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Growth and condition in relation to the lack of recovery of northern cod

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Growth and condition in fishes have been taken as indicating levels of energy available for survival and reproduction, major components of a population's productivity. After a rapid collapse in population size, northern (NAFO Division 2J3KL) cod (*Gadus morhua*) remained at a very low level of abundance for 20 years. We investigated the potential for poor growth and condition to have played a role in the collapse and lack of recovery of northern cod. Juveniles and adult males and females all showed similar patterns. Perceptions about the importance of growth and condition to population status depended on the metrics and area examined. When the northern cod population was declining, the northern areas of the population clearly had reduced growth and condition, while these metrics improved in the south. Results were equivocal as to the potential role of growth and condition in the continued low abundance of northern cod and, to some extent, depended on the nature of the metric being examined. Indices of condition, which included lipid storage in the form of liver weight, were generally lower in the north while the stock remained at a low level. Metrics associated with longer-term protein storage returned to precollapse levels quickly following the period of collapse. An index of food availability was more closely related to growth and condition than was temperature. These results point to the need both for studies of growth and condition in a population to have a comprehensive time-series of data covering the entire range of the population and the need for a better understanding of the causes and implications of changes in different metrics of condition.

Keywords: cod, condition, growth, population growth.

Introduction

Growth and condition in fishes have been taken as indicating levels of energy available for survival and reproduction, major components of a population's productivity (Lloret *et al.*, 2014; Morgan *et al.*, 2014). Studies have suggested that fish with low growth and/or poor condition have decreased survival probability (Dutil *et al.*, 1999; Lambert and Dutil, 2000; Rose and O'Driscoll, 2002). Good recruitment is more likely for fish in good condition (Marshall *et al.*, 2000; Ratz and Lloret, 2003) as a result of the impact of growth and condition on various aspects of reproduction. Fecundity is higher for larger fish and may be higher for fish in better condition (Kjesbu *et al.*, 1991; Rijnsdorp, 1994; Rideout and Morgan, 2010). Fish in good condition may produce larger, more viable eggs (Marteinsdottir and Steinarsson, 1998) and are less likely to skip spawning (Rideout *et al.*, 2006).

A variety of factors affect the growth and condition of fishes, food and temperature being two of the most important. Greater food availability can lead to increased growth and condition (Lambert and Dutil, 2000; Yaragina and Marshall, 2000; Rindorf *et al.*, 2008). Growth will increase with temperature if there is sufficient food (Bjornsson and Steinarsson 2002). Condition has also been found to increase with temperature in some studies (Jobling, 1988; Morgan, 1992; Dutil *et al.*, 1999; Sandeman *et al.*, 2008). As food availability declines, growth is most efficient at lower temperatures (Brett, 1979). Growth and condition will also be affected by decisions made about the allocation of energy to competing processes, particularly growth and reproduction (Lambert and Dutil, 2000). These decisions are often different depending on the life stage and sex of the individual (Rijnsdorp and Ibelings, 1989; Bromley *et al*., 2000; Swain and Morgan, 2001; Yoneda and Wright, 2005a,b; Jørgensen and Fiksen, 2006).

The measurement of growth in fishes is relatively straightforward and is usually expressed as size at age or the increment in size from one age to the next. Measurement of condition is somewhat more complicated. Ideally, the use of a metric of condition as an indicator of energy content or stores should be validated (McPherson *et al*., 2011; Lloret *et al*., 2014). Different metrics of condition may respond on different time-scales to availability of food resources (Holdway and Beamish, 1984; Lambert and Dutil, 1997a). In cod (*Gadus morhua*) that store lipid in the liver (Holdway and Beamish, 1984), metrics of condition based on liver size change very rapidly in relation to changes in food availability, while those based on body weight are slower to respond (Holdway and Beamish, 1984; Lambert and Dutil, 1997a). Analyses of both growth and condition can also be complicated by seasonal cycles (Holdway and Beamish, 1984; Dutil *et al*., 2003; Mello and Rose, 2005; Mullowney and Rose, 2014).

Given that growth and condition reflect the energy available to individuals in a population, low growth and condition could be expected to be related to reduced productivity. In particular, low growth and condition could cause or exacerbate population decline and delay population rebuilding. Such hypotheses have been proposed for the northern cod population off Newfoundland, Canada. This population declined dramatically during the early 1990s and, although there has been some increase in recent years, it has remained at a very low level (DFO, 2016). The collapse of the northern cod population occurred during a period of low temperature which began in the 1980s and continued into the mid-1990s (Colbourne, 2004; Colbourne *et al*., 2016). At the same time, the population of an important prey of cod, capelin (*Mallotus villosus*), declined to very low levels and, despite some increase since the mid-2000s, remains at low abundance (Buren *et al*., 2014a; DFO, 2015). A number of studies have suggested that these events are linked and that the lack of recovery (and perhaps, to some extent, the population collapse) of northern cod is a result of the low abundance of capelin (Rose and O'Driscoll, 2002; Sherwood *et al*., 2007; Buren *et al*., 2014b; Mullowney and Rose, 2014).

