørgensen 1992, Shelton et al. 1999, Dutil & Brander 2003, Peck et al. 2003, Swain et al. 2003). However, other studies have found that the impact of temperature may not be so straightforward and can differ depending on the thermal history experienced by the fish (Dutil et al. 1999, Rindorf et al. 2008). Fish can also vary in their growth response to temperature depending on size and life stage (Bjornsson et al. 2001, Yoneda & Wright 2005b) and population (Dutil et al. 2008). One important aspect that is not covered in our study is food availability. The optimum temperature for growth will depend on the amount of food available. As food availability declines, the most efficient growth occurs at lower temperatures where requirements for

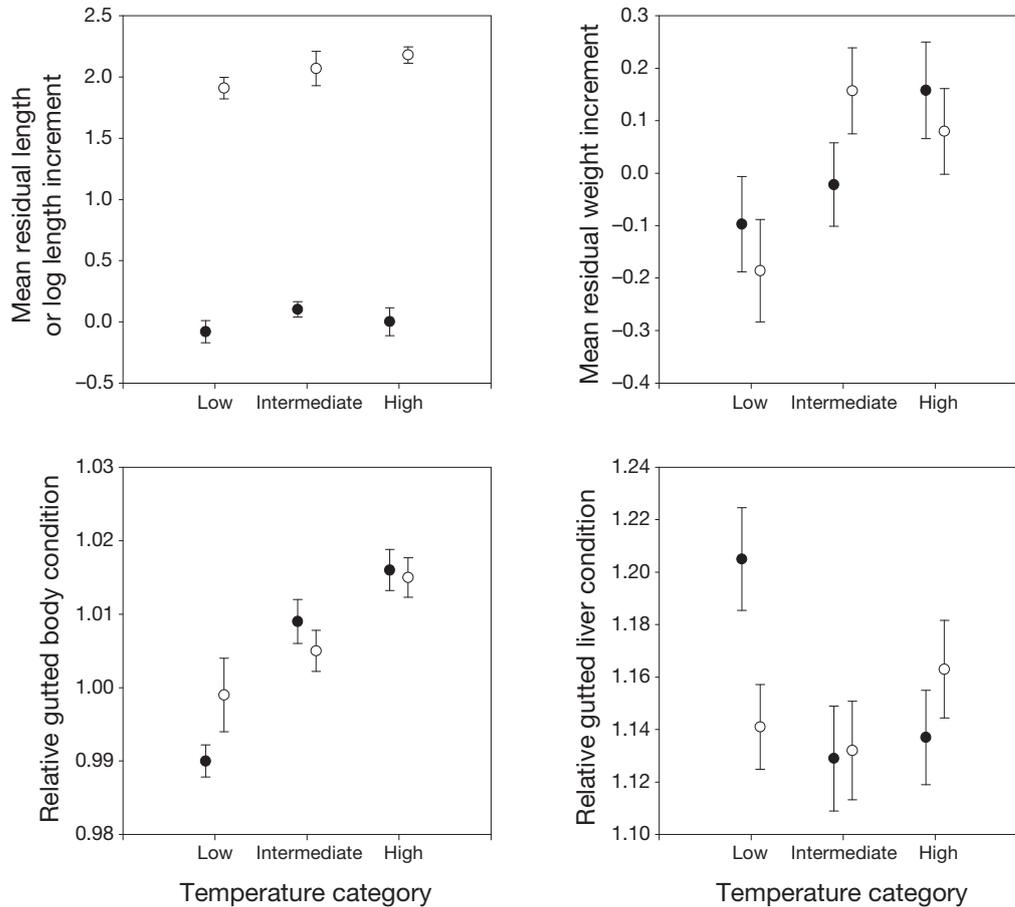


Fig. 5. *Gadus morhua*. Mean ( $\pm$ SE) of each of the growth and condition variables for each temperature category for (●) female and (○) male southern Grand Bank cod. Temperatures are anomalies for the period from June of year  $y - 1$  to May of year  $y$

maintenance are less because of lower metabolic rate (Brett 1979). However, as temperature declines further, fish can actually lose weight as feeding ceases and activity increases in an attempt to avoid cold water (Morgan 1992). A lack of increased growth at higher temperatures may indicate that prey availability was insufficient to allow for greater growth.

