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Linking population genetics and growth properties of Atlantic cod

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Contents

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Abstract

It is strongly implicated that cod in the North Atlantic Ocean is sub-structured at a small geographic scale exemplified by studies from Canadian, Icelandic, and Norwegian waters. In the first part of this review, we reviewed population genetics studies in these three areas and our conclusion is that, despite some inconsistencies in the numerous genetic studies of cod in Norwegian and Icelandic waters, and the northwest Atlantic, these studies illustrate that cod in the investigated areas consists of several distinct populations, both within and between areas. However, to understand the contradictory results obtained in some of the studies discussed in this review, more knowledge about the influence of natural selection, mutation, and genetic drift on the genetic material of cod is necessary. Such knowledge could guide us to the markers giving the best illustration of the genetic structure in these areas. Identifying and genetically characterizing wild stocks are essential steps for their conservation, since

overexploitation of genetically different populations can lead to the loss of genetic variability and productivity in subsequent generations.

Motivated by the hypothesis that growth patterns may reflect specific genotype adaptations, we reviewed stock specific responses on growth in the second part of this review and try to link these with the different life histories within the different stock units indicated in the first part of the review. An example of genetically-based differences between population units at two spawning localities off south Iceland is discussed. Studies have shown conflicting results, depending on which side of the Atlantic the problem has been investigated. We propose that a common-garden meta-analysis with several cod stocks from both sides of the Atlantic is needed to give any reasonable answer to the question of genetically-based growth differences.

In this review, we have not tried to quantify how large the environmental part of growth regulation is versus the genetic part, as this information is not available in the published literature on cod. Based on recent research on two flatfish species (turbot and Atlantic halibut), approximately 30% of growth variation is caused by genetic factors, but it remains to be seen if this is similar in cod.

Introduction

Population genetics of cod

The Atlantic cod (*Gadus morhua* Gadidae) is the major demersal fish resource distributed on the continental shelves and banks on both sides of the North Atlantic Ocean (Dahle, 1995; Galvin et al., 1995; Ruzzante et al., 1996; Figure 1) and is, and has been, one of the most valuable commercial species of the northern Atlantic region (Brander, 1995; Walters and Maguire, 1996; Kurlansky, 1997). A variety of stock identification techniques have been used to study the possible subdivision of cod populations in the north Atlantic, but without firm conclusions (Table 1). Protein variation has indicated heterogeneity of cod stocks in the investigated areas (Cross and Payne, 1978; Mork et al., 1985; Gjøsæter et al., 1992), but has not led to a clear-cut conclusion about the population structure of cod. Considerable variation has been detected at the hemoglobin (*Hb-I*) locus, showing slight spatial variation in allele frequency along the northeast coast of North America (Jamieson, 1975), an apparent cline in frequency along the Norwegian coast (Frydenberg et al., 1965; Møller, 1968; Gjøsæter et al., 1992; Dahle and Jørstad, 1993), and considerable variation in Icelandic waters (Jamieson and Jónsson, 1971).

Mitochondrial and nuclear DNA methods have given contradictory results. Most mtDNA studies show limited or no differentiation of populations (e.g., Carr and Marshall, 1991a; Árnason and Rand, 1992; Árnason et al., 1992; Pepin and Carr, 1993; Árnason and Pálsson, 1996), whereas one study (Dahle, 1991) revealed a large divergence between samples from coastal and Arctic cod in Norway, as well as within the Barents Sea area. However, studies based on minisatellite (Galvin et al., 1995) and microsatellite DNA variation (Dahle, 1995; Ruzzante et al., 1996, 1997, 1998, 2000a, b; Beacham et al., 2002), and restriction fragment length polymorphism (RFLP) of anonymous nuclear loci (Pogson et al., 1995; Fevolden and Pogson, 1995, 1997; Jónsdóttir et al., 1999, 2001, 2002; Pogson, 2001) have displayed considerable population sub-structuring of cod in the north Atlantic. The successful use of biochemical analysis to study the population structure of cod has recently been reported by Joensen et al. (2000). They found that the fatty acid profiles for three groups of lipids (total lipid, phosphatidylcholine, and phosphatidylethanolamine) in heart tissue were significantly different between cod from the Faroe Bank and the Faroe Plateau. This method might be a valuable addition to other stock identification techniques, so further studies using this method should be pursued. In conclusion, an ongoing debate on the stock structure of Atlantic cod persists and the enigma of stock identification in this species remains unresolved.

Environmental regulation of growth in cod

Fish growth is a highly complex process, influenced by numerous biotic and abiotic factors (Brett, 1979). Among abiotic factors, temperature can be regarded as a controlling factor (Brett, 1979) in poikilotherms, regulating the rate at which chemical reactions take place in cells. Information in the literature about the effect of simultaneous manipulation of environmental factors remain limited, but the interaction effect of any of these factors may well be as important as any single factor standing alone (Brett, 1979; Jobling, 1983). Generally, fish have temperature optima for

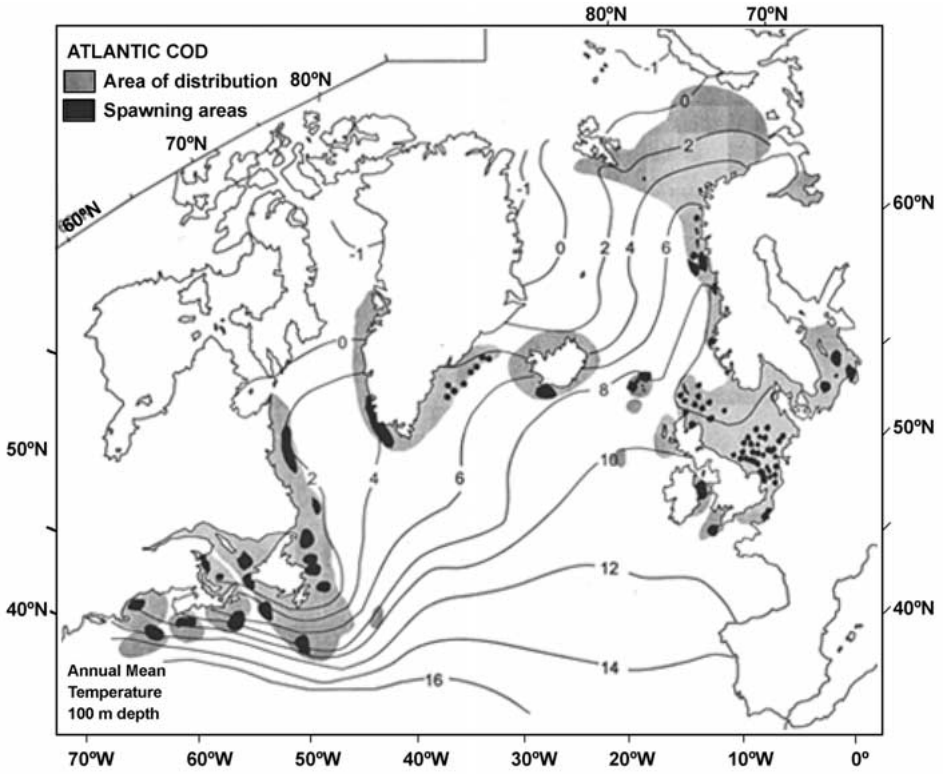

Figure 1. Spatial distribution of Atlantic cod stocks (shaded), their spawning areas (darkly shaded), and the annual mean temperature at 100 m depth in the north Atlantic (adapted from Sundby, 2000).

growth and survival (Brett, 1979; Gadomski and Caddell, 1991). These optimal values may change with age and size; growth rates of fish tend to decline as body size increases (Pedersen and Jobling, 1989; Imsland et al., 1996; Otterlei et al., 1999). Early life stages may also exhibit different optimal temperatures, possibly reflecting temporal and spatial field distributions of young and old fish of the species. A decrease in optimal temperature with increasing size (i.e., an ontogenetic shift) has been demonstrated in Atlantic cod (Pedersen and Jobling, 1989; Otterlei et al., 1999; Steinarsson and Björnsson, 1999; Björnsson et al., 2001), turbot (*Scophthalmus maximus* Scophthalmidae; Imsland et al., 1996), and Atlantic halibut (*Hippoglossus hippoglossus* Pleuronectidae; Jonassen et al., 1999). In contrast, shifts in temperature optima with increasing size have not been found in either brown trout (*Salmo trutta* Salmonidae; Elliott, 1975) or in sockeye salmon (*Oncorhynchus nerka* Salmonidae; Brett et al., 1969).

Atlantic cod in different parts of its distribution experience a wide range of environmental conditions (Brander, 1995; Planque and Frédou, 1999). Variable and changing environmental conditions may affect growth and mortality, and generate recruitment variability (Houde, 1989; Houde and Zastrow, 1993; Otterlei, 2000). Positive correlations between temperature and cod recruitment are usually found in cold northern waters, negative relationships in southern warmer waters, and no relationship at intermediate temperatures (Ottersen, 1996; Planque and Frédou, 1999). Many attempts to relate recruitment variations to environmental conditions have failed because of the interactions of co-varying factors (e.g., fish size, temperature, and food availability), making it difficult to evaluate the effect of a single factor. These attempts have also been criticized for increased type I error. By scrutinizing many environmental factors, one may find a relationship that is statistically significant but spurious. One way to avoid this is to test these hypotheses under controlled and standardized conditions in the laboratory.

Existing literature (e.g., Ottersen, 1996; Houde and Zastrow, 1993; Planque and Frédou, 1999) indicates that differences in growth of cod stocks may relate to environmental factors (i.e., temperature), selective

Table 1. Population genetics of cod in the north Atlantic. Schematic overview of results from various studies applying a suite of different methods and molecular markers

Genetic markers	Area studied	Heterogeneity found?	Data source
Allozymes	East and west Atlantic	YES	Cross and Payne (1978)
	East and west Atlantic, Baltic Sea	LIMITED	Mork et al. (1985)
	Skagerak, Norwegian coast	YES	Gjøsæter et al. (1992)
Hemoglobin	Northeast coast of Canada	YES	Jamieson (1975)
	Norwegian coast	YES	Frydenberg et al. (1965); Møller (1968); Dahle and Jørstad (1993)
	Icelandic waters	YES	Jamieson and Jónsson (1971); Jónsdóttir et al. (1999)
Mitochondrial DNA	West Atlantic	LIMITED	Carr and Marshall (1991); Pepin and Carr (1993)
	Icelandic waters	NO	Árnason and Rand (1992); Árnason et al. (1992)
	Iceland, Norway, Newfoundland	NO	Árnason and Pálsson (1996)
	Norwegian waters	YES	Dahle (1991)
Minisatellites	East and west Atlantic	YES	Galvin et al. (1995)
Microsatellites	Norwegian waters	YES	Dahle (1995)
	Northwest Atlantic	YES	Bentzen et al. (1996); Ruzzante et al. (1996, 1997, 1998, 1999, 2000a, b); Beacham et al. (2002)
Nuclear DNA RFLP	East and west Atlantic	YES	Pogson et al. (1995); Jónsdóttir (2001)
	Icelandic waters	YES	Jónsdóttir et al. (1999, 2001, 2002)
	Norwegian waters	YES	Fevolden and Pogson (1995, 1997)

mortality, food availability, or genetic factors. In all analysis with wild fish, these factors can co-vary and this can result in confounding effects where it is impossible to judge what is causing the apparent difference in growth. The simplest and most direct approach to determining whether the pattern of trait variation among locations has a genetic basis is the 'common-garden' experiment, pioneered by plant ecologists many decades ago (Conover, 1998). Here individuals from different populations or locations are reared in a controlled environment spanning the range of conditions likely to influence fitness traits in nature. Possible local adaptation of cod stocks and some recent studies where the 'common-garden' approach has been applied will be the focus of the latter part of this review, but we will start be reviewing population genetics of cod in three selected areas in the north Atlantic.