Studies that have examined growth and/or condition of northern cod relative to population trajectory have often only had data from a limited part of the geographic range of the population, from different, sometimes limited, time-periods and, to some extent, used different indices of condition. In this study, we examine both growth and condition of northern cod using multiple indices of condition. We employ data from the entire stock area with a time-scale spanning from before stock collapse and extending to a period of recent stock increase. Furthermore, we examine growth and condition for juveniles, adult males, and adult females separately and examine the possible impact of temperature and food availability. We ask whether decreased growth and condition is associated with the lack of recovery of northern cod. What can this tell us about the use of growth and condition as indicators of population productivity?

Material and methods

Data examined were from the autumn research vessel bottom-trawl survey conducted by Fisheries and Oceans Canada (Figure 1). The survey has a stratified random design, with stratification being

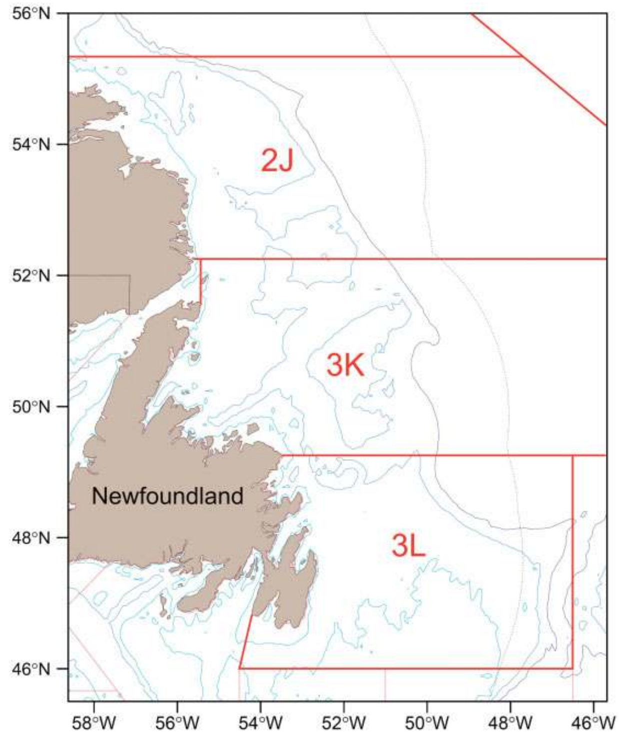

Figure 1. Map of study area showing the Northwest Atlantic Fisheries Organization (NAFO) divisions.

by depth. The survey is generally conducted during October–December, although it has occasionally extended into January. Biological data were from 1981 to 2012, years in which all three Northwest Atlantic Fisheries Organization (NAFO) divisions were covered by the survey. During the survey, fish were sampled for age, length, sex, maturity, total body weight, gutted weight, liver weight, and weight of some other internal organs. Ages 3–6 only were used in the analyses. Age 3 is well selected by the survey gear; in some years, there were very few fish older than age 6. Fish were divided into three groups (juveniles, adult males, and adult females) based on the maturity staging conducted at sea. As the main aim of the study was to examine growth and condition during periods with different levels of population size, data were divided into four time-periods based on trends in survey biomass. To do this, we used an index of population size from research vessel surveys during 1983–2012. The survey index prior to 1983 is not directly comparable, but stock size is thought to have been at least as high in 1981–1982 as in 1983 (Figure 2). We defined period 1 as 1981–1990 when the stock was at a relatively high level. During 1991–1995, the stock was in a period of rapid decline (period 2). Period 3 was 1996–2005, a time when the stock remained at an extremely low level with no sign of increase. The years 2006–2012 comprised period 4 when there was some increase in stock biomass, although the stock remained well below precollapse levels.

Growth (length at age) was analysed using generalized linear models with gamma error and an identity link function. The full model included only the two interactions of interest to this study, i.e. whether the different groups and divisions had a different pattern in length at age across period. Hence, the full model

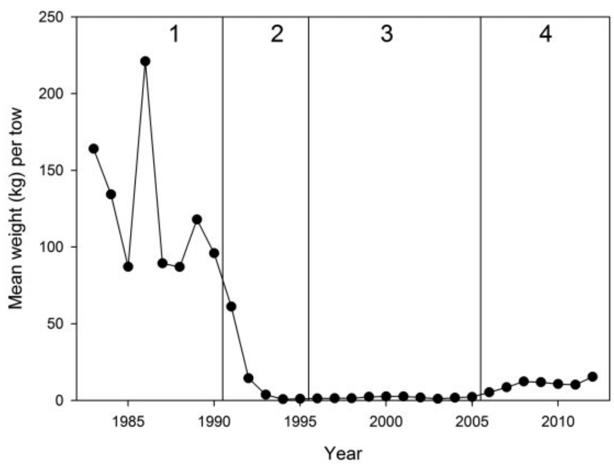

Figure 2. Biomass index (mean kg per tow) for northern cod during 1983–2012 from research vessel surveys. The lines and numbers indicate the different periods examined in the study. Period 1, the population was at a relatively high level; period 2, the population was rapidly declining; period 3, the population remained at an extremely low level; and period 4: although still at a very low level, some increase in population size was evident.

contained a factor for division (2J, 3K, or 3L), age, group (juvenile, adult male or adult female), period (1–4), a group–period interaction, and a division–period interaction. All factors were categorical. Since the proportion of adults at age changed over time, both group and age were included. The significance of factors was determined by backwards elimination, in which the full model was the starting point and factors were eliminated which did not result in a significant increase in deviance (McCullagh and Nelder, 1983).

