

Genetic variation in plasticity of life-history traits between Atlantic cod (*Gadus morhua*) populations exposed to contrasting thermal regimes

Rebekah A. Oomen and Jeffrey A. Hutchings

Abstract: We employed common-garden experiments to test for genetic variation in responses of larval life-history traits to temperature between two populations of Atlantic cod (*Gadus morhua* L., 1758) that naturally experience contrasting thermal environments during early life due to spatial and temporal differences in spawning. Southern Gulf of St. Lawrence cod larvae experienced faster growth in warmer water and low, uniform survival across all experimental temperatures (3, 7, 11 °C), consistent with previous studies on this spring-spawning population. In contrast, larvae from fall-spawning Southwestern Scotian Shelf cod collected near Sambro, Nova Scotia, lacked plasticity for growth but experienced much lower survival at higher temperatures. Phenotypes that are positively associated with fitness were observed at temperatures closest to those experienced in the wild, consistent with the hypothesis that these populations are adapted to local thermal regimes. The lack of growth plasticity observed in Sambro cod might be due to costly maintenance of plasticity in stable environments or energy savings at cold temperatures. However, additional experiments need to be conducted on Sambro cod and other fall-spawning marine fishes to determine to what extent responses to projected changes in climate will differ among populations.

Key words: Atlantic cod, climate change, early life-history traits, *Gadus morhua*, local adaptation, marine fish larvae, phenotypic plasticity, thermal reaction norm.

Résumé : Nous avons utilisé des expériences de jardin commun pour examiner la variation génétique des réactions de caractères du cycle biologique larvaire à la température entre deux populations de morues (*Gadus morhua* L., 1758) caractérisées par différents milieux thermiques naturels au début de leurs cycles biologiques respectifs, dus à des variations spatiales et temporelles du frai. Des larves de morue de la partie méridionale du golfe du Saint-Laurent sont caractérisées par une croissance plus rapide en eau plus chaude et un taux de survie faible et uniforme pour toutes les températures expérimentales (3, 7, 11 °C), ce qui concorde avec les résultats d'études antérieures sur cette population à frai printanier. En comparaison, des larves de morue de la partie sud-ouest de la plate-forme Néo-Écossaise, une population à frai automnal, prélevées près de Sambro (Nouvelle-Écosse), ne présentaient pas une plasticité de la croissance, mais étaient caractérisées par des taux de survie beaucoup plus bas aux températures plus élevées. Les phénotypes positivement associés à l'aptitude ont été observés aux températures s'approchant le plus de celles du milieu naturel, ce qui concorde avec l'hypothèse que ces populations sont adaptées à leurs régimes thermiques locaux. L'absence de plasticité de la croissance observée chez les morues de Sambro pourrait être due au coût élevé du maintien de la plasticité dans des milieux stables ou à des économies d'énergie à basse température. D'autres expériences doivent toutefois être réalisées sur les morues de Sambro et d'autres poissons à frai automnal afin de déterminer l'ampleur des variations futures entre populations des réactions aux changements climatiques anticipés. [Traduit par la Rédaction]

Mots-clés : morue, changement climatique, caractères du début du cycle biologique, *Gadus morhua*, adaptation locale, larves de poisson marin, plasticité phénotypique, norme de réaction thermique.

Introduction

Knowledge of the capacity of a species or population for phenotypic change, and how this capacity evolves, is fundamentally important for predicting how an organism will be affected by natural and anthropogenic environmental variability. Just as genetic variation can be manifested by phenotypic differences among populations, it can also underlie differences in the capacities of populations for phenotypic change (i.e., levels of phenotypic plasticity). Identifying intraspecific variation in phenotypic responses and the evolutionary mechanisms that shape it allows for better predictions of differential population responses to directional environ-

mental changes, such as those expected to occur due to global climate warming.

Examining genetic variation in reaction norms, which represent the range of phenotypes expressed by a genotype across an environmental gradient (Woltereck 1909; Schmalhausen 1949), can be extremely useful in this regard. When determined experimentally by rearing different genetic groups under the same set of environmental conditions (e.g., common-garden experiments), reaction norms allow for direct comparisons of plastic responses between families, populations, or species while controlling for environmental influences (e.g., Conover and Present 1990; Schultz et al. 1996; Broggi et al. 2005; Saldaña et al. 2005). When constructed

Received 7 September 2015. Accepted 7 December 2015.

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across both native and atypical environments, reaction norms can reveal local adaptation among populations based on whether optimal phenotypes (i.e., those associated with relatively high fitness) are produced under native conditions compared with foreign ones. Reaction-norm slopes, which represent levels of phenotypic plasticity and short-term responses to environmental change, are also expected to be under selection (Bradshaw 1965; Schlichting 1986; Lande 2009). Thus, population variability in reaction-norm slopes can be indicative of local adaptation, providing insight into how populations might respond differently to changes in their environments.