Condition of fish can also be influenced by temperature through its effects on metabolic rates and scope for growth. Dutil et al. (1999) found that populations living in warmer waters had higher whole body condition. Appetite may actually be suppressed at low temperature, leading to a decrease in condition (Jobling 1988, Morgan 1992). However, other studies have found little or no effect of temperature on condition (Yaragina & Marshall 2000, Yoneda & Wright 2005a, Pardoe et al. 2008). Changes in the abundance and type of prey available with varying temperature can also influence condition. For southern Grand Bank cod, we found that temperature significantly influenced both gutted body condition and liver condition. However, gutted body condition was highest at high tem-

peratures, while liver condition was highest at low temperatures. This is similar to the findings of Pardoe & Marteinsdóttir (2009), who found that cod in colder waters in Iceland had a lower body condition and higher liver condition than those in warmer waters. Liver and body condition respond at different rates to environmental conditions, and differences between the 2 indices could reflect differences in feeding intensity and or prey types that are available (Lambert & Dutil 1997). In the case of Icelandic cod, the fish living in colder conditions also had more prey available (Pardoe & Marteinsdóttir 2009). It is not known if there is a difference in the abundance or type of prey available in colder years in Divisions 3NO or at least in the areas inhabited by cod during colder years.

Measures of reproductive investment showed clear temperature effects. Many studies have shown that fish in warmer waters mature at a younger age (Sandstrom et al. 1995, Morgan & Colbourne 1999, Grift et al. 2003). However, for southern Grand Bank cod, both low and high temperatures resulted in earlier maturation. For this population it has also been shown that the

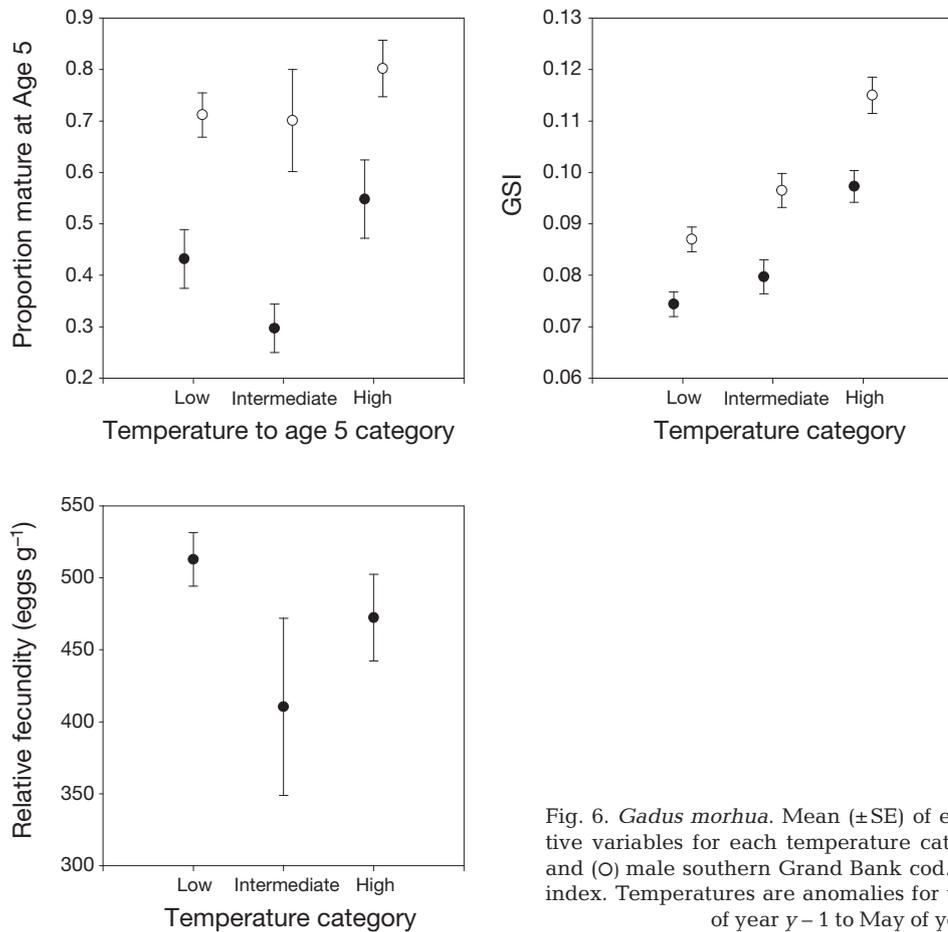


Fig. 6. *Gadus morhua*. Mean ( $\pm$ SE) of each of the reproductive variables for each temperature category for (●) female and (○) male southern Grand Bank cod. GSI: gonadosomatic index. Temperatures are anomalies for the period from June of year  $y-1$  to May of year  $y$

probabilistic reaction norm for maturation has shifted to maturation at a younger age (Olsen et al. 2005), with the conclusion that this was the result of fisheries-induced evolution. Fishing mortality has resulted in a large decline in this population (Morgan et al. 2007), and the selective effects of fishing have likely played a role. However, the results of this study indicate that the phenotypic effects of temperature have also played a role in the observed changes in maturation. An interaction between the 2 processes may have some influence on the shape of the temperature response seen here.