Three condition indices were used: total body condition, gutted body condition, and liver condition. Relative condition indices were used in order to account for the confounding effect of length on condition (LeCren, 1951). A length–weight relationship was fitted to the relevant data (i.e. total body weight vs. length, gutted weight vs. length, or liver weight vs. length). The condition factor for an individual was then the actual weight divided by the weight predicted from the length–weight relationship. Analyses for differences in condition were conducted separately for each group and for each division; therefore, the length–weight relationships were also by group and division. Given potential changes in length over the time-period that we examined, we elected not to use Fulton's condition factor. However, because relative condition indices were highly correlated ($r^2 > 0.94$) with Fulton's, results with Fulton's would be similar. Buren *et al.* (2014b) based their conclusion that lack of recovery of northern cod was related to condition on an examination of the frequency distribution of annual values of total body condition, which indicated that the variance in condition was smaller while abundance of cod was low. We, therefore, examined both the mean and variance of the condition data. We constructed hierarchical models in a Bayesian framework where condition either had a different mean and variance across time periods, a different mean but the same variance, or the same mean and variance across time-periods. The prior for mean of condition had a normal distribution with a mean of 1 and a precision of 0.001. The prior for variance was a uniform distribution from 0.01 to 1000. A total of 31 000 iterations were run for each model, with a burn-in of 1000. The model giving the lowest deviance information criteria (DIC) was taken as the best model. If models had a difference in DIC of <5, then the simplest model was taken as the best.

There is no single capelin index that covers the distribution of capelin and cod and no model of capelin stock size (DFO, 2015). Therefore, in order to investigate the relationship between food availability and growth and condition, we examined stomach weight over time as a proxy for food availability. Stomach weight was not available for all individuals, so it was calculated by subtracting the carcass gutted weight and the weight of other organs from the total body weight. This calculated stomach weight was highly correlated with measured stomach weight for those fish that had this measurement ($r^2 = 0.67$, $p < 0.0001$). Since stomach weight could be related to body size, our index of stomach weight was stomach weight/total body weight. The temperature at which each individual was captured was used as a measure of temperature occupied and was used to explore the potential impact of temperature on growth and condition. Variation in the stomach weight index and temperature occupied was analysed using generalized linear models in the same fashion as growth. The relationship of the stomach weight index and temperature with growth and condition was examined using Spearman rank correlation. Significance levels were adjusted for the number of tests conducted for each (36), leading to a significance level of 0.0014.

Sample size varied for each group, period, and metric measured (Table 1). This was because not all measurements were made on all specimens and also because, for the relative condition indices, a few observations that were obvious outliers were removed.

Results

There was a significant difference in length at age across periods (Table 2). Group, age, and NAFO division also had significant effects. For all groups in Divisions 2J and 3K, length at age was lowest in period 2, when the population was declining (Figure 3). Division 3L was more variable, but showed little indication that length at age was depressed in period 2. For all divisions, length at age in periods 3 and 4 was generally no different than in period 1, prior to the collapse of the population. Adult fish were larger than juveniles of the same age, and adult females were larger than adult males. Fish size increased with age and from north to south. There were insufficient data to include age 6 in the analyses of juveniles and age 3 in the analyses of adults, except for adult males in 2J and 3K. Age 4 could not be included for Division 3L adult females.

In Divisions 2J and 3K, condition indices for all groups were generally lowest in period 2 (Table 3, Figure 4), when the population was rapidly declining, and increased thereafter. There were some differences in the pattern, depending on the metric of condition. Both total and liver condition generally remained lower than precollapse levels in period 3, while gutted condition had returned to the levels seen in period 1. In Division 2J in period 4, total and liver condition were still lower than in period 1, while in 3K, all indices had returned to the levels of period 1. Patterns in 3L were different, with all condition indices being lowest in the period before collapse (period 1). Within a division, juveniles, adult males, and adult females tended to show the same trends in condition across period and generally had the same best model type. There were some minor exceptions, e.g. liver condition in

Table 1. Sample size for each group (juvenile, adult male, adult female), NAFO division, and time-period (1 = 1981–1990, 2 = 1991–1995, 3 = 1996–2005, 4 = 2006–2012) used in the analyses.