Due to their reliance on external heat sources, ectotherms are considered to be especially vulnerable to climate change (Krenek et al. 2012; Paaijmans et al. 2013). Predictions of their responses to directional environmental change are complicated by the fact that many species exhibit variation in levels of thermal plasticity among different latitudes (e.g., Conover and Present 1990; Liefting et al. 2009), altitudes (e.g., Sinervo and Adolph 1994; Ficetola and DeBernardi 2005), and habitats (e.g., Bronikowski 2000; Liefting and Ellers 2008) that are characterized by different levels of spatial and temporal environmental heterogeneity. Pelagic marine fish larvae can experience a variety of thermal regimes across their range due to spatial variation in hydrography. For example, the Canadian Gulf of St. Lawrence is characterized by large seasonal fluctuations (Yashayaev and Zveryaev 2001) and strong vertical gradients (Drinkwater and Gilbert 2004). In contrast, the intense tides that occur from eastern North America's Southwestern Scotian Shelf to the Bay of Fundy and Gulf of Maine cause vertical mixing that homogenizes the water column and weakens seasonal cycles (Garrett et al. 1978; Drinkwater and Gilbert 2004). Temporal variation in spawning also contributes to differences in the thermal environments marine fishes are exposed to during early life, particularly in temperate climates with large seasonal fluctuations. Understanding the impact of this thermal variation on larval plasticity is essential for predicting the short-term response of marine fish populations to global climate change because per capita population growth rate can be heavily dependent on growth and mortality during the larval stage (Anderson 1988; Cushing 1990).

Atlantic cod (*Gadus morhua* L., 1758) is a demersal marine fish of profound ecological and socioeconomic importance throughout the North Atlantic. Cod inhabit a wide variety of thermal environments that promote localized thermal adaptation across their range (Bradbury et al. 2010, 2013) and substantial variation in spawning time exists among populations (e.g., Lett 1980; Brander and Hurley 1992; Myers et al. 1993). Previous work has documented genetic variation in plasticity for larval life-history traits (Hutchings et al. 2007; Oomen and Hutchings 2015a) and juvenile body morphology (Marcil et al. 2006a, 2006b) across a limited range of temperatures. In the larval studies, these represent native or warmer conditions than those typically experienced in the wild, raising the question as to whether these responses are also observed at colder temperatures.

Here, we present evidence for genetic differences in thermal reaction norms for two key fitness-related traits, larval growth and survival, between two populations of cod that naturally experience contrasting thermal environments during early life and have been found to exhibit drastically different responses to warmer temperatures (Oomen and Hutchings 2015a). We employed a common-garden experimental protocol to construct thermal reaction norms across a two-fold wider range of temperatures than has been examined previously and that encompasses both native and atypical environments of both populations. We compare patterns of plasticity among populations and traits to assess adapta-

tion to local thermal regimes and interpret our results in light of the directional changes in temperature predicted to occur due to global climate change.

Materials and methods

Study populations

We conducted common-garden experiments on cod from (1) Southern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization (NAFO) division 4T; 47°N, 61°W) and (2) Southwestern Scotian Shelf near Sambro, Nova Scotia (NAFO division 4X; 44°25'N, 63°30'W) (Fig. 1a). Cod from these areas will be referred to throughout the text as Southern Gulf and Sambro, respectively. Southern Gulf cod spawn from April to September (ICES 1994) with peak spawning occurring in May and June (Lett 1980); the larvae experience relatively warm and highly variable temperatures (Fig. 2), increasing from 6.0 ± 2.1 °C (mean \pm SD) in June to 10.0 ± 3.9 °C in August (Fig. 1b). Sambro cod comprise a spawning group on the Southwestern Scotian Shelf and spawn from November to December (Brander and Hurley 1992; Hutchings et al. 1999). Consequently, Sambro larvae experience colder and less variable temperatures than those experienced by Southern Gulf cod (Fig. 2), decreasing from 6.8 ± 1.5 °C in November to 1.9 ± 1.5 °C in February (Fig. 1b). The duration of the larval stage (from hatch to 12 mm standard length) is dependent on growth rate and is, thus, expected to differ among temperatures and populations (e.g., 42 days at 6 °C in northeast Arctic Atlantic cod (Otterlei et al. 1999).

Common-garden experiments

Adult cod from Southern Gulf and Sambro were captured from the wild immediately prior to their peak spawning seasons in early May 2011 and early November 2011, respectively, and transported to Dalhousie University for spawning. Sample sizes were 34 and 51 cod from Southern Gulf and Sambro, respectively. Adults were allowed to spawn undisturbed in a 684 m³ pool tank at Dalhousie University at approximately 8 °C and fed dry pellets daily.

