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Cannibalistic growth polyphenism in Atlantic cod

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ABSTRACT

Background: Phenotypic variability in Atlantic cod in the Canadian Arctic is characterized by a distinctive resource polymorphism manifest by the co-existence of cannibalistic and non-cannibalistic individuals in the same populations.

Questions: What are the fitness consequences of this variation in foraging tactic? What maintains the two phenotypes?

Method: Measure and compare condition and growth trajectories between the two morphs from three meromictic lakes on Baffin Island, Canada. Use life-history invariants to estimate natural mortality and other components of fitness.

Results: Compared with non-cannibals, cannibals are predicted to achieve greater maximum size, experience higher mortality in early life, and mature at a larger size, albeit at the same age. Growth trajectories of cannibals and non-cannibals diverge as early as one year of age. Condition indices do not differ between forage morphs. The evidence does not support a genetic difference between cannibals and non-cannibals.

Conclusion: The co-existence of alternative foraging tactics by cod within Arctic lake populations can be explained as phenotypic variability maintained by environments that pose similar fitness consequences to cannibalistic and non-cannibalistic individuals.

Keywords: alternative foraging tactics, Arctic Canada, *Gadus morhua* L., life history, natural mortality.

INTRODUCTION

The killing and eating of an individual of the same species – cannibalism – is quite common (Polis, 1981), particularly among northern and alpine taxa (Amundsen *et al.*, 1999) where there is a shortage of food (Griffiths, 1994). Under these circumstances, population persistence might arguably depend on the expression of an expansively broad variability in foraging tactics, such as that generated by the co-existence of cannibals and non-cannibals (van den Bosch *et al.*, 1988). Within such populations, cannibalism might be maintained by frequency-dependent selection, manifest as one of two genetically distinct morphs (Nishimura and Hoshino, 1999).

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Alternatively, individuals adopting divergent foraging tactics might not differ genetically and there need not be differential fitness consequences associated with cannibalism and non-cannibalism.

Cannibalism is common in the most speciose of vertebrate classes (Juanes, 2003), possibly because of reproductive characteristics and indeterminate growth. Fishes that spawn over extended periods are reported to be more likely to be cannibalistic (DeAngelis and Coutant, 1982; Baras and d'Almeida, 2001), perhaps because of the resultant size heterogeneity among offspring, allowing larger individuals to cannibalize their smaller counterparts. This may be especially true for highly fecund species, which are less likely to have mechanisms to prevent filial cannibalism (references in Baras and Jobling, 2002). Species that grow slowly as juveniles may exhibit greater degrees of cannibalism, particularly when other prey are scarce (Hammar, 2000). Increased density can also be associated with increased cannibalism, although not always (e.g. Baras and Jobling, 2002).

Ever since Ricker (1954) invoked cannibalism as the ultimate mechanism of density dependence, the degree to which it represents an important source of mortality has been a matter of some debate (Polis, 1981; Bax, 1998). The demographic consequences of cannibalism for Atlantic cod (*Gadus morhua*), for example, have been reported to be negligible in over-exploited populations relative to the mortality generated by fishing (Uzars and Plikshs, 2000). Reported frequencies of conspecifics in cod diets range from 1.1% to 8.2% in marine populations (references in Palsson, 1994; Neuenfeldt and Köster, 2000), although considerably higher percentages have been documented in Canadian Arctic meromictic lakes [12.6–32.1% (Hardie and Hutchings, 2011)]. Thus, in unfished or sustainably fished cod populations, cannibalism appears likely to represent an important source of mortality. Neuenfeldt and Köster (2000) estimated that adult Baltic cod consume 25–38% of yearling and 11–17% of one-year-old conspecifics, leading to an overall loss of 31–44% of cod within the first two years of life. Patriquin (1967) estimated that cannibalism in a Canadian Arctic population (Ogac Lake) in the 1950s to 1960s accounted for the loss of 30% of cod 10–20 cm in length. Approximately 50 years later, cannibalism rates are estimated to have doubled in the same lake (Hardie and Hutchings, 2011).