Genetic studies of Atlantic cod on a small geographical scale

Here we review key studies on the genetic distribution of cod in three selected areas: Icelandic and Norwegian waters, and the northwest Atlantic. Many studies have been published on the population structure of cod in Norwegian waters and the northwest Atlantic area, and these areas were chosen to represent each side of the Atlantic Ocean. The reason for choosing these three areas is mainly related to the fact that there exists a large bulk of data covering several decades of population genetic research for these areas. Also, we have chosen to focus on genetic studies on a micro-geographical scale, as there exist many excellent papers reviewing and describing the population genetics of Atlantic cod on a macro-graphical scale (e.g., Mork et al., 1985; Shaklee and Bentzen, 1998; Ruzzante et al., 1999; Ward, 2000; Pogson et al., 2001; Smedbol and Wroblewski, 2002).

Icelandic waters

Sick (1965a) analyzed cod samples from west (Faxa Bay), north (Skjálfandi), and northeast (Langanes)

Icelandic waters, and found low *Hb-I*^{1} allelic frequencies. He concluded that the Icelandic cod population was homogeneous with respect to its hemoglobin gene frequencies. His findings of low *Hb-I*^{1} allelic frequencies is in accordance with the findings by Jónsdóttir et al. (1999, 2001), where *Hb-I*^{1} frequencies ranged from 0.005 to 0.032 with an average of 0.024. In accordance with the study of Sick (1965a), Árnason et al. (1992, 2000) found no genetic heterogeneity of cod in Icelandic waters, neither using mtDNA genotypes (Árnason et al., 1992; mean genetic distance $\tilde{\tilde{d}}$ = 0.003) or mitochondrial cytochrome *b* genotypes (Árnason et al., 2000). Árnason et al. (2000) applied a hierarchical AMOVA analysis and found that the correlation of random haplotypes within localities relative to that of random haplotypes drawn from the whole (Φ_{ST} = 0.08), the correlation of random haplotypes within localities relative to that of random haplotypes drawn from the area that the localities belong to (Φ_{SC} = 0.07), and the correlation of random haplotypes drawn from Iceland as a whole (Φ_{CT} = 0.02), were not significantly different from zero. A test between inshore and offshore samples similarly revealed no effect of geographic location (Φ_{ST} = 0.02).

Jamieson and Jónsson (1971), however, found considerable sub-structuring of cod, using transferrin and hemoglobin. They analyzed samples from several locations in Icelandic waters, as well as from East Greenland, Cape Farewell, and at intervals along the coast of west Greenland. The transferrin genotypes gave an overall indication of distinct cod stocks and the hemoglobin genotypes gave striking evidence for plurality of breeding units (Jamieson and Jónsson, 1971). Overall, the test material was not in Hardy-Weinberg equilibrium ($\chi^2 > 50$; $P < 0.001$), clearly indicting that the Icelandic cod stock consists of different breeding units. For hemoglobin, an erratic situation was observed when statistical tests were performed. More than half of the sample batches were significantly higher or lower than the overall average. They argued that during the collection period a change occurred in the composition of the Icelandic stock. They further argued that there were differences between batches of cod concentrating around Iceland at different occasions and differences between batches of cod caught there at about the same time at short distance intervals, suggested a moving mosaic effect due to the convergence of distinct genetic isolates (Jamieson and Jónsson, 1971).

Despite the conflicting conclusions obtained in these studies of hemoglobin (Sick 1965a; Jamieson and Jónsson, 1971; Jónsdóttir et al., 1999, 2001), certain consistencies were observed among the *Hb-I*^{1} allelic frequencies. Cod collected from similar sample areas by Jónsdóttir et al. (1999) and in the study of Jamieson and Jónsson (1971) all displayed low *Hb-I*^{1} allelic frequencies. The frequency of the *Hb-I*^{1} allele was also low in the study of Sick (1965a). Inconsistency was, however, found when comparing the *Hb-I*^{1} allelic frequency of cod collected from similar areas in the studies of Jamieson and Jónsson (1971) and Sick (1965a). Jamieson and Jónsson (1971) found the *Hb-I*^{1} allelic frequency to range between 0.10 and 0.51 (Faxaflói/Jökuldjúp and Langanes, respectively) whereas Sick (1965a) found the *Hb-I*^{1} allelic frequency to be zero. When comparing all samples collected from similar locations in all studies (Sick, 1965a; Jamieson and Jónsson, 1971; Jónsdóttir et al., 1999), it becomes clear that the samples showing most *HbI*^{1} allelic frequency differentiation (i.e., inconsistency) are those collected at different times of the year. Thus, the time of collection (month) seems to play an important part in the hemoglobin analysis of cod off Iceland. This observation supports the hypothesis of different cod populations in Icelandic waters (Jamieson and Jónsson, 1971; Jónsdóttir et al., 1999, 2001, 2002) and the hypothesis of a moving mosaic effect (Jamieson and Jónsson, 1971).

The findings of Jónsdóttir et al. (1999, 2001, 2002) support the sub-structuring theory of cod in Icelandic waters. The samples were analyzed using the sequenced (synaptophysin) *Syp* I locus presented by Fevolden and Pogson (1995, 1997), as well as hemoglobin (Jónsdóttir et al., 1999, 2001). This locus was originally identified as *Syp* I locus by Fevolden and Pogson (1997), but has recently been suggested to represent a cellular isoform of synaptophysin called pantophysin (*Pan* I; Pogson, 2001). Panatophysin is an integral membrane protein found in microvesicles of both neuroendocrine and non-neuroendocrine tissues that function in a variety of shuttling, secretory, and endocytotic recycling pathways (Pogson, 2001). The role of pantophysin in these pathways is currently poorly understood. To avoid confusion, the original nomenclature of *Syp* I will be used in the present discussion.

In line with the findings of Fevolden and Pogson (1997), who studied cod in Norwegian waters, significant differences were detected at the *Syp* I locus between two groups (Loftstaðahraun, Reykjanesgrunn, and Eyrabakkabugur vs. Kantur and Austfjarðadjúp; AMOVA F_{XY} = 0.201) in Icelandic

waters. The subdivision of cod into the two groups supports earlier tagging studies of cod from the investigated areas. Cod tagged near Loftstaðahraun have been recaptured along the southwest coast (e.g., Eyrabakkabugur and Reykjanesgrunn) during the feeding period, but cod tagged near Kantur have been recaptured along the southeast and east coasts (e.g., Austfjarðadjúp, Jónsson, 1996).

Like the microsatellite loci analyzed by Dahle (1991), Bentzen et al. (1996), and Ruzzante et al. (1996), the *Syp* I polymorphism revealed significant heterogeneity among cod populations at microgeographical scales (Jónsdóttir et al., 1999, 2001, 2002). However, unlike the microsatellites and in line with the findings of Fevolden and Pogson (1997), the magnitude of the population differentiation revealed by *Syp* I at a small geographic scale (Jónsdóttir et al., 1999, 2001, 2002) was large (overall F_{ST} = 0.15; Jónsdóttir et al., 1999). The largest differences in frequencies at the *Syp* I locus were observed between cod samples collected at spawning time close to shore (Loftstaðahraun; mean frequency of *Syp* I^A = 0.874) and over the continental slope (Kantur; mean frequency of *Syp* I^A = 0.247; Figures 2, 3; F_{ST} = 0.47). It is noteworthy that these sample locations (both are spawning grounds for cod) are only about 80 km apart (Jónsdóttir et al., 1999, 2001, 2002), but still the allele frequency difference is extensive. A similar pattern of *Syp* I variation was observed for cod in Norwegian waters (Fevolden and Pogson, 1995, 1997; see also below). Nordeide (1998) studied whether Norwegian coastal (NC) and Arcto-Norwegian (AN) cod intermingled at their spawning grounds in Lofoten off northern Norway. He found that NC and AN cod did not mingle randomly, although specimens from both populations may stay simultaneously at the same local spawning ground within an area of less than 0.012 km^2. In line with the findings of Nordeide (op. cit.), the data of Jónsdóttir et al. (1999, 2001, 2002) implies that some reproduction isolation might exist despite the close proximity of the spawning cod. This raises the question, what mechanisms are involved in maintaining reproductive isolation? Hutchings et al. (1999) presented results from cod spawning in tanks, and argued that cod have a lek mating system and are not a promiscuous group of spawners, as is the general view. Also, Nordeide and Folstad (2000) reviewed the literature on cod spawning behavior and concluded that a lek mating system with several options for female choice best describes the spawning behavior of cod. It is argued that courtship displays combined with mate preferences, may be important pre-mating mechanisms reducing or preventing interbreeding between groups of cod. Although our data cannot verify the hypothesis of Hutchings et al. (1999) and Nordeide and Folstad (2000), the relationship between spawning behavior and reduced interbreeding are in line with the findings of Jónsdóttir et al. (1999, 2001, 2002).

Norwegian waters

A considerable number of studies on the genetic structure of cod in Norwegian waters have been performed. The earliest studies (Frydenberg et al., 1965; Sick, 1965b; Møller, 1966, 1968, 1969) focused on hemoglobin, serum transferrin, and blood types. Based on these markers, Møller (1969) concluded that two populations of cod inhabited Norwegian waters, i.e., AN and NC cod. Further, Frydenberg et al. (1965) reported considerable subdivision of cod into several local populations based on hemoglobin. This was, however, not supported by Mork et al. (1980) who studied the LDH (Lactate dehydrogenase) enzyme. They collected samples from Lofoten (AN) and from Trondheimsfjorden (NC), and found allele frequencies of the investigated locus to be similar (0.62 vs. 0.60; $t\text{-test}_{\infty}$ = 0.27). Based on comparison with their own and the data of Jamieson (1975), Mork et al. (1980) concluded that even though Norwegian coastal cod could not be regarded as homogenous based on previous findings, the allele frequencies at the *LDH-3* locus in cod were monotonously uniform throughout the geographical range of the species.