Eggs were sampled approximately 4 weeks after they were first observed in mesh egg collectors positioned near the surface outflows of the pool tank and were incubated in 130 L flow-through tanks at 7 °C until hatching. To increase the probability that a substantial number of families was represented within each spawning group, fertilized eggs were collected over four consecutive days. To evaluate this assumption and to test for variability in family-level reaction norms, a random sample of larvae was collected from each population at the beginning and end of the experiment and tissue samples were obtained from the adults after spawning was complete. Parents and offspring were genotyped at five microsatellite loci, using established protocols (Hardie et al. 2006), and the number of families was determined to be at least 15 (Supplementary Table S1)¹ and 29 (Supplementary Table S2)¹ using COLONY (Jones and Wang 2010) (for details see Oomen and Hutchings 2015a).

The majority of eggs hatched at 10 days post fertilization. Cod larvae initially depend on their yolk sac for nutrition until exogenous feeding begins a short time after hatch (90 h post hatch at 7 °C; Hall et al. 2004). Yolk-sac larvae within 72 h post hatch were transferred to experimental tanks to a density of 60 larvae/L. Larvae were reared in 20 L aquaria with 1200 larvae per replicate at three temperatures (3 ± 1 , 7 ± 1 , and 11 ± 1 °C) with three (Sambro) or four (Southern Gulf) replicates per treatment. On the day of transfer (day 0), the temperature of all tanks was set to 7 °C. The following day, the water in the tanks was gradually changed to the experimental temperatures over the course of 12 h.

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0186>.

Fig. 1. (a) Sampling locations of spawning adults for the two study populations of Atlantic cod (*Gadus morhua*). (b) Depth-averaged (0–50 m) water temperatures (°C; mean ± 1 SD) for the first 3 months after the initial peak spawning months (i.e., June–August (Southern Gulf) and December–February (Sambro)). Mean temperatures were estimated by using all available data from 1914 to 2009 in the Bedford Institute of Oceanography’s Hydrographic Climate Database (available from <http://www.bio-iob.gc.ca/science/data-donnees/base/data-donnees/climate-climat-en.php>).

