

Countergradient variation in body shape between two populations of Atlantic cod (*Gadus morhua*)

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Variation in morphological traits is generally thought to be cogradients, with environmental effects on phenotypic expression reinforcing genetic differences between populations. We compared body shape between two populations of Atlantic cod (*Gadus morhua*). Striking shape differences occurred between juveniles from the two populations when reared in a common laboratory environment. However, no difference in body shape occurred between wild-reared juveniles from the two populations, suggesting that the genetic differences between populations were obscured by opposing effects of the environmental differences experienced in the wild. We suggest that much of the genetic diversity in body shape of fishes may be cryptic, with stabilizing selection for the same optimal phenotype resulting in genetic divergence between populations subject to contrasting environmental influences.

Keywords: countergradient variation; fish morphology; *Gadus morhua*; genetic diversity; morphometrics; phenotypic plasticity

1. INTRODUCTION

Two patterns of covariation between the genetic and environmental influences on phenotypic expression can occur between populations distributed across an environmental gradient (Levins 1968; Conover & Schultz 1995). Cogradients occur when environmental influences reinforce the genetic differences between populations, inflating the phenotypic differentiation between populations. Countergradient variation occurs when genetic differences counteract environmental effects, reducing the phenotypic differentiation between populations.

Countergradient variation is expected when stabilizing selection favours similar phenotypes in different environments. Most previous demonstrations of countergradient variation have involved physiological or life-history traits related to rates of growth, development or reproduction (e.g. Berven *et al.* 1979; Conover & Present 1990; Arendt & Wilson 1999; Trussell 2002; Kokita 2004). Countergradient variation often reflects adaptation to latitudinal or altitudinal gradients in temperature or the length of growing or reproductive seasons (e.g. Berven *et al.* 1979; Conover & Present 1990; Kokita 2004). For example, populations occurring at high latitudes, where the growing season is short, tend to evolve greater intrinsic rates of growth, though normally at some cost (Billerbeck *et al.* 2001; Lankford *et al.* 2001). Recently, countergradient variation has also been demonstrated in the secondary sexual colour of salmon, with populations occupying pigment-poor environments showing greater efficiency in the use of these pigments (Craig & Foote 2001). While countergradient variation has been identified in a growing number of cases, it is likely often overlooked because of the phenotypic similarity that it produces.

Cogradients are expected when diversifying selection favours different phenotypes in different environments. In this case, adaptation to the contrasting selection pressures between environments involves both genetic differentiation and adaptive phenotypic plasticity. Morphological traits are thought to typically exhibit cogradients variation (Levins 1968; Berven *et al.* 1979; Parsons 1997). Examples are provided by body shape in fishes. Distinct benthic and pelagic morphs occur in a number of freshwater fishes (e.g. Robinson & Wilson 1994). Predictable differences in body shape occur between the morphs. These differences, adaptations to the ecological differences between morphs (Schluter 1993; Day & McPhail 1996), reflect genetic differentiation (McPhail 1992; Robinson & Wilson 1996; Hatfield 1997) reinforced by phenotypic responses to the environmental differences between morphs (Wimberger 1991; Wimberger 1992; Day *et al.* 1994; Robinson & Wilson 1996).

Body shape in fishes is labile to a variety of environmental influences, including temperature (Martin 1949; Beacham 1990; Loy *et al.* 1996), water velocity (Imre *et al.* 2002), quantity of food (Currens *et al.* 1989) and type of food or feeding mode (e.g. Meyer 1987; Wimberger 1992; Day *et al.* 1994; Robinson & Wilson 1995). Although striking variation in body shape is evident in some fishes, body shape of other fishes is similar throughout their range. Many fishes are distributed over a wide range of latitudes, thus experiencing a wide range of environmental conditions. Similarity in body shape over these wide geographic ranges is surprising given the influence of environmental factors on body shape. A possible explanation is that, like physiological and life-history traits, morphological traits exhibit countergradient variation more commonly than currently thought.