Given that cannibalism is more likely to impose mortality on small, slow-growing individuals, it is not surprising that cannibals are reported to exhibit faster growth and attain larger sizes than their non-cannibalistic counterparts (Fox, 1975; Smith and Reay, 1991; Elgar and Crespi, 1992; Le Cren, 1992; Claessen *et al.*, 2000; Juanes, 2003; Finstad *et al.*, 2006). Such growth divergence can contribute to bimodal size distributions, populations being comprised of many small and few very large individuals (Le Cren, 1992). Bimodality of size structure can arise because of a combination of extended spawning period and the foraging advantage benefiting larger individuals (references in DeAngelis and Coutant, 1982), or in a cyclic manner following recruitment pulses or other periods of occasional high densities of small individuals, which might then enable a few cannibals to reach very large sizes (Bystrom, 2006).

However, bimodal size-frequency distributions provide little information on the population dynamical causes and consequences of cannibalism. To explore this further, it can be advantageous to monitor size distributions over time, as has been done to great effect (Shelton *et al.*, 1979; Timmons *et al.*, 1980; Persson *et al.*, 2004), although this approach is not always logistically feasible. A second approach, once it has been established that cannibalistic growth polyphenism exists, is to study the growth trajectories of the two feeding types throughout their lives to reveal at what point it arises and to examine the consequences thereof (Le Cren, 1992). This is the protocol adopted here to study cannibalism by Atlantic cod in Arctic lakes.

Persisting at relatively high densities in small, depauperate lakes devoid of alternative prey fish species (Hardie and Hutchings, 2011) at the northern extreme of the species' range in Canada, cannibalism is arguably unavoidable. Our purpose here is to explore the consequences of cannibalism to metrics of condition, growth, mortality, and life history for cod in three of these near-pristine populations.

MATERIALS AND METHODS

Sampling

We sampled Atlantic cod from three meromictic lakes (Ogac Lake, Qasigialiminiq, and Tariujarusiq) on Baffin Island, Nunavut, Canada, using hook and line, gill nets, and minnow traps in July and August 2003, and from Ogac Lake only in July and August 2004 and July 2005. Given that general descriptions of these populations have been reported elsewhere (Hardie *et al.*, 2008; Hardie and Hutchings, 2011), including comparative genetic analyses (Hardie *et al.*, 2006), we will not provide a detailed description of the study sites here.

Individuals sampled to identify stomach contents were classified as cannibals if they had any part of a juvenile or adult cod in their stomachs. Once cod with empty stomachs had been excluded from the dataset, we analysed growth trajectories of 28 cannibalistic and 22 non-cannibalistic individuals from Ogac Lake (OG), 11 cannibals and 45 non-cannibals from Qasigialiminiq (QL), and 17 cannibals and 35 non-cannibals from Tariujarusiq (TL).

Condition and age determination

Metrics of body condition were estimated from data on individual body weight, body length, liver weight, and white muscle. These included the hepatosomatic index (HSI = liver weight × total weight^{-1}), Fulton's condition factor [$K = 100 \times$ total weight (g) × total length (cm)$^{-3}$], and a size-corrected condition factor (K_{adj}). Given that K in these cod populations is known to increase with length (Hardie and Hutchings, 2011), we employed population-specific exponents of the length–weight (L-W) relationship to calculate K_{adj} [100 × total weight (g) × total length (cm)$^{-b}$] for intra-population comparisons of condition between cannibals and non-cannibals: $b_{\text{OG}} = 3.30$, $b_{\text{QL}} = 3.49$, and $b_{\text{TL}} = 3.26$ (Hardie and Hutchings, 2011). Wet-weighed samples of liver and white muscle of cannibalistic ($n = 8$) and non-cannibalistic ($n = 16$) Ogac Lake cod were collected and preserved in chloroform : methanol (2:1) in the field. The lipid content of these samples was measured following the protocol described by Budge *et al.* (2006).

For age determinations, one sagittal otolith from each individual ($n = 447$) was sectioned and resin-mounted at the Otolith Research Laboratory at the Bedford Institute of Oceanography, Dartmouth, NS, Canada, using equipment and protocol described elsewhere [http://www.marinebiodiversity.ca/otolith/english/home.htm]. For sectioned otoliths that were difficult to read or appeared not to have been sectioned through the nucleus (53/447), the second sagittal otolith was broken by hand and wet-polished on emery cloth (200–800 grit) mounted on a Plexiglasfi board. Digital images of both types of otolith preparations were obtained, using a Nikon DXM1200 camera mounted on a Nikon C-DSD115 stereo microscope under reflected light and using the image analysis program ACT 1 (Nikon Instruments, Inc., Melville, NY). Digital images of magnified otoliths were manipulated by Photoshop 7.0 (Adobe Systems, Inc.) to optimize the contrast between