		Juvenile				Adult male				Adult female			
Division 2J	**Age**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Length	3	438	157	392	377	59	90	278	249				
	4	242	94	115	100	174	144	178	210	20	57	110	97
	5	98	25	6	23	201	89	54	72	136	103	60	87
	6					168	23	10	22	176	48	13	27
Total condition		795	319	580	501	602	347	534	553	333	214	220	241
Gutted condition		792	276	514	502	602	346	520	553	332	211	217	241
Liver condition		672	299	544	455	494	327	510	516	272	201	215	229
Stomach weight		654	298	542	491	526	347	514	547	306	208	185	208
Division 3K	**Age**	**Juvenile**				**Adult male**				**Adult female**			
		1	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Length	3	388	345	815	536	32	93	351	248				
	4	227	121	247	199	100	145	251	276	19	73	153	191
	5	53	24	31	43	100	125	113	248	71	165	110	269
	6					94	80	10	152	115	23	201	94
Total condition		681	506	1389	789	324	443	768	926	216	359	334	704
Gutted condition		680	493	1094	783	326	443	725	924	216	357	332	702
Liver condition		506	481	1285	738	265	419	731	889	200	342	326	682
Stomach weight		506	490	1269	753	271	441	735	905	174	350	292	649
Division 3L	**Age**	**Juvenile**				**Adult male**				**Adult female**			
		1	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Length	3	294	253	499	551								
	4	228	149	139	252	34	108	130	204				
	5	86	55	42	57	50	96	63	163	26	81	56	199
	6					70	94	29	134	114	32	128	70
Total condition		559	489	700	876	161	354	354	670	102	251	163	472
Gutted condition		628	481	684	868	159	350	349	663	101	244	161	468
Liver condition		500	443	652	815	151	321	341	635	93	234	152	456
Stomach weight		535	455	666	849	153	297	222	496	98	193	88	322

The sample size for temperature is not given as it is the same as for total condition. Stomach weight refers to the calculated stomach weight index.

Division 3K (Table 3). The results for variance in the condition indices were somewhat equivocal; in 13 of 27 cases, the best model had the same variance in all periods. For relative gutted condition, in no case was the best model the one with different variance across period (Table 3).

For the stomach weight index, there was a significant NAFO division–period interaction (Δ deviance 56.2, Δ d.f. = 6, $p < 0.0001$), indicating that the change in stomach weight across period differed significantly by area. There was no significant group–period interaction (Δ deviance 1, Δ d.f. = 6, n.s.); although the pattern in the stomach weight index differed across period between divisions, within a division the pattern was the same for all groups (Figure 5). The stomach weight index was lowest in period 2 in Division 2J, in period 3 in Division 3K, and in period 1 in Division 3L. The change in temperature across period also differed by area (Δ deviance 30, Δ d.f. = 6, $p < 0.0001$), but the change was the same across groups within a division (Δ deviance 5, Δ d.f. = 6, n.s.). The temperature occupied by all groups was lowest in period 1, with a general increase across periods. Temperature in period 4 was similar to that in period 3 in 2J and 3K, while temperature in 3L continued to increase in period 4 (Figure 6).

Correlations of condition and length with the stomach weight index were generally stronger than the correlations with temperature (Table 4). All but one of the correlations with the stomach weight index were significant, and particularly for relative liver condition and length, the magnitude of the correlation coefficient was much larger than for the correlations with temperature. The correlation of the stomach weight index with total condition is confounded by the fact that total condition includes the weight of the stomach, but is included in Table 4 for completeness.

Discussion

Fish condition and growth are dependent on the environment to which the fish are exposed. A decline in growth and condition when the environment is poor can indicate reduced productivity, including increased mortality (Lloret *et al.*, 2014). Low condition and growth have been associated with population decline in a number of cases (Lambert and Dutil, 1997a,b; Marshall *et al.*, 2000; Bundy and Fanning, 2005; Zimmerli *et al.*, 2007) and may have also contributed to the decline in northern cod, at least in the northern areas. Growth and condition were clearly depressed in the two northern divisions while the population was collapsing during period 2. This may have exacerbated the effect of fishing mortality (Shelton, 2005; Lilly *et al.*, 2013).

Previous studies have suggested that poor growth and/or condition were also related to the lack of recovery of northern cod (Rose and O'Driscoll, 2002; Sherwood *et al.*, 2007; Buren *et al.*, 2014b; Mullowney and Rose, 2014). However, only Buren *et al.* (2014b) used a time-series extending from before the period of collapse and covering the geographic range of northern cod. They examined Fulton's K based on total body condition during 1978–