Two publications (Jørstad, 1984; Mork et al., 1985) presented allozyme data from cod in the waters of northern Norway. In both studies, two loci revealed the most variability (*LDH-3* and *PGI-1*). Jørstad (1984) concluded that his findings reflected the existence of several genetically differentiated groups in this area. Mork et al. (1985), however, did not agree with this conclusion and argued that the statistical analyses used were inappropriate. They concluded that Atlantic cod populations were homogenous and sufficient gene flow prevents substantial genetic divergence on a large geographical scale. Mork et al. (1985) reported an overall F_{ST} of 0.014 based on 10 allozyme loci (single locus F_{ST} = 0.003 − 0.031), consistent with low to moderate population divergence. Mork and Giæver (1999) further supported these results in their allozyme study on cod along the coast of Norway, from the Russian border to mid-Norway (overall F_{ST} = 0.012). As in previous studies (Jørstad, 1984; Mork

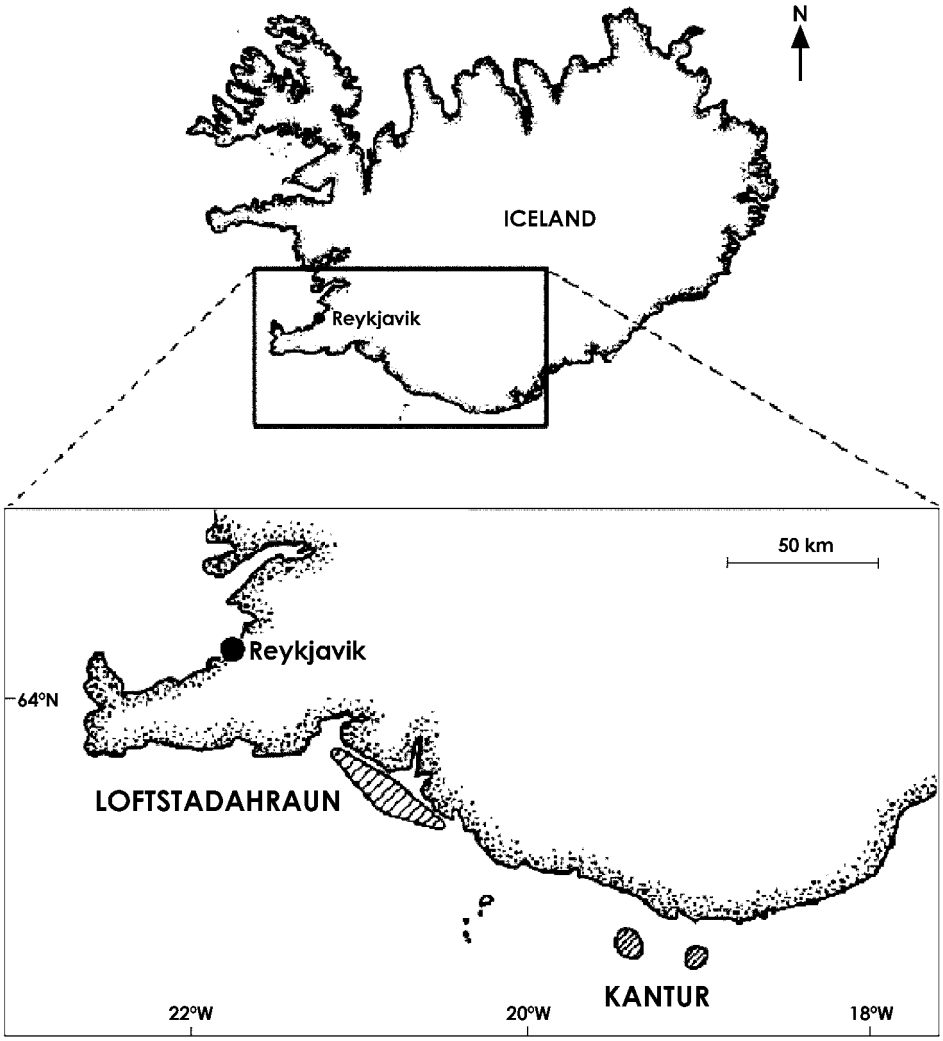

Figure 2. Sampling sites of Atlantic cod from two spawning locations off south Iceland (adapted from Jónsdóttir et al., 2001).

et al., 1985), *LDH-3* was the most variable and showed substantial inter-sample genetic heterogeneity, in sharp contrast to the five remaining analyzed loci. The authors argued that the cod *LDH-3* locus is strongly affected by natural selection and that much, if not all, of the heterogeneity at this locus was due to selection (Mork and Giæver, 1999). The authors concluded that they do not find it justified to use the observed allele frequencies at this locus in models of cod genetic population structure in Norwegian fjords and coastal waters (Mork and Giæver, 1999). In their view, isolation by distance is the principal basis for genetic differentiation in cod.

However, the subdivision of Atlantic cod into AN cod and NC cod has been supported and discussed in later studies (Dahle, 1991; Fyhn et al., 1994; Fevolden and Pogson, 1995, 1997). Fyhn et al. (1994) documented a new *Hb-I* polymorphism using isoelectric focusing electrophoresis and described new phenotypes. They distinguished the AN cod from NC cod by an absence of double bands for both *Hb-I(1/2)* and *Hb-I(2/2)* phenotypes. No difference in hemoglobin components was detected between subgroups within the AN and NC cod.

Dahle (1991) analyzed cod samples from the Barents Sea and along the coast of Norway, from Eidsfjorden to Austevoll, using mtDNA. He found a large divergence between samples from the Barents Sea and the coastal area ($\delta\%$ = 5.62). Significant divergence was further detected between local-

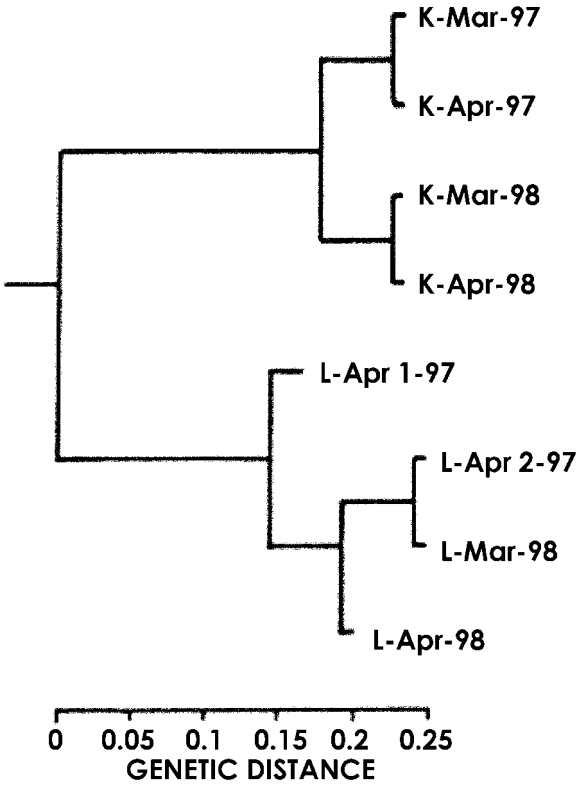

Figure 3. Temporal and spatial stability of cod from two spawning locations (Loftstaðahraun [L] and Kantur [K]) off south Iceland. Samples were taken in March (Mar) and April (Apr) in 1997 and 1998. The figure shows an UPGMA dendrogram of the eight sampling groups, based on Reynolds genetic distance (adapted from Jónsdóttir et al., 2001).

ities within the Barents Sea, where Bear Island and Spitsbergen (west) samples differed significantly from the Barents Sea (east) sample. No genetic subdivision were found among cod samples along the Norwegian coast, not even in the spawning area of the AN cod (Henningsvær) or in the suspected migration route (Moskenes) of the AN cod from the Barents Sea to the spawning area (Dahle, 1991).

A substantial genetic subdivision of AN cod (Barents Sea) and NC cod (Trondheimsfjorden) has been indicated in the study of Fevolden and Pogson (1995). They used 17 anonymous nuclear RFLPs loci in the analyses of samples from Fugløybanken (off the coast of Tromsø, northern Norway) and Balsfjorden (coastal area south of Tromsø). These two sites are known spawning areas for AN and NC cod, respectively. They found only three polymorphisms (all in linkage disequilibrium), revealed by the same GM798 cDNA probe (using three different restriction enzymes), to show significant differences between the two samples (the combination of GM798 probe with *Dra* I restriction enzyme is synonymic with the *Syp* I locus discussed in the papers presented here). In a later study by Fevolden and Pogson (1997), they used the *Syp* I locus to analyze over 900 specimens from the Barents Sea, coastal area and fjords in northern Norway (Figure 4). Their results confirmed the existence of highly significant differences between AN and NC cod (Figure 5). Applying Wright (1978) hierarchical F statistics, they found that 38.9% (F_{XY} = 0.389) of allelic variance was attributable to differences between coastal and Arctic cod. Further, they indicated that genetic heterogeneity might exist among resident populations of cod in different fjords. Thus, they speculated that gene flow among populations throughout northern Norway might be considerably lower than previously believed (Fevolden and Pogson, 1997).

One publication is in sharp contradiction with the studies discussed above. The analyses of Árnason and Pálsson (1996) revealed no substructure of cod collected from nine sampling localities in Norwegian waters, representing three overall areas: Arctic, coastal, and middle, using the mitochondrial cytochrome *b* method. They found little or no evidence for genetic distinctness among Norwegian cod stocks, not even between the Barents Sea and coastal cod (AMOVA among areas Φ_{CT} = 0.008; θ_{ST} (analogous to F_{ST}) = 0.018). Further, they found little or no evidence for the historical view of a long-standing and permanent genetic structure of cod populations, neither among localities nor areas (Árnason and Pálsson, 1996). Several plausible explanations have been suggested to explain the sharp differences between the results of mtDNA studies on the one hand and most other studies on the other hand. These explanations are discussed in detail later in this review.

It is clear from the discussion above that different classes of markers differ in their likelihood of revealing genetic divergence at spatial scales. Early population surveys of hemoglobin and transference found significant differences between populations at the Norwegian coast and the Barents Sea (Frydenberg et al., 1965; Sick, 1965a; Møller, 1968; see later study by Dahle and Jørstad, 1993; Fyhn et al., 1994). Conclusions from mtDNA are conflicting, ranging from panmixia (Árnason and Pálsson, 1996) to significant differences between Norwegian coastal and Arcto-Norwegian populations (Dahle, 1991). Conflicting results are also found when comparing the allozymes

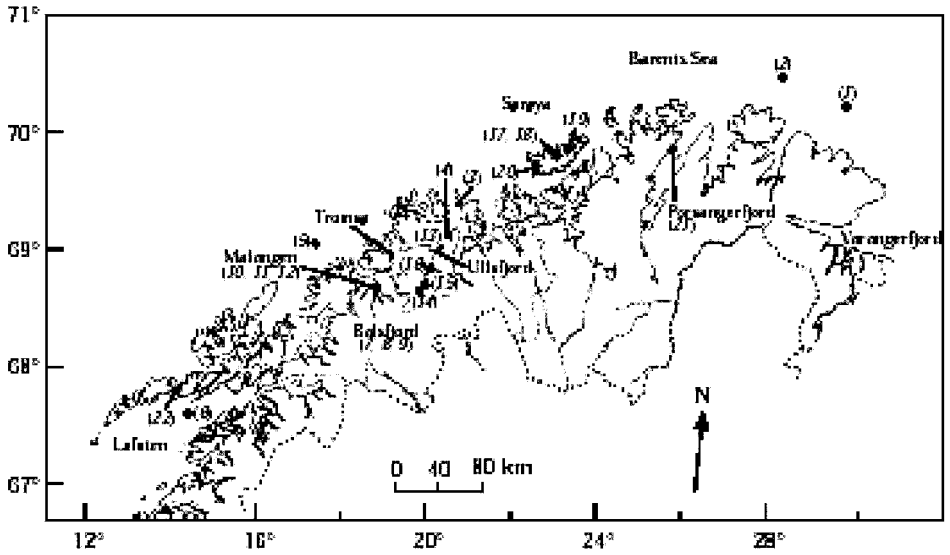

Figure 4. Approximate locations of 22 sampling stations of Atlantic cod off northern Norway (from Fevolden and Pogson, 1997).