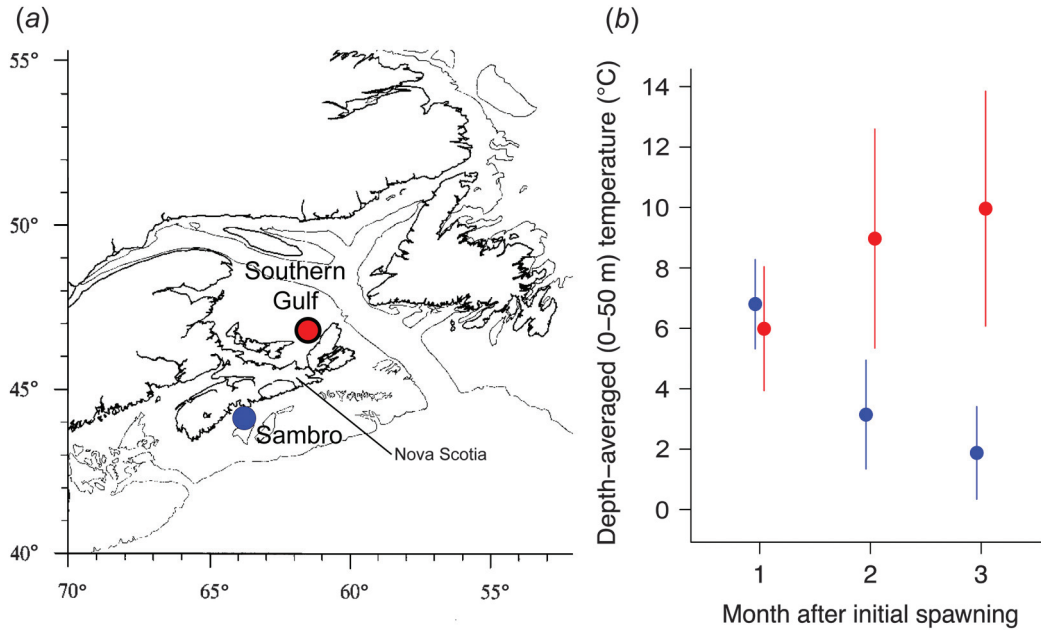
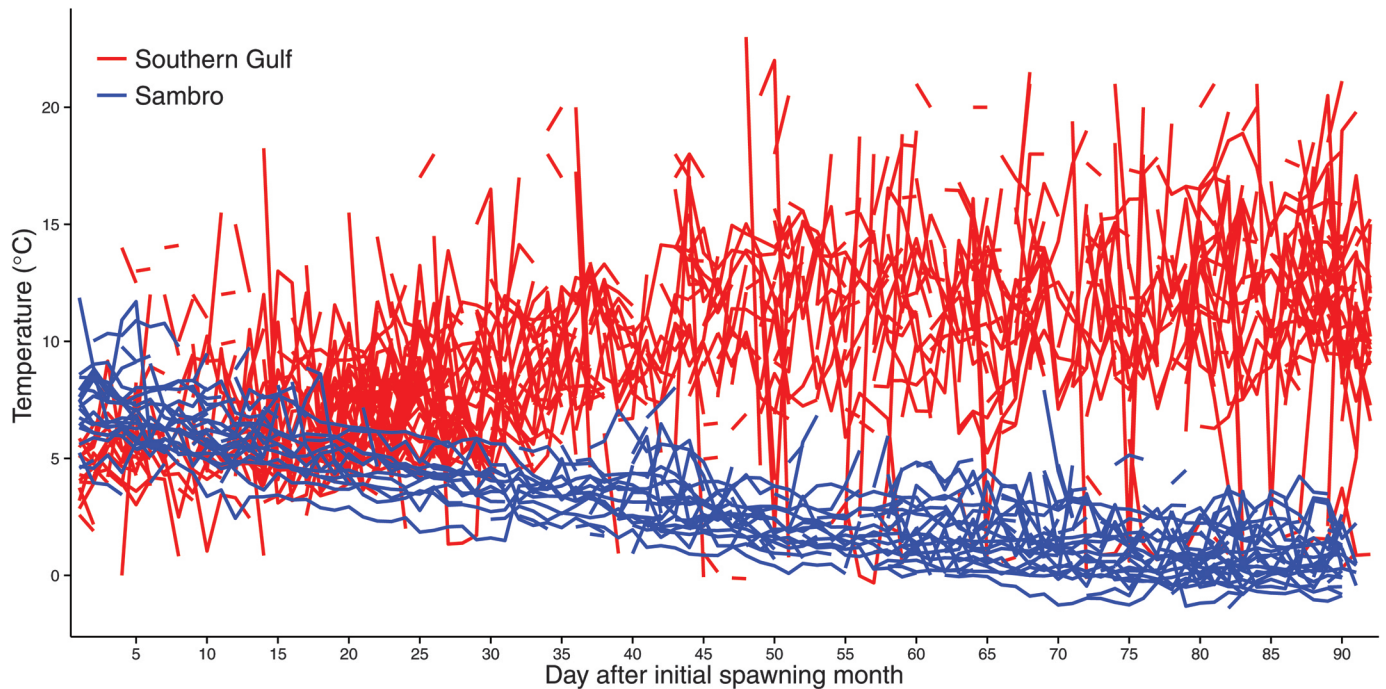


Fig. 2. Depth-averaged (0–50 m) water temperatures for the first 3 months after the initial peak spawning months (i.e., 1 June to 31 August (Southern Gulf) and 1 December to 29 February (Sambro)) using all available data from 1914 to 2009 in the Bedford Institute of Oceanography’s Hydrographic Climate Database (available from <http://www.bio-iob.gc.ca/science/data-donnees/base/data-donnees/climate-climat-en.php>).



Larvae were fed rotifers at a density of 4500 prey/L, three times per day (at approximately 0900, 1300, and 1700). Larvae were fed *Isochrysis*-enriched rotifers from day 1 to day 10 and then Ori-Green (Skretting) enriched rotifers from day 11 to day 29. Larvae were reared under 24 h light (as recommended by Puvanendran and Brown 2002) at 2000 lx; water temperatures were monitored daily.

On day 0, 60 larvae were randomly sampled for initial length measurements, hereafter referred to as “length at hatch”. On day 29, the number of larvae alive in each tank was counted and 10 larvae from each tank were sampled for length measurements. Survival was recorded as the number of larvae alive in each tank, relative to the number alive at day 0. We used AxioVision image

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analysis software (Zeiss) to measure standard length, according to Kahn et al. (2004). Length at day 29 was used as a proxy for growth, following Hutchings et al. (2007).