The Atlantic cod *Gadus morhua* is widely distributed over the continental shelves of the northwest and northeast Atlantic Ocean. In this paper, we compare body shape

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between cod from two populations, one occurring off the southwest coast of Nova Scotia and the other occurring off the northeast coast of Newfoundland. Body shape did not differ between wild-reared juveniles from the two populations. However, striking differences in body shape occurred between juveniles from the two populations when reared in a common laboratory environment, indicating that genetic divergence between the two populations underlies their phenotypic similarity in the wild. We suggest that much of the genetic diversity in body shape of fishes may be cryptic, with stabilizing selection for the same optimal phenotype resulting in genetic divergence between populations subject to contrasting environmental influences.

2. MATERIAL AND METHODS

(a) *Study populations*

Juvenile cod were compared between two populations, referred to here using their Northwest Atlantic Fisheries Organization division names (4X and 3L). The 4X population occurs on the southwest Scotian Shelf off the south coast of Nova Scotia, Canada. Cod in this population spawn in winter (Rowe & Hutchings 2004). The 3L population, part of the once-large 'northern cod' stock complex, occurs off the northeastern coast of Newfoundland, Canada. Cod in this population spawn in early summer (Hutchings & Myers 1994). Further details on these populations are given in Marcil *et al.* (in press).

(b) *Wild-reared juveniles*

Juvenile cod were collected from the 4X population by otter trawling off Cape Sable, Nova Scotia (43°26' N 65°41' W) on July 9, 2003. These cod averaged 80.8 mm in standard length (s.e. = 2.1). Juveniles were collected from the 3L population by beach seining at Newman Sound in Bonavista Bay, Newfoundland (48°34' N 53°57' W) on May 28, 2003. These cod averaged 76.7 mm in standard length (s.e. = 1.7).

(c) *Common-garden experiment*

Mature, pre-spawning cod (58–60 individuals per population) were collected from each of the populations and allowed to spawn in laboratory tanks. Cod were collected from the 4X area on January 16, 2003 and from the 3L area on June 1, 2003. Four batches of fertilized eggs were collected from each of the populations. Each batch consisted of eggs from two consecutive days of spawning. All eggs were incubated at the Ocean Sciences Centre (St John's, Newfoundland) in 250 l flow-through tanks held between 5 and 8 °C until hatching.

When almost all eggs had hatched, larvae were transferred to 500 l circular flow-through tanks (50 larvae/l), with four replicate tanks for each population (one per batch). Larvae were reared under a 24 h light photoperiod at 11 ± 1 °C and fed to satiation three times daily (morning, afternoon, and evening). Larvae were fed live food (rotifers and, at larger sizes, *Artemia*) for the first 49 days (see Marcil *et al.* (in press) for details), and then slowly weaned to dry food which they were fed for the remainder of the experiment. All other rearing parameters, such as light intensity, water flow and weaning times, were kept constant between populations. After 60 days post-hatch, the juveniles from all four replicate tanks were combined and graded regularly (every 3–4 weeks) into new tanks, one per size class (small, medium, large) to

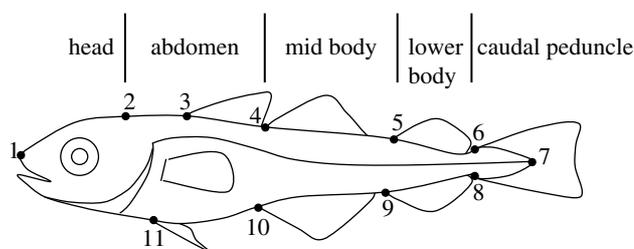


Figure 1. Location of the 11 homologous landmarks used to describe the shape of juvenile cod.

promote more even growth and prevent cannibalism. After four months of rearing in a common environment, a random sample of 50 juveniles, drawn from all three size classes in proportion to their relative abundance, was obtained from each of the populations. Average standard lengths were 101.5 mm (s.e. = 1.5) for the 4X population and 93.6 mm (s.e. = 2.4) for the 3L population.

(d) *Morphometric data collection*

All specimens were stored frozen for a minimum of two months to ensure that any shrinkage due to freezing was comparable between groups (maximum shrinkage due to freezing occurs within two months). The cod were then thawed and a photograph of each individual was taken with a digital camera. Homologous landmarks, corresponding to 11 anatomical structures, were digitized along the lateral profile of the fish (figure 1) using the tpsDig program (Rohlf 2003a).