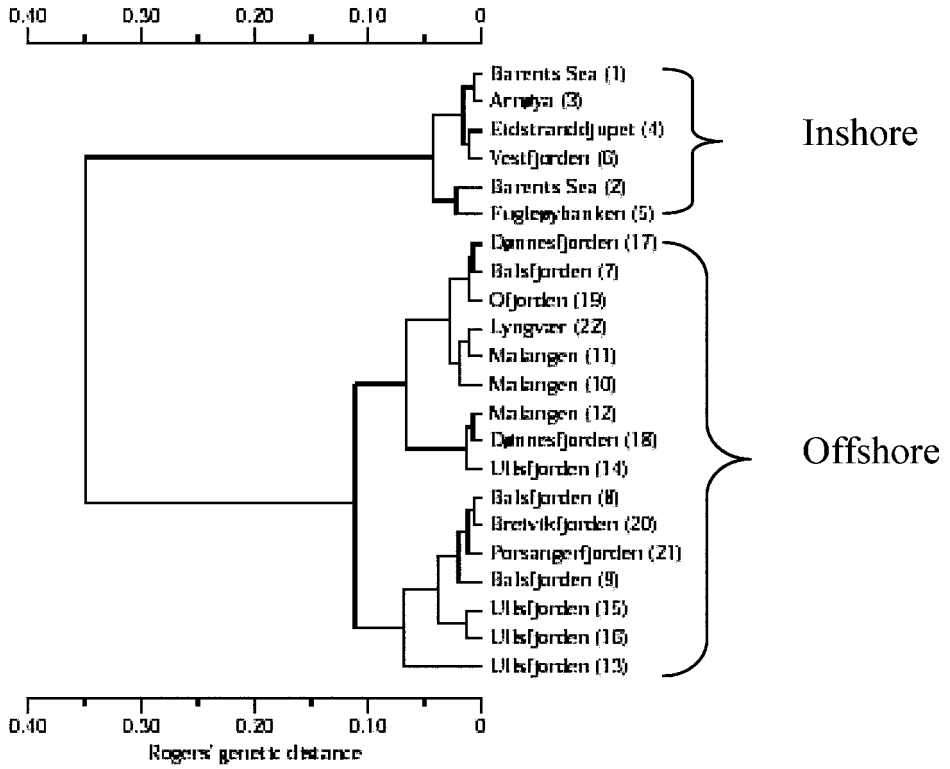

Figure 5. UPGMA dendrogram of the 22 subsamples (see Figure 4) based on Rogers genetic distance. Sample numbers given in parentheses refer to numbers in Figure 4 (adapted from Fevolden and Pogson, 1997).

studies of Mork and Giæver (1999) who conclude (when excluding LDH from their analysis) that, cod along the Norwegian coast are genetically homogeneous, and the studies of Jørstad and Nævdal (1989) and Gjøsæter et al. (1992) indicating moderate heterogeneity. The only non-conflicting markers are cDNA, as the studies of Fevolden and Pogson (1995, 1997) show highly significant differences between Norwegian coastal and Arcto-Norwegian populations (AMOVA, F_{ST} = 0.398). Mork and Giæver (1999) argued against the use of all markers affected by natural selection (*LDH-3*, *Hb-I*, and *Syp* I) and recommended the use of mtDNA markers as used by Árnason and Pálsson (1996). We feel that this will not solve the issue of genetic differentiation in cod in Norwegian waters, as mtDNA studies have also lead to conflicting results (see Dahle, 1991). Although undetectable by some markers, less profound genetic structures may exist which are of sufficient stability to allow a realistic biological stock delineation, and hence aid in a rational resource utilization (Mork and Giæver, 1999). What is clearly needed are studies based on genetic markers with sufficient temporal stability and with sufficiently high evolutionary rates to dominate over current levels of gene flow. Such markers are available, i.e., DNA microsatellites, and these have been applied with success to detect genetic differentiation in cod at localized scales in the northwest Atlantic and Canada. The results from these studies are discussed in the next section of the review.

Northwest Atlantic

Substantial genetic sub-structuring has been reported for cod in the northwest Atlantic. Already in the 1960s, a genetic study using hemoglobin revealed a polymorphic ratio cline along the coast of North America (St. John's, Newfoundland; Woods Hole, Gulf of Maine; and Ocean City, Maryland; Sick, 1965a). Significant frequency differences were observed for *Hb-I* alleles between Newfoundland ($Hb\text{-}I^1$ = 4.2%) and the Gulf of Maine (HbI^1 = 8.0%), but the difference between the Maryland and Gulf of Maine samples was insignificant (Sick, 1965a). Moreover, the frequency of this allele in the Newfoundland sample was significantly higher than the value of 0.016 for the pooled Greenland and Icelandic samples (Sick, 1965a). It is noteworthy that the American cline is much less steep than the one found in the eastern Atlantic, where the $Hb\text{-}I^1$ allelic frequency ranged from about 0.10 to 0.60 (Barents Sea and North Sea/Skagerrak/Danish Belt Sea, respectively) over a latitudinal distance which is only about half of that between Disco Bay (Greenland, the northernmost west Atlantic sample) and Maryland (North America, the southernmost west Atlantic sample; Sick, 1965a). Jamieson and Birley (1989) supported the genetic heterogeneity at the *Hb-I* locus in a later study.

Cross and Payne (1978) analyzed cod samples from Hamilton Inlet Bank in the north to South Channel in the southwest and Flemish Cap in the east, using transferrin and *PGI-2* loci. In accordance with Jamieson (1975), they found a decrease of *Tf2* and an increase of *Tf5* allele frequencies from north to south, but, unlike Jamieson (1975), they did not observe the striking heterozygote deficiencies that Jamieson (1975) interpreted as evidence of major genetic divergence. Overall, the transferrin and *PGI-2* combined indicated a separation of cod into at least two groups, the Flemish Cap and the adjacent northern Grand Bank, but the transferrin subdivided the cod stock further into populations north (Hamilton Bank to Gulf of St. Lawrence) and south (Scotian Shelf to South Channel) of Laurentian Channel (Cross and Payne, 1978). They speculated that the Flemish Cap may have maintained a relict cod population during the last glaciation while the North American shelf cod populations were forced farther south of their present range by low sea temperature and that the two relict groups have not introgressed subsequently. Further subdivision of cod populations were observed within the north Laurentian Channel group, where a significant dichotomy was observed between northern (Hamilton Inlet Bank to Northern Grand Bank east) and southern (Northern Grand Bank west to Gulf of St. Lawrence) components. The results of Cross and Payne (1978) were supported in later research (Galvin et al., 1995; Pogson et al., 1995; Bentzen et al., 1996) and further subdivision of cod populations was observed (Ruzzante et al., 1998).

Both the studies of Pogson et al. (1995) using anonymous nuclear RFLPs loci and of Galvin et al. (1995) using the *Mmer*-AMP2 minisatellite locus, revealed clear genetic subdivision of cod off Newfoundland and on the Scotian Shelf. The overall F_{ST} (= 0.03) in the study of Galvin et al. (1995) was in the range of single-locus F_{ST}'s reported by Pogson et al. (1995) for anonymous nuclear RFLP loci (F_{ST} = 0.008 − 0.309; average = 0.069). Bentzen et al. (1996) surveyed cod populations from the Scotian shelf, the northern cod stock complex (Labrador to

northern Grand Bank), and the Flemish Cap with a suite of six microsatellites. Both the number of alleles (40.8) and the mean heterozygosity (0.86) were very high. A number of single and multi-locus measures supported the findings of three genetically distinct populations of cod (Flemish Cap, Scotian Shelf, and Northern cod), and of further division of Northern cod into northern and southern components. However, the distinct split between populations south of the Laurentian channel and those to the north observed by Cross and Payne (1978) was only weakly supported, although the Laurentian channel marked a discontinuity in geographic variation at one locus (Gmo132). They argued that the deep ocean trenches separating the three genetically different populations act as barriers to gene flow, and further that genetic divergence is caused by genetic drift and mutation acting in reproductively isolated populations (Bentzen et al., 1996).

The finding of northern and southern components of Northern cod were further supported by Ruzzante et al. (1998), where variation in five microsatellite DNA loci scored in approximately 1300 individuals provided evidence of genetic structure among 14 cod populations spanning the range of the species in the northwest Atlantic (from the northeast Newfoundland Shelf in the north to the Bay of Fundy and Georges Bank in the south). Moreover, they found significant genetic differences among populations that had been considered to be homogeneous (Ruzzante et al., 1996, 1998). They demonstrated that cod overwintering in the inshore area of Trinity Bay were genetically different from offshore overwintering cod (Ruzzante et al., 1996, 1997). These findings were consistent with morphometric differences between cod populations off Newfoundland (Pepin and Carr, 1993). Moreover, Ruzzante et al. (1997) indicated temporal stability between inshore overwintering cod from Trinity Bay and offshore overwintering cod from the Grand Bank as the magnitude of genetic distance between these groups, however measured remained virtually identical (F_{ST} = 0.001). In a later study, Ruzzante et al. (1998) documented differences among cod populations at a continental shelf scale involving the NE Newfoundland Shelf, the Grand Banks, the Flemish Cap, the Scotian Shelf, and George Bank, and emphasized that each group was separated from the next by a series of submarine saddles, channels, or trenches. They also found evidence of genetic structure in cod populations at spawning bank scales that can be characterized by distinct oceanographic features (Ruzzante et al., 1998). A hierarchical analysis of F_{ST} revealed evidence of genetic population structure at several geographical scales, including when all 14 populations were considered separately (F_{ST} = 0.0084; $P < 0.001$). Genetic differentiation increased if populations were pooled into six shelf-scale groups: northern cod, Flemish Cap, south Newfoundland, Scotian Shelf, Georges Bank, and Bay of Fundy (F_{ST} = 0.011). In all, Ruzzante et al. (1998) separated their 18 sample locations into 14 populations based on differences in geographical locations or genetic differences, or both. Beacham et al. (2002) examined variation at seven microsatellite loci and one nuclear RFLP locus (*Pan* I, i.e., former *Syp* I) from 19 inshore and offshore locations around Newfoundland and Labrador (Figure 6). The mean F_{ST} over all loci was 0.008 and regional differences in allele frequencies were seven times larger than annual variation, indicating several different stock units (Figure 7). Overall, the cod populations surveyed conformed to an isolation-by-distance structure rather than a strict inshore-offshore division as suggested by Ruzzante et al. (1996, 1997, 1998). The study of Beacham et al. (2002) differed from the studies of Ruzzante et al. (1998) as it was based on other genetic markers (seven new microsatellite loci and the *Pan* I locus), more samples were taken from the insular Newfoundland area, and only mature fish were collected. However, while both the studies of Beacham et al. (2002) and Ruzzante et al. (1996, 1997, 1998), and tagging studies in this area (Taggart et al., 1995) have indicated that there is little exchange between cod stocks in these areas, Ruzzante et al. (2000a) suggested (based on microsatellite data) that cod aggregations characteristically found in the overwintering region in the Gulf of St. Lawrence represent population mixtures that differ in the proportion of cod contributed to them by the various stock components. Two general conclusions can be drawn from these studies. First, given the population substructure detected between most inshore and offshore areas, and among offshore areas themselves, the likelihood that the inshore-spawning stock will contribute to offshore recovery is low (Beacham et al., 2002). Second, future management should be designed around the spatial and temporal scale of the stock structure identified between inshore and offshore populations (Ruzzante et al., 1996, 1997, 1998; Beacham et al., 2002), and during overwintering in the Gulf of St. Lawrence (Ruzzante et al., 2000a).