Data analysis

The experiments described here differ from a classical common-garden experimental design in that populations were studied at different times, necessitated by differences in spawning times. Although this variation might influence the mean trait values of a reaction norm, it is unlikely to affect the slopes unless the unknown factor also has an interacting effect with temperature for the traits in question. However, we previously found that reaction-norm slopes did not differ for larval growth (Supplementary Table S3)¹ or survival (Supplementary Table S4)¹ between the experiment performed on Southern Gulf cod in the present study and one performed using similar protocols in 2003 by Hutchings et al. (2007), despite differing reaction-norm elevations (Oomen and Hutchings 2015a). Therefore, we only compare reaction-norm slopes and refrain from interpreting population differences in reaction-norm elevations between experiments conducted at different times.

All statistical analyses were performed in R (R Development Core Team 2012). A one-way analysis of variance (ANOVA) was conducted on length at hatch to determine whether or not the size of newly hatched larvae differed among populations. Reaction norms for larval growth were constructed for each population, using a linear mixed-effects model with population, temperature, and their interaction as fixed effects and tank as a random effect nested within temperature. A significant interaction term is indicative of a genotype \times environment interaction (i.e., genetic variation in reaction-norm slopes). Post hoc contrasts were used to determine population-specific levels of plasticity (i.e., temperature effects) and identify significant differences in reaction-norm slopes between populations.

Reaction norms for growth have been shown to differ at the family level in some fish species (e.g., Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum in Ardeidi, 1792); Evans et al. 2010). If this is true for cod, then there is the potential for families present in high proportions in the experiment to bias the resulting reaction norms. However, we found no significant difference in reaction-norm slopes among Sambro families ($F_{[8,54]} = 0.98$, $P = 0.46$; Supplementary Table S5³). Although it was not possible to test for a family effect in Southern Gulf cod, the growth reaction-norm slope in the upper temperature range did not differ from that documented in a previous experiment having more than twice the number of confirmed families (Oomen and Hutchings 2015a; Supplementary Table S3³).

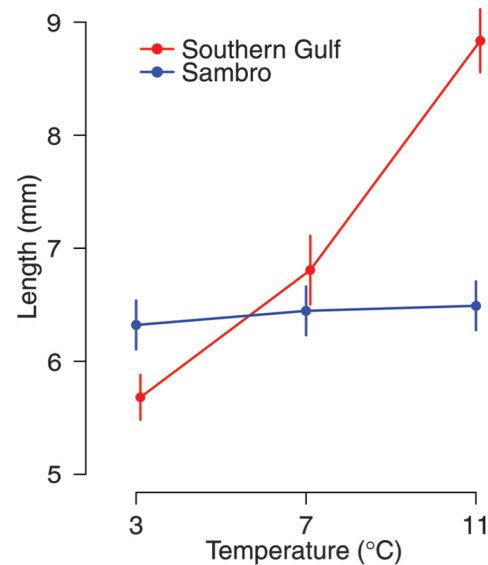
Survival reaction norms were constructed using back-transformed model estimates from a generalized linear model with a quasi-binomial distribution and logit link with population, temperature, and their interaction as the fixed effects. To test for an interaction, survival for all tanks was increased by one larva (0.08%) to eliminate zeros in the data set. The identity link was used instead of the logit link so that the reaction-norm elevations (i.e., intercepts) did not influence the test. Deviance tables were used to determine the best model, using χ^2 tests and the forward stepwise method. Post hoc contrasts were used to identify population-specific temperature effects and differences in reaction-norm slopes among populations.

Results

Growth reaction norms

Larval length at hatch differed among populations ($F_{[1,118]} = 136.96$, $P < 0.001$) with Sambro larvae (4.92 ± 0.03 mm; mean \pm SE) being larger than Southern Gulf larvae (4.18 ± 0.03 mm). Growth reaction norms revealed significantly different responses to temperature between Sambro and Southern Gulf larvae (Fig. 3), re-

Fig. 3. Thermal reaction norms for growth of larval Atlantic cod (*Gadus morhua*) based on standard length at 29 days post hatch (mean \pm 1 SE).



flected by a significant population \times temperature interaction ($F_{[2,127]} = 21.26$, $P < 0.001$; Table 1). A contrast analysis revealed that Southern Gulf larvae exhibited thermal plasticity for growth, with a $\approx 56\%$ greater length when reared at 11 °C (8.84 ± 0.28 mm) than when reared at 3 °C (5.68 ± 0.20 mm), whereas the growth of Sambro larvae did not change significantly with temperature (Table 2). The population variation in growth responses was evident at both the lower (3–7 °C: $t = -2.111$, $P = 0.018$) and the upper (7–11 °C: $t = 3.869$, $P < 0.001$) ranges of experimental temperatures, although the difference in slopes at the lower temperature range was not significant after correcting for multiple comparisons (Table 2).