Table 1. Summary of the linear regression of our age estimates against age estimates from the same otoliths by researchers at the Iceland Marine Research Institute

Population	Slope	*P*-value	*r*	*n*	Mean age estimate difference ± S.E.
Ogac Lake	0.96	<0.00001	0.98	112	−0.13 ± 0.05
Qasigialiminiq	0.90	<0.00001	0.95	48	0.04 ± 0.09
Tariujarusiq	0.94	<0.00001	0.96	51	−0.04 ± 0.09

opaque and hyaline zones, which were interpreted as representing summer and winter growth periods, respectively.

Although age validation was not possible for these populations, several measures were taken to ensure the best possible interpretation of otolith annular patterns. Experts at the Marine Research Institute, Reykjavik, Iceland aged a subsample of otoliths. Altogether, 49 of 213 age interpretations differed from those estimated by the authors, although most of these ($n = 39$, or 18.3%) were by only one year, and 10 (4.7%) by a maximum of three years. Linear regressions of our data against age estimates from the Marine Research Institute suggested no systematic bias (Table 1).

Four different nucleus–margin otolith transects were tested to verify the proportionality of otolith length to fish length. A transect through the ventral plane of the otolith yielded a strongly linear relationship between otolith and fish length for all populations ($r = 0.81$–0.88; $P < 0.0001$). Relative inter-annular distances were digitized starting from a landmark at the centre of the nucleus, with subsequent landmarks placed at the start of each opaque summer growth zone, using the programs tpsDig2 and tpsUtil (Rohlf, 2004, 2005). Relative distances were converted to absolute distances in millimetres to apply the biological intercept method (Campana, 1990), using a published biological intercept value for Atlantic cod reported by Sinclair *et al.* (2002) and converted to back-calculated lengths-at-age by the equation:

$$L_a = L_c + (O - O_c)\,(L_c - L_i)\,(O_c - O_i)^{-1},$$

where L_a is the estimated length at age a, L_c is the length at capture, O is the distance from the centre of the nucleus to the outer edge of the opaque annulus corresponding to age a, O_c is the distance from the centre of the nucleus to the outer edge of the otolith, and L_i and O_i are the fish length and otolith length at the biological intercept, 2.44 mm and 0.44 mm, respectively (Sinclair *et al.*, 2002).

Growth and metrics of life history

The life histories of cannibals and non-cannibals were compared within and between the three populations. Although not measured directly, life-history traits (or metrics thereof) were derived from parameters associated with individual growth trajectories, as modelled by the classic von Bertalanffy growth model (VBGM). To account for non-independence (serial correlation) of back-calculated lengths-at-age from otolith annulus measurement, we used a non-linear mixed effect (NLME) approach to fit the VBGMs:

$$L_{a,i} = (\mu L_\infty + L_{\infty,i})\,(1 - \exp(-(\mu k + k_i)\,(t_{a,i} - \mu t_0 + t_{0,i}))),$$

where $L_{a,i}$ is the predicted length of individual i at age a, μL_∞ is the mean VBGM asymptotic length parameter, $L_{\infty,i}$ is deviation of the asymptotic length for individual i from μL_∞, μk is the mean VBGM growth parameter, k_i is deviation of the growth parameter for individual i from μk, μt_0 is the mean VBGM asymptotic length parameter, and $t_{0,i}$ is deviation of the asymptotic length for individual i from μt_0. The overall VBGM and the k, L, and t_0 parameters were compared between pairs of populations, using PROC NLMIXED in SAS (SAS Institute, Inc., 1999) to apply the maximum likelihood test described by Kimura (1980), as recommended for the analysis of annulus-based, size-at-age data (Schaalje *et al.*, 2002). This method employs likelihood-ratio tests to compare models. For example, to test the difference in L_∞ between two datasets (e.g. populations or sexes), the likelihood of an unconstrained model with separate values for all three parameters is compared to the likelihood of a constrained model assuming a common L_∞. If the likelihood of the two models differs significantly, then the L_∞ parameter differs significantly between the two datasets. The same approach was used to compare growth between the sexes for cod in Ogac Lake.