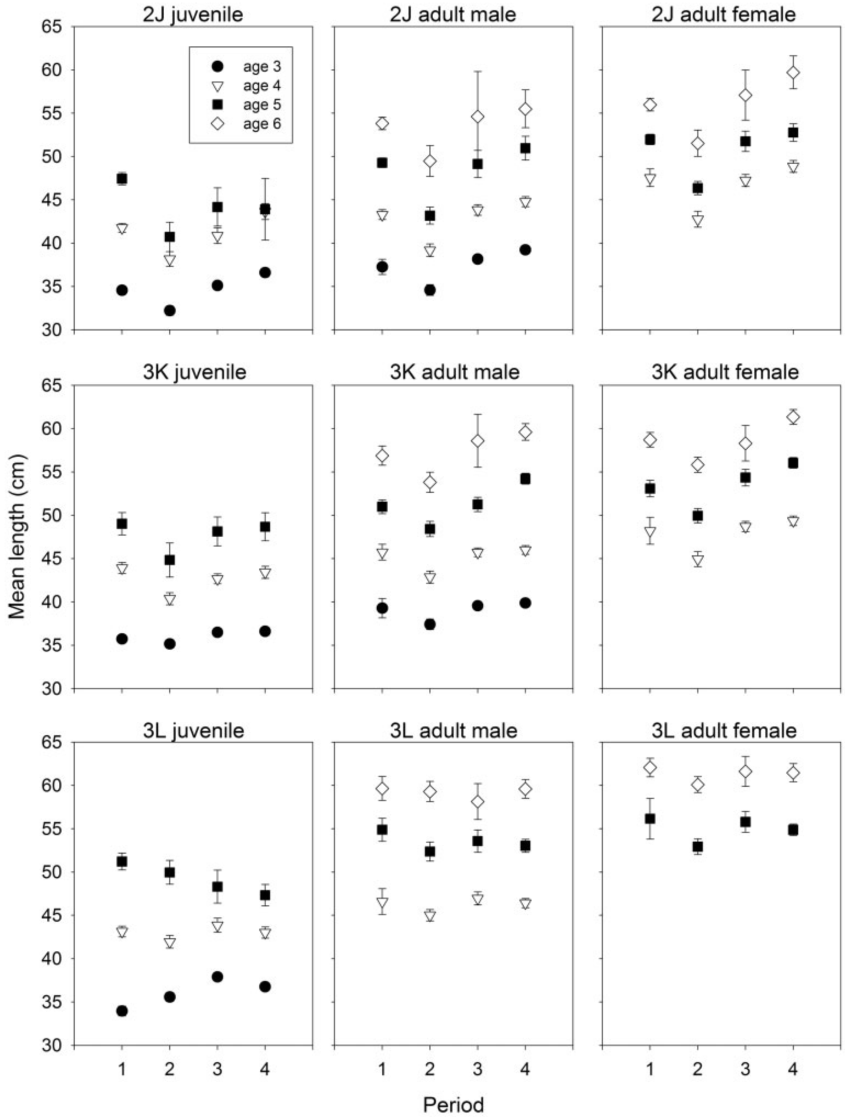

Figure 3. Mean length at age (cm) for ages 3–6 for juveniles, adult males, and adult females in each NAFO division (2J, 3K, 3L) in each period (see Figure 2). Mean and 95% CIs are shown.

Table 2. Results of model comparisons for length at age using backwards elimination of factors.

Model	Δ deviance	Δ d.f.	*p* value
NAFO age group period group*period NAFO*period			
NAFO age group period group*period	3.4	6	n.s.
NAFO age group period NAFO*period	0.9	6	n.s.
NAFO age group period	3.7	6	n.s.
NAFO age group	15	3	0.002
NAFO age period	18.2	2	0.0001
NAFO group period	173.7	3	0.0001
Age group period	7.6	2	0.02

The change in deviance, change in degrees of freedom (d.f.), and *p* value are given; n.s., not significant.

2006 and found lower mean condition in Divisions 2J and 3K in the 1990s and 2000s and a tendency for a narrower distribution of condition. Although our findings for total body condition are generally in agreement, overall results of our study are equivocal as to the potential role of growth and condition in the continued low abundance of northern cod and depend on the nature of the metric being examined. Indices of condition with some association with lipid storage, relative liver condition, and relative total condition (which includes the weight of the liver) were generally lower in the two northern divisions in period 3 than in the period