Survival reaction norms

Survival differed among temperatures and populations, ranging from 0.2% (Southern Gulf at 7 °C) to 27.3% (Sambro cod at 3 °C). Thermal reaction-norm slopes for survival differed significantly between Southern Gulf and Sambro larvae ($P < 0.001$; Fig. 4, Table 3), with Sambro larvae experiencing greater plasticity than Southern Gulf larvae. Survival of Sambro larvae decreased with increased temperature: survival at 7 °C was 19% lower than that at 3 °C ($P < 0.001$; Table 4) and declined an additional 4% at 11 °C, although this decrease was not significant ($P = 0.109$; Table 4). Conversely, survival of Southern Gulf larvae did not differ between temperature treatments (3–7 °C: $P = 0.352$; 7–11 °C: $P = 0.648$; Table 4). The thermal responses exhibited by the two populations differed significantly at the lower (3–7 °C: $P = 0.001$) and marginally in the upper (7–11 °C: $P = 0.098$) range of temperatures studied, although variation in slopes in the upper range was not significant after correcting for multiple comparisons (Table 4).

Discussion

Larval cod plasticity in growth and survival

We found highly divergent thermal reaction norms for larval growth and survival between two Atlantic cod populations that naturally experience contrasting thermal environments during the larval stage: relatively warm and variable (Southern Gulf) and relatively cold and invariant (Sambro) (Fig. 2). When plasticity was observed for either trait, the best phenotype, from a fitness perspective, was observed at temperatures similar to those typically experienced in the wild: Southern Gulf larvae grew faster at warmer temperatures and survival of Sambro larvae was higher at

Table 1. Effects of population and temperature on growth of larval Atlantic cod (*Gadus morhua*).

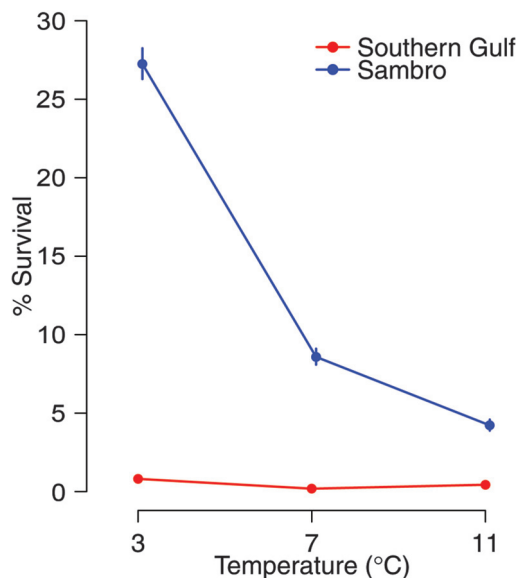
Model term	df	Sum of squares	Mean of squares	F	P
Population	1	1.59	1.59	3.18	0.077*
Temperature	2	21.23	10.61	21.16	<0.001**
Population × temperature	2	21.33	10.66	21.26	<0.001**
Model term	Variance		Standard deviation		
Tank	0.09		0.30		
Residual	0.50		0.71		

Note: Symbols denote significance at the following levels of α : *, 0.1; **, 0.05.

Table 2. Contrast analysis of the effects of population and temperature on growth of larval Atlantic cod (*Gadus morhua*).

Contrast	Estimate	SE	t	P
Temperature effects				
Sambro at 7 °C vs. Sambro at 3 °C	-0.13	0.30	-0.41	0.342
Sambro at 7 °C vs. Sambro at 11 °C	0.04	0.30	0.15	0.442
Southern Gulf at 7 °C vs. Southern Gulf at 3 °C	-1.13	0.36	-3.10	0.006**
Southern Gulf at 7 °C vs. Southern Gulf at 11 °C	2.03	0.41	4.92	<0.001**
Interactions				
Sambro slope vs. Southern Gulf slope (from 7 to 3 °C)	-1.00	0.47	-2.11	0.032**
Sambro slope vs. Southern Gulf slope (from 7 to 11 °C)	1.98	0.51	3.87	<0.001**

Note: Symbols denote significance at the following levels of α : **, 0.05 (with Bonferroni correction); ++, 0.05 (without Bonferroni correction). A Bonferroni correction for all possible contrasts of interest ($n = 6$) changes the critical P values to 0.017 ($\alpha = 0.1$) and 0.008 ($\alpha = 0.05$). Contrasts are described as A vs. B, where the estimate is the change in length from A to B.

Fig. 4. Thermal reaction norms for percent survival of larval Atlantic cod (*Gadus morhua*) at 29 days post hatch (mean \pm 1 SE; contained within the symbols for the Southern Gulf).

colder temperatures. Presuming that high survival during the larval stage results in higher fitness, the observed variation in reaction norms is consistent with the hypothesis that these populations are adapted to their local thermal regimes.