The ages at which the VBGMs for cannibals and non-cannibals would predict a significant difference in length were estimated by plotting the 95% confidence intervals associated with the predicted length differences between the two VBGMs. The age at which the lower bound of the 95% confidence interval exceeds a length difference of zero predicts the age at which growth polyphenism is predicted to result in a significant difference in length.

The growth coefficient, k, and asymptotic length, L_∞, provide the basis for life-history invariants (Charnov, 1993) that can be used to estimate key components of fitness for the Canadian Arctic populations, such as the instantaneous rate of natural mortality (M), length at maturity (L_α), and age at maturity (α). Mortality (M) at a specific length L can be estimated as $M = (L/L_\infty)^{-1.5} \times k$ (Charnov *et al.*, 2012); mortality across all ages can be estimated as $4.31 \times T_{\mathbf{max}}^{-1.01}$ (Hoenig, 1983), where $T_{\mathbf{max}}$ is maximum age. Length at maturity can be approximated by the life-history invariant $L_\alpha/L_\infty = 0.67$ (Charnov, 1993; Charnov *et al.*, 2012). Based on their respective estimates of L_α, and using the VBGMs depicted in Fig. 1, age at maturity (α) could be estimated for cannibals and non-cannibals.

Genetic analysis

We undertook an exploratory analysis of potential genetic differences between cannibals and non-cannibals, using previously published data obtained for cod in Ogac Lake (Hardie *et al.*, 2006). A Bayesian model-based clustering method was used to infer population structure from the microsatellite DNA data, using *structure* v.2.1 (Pritchard *et al.*, 2000). We simulated one to three sub-populations in the data, using burn-in and run lengths of 10^4 iterations each and using the admixture ancestry and correlated allele frequency models without prior population information. The greatest mean estimated *ln* probability of the data was considered to be the most parsimonious estimate of the number of populations represented by the data.

RESULTS

In general, although most measures of condition were greater among cannibalistic than non-cannibalistic cod, few of these differences were significant (Table 2). The mean hepatosomatic index of cannibalistic cod was significantly greater than that of non-cannibals in

Table 2. Hepatosomatic index (HSI), condition factors (Fulton's K and adjusted K_{adj}), and liver/white muscle lipid content for Atlantic cod in three Arctic lake populations

	Ogac		Qasigialiminiq		Tariujarusiq	
	Cannibals	Non-cannibals	Cannibals	Non-cannibals	Cannibals	Non-cannibals
HSI	0.021	0.015	**0.022**	**0.017**	0.013	0.015
Fulton's K	**0.72**	**0.66**	**0.69**	**0.62**	0.65	0.62
K_{adj}	0.23	0.22	0.11	0.10	0.25	0.25
% Lipid (liver)	22.43%	19.73%	—	—	—	—
% Lipid (white muscle)	1.39%	0.95%	—	—	—	—

Note: Significantly different values between cannibals and non-cannibals are in **bold** font.

Table 3. Maximum likelihood comparison of the mixed-effects von Bertalanffy growth curves fit to individual back-calculated growth trajectory data for non-cannibal and cannibal Atlantic cod from Ogac Lake (d.f. = 31), Qasigialiminiq (d.f. = 50), and Tariujarusiq (d.f. = 33) populations

Population	Phenotype	L_∞	k	t_0
Ogac Lake	Non-cannibal	**92.58** (7.10)	0.17 (0.01)	0.08 (0.06)
	Cannibal	**133.20** (11.34)	0.14 (0.02)	0.07 (0.08)
Qasigialiminiq	Non-cannibal	88.98 (5.61)	0.15 (0.01)	−0.10 (0.05)
	Cannibal	95.97 (13.84)	0.13 (0.01)	−0.21 (0.11)
Tariujarusiq	Non-cannibal	**95.81** (10.02)	0.18 (0.02)	**−0.07** (0.05)
	Cannibal	**129.32** (13.05)	0.18 (0.04)	**0.16** (0.07)

Note: Standard errors are in parentheses. Significantly different values ($P < 0.05$) between cannibals and non-cannibals are in **bold** font.

Qasigialiminiq (t-test, $P < 0.005$), but not in Ogac Lake ($P > 0.1$) or Tariujarusiq. Estimates of Fulton's K suggest that the condition of cannibalistic cod is significantly greater than that of non-cannibals in Ogac Lake and Qasigialiminiq (t-test, $P < 0.001$). However, this statistic suffers from a positive bias with increasing length, which is probably important here, given that cannibals are much larger, on average, than non-cannibals. Not surprisingly, then, there is no significant difference in the mean condition factor adjusted for the allometric exponent of the L-W relationship between cannibals and non-cannibals (K_{adj}, all $P > 0.5$). Although lipid concentrations were greater in both the livers and white muscle of cannibalistic cod, these differences were not significant (t-test, $P > 0.25$).