A generalized least-squares Procrustes superimposition (Rohlf & Slice 1990) was performed on all the digitized sets of coordinates using the tpsRelw program (Rohlf 2003c). This procedure aligned each set of coordinates by translation, scaling and rotation, so that corresponding homologous landmarks lay as close as possible to each other. A consensus configuration was then computed on the set of scaled and aligned specimens. This configuration served as a reference to compute the partial warps and uniform components which are used as shape variables in geometric morphometric analyses. Uniform components represent the shape change associated with uniform stretching or compression of all landmarks along their x and y axes (Rohlf & Bookstein 2003). Partial warps are parameters describing the non-uniform deformations in shape between the consensus configuration and the specimens (Rohlf 1990). The 11 pairs of x and y coordinates were transformed into 16 partial warps and 2 uniform components for each specimen.

(e) *Statistical analysis of shape variation*

Morphometric variation was summarized by relative warp (RW) analysis, calculated using tpsRelw (Rohlf 2003c). This procedure extracts principal components, termed RWs, from the covariance matrix of the partial warp and uniform component scores. To test for shape differences between populations and rearing environments, scores of the first three RWs were used as dependent variables in analyses of covariance (ANCOVA), computed using the SAS procedure GLM (SAS 1999–2001). \log_{10} centroid size was included as a covariate to control for allometric effects of size on shape. Since covariate slopes were homogeneous among groups in all cases ($p > 0.1$), common-slope models were used. Homogeneity of variance was tested by comparing the residual mean squares from separate within-group regressions using F -max tests. These tests indicated that

variance was homogeneous between groups for RW2 and RW3 ($p > 0.05$) but not for RW1 ($p < 0.05$). Heterogeneity in variance of RW1 was due to low variance in one group, a case which is not a problem for ANOVA (Underwood 1997). Effects of population, rearing environment and their interaction were tested using type III sums of squares. Mean RW scores adjusted to the average log centroid size were obtained for each population \times rearing environment group using the least square means option of GLM. Deformations associated with the first three RWs were obtained using the tpsRegr program (Rohlf 2003b).

3. RESULTS

RW analysis revealed two distinct patterns in shape variation. RW1, accounting for 39% of the variation in body shape, summarized variation in the orientation of the head. Laboratory-reared juveniles were distinguished from wild-reared juveniles along RW1 (figure 2). The effect of centroid size on RW1 was significant (table 1), indicating an allometric effect of size on this aspect of body shape. However, the difference in RW1 between rearing environments remained highly significant controlling for this allometric effect of size (table 1, figure 3a). The effect of rearing environment was parallel between the two populations (figure 3a). Laboratory-reared juveniles had a straight dorsal profile with an obliquely positioned mouth, while wild-reared juveniles had an arched dorsal profile with a terminal mouth (figure 3a).

RW2 and RW3, together accounting for 28% of the variation in body shape, summarized variation in body depth. There was a significant allometric effect of size on RW2 but not on RW3 (table 1). For both RW2 and RW3, there was a highly significant interaction between the effects of population and rearing environment (table 1, figure 3). Body depth was the same in the two populations when reared in the wild. However, when reared in the laboratory, body depth differed dramatically between populations, with 4X juveniles having a deep body and 3L juveniles a shallow body.

4. DISCUSSION

Striking differences in body shape occurred between wild- and laboratory-reared cod in our study. Strong environmentally induced differences in body shape have also been demonstrated between wild- and laboratory-reared individuals in other fishes (e.g. Swain *et al.* 1991). Such differences are not unexpected given the strong influence of environmental factors on body shape in fishes (see §1). More surprising was the strong interaction between the effects of rearing environment and population on a second aspect of body shape (summarized by RW2 and RW3), mostly involving body depth. Body depth did not differ between populations in wild-reared individuals but differed sharply between populations when reared in a common environment. This suggests that countergradient variation in body shape occurs between these two populations, with genetic divergence counteracting contrasting environmental effects to produce the same phenotype in the two populations in the wild.