The thermal response of Southern Gulf larvae was consistent across a wide range of temperatures potentially encountered in the wild, and the response to warmer temperatures was similar to those previously documented for spring-spawning cod populations (Hutchings et al. 2007; Oomen and Hutchings 2015a). However, unlike Hutchings et al. (2007), we did not find survival to be greater at higher temperatures for cod that experience relatively cold temperatures during the larval stage. Sambro larvae generally experience colder temperatures than previously studied

Northwest Atlantic cod populations (Oomen and Hutchings 2015a), yet experience a drastic decrease in survival in the laboratory with increasing temperature. Therefore, mean water temperatures alone are insufficient in explaining population variation in thermal reaction norms. Our findings suggest that thermal variability might play a major role in shaping thermal responses in larval cod, although the relative importance of stochastic fluctuations and predictable seasonal changes in temperature (i.e., spring warming in the Southern Gulf and autumn cooling on the Scotian Shelf) remains unclear.

Contrasting patterns of plasticity and canalization between direct fitness traits (e.g., survival and reproduction) and those indirectly related to fitness (e.g., morphological or physiological traits) are predicted between populations that experience different levels of environmental variability (Conover and Schultz 1995; Liefting et al. 2009), although the distinction between trait types is not always clear. For example, growth rate is widely regarded as a fitness trait; however, it is not always maximized. Many ectotherms exhibit countergradient variation in growth (e.g., Schultz et al. 1996; Conover et al. 1997; Richter-Boix et al. 2010), wherein southern genotypes have lower growth-rate capacities than northern ones (Conover and Schultz 1995; Yamahira and Conover 2002). The apparent environmental canalization of growth in Sambro larvae might be due to a cost associated with maintaining a plastic growth response or a lack of compensatory evolution in stable environments. Conversely, survival was severely reduced in Sambro larvae as temperatures diverged from those experienced in the wild. Survival (to a given age) represents an ultimate fitness trait in the sense that high survival is essentially always adaptive and thus should be resistant to environmental perturbation within the natural range. Our findings suggest that Sambro larvae have not evolved a compensatory response to cope with temperatures beyond the narrow range they experience, resulting in decreased fitness in new environments, while greater growth plasticity in Southern Gulf larvae suggests they might have evolved flexibility in the face of thermal variability that enables them to adjust energy expenditures so that survival is unaffected across a wide range of temperatures.

Table 3. Deviance table of the effects of population and temperature on survival of larval Atlantic cod (*Gadus morhua*) from Southern Gulf and Sambro.

Model term	df	Deviance	Residual df	Residual deviance	P
Null	—	—	20	2774.97	—
Population	1	1819.71	19	955.26	<0.001**
Temperature	2	118	17	837.26	0.312
Population × temperature	2	577.03	15	260.23	<0.001**

Note: Symbols denote significance at the following level of α : **, 0.05. *P* values were obtained from χ^2 tests that were used to determine if the model fit improved significantly by sequentially adding population, temperature, and their interaction to the null model.

Table 4. Contrast analyses of the effects of population and temperature on survival of larval Atlantic cod (*Gadus morhua*).

Contrast	Estimate	SE	<i>t</i>	<i>P</i>
Temperature effects				
Sambro at 7 °C vs. Sambro at 3 °C	13.49	3.11	4.34	<0.001**
Sambro at 7 °C vs. Sambro at 11 °C	-3.85	2.26	-1.70	0.109
Southern Gulf at 7 °C vs. Southern Gulf at 3 °C	0.62	0.64	0.96	0.352
Southern Gulf at 7 °C vs. Southern Gulf at 11 °C	0.25	0.53	0.47	0.648
Interactions				
Sambro slope vs. Southern Gulf slope (from 7 to 3 °C)	-12.87	3.17	-4.06	0.001**
Sambro slope vs. Southern Gulf slope (from 7 to 11 °C)	4.10	2.32	1.77	0.098+

Note: Symbols denote significance at the following levels of α : **, 0.05 (with Bonferroni correction); +, 0.1 (without Bonferroni correction). A Bonferroni correction for all possible contrasts of interest ($n = 6$) changes the critical *P* values to 0.017 ($\alpha = 0.1$) and 0.008 ($\alpha = 0.05$). Contrasts are described as A vs. B, where the estimate is the change in survival from A to B.