Convergence of the NLMIXED model to the back-calculated length-at-age data was achieved for individuals aged 7 years and older in Ogac Lake, 6 years and older in Qasigialiminiq, and 5 years and older in Tariujarusiq. There were strongly significant differences in some VBGM parameters between cannibalistic and non-cannibalistic cod, notably those related to L_∞ (Fig. 1, Table 3). Growth data for cod in Ogac Lake and Tariujarusiq indicated that cannibals are characterized by greater asymptotic sizes (~130 cm) than non-cannibals (≈95 cm). The VBGMs for cannibalistic and non-cannibalistic individuals predict that cannibalistic growth polyphenism will result in

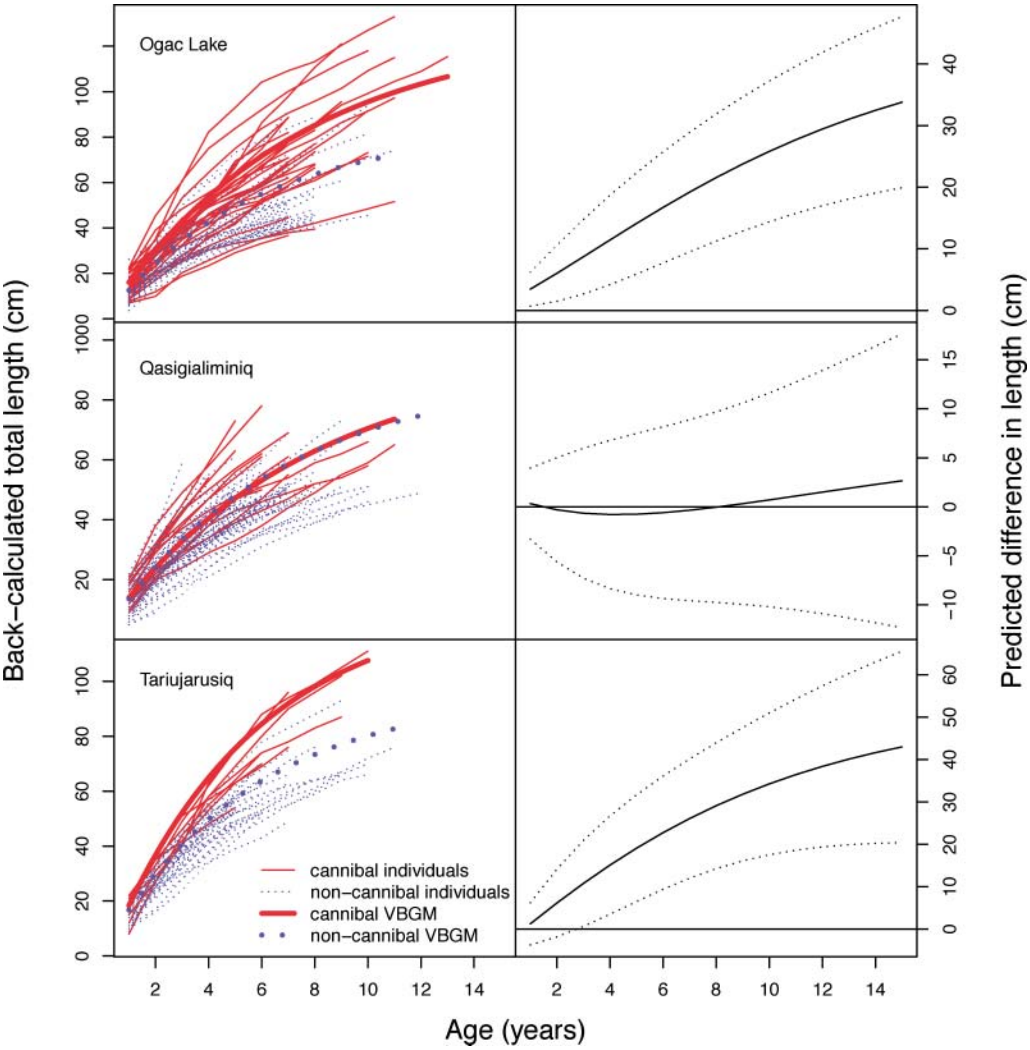

Fig. 1. Individual growth trajectories and predicted von Bertalanffy growth model (VBGM) differences between cannibals and non-cannibals from Ogac Lake, Qasigialiminiq, and Tariujarusiq on the right, with corresponding predicted differences in length-at-age shown within 95% confidence intervals. The point at which the lower bound of the confidence interval exceeds a length difference of zero is the age at which cannibals and non-cannibals are predicted to differ significantly in length.