The genetic differences between these populations may be an adaptation to divergent effects of temperature at early life history stages in the wild. Cod from the 4X

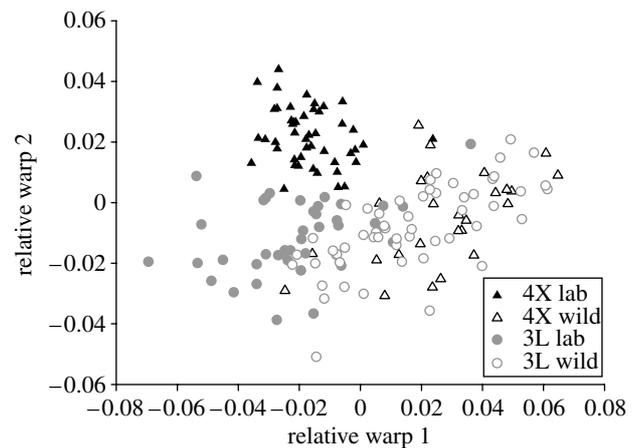


Figure 2. Relative warp scores of wild- and laboratory-reared juvenile Atlantic cod from two populations. No adjustments have been made for allometric effects of size variation between individuals.

Table 1. ANCOVA on relative warp scores of wild- and laboratory-reared juvenile Atlantic cod from two populations. (Log transformed centroid size was used as covariate to account for allometric effects of size variation. Mean squares (MS) are based on type III sums of squares.)

source	MS	$F_{1,163}$	p
<i>relative warp 1</i>			
log centroid size	0.002 076	5.72	0.0179
population	0.001 074	2.96	0.0873
rearing environment	0.053 206	146.61	<0.0001
population \times rearing	0.000 411	1.13	0.2887
error	0.000 363		
<i>relative warp 2</i>			
log centroid size	0.004 023	29.71	<0.0001
population	0.009 453	69.81	<0.0001
rearing environment	0.000 484	3.57	0.0605
population \times rearing	0.007 911	58.43	<0.0001
error	0.000 135		
<i>relative warp 3</i>			
log centroid size	0.000 075	0.56	0.4554
population	0.001 968	14.69	0.0002
rearing environment	0.001 630	12.16	0.0006
population \times rearing	0.004 094	30.55	<0.0001
error	0.000 134		

population spawn in winter, whereas the cod that we used from 3L were summer spawners. Larvae and early juveniles of Atlantic cod are pelagic, occurring in the upper water layers. Temperatures in these waters in the months following spawning are cooler in the 4X area (e.g. averaging 2.4–3.4 °C at 20 m in March–April) than in the 3L area (e.g. averaging 5.7–7.3 °C at 20 m in July–August; see Marcil 2004 for further details). Marcil *et al.* (in press) delineated reaction norms of body shape to temperature for juvenile Atlantic cod. Colder rearing temperatures produced a shallower body shape. When reared in a common laboratory environment, 4X juveniles had a deeper body than those from 3L. Thus, the genetic difference observed between the 4X and 3L populations counteracts the temperature effects expected in the wild.