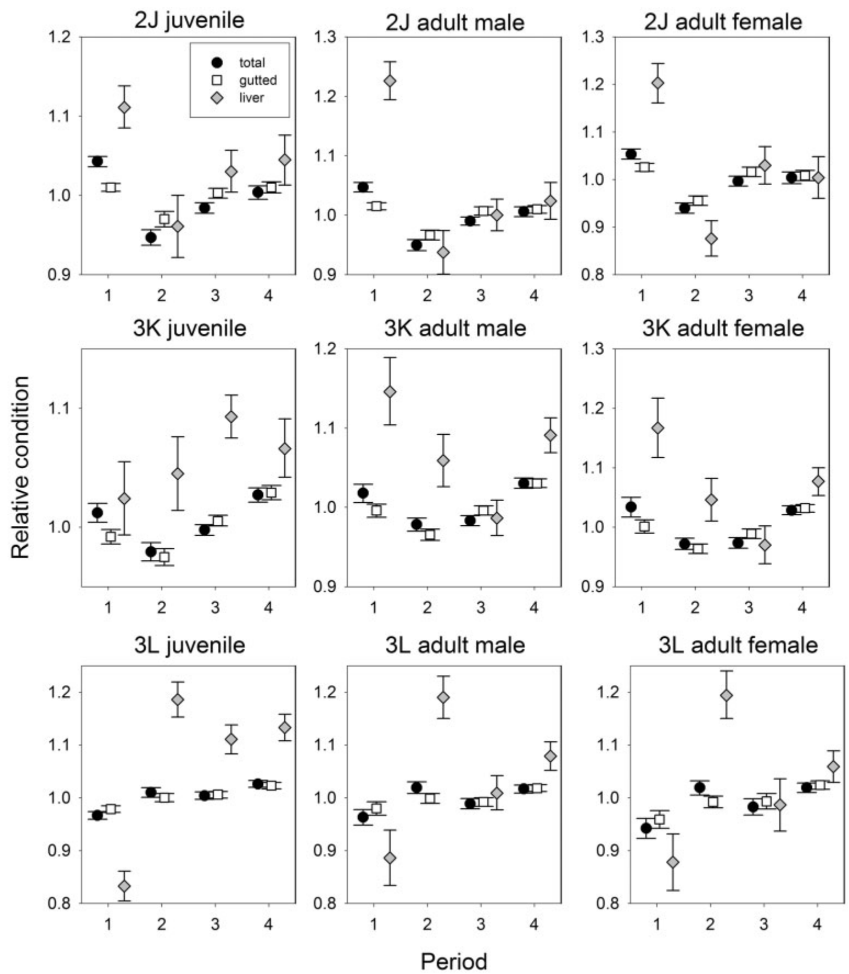

Figure 4. Relative condition (total, gutted, and liver) for adult females, adult males, and juveniles in each NAFO division (2J, 3K, 3L) in each period (see Figure 2). Median and 95% credible intervals are shown.

Table 3. Results of hierarchical Bayesian models examining condition for constant mean and variance.

	Total condition			Gutted condition			Liver condition		
	Best model	**Lowest mean**	**Lowest variance**	**Best model**	**Lowest mean**	**Lowest variance**	**Best model**	**Lowest mean**	**Lowest variance**
Division 2J									
Juvenile	DMDV	2	3	DMSV	2	NA	DMDV	2	2=3=4
Male	DMDV	2	3	DMSV	2	NA	DMDV	2=3	2=3
Female	DMDV	2	2=3	DMSV	2	NA	DMDV	2	2=3
Division 3K									
Juvenile	DMDV	2	2=3	DMSV	2	NA	DMSV	1=2=4	NA
Male	DMDV	2=3	2=3	DMSV	2	NA	DMDV	3	3
Female	DMDV	2=3	3	DMDV	2	1=2=3	DMDV	3	3=4
Division 3L									
Juvenile	DMDV	1	1	DMSV	1	NA	DMSV	1	NA
Male	DMSV	1	NA	DMSV	1=2=3	NA	DMDV	1	1=3
Female	DMSV	1	NA	DMSV	1	NA	DMSV	1	NA

The period with the lowest mean and variance is given if the model indicated significant differences across period. DMDV indicates the best model had a different mean and variance across periods; DMSV indicates a different mean, but the same variance across periods, in which case, the period with the lowest variance is given as NA. See text and Figure 2 for definition of periods.

prior to collapse, and variance in these indices was generally less in period 3. Metrics more associated with longer-term protein storage, growth and gutted condition, did not match the results of Buren *et al.* (2014b) and had returned to precollapse levels by period 3, while variance in gutted condition did not change over time.

Inconsistent patterns in liver and body condition are common in cod (Marshall *et al.*, 2004; Pardoe *et al.*, 2008; Pardoe and