Fecundity of southern Grand Bank cod varied significantly with temperature, a finding that has been reported for other cod populations (Kjesbu et al. 1998, Kraus et al. 2000, Pörtner et al. 2001), as well as other Grand Bank groundfish species (Hodder 1965). There are several mechanisms through which temperature can influence fecundity, including through effects on metabolic rates, atresia, and gametogenesis (Fedorov 1971, Van Der Kraak & Pankhurst 1997, Pawson et al. 2000). Similar to liver condition, relative fecundity was highest at low temperatures, and this may be related to the greater stores of lipids at these temperatures.

GSI increased with increasing temperature. However, GSI was not correlated with relative fecundity. In fact, relative fecundity was low from 1996 to 2004, a period when GSI reached its peak. The lack of correlation with fecundity indicates that GSI may not be a good metric of reproductive investment, at least for females, a conclusion also drawn for northeast Arctic cod (Kjesbu et al. 1998). GSI may be better as an indicator of how close fish are to spawning. Potential fecundity can be set months before spawning, with the increase in GSI attributable to the development of oocytes rather than to an increase in their number (Zamarro 1992). The higher GSI of fish from warm years would thus suggest that fish are at a later stage of oocyte development (i.e. closer to spawning).

Males are thought to invest less energy into reproduction than females, at least in terms of energy allocated to the gonads (Rijnsdorp & Ibelings 1989, Bromley et al. 2000). As a result of this the effect of temperature on energy allocation, decisions may differ between the sexes. Yoneda & Wright (2005a,b) found that low temperatures had more of an effect on reproduction of first-time spawning females than males. In our study, all of the metrics, except the measure of

growth in weight, were highly correlated between males and females. In this population, the sexes seem to make the same types of decisions about energy allocation over a range of temperatures. It would be interesting to be able to evaluate these decisions on a finer scale to determine if the magnitude as well as the direction of the decisions about energy allocation is the same for the sexes.

For southern Grand Bank cod, varying temperature resulted in differences in energy allocation. Although there was no effect of temperature on growth, there were significant temperature effects on energy storage and on reproductive investment. It would appear that decisions about energy allocation to growth were independent of temperature and that variation in growth was more related to some other factor, perhaps prey availability. Reproductive investment seemed to be higher at both lower and higher temperatures, with both sexes maturing younger at these temperatures and females investing less into egg production at intermediate temperatures. The quality and quantity of prey can play a role in the amount of energy invested in reproduction (Rideout & Rose 2006), and temperature may impact prey available to cod.

The effects of temperature on condition and reproduction occur at different times of the year. Temperature affects body and liver condition (in females) in a similar way throughout the year, with lower temperatures resulting in more storage in the liver and higher temperature leading to higher body condition. On the other hand, the effects of temperature on reproductive investment occur during the October to May period, which is the time when cod are developing their gonads. Temperature impacts may not be equal throughout this period. Skjæraasen et al. (2006, 2009) found that decisions about fecundity and skip-spawning are made early in the oocyte ripening period.

The effects of temperature on allocation of energy observed here mean that temperature variation will affect the productivity of the population through effects on reproductive potential. Lower reproductive potential at intermediate temperatures could lead to lower recruitment. If such conditions persisted, weaker year classes would lead to a lower level of sustainable harvest. Incorporating these changes into our understanding of sustainable fishing rates should improve our ability to successfully manage this population.

*Acknowledgements.* We thank the many people involved in the collection and processing of these samples and oceanographic data. This paper was greatly improved by the comments of reviewers. This is a contribution of the NAFO Working Group on Reproductive Potential. The study was funded in part by the International Governance Strategy of Fisheries and Oceans Canada.