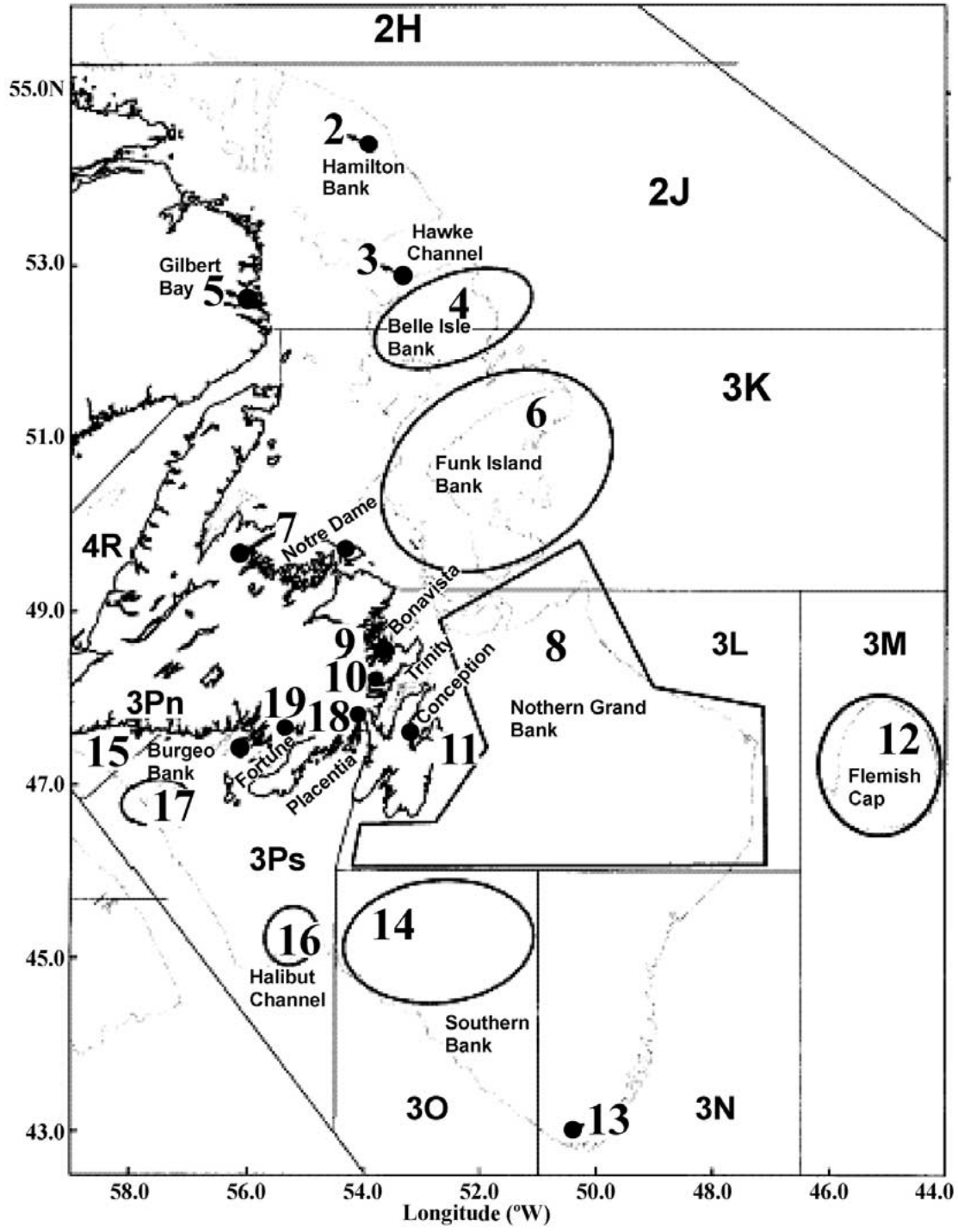

Figure 6. Sampling locations in the Beacham et al. (2002) study. Inshore samples: 5, 7, 9, 10, 11, 18, 19; Offshore samples: 2, 3, 4, 6, 8, 12, 14, 15, 17. Boundaries of NAFO divisions and the 300 m depth contour are indicated (from Beacham et al., 2002).

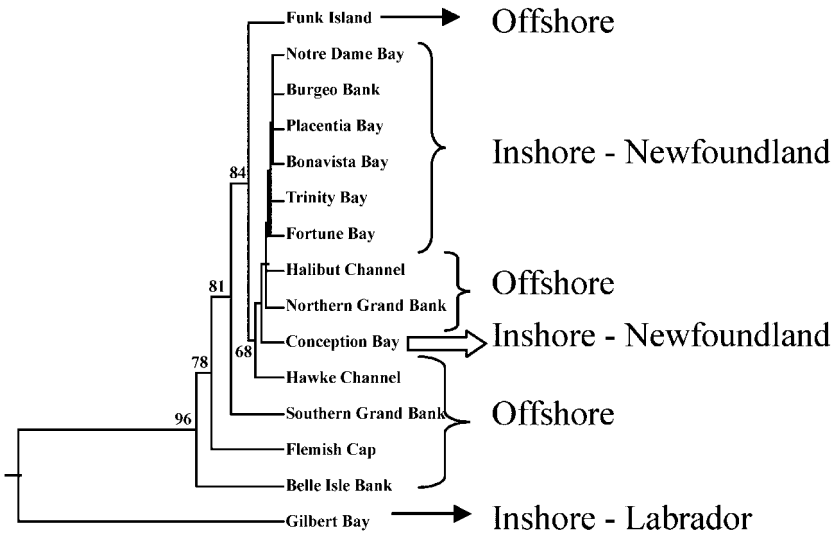

Figure 7. UPGMA dendrogram based on Cavalli-Sforza and Edward's chord distance for cod from 15 sampling sites in the northwest Atlantic adjacent to Newfoundland and Labrador. Only samples of at least 20 fish were included in the analysis (adapted from Beacham et al., 2002).

Why do mitochondrial and nuclear DNA studies give such contradictory results?

In the studies discussed above, the results indicate subdivision of Atlantic cod where microsatellites, minisatellites, and anonymous nuclear DNA RFLP markers have been applied, and at least some protein loci reveal differences among western Atlantic stocks. This is in sharp contrast to most studies based on mitochondrial DNA variation, as these have shown limited or no differentiation of populations (e.g., Árnason and Rand, 1992; Árnason et al., 1992, 2000; Pepin and Carr, 1993; Árnason and Pálsson, 1996). The question must arise as to why the RFLP analyses of mitochondrial, on the one hand, and most other markers, on the other, give such contrasting results.

First, as mitochondrial DNA is predominantly maternally inherited it is important to sample individuals from many locations to avoid sampling individuals belonging to the same mtDNA clone (descending from a common female; Dahle, 1991). In the study of Árnason et al. (1992), the majority of samples were sampled from only six catches but not spread across the spatial and temporal scale as recommended (e.g., Dahle, 1991).

Second, all samples in the Árnason et al. (1992) study were taken from coastal areas, making it impossible to test whether an off-coastal population might exist off Iceland. Further, the vast majority of samples were sampled from depths shallower than 90 m thus ignoring the fact that cod off Iceland are predominantly caught at depths exceeding 90 meters. It is possible that this sampling procedure, which is biased towards shallow depths and coastal areas, might not be adequate if the aim is to describe the population structure of cod off Iceland. In another study of cod population genetics off Iceland, Jamieson and Jónsson (1971) investigated a total of 2549 specimens caught at 62 localities and at various depths (50–253 m). Their study demonstrated that the frequency of the *Hb-I* locus varied highly between cod caught at the southwest coast (characterized by low $Hb1^1$ allele frequencies) and cod caught at the northwest, north, and northeast coast (characterized by high $Hb\text{-}I^1$ allele frequencies).

Third, the phenograms in the Árnason et al. (1992) study show a large individual variation within samples taken from the same sampling site and in many cases this variation is greater than the variation between the different sampling sites. It follows then, that it is possible that the large intra-population variation between mitochondrial DNA genotypes seen in the Árnason et al. (1992) study might be masking some of the inter-population variation, and making it difficult to draw firm conclusions regarding the population structure. To overcome statistical problems related to large individual variation within samples, a large sample size is required to reveal inter-population variation.

Finally, the contrast between mitochondrial DNA and nuclear DNA analysis in resolving population structure may relate to different potential for detecting

variation. It has been suggested by some workers (e.g., Carvalho and Hauser, 1994; Ward and Grewe, 1994; Ruzzante et al., 1996) that, if they exist, genetic differences are more likely to be detected by nuclear than by mitochondrial DNA studies. This is supported by the fact that in many cases, mtDNA analysis has not lead to enhanced resolution of stock issues compared with other molecular methods (Ward and Grewe, 1994 and references therein). MtDNA is usually treated as a single locus, with the composite genotypes equivalent to alleles, whereas allozyme and nuclear DNA analysis permits the examination of many independent loci (Ward and Grewe, 1994). Further, in many marine fishes common genotypes are frequently widely distributed (Smith et al., 1990; Carvalho and Hauser, 1994). It has, thus, been suggested that analysis of frequencies distributions demands larger sample sizes than traditionally has been employed in many mtDNA studies (e.g., Dahle, 1991; Árnason et al., 1992; Árnason and Pálsson, 1996), and that the use of too few individuals may contribute to the mtDNA homogeneity commonly observed (e.g., Árnason et al., 1992).

Population separation and growth differences

The discussion in the first section of this review clearly indicates that, despite some inconsistencies among the numerous genetic studies of cod in Norwegian waters and the northwest Atlantic, these studies illustrate that cod in the investigated areas consists of several distinct populations both within and between areas. Accordingly, we will now shift focus to an important question: given that different population units of cod exist, does life history vary between these units? To answer this question, we will first address the possibility of population specific variation in life history parameters, focusing on differences in growth. First, the theory behind such differences will be elucidated. Second, population specific differences in growth physiology will be reviewed with examples from cod and other fish species. The focus will then be shifted from population specific to the next level below, i.e., genotype specific differences in growth physiology exemplified by two well studied loci (*Hb-I* and *Syp/Pan* I) in cod.