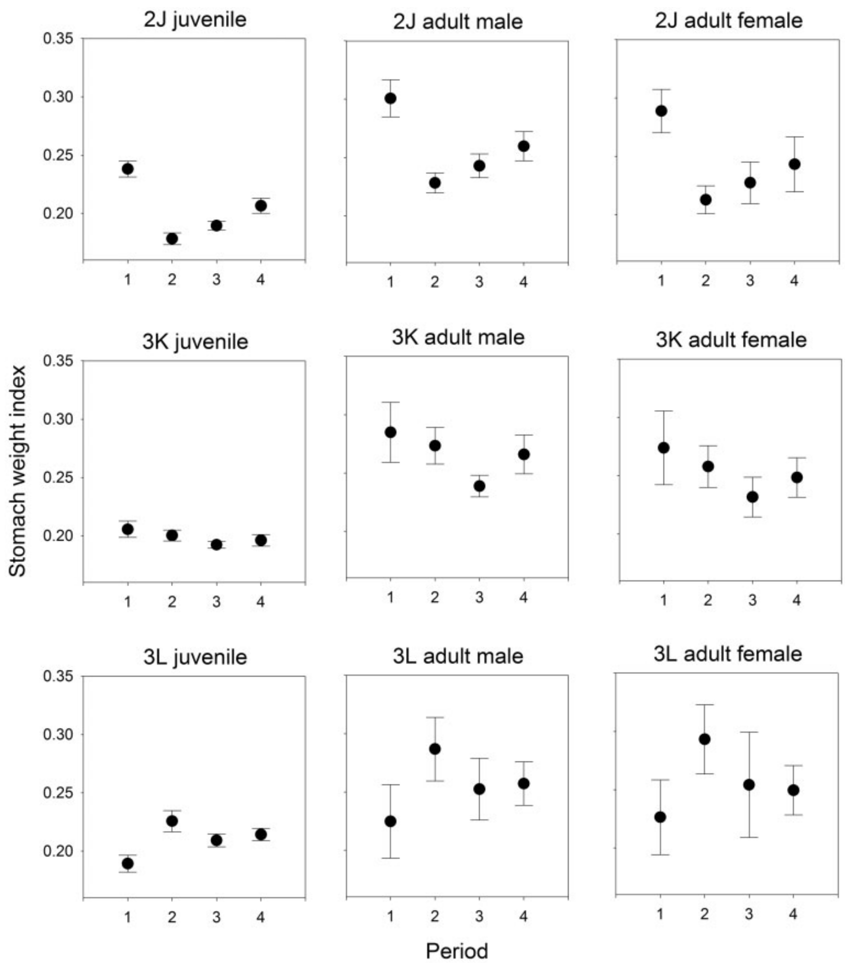

Figure 5. Stomach weight index (stomach weight/total body weight) for juveniles, adult males, and adult females in each NAFO division (2J, 3K, 3L) in each period (see Figure 2). Mean and 95% CIs are shown.

Marteinsdottir, 2009; Morgan *et al.*, 2010). Indices of liver condition respond quickly to differences in food abundance (Foster *et al.*, 1993; Lambert and Dutil, 1997a,b). Body condition and growth respond on a longer time-scale, with muscle proteins only being used for energy when lipid reserves are depleted (Holdway and Beamish, 1984; Black and Love, 1986). Therefore, while low liver condition may indicate a lack of lipid-rich prey in the recent past, low gutted body condition and growth may be more indicative of a level of food depletion that could lead to increased mortality (Dutil and Lambert, 2000).

The energy required for reproduction in adults means that the energy allocation decisions of juveniles and adults are different (Yoneda and Wright, 2005a,b; Jørgensen and Fisksen, 2006). In our study, adult fish were larger than juveniles at the same age, but there were no differences in trends in growth over time between juveniles and adults. Patterns in condition over time were also very similar between juveniles and adults, and it would seem that whatever factors were driving the changes in condition and growth affected juveniles and adults in a similar fashion. Furthermore, adult males and females also exhibited similar temporal patterns. The metrics examined here do not tell us about possible changes in allocation of energy to reproduction by adults. It is not known whether adults were decreasing their reproductive effort at the same time as condition was low or whether they maintained reproduction at the expense of condition. If reproductive effort declined when lipid storage in the liver was lower, this could affect population abundance through an impact on recruitment (Marshall *et al.*, 1998, 2000; Ratz and Lloret, 2003). Cod have a seasonal cycle in growth and condition related to the use of energy for reproduction and subsequent rebuilding of energy reserves (Holdway and Beamish, 1984; Lilly, 1998; Mello and Rose, 2005). Our samples were collected during the period when cod were feeding and building reserves. Observations at a different part of the annual cycle may show a greater difference between juveniles and adults and/or between adult males and females.

There were geographic differences in the trends in growth and condition, the biggest difference being between Division 3L and the two divisions to the north. There were no clear trends in growth in 3L, and all indices of condition were lowest in the first period. It is not known why trends would be so different in 3L, but regional variation in condition and growth has been found