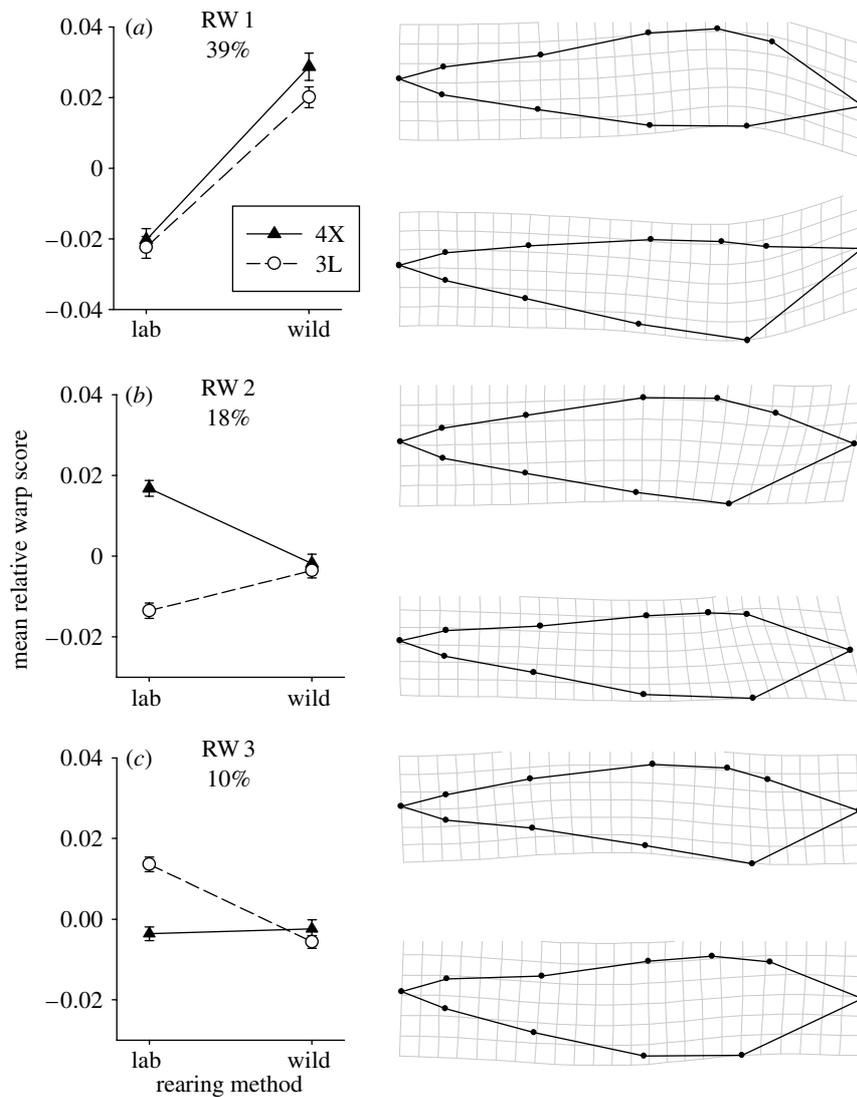


Figure 3. Mean relative warp (RW) scores of wild- and laboratory-reared juvenile Atlantic cod from two populations. For (a) RW1, (b) RW2, (c) RW3. For RW1 and RW2 scores are adjusted to the grand mean log centroid size to control for allometric effects of size differences between groups. Vertical lines show standard errors for each group. Percentages indicate the proportion of shape variation accounted for by each relative warp. Thin-plate spline deformations corresponding to the extreme positive and negative phenotypic values are depicted on the right hand side of each graph.

Marcil *et al.* (in press) conducted more extensive common-garden experiments on body shape of cod at an earlier ontogenetic stage (early post-metamorphosis, average length 25 mm). They reported results for four populations, the two examined here and two additional populations spawning in late spring–early summer. Although they had no information on the body shape of wild-reared juveniles, their results for laboratory-reared juveniles are consistent with those reported here. When reared in a common laboratory environment, 4X juveniles were deeper bodied than those from all three populations spawning in late spring–early summer. This result was consistent across a number of environments (different food treatments), across several batches (egg collections) for each population and across 2 years for the 4X population.

The difference in body shape between wild- and laboratory-reared juveniles may have been induced by differences in diet or feeding behaviour. For the last four months of rearing, laboratory juveniles were fed dry food introduced at the water surface. In the wild, juvenile cod in

these populations adopt a demersal lifestyle after reaching lengths of about 30–60 mm (Methven & Bajdik 1994; Tupper & Boutilier 1995), feeding on zooplankton and a variety of benthic prey. The differences in shape between wild- and laboratory-reared juveniles mostly involved the dorsal profile of the body and the position of the mouth. Phenotypic plasticity in body shape and trophic morphology in response to differences in food type and feeding orientation has been demonstrated in a variety of fishes (e.g. Meyer 1987; Wimberger 1992; Day *et al.* 1994; Robinson & Wilson 1995).