Population-by-environment interactions

Studies on many fish species, particularly salmonids, have clearly demonstrated that production characteristics often vary between different populations (see review in Gjedrem et al., 1988). The hypothesis that growth and other life history traits in fish can vary between latitudes was suggested by Conover and Present (1990) and Conover (1990). The driving selective force for this variation in growth has been demonstrated to be size-dependent winter mortality in young-of-the-year (YOY) fish, which is greater in smaller fish (Shuter and Post, 1990; Conover, 1992 and references therein) and at higher latitudes (Conover and Present, 1990). Such size-dependent winter mortality results in a strong selection pressure towards fast growing fish at higher latitudes. This selection pressure will increase as the growing season becomes shorter and as winter temperature decreases with increasing latitude. Conover (1992) noted that, to the extent that growth rate is heritable, local populations that experience size-selective winter mortality should evolve higher growth rates than those that do not, given an absence of confounding factors. The end result may be a countergradient variation in growth: genetic variation that compensates for environmental influences on phenotype across an environmental gradient (Conover and Present, 1990; Conover, 1998). The simplest and most direct approach to determining whether the pattern of trait variation across multiple field locations has a genetic basis is the 'common-garden' experiment, pioneered by plant ecologists many decades ago (Conover, 1998). Individuals from different populations or locations are reared in controlled environments that span the range of conditions likely to influence fitness traits in nature, e.g., growth and food conversion efficiency. Reaction norms are measured for the traits of interest and compared across populations. A significant difference among populations in the mean or variance of traits in a common environment indicates a genetic basis. Differences in the slope of reaction norms indicate that the relative performance of each population depends on the environment (i.e., genotype by environment [G×E] interaction), whereas differences in elevation of the reaction norms indicates covariance (Cov G,E) (Stearns, 1992; Conover, 1998). In an ocean-wide common garden study, it would be important to have as many families as possible represented from each population. Simulation studies (e.g., Bentsen and Olesen, 2002) have been used to determine the effect of the number of breeders (4–100 pairs), the number of progeny tested (5–150 progeny per pair), and the magnitude of the heritability ($h^2 = 0.1 - 0.4$) on the rate of inbreeding, and the response to selection

through 15 generations of mass selection. The mean h^2 of life history traits (including growth) is found to be 0.26 (Law, 2000). For $h^2 = 0.2$, the simulation study of Bentsen and Olesen (2002) implied that a combination of at least 10 broodstock pairs and 50 progeny from each pair would reduce the variation in response to selection by 20% compared with 4 pairs, and a further increase to 50 pairs and 50 progeny from each pair would reduce the variation by 60% compared to 4 pairs. Accordingly, 10–50 broodstock pairs with at least 50 progeny from each broodstock pair would be more than adequate in a common-garden study to achieve a precise estimate of the genetic effect in each population. Such an experimental design would have a statistical power ($1\text{-}\beta$) of 0.86–0.95 (Lynch and Walsh, 1998).

Theoretically, faster growth of northern fish must be achieved by either (a) higher consumption or (b) better food conversion efficiency, or (c) a combination of the two. If physiological efficiency is maximized by natural selection, the faster growth of higher-latitude halibut should result solely from higher consumption rates. In the study by Imsland et al. (2000a), gross energy conversion efficiency (K; defined as: K = growth/daily energy consumption) differed between the three populations of Atlantic halibut, with 24.9, 22.3, and 19.9% of the consumed energy accumulated in Atlantic halibut from Norway, Iceland, and Canada, respectively. This indicates 25% better energy utilization in the Norwegian population compared to the Canadian. This suggests that inter-population differences in utilization of energy may exist. This intra-specific variation in energy utilization between populations of juvenile Atlantic halibut is surprising because evolutionary theory (Falconer, 1989) predicts that if the utilization of energy increases an individual's fitness, selection should drive utilization of energy to fixation at some physiologically maximal species-specific level. This may suggest that the selection force for energy utilization and allocation can vary within the species level in response to environmental differences. Consequently, the underlying 'growth factor' (Imsland et al., 1998) can vary at the species level in response to different environments. Very few studies have addressed the possibility of intra-specific genetic variation in utilization of energy in poikilotherms. Reinitz et al. (1978) found significant differences in food conversion among different populations of rainbow trout (*Oncorhynchus mykiss*, Salmonidae). Also, Present and Conover (1992) found differences in food conversion efficiency and in food consumption in two populations of Atlantic silverside (Nova Scotia vs. South Carolina).

Variation in life history parameters in different population units

Conover and Present (1990) found that the strength of size selective winter mortality was positively correlated with latitude, representing a directional selection factor for increased body size. Further, geographical variation in growth with a general tendency towards lower temperature optima and larger size at first maturity in higher (northern) latitudes (Conover and Present, 1990) has been described for some marine fish species (Leggett and Carscadden, 1978; Boehlert and Kappenman, 1980; Castro and Cowen, 1991; Conover, 1992). In addition to such north-south adaptations in growth related to differences in temperature and day length, similar adaptations may take place between different ecosystems at the same latitude, and hence, cannot be categorized as countergradient variation in growth because of the same day length at the same latitude. Such adaptation should be categorized as 'local adaptation'. A mixture of local adaptation and latitudinal variation has been observed in turbot and halibut (Jonassen et al., 2000; Imsland et al., 2000a, b, 2001a, b, c), with high latitude populations showing faster growth compared to low latitude populations. Data from turbot (Imsland et al., 2001c) is shown in Figure 8. Here, food conversion efficiency, food intake, and growth of juvenile turbot reared under different temperatures (14–22 °C) were found to be higher in fish in a higher latitude (Norway and Iceland) strains than lower latitude (France and Scotland) strains in two confirmatory studies (experiment 1, size range 7–70 g fish, and experiment 2, size range 20–150 g fish). The slope of the reaction norms differs for both species (halibut, Jonassen et al., 2000; turbot, Imsland et al., 2001a, c), indicating that significant GxE interactions may be found for these species. The differences in growth may reflect adaptation to temperature (i.e., local adaptation), demonstrated by variation in optimum temperature for growth ($T_{opt}G$) or adaptation to length of the growing season, seen as higher growth rates in northern populations across all temperatures that permit growth (e.g., 14 °C, 18 °C, and 22 °C in Figure 8). Temperature compensation or decreased temperature interval for growth as an adaptation to the colder environment at higher latitude is seen as the alternative to countergradient adaptation. However, the two strategies are

not mutually exclusive, and the data of Jonassen et al. (2000) and Imsland et al. (2000a, b, 2001a, b, c) show indications that a combination of these two forms of growth regulation exist in Atlantic halibut and turbot.

These findings have two major implications. First, for culture of these species, particularly in selection work focusing on growth performance, it is suggested that northern populations may be more suitable for commercial aquaculture because they grow faster and convert food better than southern populations. Second, if countergradient variation in growth performance takes place within a species, it is insufficient to compare populations on the basis of only environmental data and a single growth model. One cannot automatically assume that one set of physiological parameters, in this case growth-related parameters, is satisfactory to predict growth for a species throughout its range, as different populations might show a difference in response towards different physiological parameters.

Do life history parameters vary between different cod stocks?

The findings on Atlantic cod do not show a clear consistent trend. Faster somatic growth of the southern NC cod, as compared with AN through the larval and early juvenile periods (van der Meeren et al., 1994; Otterlei et al., 1999) does not support the hypothesis of countergradient latitudinal variation in growth of cod. Otterlei et al. (1999) found only minor differences in larval and juvenile growth between the NC and NA stocks. The fish were reared at six temperatures in the temperature interval of 4–14 °C and, except for the occurrence of NC larvae growing faster than the NA larvae at 4 °C, the differences in specific growth and maximal growth (G_{max}) between the two stocks were minor relative to the significance of temperature. Svåsand et al. (1996) investigated the growth performance of NC and NA juveniles, which were reared together in net pens until maturation (approx. two years old). NC displayed significantly higher growth rate during the spring/summer season. The NA had significantly lower hepatosomatic and gonadosomatic indices, and were thinner than the NC, indicating differences in body form and energy allocation patterns between the two strains. The final weight of the NC cod was 15% higher than that for the NA cod. Growth performances for NC and NA stocks may reflect differences in life history strategy adapted to different environmental conditions. In nature, the NA grows to a greater maximum size in length and weight compared to the NC, although they grow slower and mature at a more advanced age (Godø and Moksness, 1987).

In two recent studies on the western side of the Atlantic (Purchase and Brown, 2000, 2001), differences in growth of cod reared in a common-garden experiment were found. Purchase and Brown (2000) reared cod larvae and juveniles from Grand Banks (GB) and the Gulf of Maine (GOM) at 7 and 12 °C, and found that larvae from the GB grew faster than GOM larvae at both temperatures. Gross food conversion efficiency (GFCE) also varied between the stocks, as the GB cod had significantly higher GFCE than the GOM cod at both temperatures. In the wild, GOM cod grow much faster than cod on the GB, probably due to a better combination of higher temperatures and higher prey density in the GOM. The authors concluded that environmental factors in the northwest Atlantic that result in slower growth in northern areas have also resulted in the evolution of higher maximum growth rates and better food conversion efficiencies in northern cod. They also concluded that genetic differences among stocks in these highly selected traits existed, corresponding to observed genetic differences found by researchers using molecular techniques (Bentzen et al., 1996; Ruzzante et al., 1996, 1998). In a replicated study, similar differences between GOM and GB cod were reported (Purchase and Brown, 2001). Other studies report differences in activity and metabolism (Hunt von Herbing and Boutilier, 1996) and growth (Hunt von Herbing et al., 1996) between larval cod from Newfoundland and Nova Scotia. Together, these studies suggest that adaptation to different environmental conditions may be widespread among populations of cod in the northwest Atlantic.

However, it is premature to conclude that population differences seen in the study of Svåsand et al. (1996) and Purchase and Brown (2000, 2001) are genetic in origin for two reasons. First, gametes were collected from wild adults and parental effect may have been present. Second, common-garden studies are often performed with small sample sizes of adults (7 family groups in Svåsand et al., 1996, and 7 (GB) and 27 (GOM) crossings in Purchase and Brown, 2000), so that the results may not accurately represent the whole population. It is possible that not all families are represented in the study material and that one or a few families are dominating the findings. It is also