Caveats

Common-garden experiments are one of the most effective means of isolating the genetic basis of phenotypic variation, assuming maternal effects (nongenetic effects of the mother's environment or phenotype on the offspring phenotype; Marshall 2008) are controlled to the greatest extent possible (Conover and Baumann 2009; Hutchings 2011). Ideally, second- or third-generation laboratory cod would be used to eliminate maternal effects. However, the long generation time of Atlantic cod makes this unfeasible. To reduce potential maternal effects that can be exacerbated by stress in breeding females, adults in the present study were acclimatized to a common spawning environment for at least 4 weeks prior to the first egg collection and spawning was allowed to proceed undisturbed in a semi-natural environment. Maternal effects in fishes are mainly caused by variation in egg size, which influences size at hatch (Conover and Schultz 1995; Marshall 2008). Although length at hatch differed between populations, it was not positively associated with growth. Southern Gulf larvae were smaller at hatch, yet grew equal to or more than Sambro larvae, depending on temperature. Indeed, we found no relationship between length at hatch and growth or survival responses in common-garden experiments on five populations (Oomen and Hutchings 2015a). Furthermore, the optimal phenotypes were not observed at temperatures most similar to those experienced by the adults prior to (4 and 9 °C for Southern Gulf and Sambro, respectively; data not shown) or during (8 °C) spawning, as was the case in a rare example of transgenerational plasticity in a vertebrate (Salinas and Munch 2012). Therefore, we interpret the observed variation in growth and survival reaction norms as being the result of genetic differences between populations, although it is not possible to entirely rule out the influence of maternal effects.

High mortality is natural for early life stages of marine fish (Anderson 1988) and is common in laboratory-reared larval cod (e.g., Otterlei et al. 1999, 2002; Hutchings et al. 2007). For example, Hutchings et al. (2007) reported survival rates of 1.6%–5.7% using nearly identical protocols to the present study. Survival of Southern Gulf larvae was relatively low in the present study (0.2%–0.8%), which may have resulted in a lack of sensitivity for detecting temperature effects on survival for this population. However,

none of the treatments suffered complete mortality and the response did not differ from that documented by a previous experiment with higher survival rates (Supplementary Table S4).¹

If size-selective mortality were responsible for the observed differences in growth reaction norms, we would expect to see changes in length corresponding to changes in survival. This was not the case. For example, there was no difference in length of Sambro larvae between temperature treatments despite a more than six-fold difference in survival. Furthermore, growth reaction norms for Southern Gulf cod did not differ between two experiments with different survival rates (Supplementary Table S3).¹

Plastic responses to directional shifts in temperature

Given the high levels of plasticity in life-history traits in some cod populations, even a small, sustained change in ocean temperature could have major impacts on per capita population growth rate and recovery (Drinkwater 2005). Our study suggests that a 2–4 °C increase in mean temperature, as predicted by climate models to occur by the year 2100 (IPCC 2007), could potentially result in faster larval growth for Southern Gulf cod. Although we did not find a direct effect of temperature on Southern Gulf larval survival, in the wild survival would likely increase with growth, as a shorter larval stage reduces the risk of predation (Anderson 1988). Conversely, our findings suggest that Sambro larval growth would be unaffected by rising water temperatures, but they would experience higher mortality. Thus, rising ocean temperatures might be associated with a net increase in productivity for Southern Gulf cod but a decline in that of Sambro cod. Such variation in thermal responses should be considered along with behavioural responses (i.e., range shifts) and other ecosystem variables (reviewed by Pörtner and Peck 2010) to form population-specific management and recovery plans for cod in the face of global environmental change.

Conclusion

We documented genetic divergence in thermal plasticity for larval growth and survival between two cod populations across a broader range of thermal environments than had been examined previously. Variation in thermal reaction norms suggests these populations might be adapted to their local thermal regimes and

that their responses to potential future changes in ocean temperature will differ substantially. Furthermore, our findings suggest that spatial variation in mean water temperature is not sufficient for explaining adaptive divergence in thermal responses among cod populations and that thermal variability might play a role in shaping plasticity. The present study contributes to a rich and rapidly expanding body of knowledge on genetic variation in plastic responses in fishes (reviewed by Hutchings 2011 and Oomen and Hutchings 2015b), information vital to enhancing our understanding of how ectotherms respond to changing environments.

Acknowledgements

We thank C. Boaler, P. Debes, C. Kozela, B. Mosher, E. Reuchlin-Hugenholtz, N. Roney, and the staff at the Aquatron Laboratory at Dalhousie University for their assistance in rearing larval cod. Thanks go to V. Yaroshewski and C. Herlinger for assistance with genetic analyses, D. Keith and D. Hamilton for statistical advice, and P. Bentzen, S. Walde, and M. McBride for helpful comments and discussion. The work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a Strategic Research Grant and a Discovery Grant to J.A.H. and a Canada Graduate Scholarship to R.A.O., as well as by Loblaw Companies Limited, the Canadian Wildlife Federation, Sushi Nami Royale, and the Phi Kappa Pi Joe Ghiz Memorial Fund.

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