#### LITERATURE CITED

- Bjornsson B, Steinarsson A (2002) The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 59:494–502
- Bjornsson B, Steinarsson A, Oddgeirsson M (2001) Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). *ICES J Mar Sci* 58:29–38
- Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish physiology*, Vol III. Academic Press, New York, p 599–675
- Bromley PJ, Ravier C, Witthames PR (2000) The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawning turbot. *J Fish Biol* 56:264–278
- Claireaux G, Webber DM, Kerr SR, Boutilier RG (1995) Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. *J Exp Biol* 198:49–60
- Colbourne EB, Fitzpatrick C, Sencial D, Stead P, Craig J, Bailey W (2005) An assessment of physical oceanographic environment in NAFO sub-areas 2 and 3 for 2004. NAFO SCR Doc 23, Ser No 5107, Dartmouth, NS
- Doubleday WG (1981) Manual on groundfish surveys in the Northwest Atlantic. NAFO Sci Coun Stud 2:7–55
- Dutil JD, Brander K (2003) Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. *Fish Oceanogr* 12:502–512
- Dutil JD, Castonguay M, Gilbert D, Gascon D (1999) Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the northwest Atlantic. *Can J Fish Aquat Sci* 56:1818–1831
- Dutil JD, Jabouin C, Larocque R, Desrosiers G, Blier PU (2008) Atlantic cod (*Gadus morhua*) from cold and warm environments differ in their maximum growth capacity at low temperatures. *Can J Fish Aquat Sci* 65:2579–2591
- Fedorov KY (1971) The state of the gonads of the Barents Sea Greenland halibut [*Reinhardtius hippoglossoides* (Walb.)] in connection with failure to spawn. *J Ichthyol* 11:673–682
- Goddard SV, Morgan MJ, Fletcher GL (1997) Influence of plasma antifreeze glycoproteins on temperature selection by Atlantic cod (*Gadus morhua*) in a temperature gradient. *Can J Fish Aquat Sci* 54(Suppl 1):88–93
- Griff RE, Rijnsdorp AD, Barot S, Heino M, Dieckman U (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar Ecol Prog Ser* 257:247–257
- Hodder VM (1965) The possible effects of temperature on the fecundity of Grand Bank haddock. *ICNAF Spec Publ* 6: 515–522
- Jobling M (1988) A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture* 70: 1–19
- Jørgensen T (1992) Long-term changes in growth of Northeast Arctic cod (*Gadus morhua*) and some environmental influences. *ICES J Mar Sci* 49:263–277
- Jørgensen C, Fiksen O (2006) State-dependent energy allocation in cod (*Gadus morhua*). *Can J Fish Aquat Sci* 63: 186–199
- Kjesbu OS, Witthames PR, Solemdal P, Greer Walker M (1998) Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J Sea Res* 40:303–321
- Kraus G, Müller A, Trella K, Köster FW (2000) Fecundity of Baltic cod: temporal and spatial variation. *J Fish Biol* 56:1327–1341
- Lambert Y, Dutil JD (1997) Can simple condition indices be