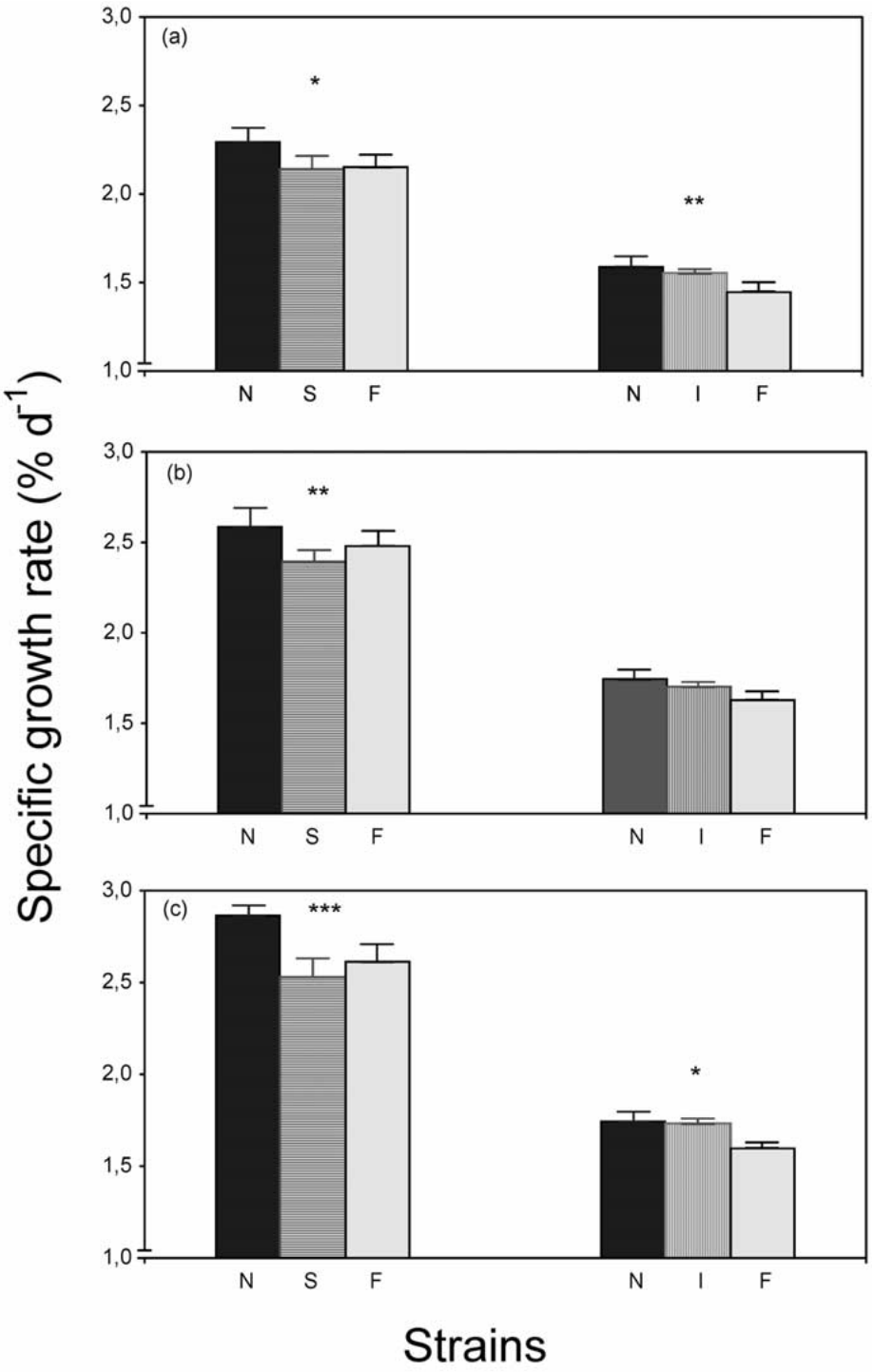

Figure 8. Comparison of mean (+SE) specific growth rates of four different strains of juvenile turbot in two confirmatory studies; Experiment 1 on the left (size range 7–70 g) and Experiment 2 on the right (size range 20–150 g); (a) 14 °C; (b) 18 °C; (c) 22 °C. $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$. N – Norway; S – Scotland; F – France; I – Iceland (adapted from Imsland et al., 2001c).

possible that the proportion of fast and slow growing fish is not equal in the experimental populations.

Overall, these studies reveal that there is still an urgent need to investigate this problem further if we are to be able to answer the question as to whether or not there is a genetic basis for geographical variation in growth rates of cod. The common-garden approach has given contradictory answers depending on which side of the Atlantic the problem has been investigated. We propose that a common-garden meta-analysis with several cod stocks from both sides of the Atlantic is needed to give any reasonable answer to the question of genetically-based growth differences. To conduct such a study, fertilized eggs from different stocks will have to be hatched and reared through the larval phase under identical environmental conditions in a single hatchery. All the fish will have to be tagged so different stocks can be identified and then reared under a range of environments (i.e., reaction norms; Stearns, 1992), but in the same experimental units (tanks). Until such studies have been conducted, it is premature to conclude one way or the other.

Genetic properties and growth performance: growth properties of different cod genotypes

Biochemical genetic variation of commercially important fish species has now been studied for three decades (reviewed by Smith et al., 1990; Carvalho and Hauser, 1994, Shaklee and Bentzen, 1998). However, the biological significance of biochemical genetic variation is still generally unknown, and few studies have tried to link the functional relationship between genetic variation and physiological parameters. For cod notable exceptions exist in the *Hb-I* and *Syp* I loci, and in the next section, we review results found in these loci.

Hemoglobin

The hemoglobin locus in Atlantic cod is characterized by at least three different genotypes called, *Hb-I(1/1)*, *Hb-I(1/2)*, and *Hb-I(2/2)*. Mork et al. (1984a, b), Mork and Sundnes (1984), and Nævdal et al. (1992) have reported growth differences related to hemoglobin polymorphism. These genotype dependent growth rates are probably correlated with differences in functional properties of the hemoglobins, as Karpov and Novikov (1980) reported specific temperature dependence of oxygen dissociation curves for cod hemoglobins. They found that oxygen affinity of *Hb-I(2/2)* was greatest at low (0 °C, 5 °C, and 10 °C) temperatures, but declined at higher temperatures (15 °C, 20 °C), whereas the reverse was found for *Hb-I(1/1)*, and *Hb-I(1/2)* displayed intermediate properties of the homozygotes. Brix et al. (1998) investigated the genetic variation and functional properties of Atlantic cod hemoglobins and found that the oxygen affinity of the hemoglobins varied between the genotypes. The *Hb-I(2/2)* genotype had the highest oxygen affinity in the temperature range of 10–20 °C (Figure 9). A similar system has been reported for other species. Samuelsen et al. (1999) estimated the oxygen affinities of the different turbot hemoglobin genotypes at 10°, 16°, and 19 °C, and at pH values 7.2, 7.5, and 7.8, and found that *Hb-I(2/2)* had the highest oxygen affinity at all three temperatures, followed by *Hb-I(1/2)* and *Hb-I(1/1)*. For both species, temperature sensitivity of O_2 binding for hemoglobin was low, but increased with increasing pH. It was hypothesized that the relatively temperature insensitive hemoglobins might be an adaptation to variable temperature conditions in the distribution area of the species. These studies demonstrate a functional relationship between particular biochemical genetic variants and physiological capacity. However, it is possible that other physiological processes, e.g., growth, may also vary between genotypes. Mork et al. (1984a, b) and Nævdal et al. (1992; Figure 9) indicated a genotype dependent growth rate in Atlantic cod, although in other studies no such dependence has been found (Jørstad and Nævdal, 1994; Glover et al., 1997). To test the correlation of growth and feeding behavior Salvanes and Hart (2000) compared the competitive performance of cod of the three *Hb-I* genotypes. Randomly chosen one-year-old cod were tested for individual responses to prey offered sequentially, and the results indicated that the most successful fish were usually among the first to feed and tended to possess hemoglobin genotype *Hb-I(2/2)*. Their findings indicate that there might be a link between genotype, growth and feeding behavior. Accordingly, it may be postulated that physiological factors are to some extent correlated, as the hemoglobin genotype in Atlantic cod with the highest affinity to oxygen also displays the highest overall growth and highest competitive performance. Such an interrelation between physiological factors is indicated for turbot, as the hemoglobin genotype with the highest oxygen affinity (*Hb-I(2/2)*) in turbot displays the fastest growth (Imsland et al., 1997, 2000c) and lowest age at first maturity (Imsland, 1999). There are not many examples of such relations between

physiological properties and biochemical genetic variation in the literature, but studies of Atlantic salmon (*Salmo salar* Salmonidae) and Arctic charr (*Salvelinus alpinus* Salmonidae) indicate that homozygotes of the trypsin isozyme allele 92 [*TRP-2 (92/92)*] have faster growth than other TRP genotypes (Torrisen, 1991; Torrisen and Shearer, 1992). This appears to relate to a higher protein conversion efficiency ratio of *TRP-2 (92/92)* homozygotes.

Syp *I genotypes and other RFLP genotypes*

In recent studies (Fevolden and Pogson, 1995, 1997; Jónsdóttir et al., 2001, 2002), the possibility of a correlation between growth properties and different genotypes at the synaptophysin (*Syp* I) locus in Atlantic cod has been investigated. Jónsdóttir et al. (2002) investigated the population genetics and genetically-based growth properties at two spawning sites off south Iceland (Kantur and Loftstaðahraun, Figure 2) and found large size differences between cod from the different sampling sites. Whenever significant differences were found between genotypes, the *Syp* I^{AA} displayed the highest weight at age and the *Syp* I^{BB} the lowest (Figure 10). No differences in weight between genotypes were found for the youngest and the oldest age groups. Genetically-based differences in condition factor were found for males at both sites and for females at Kantur. In all cases the *Syp* I^{AA} genotype had the highest and the *Syp* I^{BB} the lowest condition factor. Differences in growth, weight, and length were observed, and condition factor (CF) varied between the genotypes, as the *Syp* I^{AA} had significantly higher CF than did *Syp* I^{BB} (Jónsdóttir et al., 2002). Further, as there was a clear difference in the genetic composition of the Loftstaðahraun and Kantur samples, with significantly lower *Syp* I^{A} allele frequencies in Kantur samples, these differences in weight at age and CF could reflect differences in growth performance of the two sampling groups. This difference in condition of the *Syp* I genotypes might influence the viability characteristics of cod larvae. Marteinsdóttir and Steinarsson (1998) investigated maternal influence on egg size and viability of Iceland cod eggs and larvae, and found significant correlations between the CF of female cod and mean egg size, as well as larval feeding success. Genetically-based differences in condition of the different *Syp* I genotypes (Jónsdóttir et al., 2002) could lead to different quality and viability of larvae. At present, little is known regarding the physiological basis of the growth variation among fish with different *Syp* I genotypes and it is premature to conclude anything before controlled experiments with different genotypes have been performed. Pogson (2001) suggested that the polymorphism could relate to the differential expression and/or functioning of the protein (synaptophysin) in different tissues. This possibility can be tested by comparing the *in situ* levels and/or distribution of pantophysin/synaptophysin in different tissues for different *Syp* I genotypes. The intravesicular loops of physins (including synaptophysin) have not previously been identified as being important domains of the protein (Pogson, 2001), but the strong footprint of selection (e.g., differences in growth; Fevolden and Pogson, 1995; Jónsdóttir et al., 2002) found for this locus strongly suggests that it must be performing some critical function(s). Alternatively, the *Syp* locus may be linked to another locus performing these functions, as Pogson (2001) data indicate strong linkage disequilibrium at the *Syp* I gene region. A fruitful way to continue this research might be to conduct controlled experiments where performance (growth, food intake, feed conversion efficiency, feeding behavior, etc.) and environmental factors (e.g., temperature, oxygen, photoperiod, predation risk, and food availability) are studied simultaneously for different *Syp* I genotypes.

There are indications that growth differences may be found in nuclear loci other than the *Syp* I locus and that higher heterozygosity at these loci is linked to a fitness character i.e., overdominance. Jónsdóttir (2001) found genetically-based differences in length- and weight-at-age at two other loci (GM860 and GM865) in two populations of cod, i.e., Loftstaðahraun (south Iceland) and Trondheimsfjorden (west Norway). In both cases, heterozygotes displayed the highest growth. But as these overdominance differences were found in only two of six locations in the northeast Atlantic, the authors concluded that it is important to clarify whether differences in growth performance between genotypes at these loci are manifested when the fish is reared under controlled and equal conditions in the laboratory or if these differences were simply a coincidence.

Possible mechanisms behind growth differences

There are at least three interrelated explanations of the differences in growth and condition properties found between genotypes and populations.