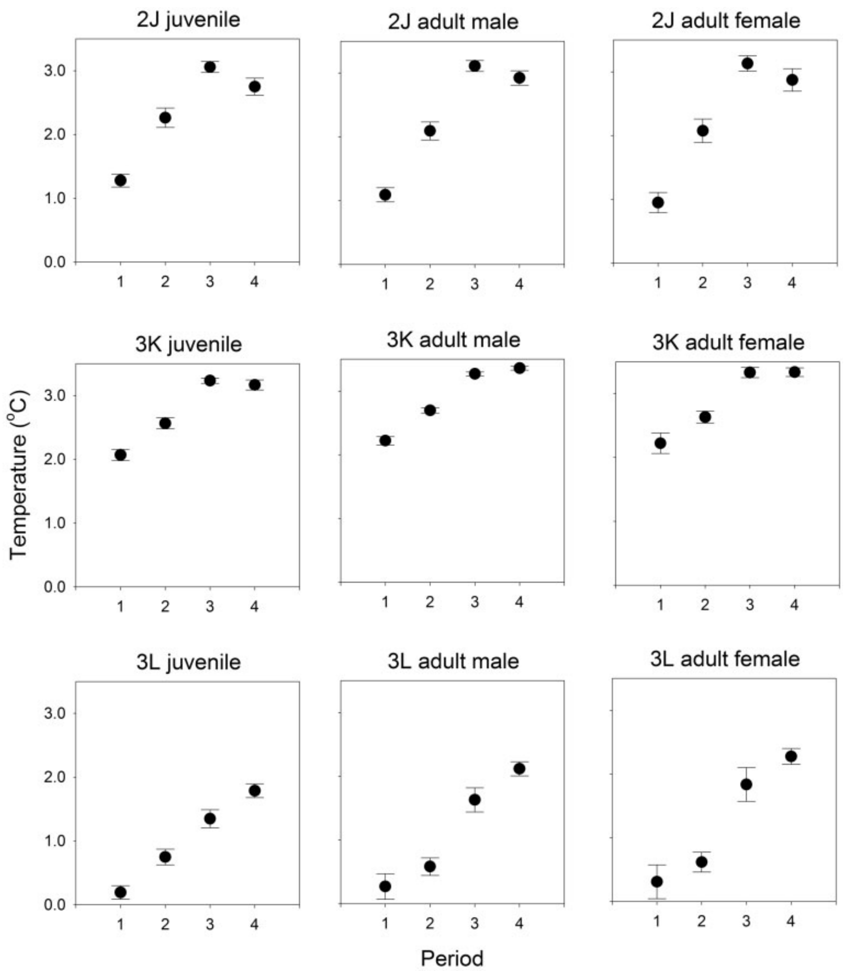

Figure 6. Mean temperature (°C) occupied for juveniles, adult males, and adult females in each NAFO division (2J, 3K, 3L) in each period (see Figure 2). Mean and 95% CIs are shown.

previously for cod (Pardoe *et al.*, 2008; Pardoe and Marteinsdottir, 2009). The northern cod population inhabits a large geographic range with heterogeneous conditions, which might be expected to lead to variation in condition and growth within the population. The two northern divisions have been identified as belonging to a different ecoregion than 3L, based on biological and physical variables (Pepin *et al.*, 2000). The fish are also very mobile, undertaking annual migrations (Rose, 1993), and some of the patterns may be related to fish moving from one area to another.

Both temperature and stomach weight had some effect on growth and condition in northern cod. The influence of stomach weight was consistent for all groups, NAFO divisions, and measures of condition and growth; higher stomach weight (and presumably food availability) led to better condition and growth. However, the relationship is not necessarily linear because by the end of the study period, growth and, in many cases, condition had returned to precollapse levels in the northern areas, while the stomach weight index remained lower than in period 1. Other studies have also found a relationship between stomach weight and condition (Lilly, 1994; Sandeman *et al.*, 2008). The impact of temperature was less than that of stomach weight. In the north, the coldest temperatures occupied were in the precollapse period when growth and condition were highest. Effects of temperature and food availability interact (Brett, 1979), making it difficult to separate their impact.

It is not clear that low growth and condition contributed to the lack of recovery of northern cod. Perceptions about the importance of growth and condition to population status depended on the metrics and area examined, but there was little indication that growth and condition remained consistently low over the entire time-period since the stock collapsed. In the northern part of the population's distribution, it did seem clear that all indices of condition and growth were depressed while the population was collapsing, and this information may be helpful in monitoring the status of populations. The interpretation of changes in condition and growth are generally complex. This study and others have found trends that vary, depending on the index of condition and geographic area examined (Marshall *et al.*, 2004; Pardoe *et al.*, 2008; Pardoe and Marteinsdottir, 2009; Morgan *et al.*, 2010). These results point to the need both for studies of growth and condition in a population to have a comprehensive time-series of data covering the entire range of the population and the need for a better understanding of the causes and implications of changes in different metrics of condition.

Table 4. Results of Spearman rank correlations for temperature and stomach weight index with the three indices of condition (total body condition, gutted condition, liver condition) and with length at age for each group (juvenile, adult male, adult female) and NAFO division.

	Temperature				Stomach weight index			
	Total	Gutted	Liver	Length	Total	Gutted	Liver	Length
Division 2J								
Juvenile	−0.05	0.12	0.15	−0.01	0.55	0.13	0.55	0.27
	0.02	<0.0001	<0.0001	0.58	<0.0001	<0.0001	<0.0001	<0.0001
Male	0.0001	0.12	0.04	−0.22	0.48	0.10	0.43	0.49
	0.99	<0.0001	0.067	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Female	−0.05	0.09	0.03	−0.19	0.54	0.17	0.63	0.36
	0.09	0.0039	0.29	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Division 3K								
Juvenile	0.06	0.19	0.17	0.06	0.47	0.08	0.60	0.13
	0.0002	<0.0001	<0.0001	0.0003	<0.0001	<0.0001	<0.0001	<0.0001
Male	0.11	0.19	0.14	−0.10	0.50	0.09	0.46	0.36
	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Female	0.09	0.18	0.17	0.003	0.53	0.14	0.67	0.16
	0.0002	<0.0001	<0.0001	0.91	<0.0001	<0.0001	<0.0001	<0.0001
Division 3L								
Juvenile	0.26	0.20	0.22	0.0007	0.53	0.14	0.56	0.11
	<0.0001	<0.0001	<0.0001	0.96	<0.0001	<0.0001	<0.0001	0.0002
Male	0.08	0.13	0.13	−0.04	0.55	0.14	0.50	0.16
	0.0027	<0.0001	<0.0001	0.09	<0.0001	<0.0001	<0.0001	<0.0001
Female	0.08	0.18	0.09	−0.04	0.55	0.15	0.68	−0.07
	0.015	<0.0001	0.006	0.24	<0.0001	<0.0001	<0.0001	0.11

In each cell, the top number is the correlation coefficient and the bottom number is the p value. With correction for number of correlations, the significance level is $p < 0.0014$.

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