Common-garden experiments ideally use individuals from lineages reared in common environments for two or more generations in order to eliminate the possibility that differences between groups are due to maternal effects or other pre-fertilization environmental influences (Conover & Schultz 1995). Unfortunately, this was not possible in our study on Atlantic cod, a marine fish with a long generation time. Maternal effects have frequently been demonstrated in traits like early survival, size and growth rate in fishes and are generally attributed to effects of egg

size. These effects are usually substantial only at early developmental stages (Heath *et al.* 1999). Pre-fertilization environmental effects have also been demonstrated for meristic characters in fishes (Swain & Lindsey 1986). These characters are determined by processes occurring soon after fertilization and are fixed early in life (typically before hatching). We do not expect a large effect of egg size or early embryonic processes on body shape of juveniles, months after hatching. Thus, we believe that the differences reported here between populations reared in a common environment are probably genetic differences. If not, then pre-fertilization and post-fertilization environmental effects appear to be countergradient in these cod populations.

Cryptic genetic variation, whose expression is suppressed by the buffering systems that ensure normal development, may be revealed when environmental stress compromises these buffering systems (e.g. Queitsch *et al.* 2002). This could provide an alternative explanation for our results, with accumulated genetic differences between populations unexpressed in their normal developmental environment in the wild but revealed in the novel laboratory environment. However, the observation that the effect of genetic differences between populations on body shape counteracts the predicted effect of temperature differences in the wild suggests that this is instead a case of countergradient variation.

Most previous demonstrations of countergradient variation have been in physiological traits such as growth rate (e.g. Conover & Present 1990; Parsons 1997; Arendt & Wilson 1999; Trussell 2002; Salvanes *et al.* 2004), developmental rate (Berven *et al.* 1979; Laugen *et al.* 2003), reproductive rate (Kokita 2004) and the use of dietary pigments (Craig & Foote 2001). In these cases, genetic differences have evolved to compensate for environmental effects, reducing phenotypic variation across environmental gradients. Most of these cases involve latitudinal or altitudinal gradients in temperature and length of the growing season, though countergradient variation has also been demonstrated for other environmental factors such as resource availability (Craig & Foote 2001) and water velocity (Trussell 2002). In contrast, most previous studies have reported cogradients in morphological characters such as body shape, with genetic effects and plastic responses reinforcing each other (e.g. Day *et al.* 1994; Robinson & Wilson 1996; Parsons 1997). In these cases, different phenotypes are favoured in the different environments, and both genetic divergence and adaptive phenotypic responses have evolved in response to contrasting selection pressures. To our knowledge, countergradient variation in body shape has been reported in only two cases, the present study on Atlantic cod and an earlier study comparing autumn- and winter-spawning populations of chum salmon (*Oncorhynchus keta*) (Tallman & Healey 1991).

Conover & Schultz (1995) noted that countergradient variation, though firmly established, had been demonstrated in only a few cases. They suggested that this may reflect the tendency to focus research efforts on the causes of phenotypic diversity rather than on understanding the evolutionary basis of phenotypic similarity between habitats or populations. Since then, countergradient variation has been demonstrated in growth rate, developmental rate and other physiological

traits in an increasing number of cases (e.g. Conover *et al.* 1997; Parsons 1997; Purchase & Brown 2000; Trussell 2002; Laugen *et al.* 2003; Kokita 2004; Salvanes *et al.* 2004). However, variation in morphological traits is still thought to be predominantly cogradients (e.g. Parsons 1997; Trussell 2002). This may be because environmental effects on traits like body shape are less well known than the effects of factors like temperature on rates of physiological processes, so that phenotypic similarity in body shape between areas or populations continues to attract little attention. However, given the demonstrated influences of the environment on body shape in fishes (see above), phenotypic similarity between populations occurring at different latitudes or in different habitats is more likely to reflect genetic differentiation than genetic homogeneity. Many marine fishes occur across a broad range of latitudes (and thus environments) but fail to show the striking phenotypic diversity evident in many freshwater fishes. We suggest that much of the genetic diversity in these widespread marine fishes may be overlooked, with stabilizing selection for the same optimal phenotype resulting in genetic differentiation to counteract the environmental differences between populations.

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