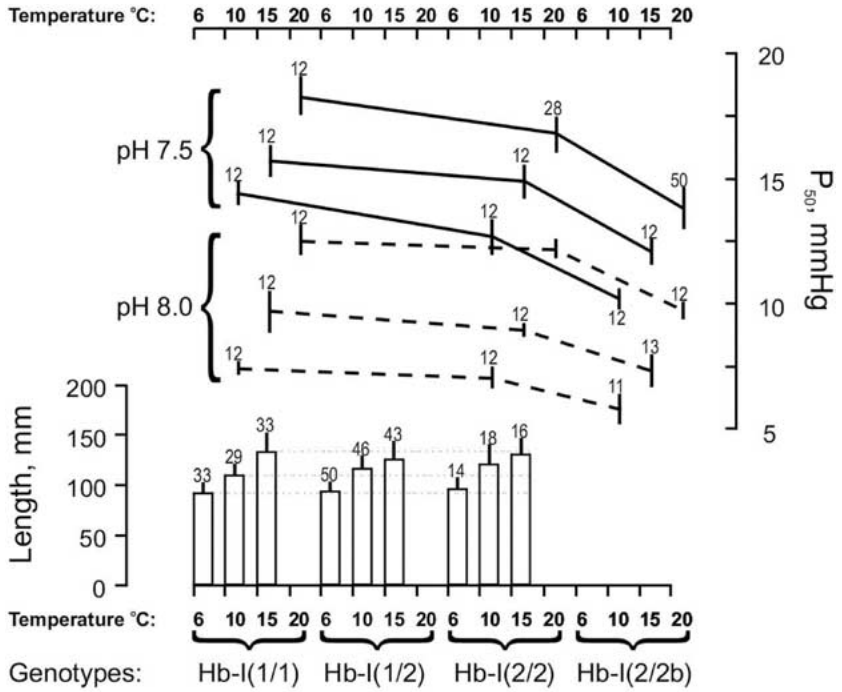

Figure 9. Oxygen affinity (P_{50}, mmHg) and growth data (length, mm) for three different hemoglobin genotypes in Atlantic cod as a function of temperature. Bars indicate SD and numbers on top of the bars N. Lines from above at both pH 7.5 and pH 8.0: *Hb-I(1/1)*, *Hb-I(2/2)*, and *Hb-I(2/2b)*. Oxygen affinity data from Brix et al. (1998) and growth data from Nævdal et al. (1992).

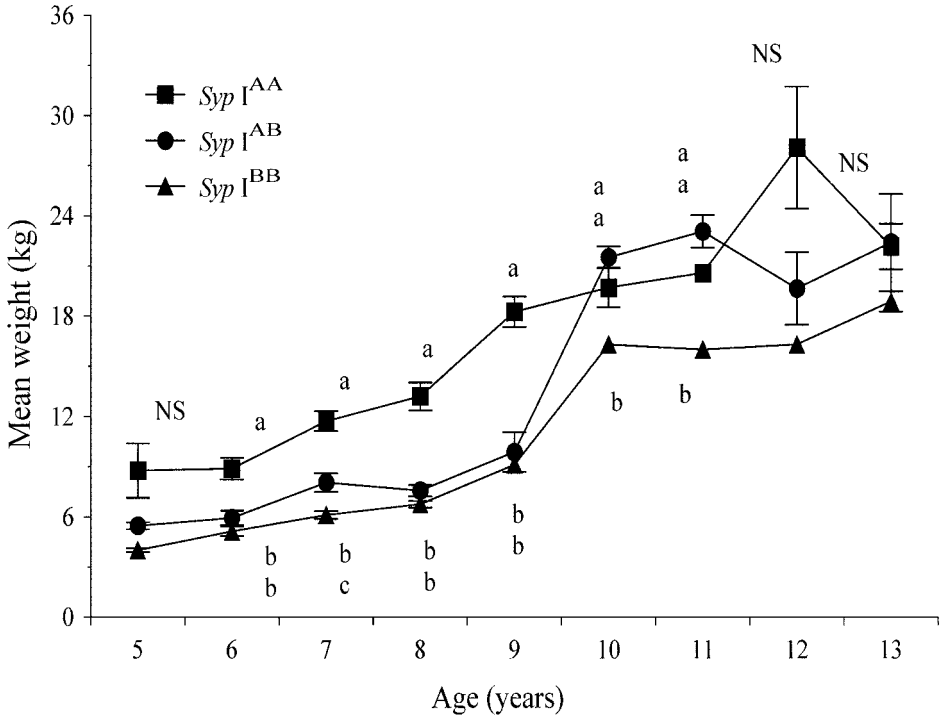

Figure 10. Mean weight at age of three *Syp* I genotypes of Atlantic cod at different ages. Data from the different sampling sites are compiled. Vertical lines indicate standard errors (SE). Different letters indicate significant differences (one way ANOVA followed by Student-Newman-Keuls multiple comparison test) within each age group; NS, not significant (adapted from Jónsdóttir et al., 2002).

Differences in population growth performance

Recent 'common-garden' studies on cod at the Faeroes in Norway and in Canada have indicated differences in growth performance of different cod populations (van der Meeren et al., 1994; Fjallstein and Magnussen, 1996; Svåsand et al., 1996; Otterlei et al., 1999; Purchase and Brown, 2000). Such differences in growth performance among populations have also been reported for several teleost species including American shad (*Alosa sapidissima* Clupeidae; Leggett and Carscadden, 1978), splitnose rockfish (*Sebastes diplopora* Scorpaenidae; Boehlert and Kappenman, 1980), weakfish (*Cynoscion regalis* Sciaenidae; Shepherd and Grimes, 1983), Atlantic silversides (*Menida menida* Atherinidae; Conover and Present, 1990), striped bass (*Morone saxatilis* Percichthyidae; Conover et al., 1997), Atlantic halibut (Jonassen et al., 2000; Imsland et al., 2000a), and turbot (Imsland et al., 2000b, 2001a, b).

These findings indicate that inter-population variation in life history traits may be a widespread pattern in temperate fishes and illustrate the important role of such variation in growth as a regulator of life history strategies in many temperate fishes.

Environmental influences on genetic variation in growth rates

It is also possible that the differences in growth properties reflect differences in environmental temperatures in the feeding areas of the groups under study, as adaptation to different migration and environmental patterns can influence life history traits in different fish populations. Earlier studies have shown a general tendency towards lower condition in fish from lower environmental temperatures (Haug et al., 1989; Solbakken et al., 1994; Imsland et al., 1995). In Iceland, the data of Jónsdóttir et al. (1999) indicate that part of the cod spawning at Kantur (south Iceland) migrates towards feeding areas off the east coast of Iceland, whereas cod spawning at Loftstaðahraun (south-east Iceland) migrate towards the west coast. Earlier tagging studies off Iceland have also indicated similar migration patterns (Jónsson, 1996). In the areas off east Iceland, the sea temperature is lower than off the southwest and west coast (Stefánsson and S. Jónsdóttir, 1974). It may thus be speculated that the genetically-based difference in growth seen in the study of Jónsdóttir et al. (2002) is partly related to differences in migratory patterns of the cod populations. Pogson and Fevolden (1998) found a relationship between growth rate and degree of individual heterozygosity at ten nuclear RFLP loci in one population of Atlantic cod (Balsfjorden, north Norway), but not in the other population studied (Barents Sea). To explain this discrepancy in their findings, Pogson and Fevolden (1998) pointed out that the Balsfjord population experiences harsher environmental conditions compared to the Barents Sea population, so that this could be an example of a genotype-environment interaction. If so, these loci may possess mutations that are deleterious in Balsfjord, but neutral in the Barents Sea.

Individual genetically-based growth differences

Individual differences in growth performance might explain the observed difference in growth indices. Every individual in a group of fish can be assigned an individual growth factor X_{i} that indicates the relative growth rate of the individual in relation to the average growth rate in the population. Few studies have tried to assess this underlying individual genetic growth factor (Forsberg, 1995; Imsland et al., 1998; Imsland, 2001), although it is axiomatic that individuals vary in growth. Imsland et al. (1998) suggested, based on modeling investigations of individual growth trajectories, that the individual growth trait X_i is stochastic with some kind of 'memory', i.e., the relative growth rate of individual i is to some extent correlated with its relative growth rate in the previous period. The authors suggested that the genetic component influencing growth and its autoregressive behavior have a large impact on growth variability in fish. Such growth variability can have a large effect on the dynamics of a cohort (Chambers and Leggett, 1992; DeAngelis et al., 1993; Rice et al., 1993). The positive correlation between imminent growth rates (Imsland et al., 1998) suggests that the individual growth factor X_i is inherent. The genetically-based growth reported by several authors (Torrisen, 1991; Nævdal et al., 1992; Forsberg, 1995; Fevolden and Pogson, 1997; Imsland et al., 1997, 2000c) supports this view. Fevolden and Pogson (1995) reported genetically-based differences in growth of *Syp* I genotypes. Using length/age ratio as an index of growth, they found that the *Syp* I^{AA} genotype displayed the highest mean growth and *Syp* I^{BB}, the lowest growth. Further, they found significant differences in *Syp* I allele frequencies between two samples of Arctic and Norwegian coastal cod populations. A later study confirmed this difference in allelic frequencies (Fevolden and Pogson, 1997). In

both studies the *Syp* I^{AA} genotype is more common in coastal cod samples, indicating higher growth of Norwegian coastal cod compared with Arctic cod, which conforms to the findings of Svåsand et al. (1996). The correlation between growth and *Syp* I genotypes is supported by Jónsdóttir et al. (2002). However, it is important to clarify whether differences in growth performance between genotypes and sampling groups are manifested when fish are reared under controlled and equal conditions in the laboratory. Mature fish at different localities need to be stripped in the field and eggs brought to the laboratory. After hatching larvae and juveniles will be reared together in common tanks so that the possible population specific difference in life history traits can be estimated.

Conclusions

In this review, we have discussed various aspects of the population genetics of Atlantic cod, and have tried to link a functional relationship between genetic variations and physiological parameters. It has been strongly implicated that cod in the north Atlantic Ocean is sub-structured. The study of cod stock structure in Norwegian and Icelandic waters, and in the northwest Atlantic area revealed considerable genetic differentiation between populations at localized scales using some genetic markers.

Observed growth differences between cod stocks may relate to environmental (not the focus of this review) factors (i.e., temperature), selective mortality, or food availability, or may have a genetic basis. The genetic growth regulation can be related to (a) superior growth performance of some cod stocks based on inherent population-based differences in growth, (b) changes in genetic composition of cod stocks where some stocks have higher frequency of 'high-growth-genotypes', or (c) a combination of the two first mechanisms. An example of the second mechanism (high growth genotypes) would be the synaptophysin (*Syp* I) and hemoglobin loci.

Future prospects

Different genetic markers, which assay genes with different mutation rates, allow us to view various aspects of genetic structure arising on various temporal and spatial scales. Accordingly, a particular method defines, or limits, the kind of questions that can be investigated and this should be taken into account in future population genetic studies. Also, this review illustrates the usefulness of knowing more about the general biology of cod. Knowing the migration pattern of cod, i.e., if cod migrate to the same spawning areas year after year, and knowing the behavior of cod, especially in the mating period, is important in relation to population genetics. Such behavior can greatly influence reproductive isolation and genetic stability of a population. Also, more knowledge about the influence of natural selection, mutation, and genetic drift on the genetic material of cod is necessary to understand why contradictory results are obtained using the different genetic markers discussed here. Identifying and genetically characterizing wild stocks are essential steps for their conservation, since overexploitation of genetically different populations can lead to the loss of genetic variability and productivity in subsequent generations.

As this review shows, there are many questions yet to be answered concerning the population genetic structure of cod. Future research should focus on gaining a thorough understanding of the biological, physiological and behavioral mechanisms that can cause reproductive isolation of cod. We must try to answer the questions of why different methods give contradictory results and how natural forces influence the genetic material, and also try to link in a coherent manner the interplay between genetically different populations and life histories.

Further, it is important to clarify whether differences in growth performance between genotypes and sampling groups are manifested when fish are reared under controlled and equal conditions in the laboratory. We propose that a common-garden meta-analysis with several cod stocks from both sides of the Atlantic is needed to give any reasonable answer to the question of genetically-based growth differences. Until such studies have been conducted it is premature to conclude one way or the other.

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