significant length differences by age 1 (the youngest age of our back-calculated data) in Ogac Lake and by age 3 in Tariujarusiq (Fig. 1).

The growth trajectories suggest that cannibals and non-cannibals differ in life history. Based on the estimates generated by the VBGM parameters for cod in Ogac Lake and Tariujarusiq, cannibals differ in some respects from non-cannibals but not others (Table 4). Cannibals are predicted to attain larger maximum sizes, mature at larger sizes, and experience higher mortality at smaller sizes (e.g. at 50 cm). In Ogac Lake (but not Tariujarusiq), cannibals are forecast to experience lower average mortality throughout their

Table 4. Life-history metrics estimated for non-cannibal and cannibal Atlantic cod in two Arctic lakes

Population	Phenotype	L_∞	$M_{50\text{cm}}$	M_{lifetime}	$T_{\max}$	L_α	α
Ogac Lake	Non-cannibals	92.6	0.43	0.47	9	62.0	8.0
	Cannibals	133.2	0.61	0.32	13	89.2	8.0
Tariujarusiq	Non-cannibals	95.8	0.48	0.38	11	64.2	7.0
	Cannibals	129.3	0.75	0.42	10	86.6	6.5

Note: L_∞ = asymptotic length (a metric of maximum size, cm); $M_{50\text{cm}}$ = natural mortality at 50 cm; M_{lifetime} = natural mortality during lifetime; $T_{\max}$ = maximum observed age (years); L_α = length at maturity (cm); α = age at maturity (years).

life because of their older maximum age. Interestingly, age at maturity is predicted to be similar for both foraging phenotypes within each population.

Our analyses of microsatellite DNA allelic frequencies for cod in Ogac Lake indicated that the most parsimonious estimate for the number of genetically different groups in this population was 1. That is, there was no evidence that cannibals could be distinguished from non-cannibals in Ogac Lake, based on allelic frequency data at presumably selectively neutral loci.

DISCUSSION

Phenotypic variability within isolated populations of Atlantic cod in Canadian Arctic lakes is dominated by a distinctive resource polymorphism manifest by the co-existence of cannibalistic and non-cannibalistic individuals. In some populations, these differences in foraging tactics are reflected by differences in growth trajectories that are implicitly suggestive of differential mortality and life history. Interestingly, based on these estimates, one can make the argument that adoption of the cannibalistic and non-cannibalistic tactics has similar consequences for fitness. Fitness advantages associated with the greater size of cannibals (such as increased fecundity) appear to be offset by higher mortality prior to maturity, consistent with the outcome of a mortality–growth trade-off (Metcalfe and Monaghan, 2001; Yurewicz, 2004). Age at maturity, a key correlate of fitness (Hutchings *et al.*, 2012), is predicted to be similar between tactics, as are metrics of physiological condition; there is also no evidence of genetic differentiation. Thus, the co-existence of alternative foraging tactics by cod in Arctic lakes can be explained as phenotypic variability maintained by environments that pose similar fitness consequences to cannibalistic and non-cannibalistic individuals.

From a methodological perspective, it is noteworthy that significant cannibalistic growth polyphenism was detected despite a relatively crude means (visual inspection of stomach contents) of classifying individuals as cannibals or non-cannibals. If a more refined technique had been applied (such as stable isotope analyses), statistical power would have increased and sample sizes would have been larger (given that they would have included individuals sampled when their stomachs were empty), meaning that apparent differences documented here might well have been more evident. That diverse measures of condition were consistently higher, albeit not statistically so, among cannibals than non-cannibals in all three lakes is consistent with expectations. However, this difference is lower than might have been expected, given the lack of alternative prey available to non-cannibals. One possible explanation is that the lipid content of juvenile cod – the primary prey of cannibals – does not differ from that of most other benthic prey (Hardie and Hutchings, 2011), which may be less energetically expensive to obtain.