- used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? Can J Fish Aquat Sci 54(Suppl 1):104–112
- Lambert Y, Dutil JD (2000) Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Can J Fish Aquat Sci 57:815–825
- Lambert Y, Yaragina NA, Kraus G, Marteinsdottir G, Wright PJ (2003) Using environmental and biological indices as proxies for egg and larval production of marine fish. J Northwest Atl Fish Sci 33:115–159
- Mello LGS, Rose GA (2005) Seasonal growth of Atlantic cod: effects of temperature, feeding and reproduction. J Fish Biol 67:149–170
- Morgan MJ (1992) Low-temperature tolerance of American plaice in relation to declines in abundance. Trans Am Fish Soc 121:399–402
- Morgan MJ, Colbourne EB (1999) Variation in maturity-at-age and size in three populations of American plaice. ICES J Mar Sci 56:673–688
- Morgan MJ, Hoenig JM (1997) Estimating maturity-at-age from length stratified sampling. J Northwest Atl Fish Sci 21:51–63
- Morgan MJ, Murphy EF, Bratley J (2007) An assessment of the cod stock in NAFO Divisions 3NO. NAFO SCR Doc 40, Dartmouth, NS
- Myers RA, Mertz G, Bishop CA (1993) Cod spawning in relation to physical and biological cycles of the northern North-west Atlantic. Fish Oceanogr 2:154–165
- Neat F, Righton D (2007) Warm water occupancy by North Sea cod. Proc Biol Sci 274:789–798
- Olsen EM, Lilly GR, Heino M, Morgan MJ, Bratley J, Dieckman U (2005) Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 62:811–823
- Pardoe H, Marteinsdóttir G (2009) Contrasting trends in two condition indices: bathymetric and spatial variation in autumn condition of Icelandic cod *Gadus morhua*. J Fish Biol 75:282–289
- Pardoe H, Thordarson G, Marteinsdottir G (2008) Spatial and temporal trends in condition of Atlantic cod *Gadus morhua* on the Icelandic shelf. Mar Ecol Prog Ser 362: 261–277
- Pawson MG, Pickett GD, Witthames PR (2000) The influence of temperature on the onset of first maturity in sea bass. J Fish Biol 56:319–327
- Peck MA, Buckley LJ, Caldarone EM, Bengston DA (2003) Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Mar Ecol Prog Ser 251: 233–243
- Pörtner HO, Berdal B, Blust R, Brix O and others (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Cont Shelf Res 21:1975–1997
- Rideout RM (1999) Aspects of the reproductive cycle of Atlantic cod, *Gadus morhua* L., from inshore Newfoundland. MSc thesis, Memorial University of Newfoundland and Labrador, St. Johns, NL
- Rideout RM, Rose GA (2006) Suppression of reproduction in Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 320: 267–277
- Rideout RM, Rose GA, Burton MPM (2005) Skipped spawning in female iteroparous fishes. Fish Fish 6:50–72
- Rijnsdorp AD (1994) Population-regulating processes during the adult phase in flatfish. Neth J Sea Res 32:207–223
- Rijnsdorp AD, Ibelings B (1989) Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. J Fish Biol 35:401–415
- Rindorf A, Jensen H, Schrum C (2008) Growth, temperature, and density relationships of North Sea cod (*Gadus morhua*). Can J Fish Aquat Sci 65:456–470
- Roff DA (1983) An allocation model of growth and reproduction in fish. Can J Fish Aquat Sci 40:1395–1404
- Sandstrom O, Neuman E, Thoresson G (1995) Effects of temperature on life history variables in perch. J Fish Biol 47: 652–670
- Shelton PA, Lilly GR, Colbourne E (1999) Patterns in the annual weight increment for Div. 2J+3KL cod and possible prediction for stock projection. J Northwest Atl Fish Sci 25:151–159
- Skjæraasen JE, Nilsen T, Kjesbu OS (2006) Timing and determination of fecundity in Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 63:310–320
- Skjæraasen JE, Kennedy J, Thorsen A, Fonn M, Strand BN, Mayer I, Kjesbu OS (2009) Mechanisms regulating oocyte recruitment and skipped spawning in Northeast Arctic cod (*Gadus morhua*). Can J Fish Aquat Sci 66:1582–1596
- Steffel S, Dizon AE, Magnusson JJ, Neill WH (1976) Temperature discrimination by captive free-swimming tuna, *Euthynnus affinis*. Trans Am Fish Soc 105:588–591
- Swain DP, Morgan MJ (2001) Sex-specific temperature distribution in four populations of American plaice *Hippoglossoides platessoides*. Mar Ecol Prog Ser 212:233–246
- Swain DP, Sinclair AF, Castonguay M, Chouinard GA, Drinkwater KF, Fanning LP, Clark DS (2003) Density- versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and on the Scotian Shelf. Fish Res 59:327–341
- Templeman W, Hodder VM, Wells R (1978) Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. ICNAF Res Bull 13:53–65
- Van Der Kraak G, Pankhurst NW (1997) Temperature effects on the reproductive performance of fish. In: Wood CM, McDonald DG (eds) Global warming: implications for freshwater and marine fish. Cambridge University Press, Cambridge, p 159–176
- Wiborg KF (1951) The whirling vessel. An apparatus for the fractionating of plankton samples. Fiskeridir Skr Ser Havunders 9:1–16
- Wootton RJ (1990) Ecology of teleost fishes. Fish and fisheries, Ser 1. Chapman & Hall, London
- Yaragina NA, Marshall CT (2000) Trophic influences on inter-annual and seasonal variation in the liver condition index of northeast Arctic cod (*Gadus morhua*). ICES J Mar Sci 57:42–55
- Yoneda M, Wright PJ (2005a) Effect of temperature and food availability on reproductive investment of first-time spawning male Atlantic cod *Gadus morhua*. ICES J Mar Sci 62:1387–1393
- Yoneda M, Wright PJ (2005b) Effects of varying temperature and food availability on growth and reproduction in first-time spawning female Atlantic cod. J Fish Biol 67: 1225–1241
- Zamarro J (1992) Determination of fecundity in American plaice (*Hippoglossoides platessoides*) and its variation from 1987 to 1989 on the tail of the Grand Bank. Neth J Sea Res 29:205–209