Although strong growth divergence was evident in two populations, it was not a prominent feature of cod inhabiting Qasigialiminiq. There are potential reasons for this observation. The size distribution of sampled cod in Qasigialiminiq was narrower than that in the other lakes. This may be attributable to a lack of lipid-rich sea urchins (*Strongylocentrotus droebachiensis*) in the diets of the non-cannibals, whose stomachs were dominated by lipid-poor cone-worms (*Cistenides granulata*). The sample size of cannibals in Qasigialiminiq was likely too low ($n = 11$) to resolve growth differences at the population level. Harvesting during the decade that preceded our sampling might have removed many large, potentially cannibalistic individuals (Hardie and Hutchings, 2011), which could have contributed to the lack of significant differences in predicted VBGMs between cannibals and non-cannibals in Qasigialiminiq. Also, as a result of our inability to fit the comparative VBGM to individuals younger than age 6 years, we excluded several fast-growing Qasigialiminiq cannibals from the analysis; the individual growth trajectories of large, young cannibalistic cod are visible above the predicted curves in Fig. 1. Thus, there is reason to believe that growth divergence between cannibals and non-cannibals may have once been (and may be again) a feature of cod in Qasigialiminiq.

The early divergence of growth trajectories between cannibals and non-cannibals documented here is remarkable if for no other reason than it is rare within fish populations, for which growth divergence usually arises much later in life (Campbell, 1979; Mangel, 1996; Persson *et al.*, 2004; but see Baras *et al.*, 2000). One plausible explanation is that an initial bimodality (in the first year of life) amplifies quickly due to a feeding advantage (DeAngelis and Coutant, 1982), which is then further amplified as a result of the foraging gains of cannibalism, coupled with the less efficient foraging among non-cannibals owing to the risk of cannibalism (Griffiths, 1994; Baras *et al.*, 2000).

The acceleration of growth in many cannibals can produce a so-called ‘double growth curve’ marking the point of growth acceleration. Campbell (1979), for example, reported biphasic growth in giant ‘ferox’ trout relative to ‘normal’ brown trout (*Salmo trutta*) in the same populations, and Le Cren (1992) documented double growth trajectories among perch (*Perca fluviatilis*) in Lake Windermere (UK). In the former, growth accelerated at the onset of (primarily non-cannibalistic) piscivory (Campbell, 1979; Mangel, 1996). In the latter case, a 10-year study by Persson *et al.* (2004) revealed that the acceleration of growth of giant cannibalistic perch occurred at a point in population dynamic time initiated by an episode of high adult mortality. Although there is strong potential for selection on rapid growth to large size when cannibalism is intense, a genetic basis for cannibalistic growth polyphenism has been documented within few populations [Arctic char, *Salvelinus alpinus* (Jonsson and Jonsson, 2001) and brown trout (McVeigh *et al.*, 1995)].

The hypothesis that early diverging cannibals differ genetically from non-cannibals was not supported here, notwithstanding some limitations in the analyses (Evanno *et al.*, 2005). The lack of compelling evidence of intra-population genetic differentiation between morphs suggests that the growth polyphenism in early life might be attributable to a high degree of spatiotemporal environmental variability within lakes. Patriquin (1967) suggested that the unusually high heterogeneity in the size of eggs and larvae in Ogac Lake was too great to be explained solely by temperature and was inconsistent with spatial variability in salinity. He suggested that this variability might be caused by pre-spawning effects of differences in feeding condition, size, and growth rate among adults. Consistent with this hypothesis is the significant length heterogeneity observed among 197 cod larvae collected from Ogac Lake in July 2004, ranging from 2.5 to 23.5 mm and reflecting a highly skewed distribution biased towards small individuals (D.C. Hardie and J.A. Hutchings, unpublished data).

In summary, relative to non-cannibals in the same population, we document supportive evidence that cannibalistic Atlantic cod diverge in growth as early as the second year of life, achieve greater maximum size, experience higher mortality in early life, and mature at a larger size. Neither predicted age at maturity nor observed condition indices differ between morphs; data do not reveal genetic differences between cannibals and non-cannibals. Thus, the co-existence of alternative foraging tactics by cod within Arctic lake populations can be explained as phenotypic variability maintained by environments that pose similar fitness consequences to cannibalistic and non-cannibalistic individuals.

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