STOCK IDENTIFICATION METHODS
Applications in Fishery Science

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Environmental and Genetic Influences on Stock Identification Characters

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I. Introduction

II. Factors Underlying Intraspecific Patterns of Phenotypic and Genetic Diversity

III. Meristic Characters
   A. Environmental Influences
   B. Genetic Influences
   C. Variation Among Populations

IV. Morphometric Characters
   A. Environmental Influences
   B. Genetic Influences
   C. Variation Among Populations

V. Life History Characters
   A. Environmental Influences
   B. Genetic Influences
   C. Variation Among Populations

VI. Conclusions

References

I. INTRODUCTION

Characters used to identify fish stocks can be divided into three groups: those that are purely genetic, those that are purely environmental, and those that may reflect both genetic and environmental variation. Early studies characterized
stocks on the basis of phenotypic variation in life-history, meristic, morphometric, and life history traits. These characters are quantitative genetic traits, typically controlled by many genes and affected by the environment in which those genes are expressed (Falconer, 1981; Hard, 1995). They also are generally related to fitness and thus, molded by natural and sexual selection, they reflect local adaptation (e.g., Carvalho, 1993; Hard, 1995; Conover, 1998). Over the past 40 years, several molecular genetic techniques have been developed to directly examine genetic variation within and between groups (e.g., protein allozymes, mitochondrial DNA, microsatellite DNA). These genetic markers usually are assumed to be neutral or nearly neutral to selection (Carvalho and Hauser, 1994; McKay and Latta, 2002), although this is not always the case (e.g., Karl and Avise, 1992; Pogson et al., 1995; Streelman et al., 1998; Merila and Crnokrak, 2001). Finally, environmental markers, such as the elemental composition of otoliths, have also been used to delineate stock structure in recent decades (e.g., Thresher, 1999; Campana et al., 2000). These markers, signatures of the habitats or areas occupied at each life history stage, are usually thought to reflect purely environmental differences between groups of fish, although it has been suggested that genetic effects also may contribute to differences between individuals, stocks, or species (Kalish, 1989; Thresher et al., 1994). In this chapter, we focus on a comparison between the "traditional" approaches to stock identification using phenotypic characters, in particular meristic, morphometric, and life history traits, and the newer approaches using molecular genetic markers.

The strengths and weaknesses of the different approaches depend on the working definition of the term stock. A wide range of definitions has been used, spanning a continuum from the "fishery stock," a group of fish exploited in a specific area, to the "genetic stock," a reproductively isolated unit, genetically different from other such units (Carvalho and Hauser, 1994). Most commonly, a stock is considered equivalent to a population, at least partly reproductively isolated from other populations, and genetically different from them as a result of adaptation to its local environment (e.g., MacLean and Evans, 1981). However, the importance of delineating "phenotypic" stocks (Booke, 1981), groups of fish characterized by phenotypic differences that may be entirely environmentally induced, is being increasingly emphasized (e.g., Shepherd, 1991; Haddon and Willis, 1995; Jerry and Cairns, 1998; Lowe et al., 1998; Cadrin, 2000). For example, Cadrin and Friedland (1999) argue that intraspecific groups with persistent phenotypic differences in life history traits need to be recognized in stock assessment and fisheries management, even if these differences do not reflect genetic differentiation. Meristic, morphometric, and life history characters are clearly appropriate for delineating phenotypic stocks. In this chapter, we focus on the advantages and disadvantages of these types of characters for delineating genetically distinct, locally adapted stocks.
II. FACTORS UNDERLYING INTRASPECIFIC PATTERNS OF PHENOTYPIC AND GENETIC DIVERSITY

Genetic divergence between intraspecific groups depends on the level of gene flow between the groups, genetic drift, and selection (Endler, 1986). Genetic drift refers to the random fluctuation in allele frequencies that arises from the sampling of gametes in finite populations. Gene flow is the change in allele frequency that results from the movement of gametes or individuals between groups. Gene flow reduces or prevents differentiation, while drift promotes it. Selection can do either, depending on whether the same or different genotypes are favored in the different groups.

On evolutionary time scales, neutral molecular evolution between reproductively isolated groups appears to proceed at a steady pace, with the extent of neutral genetic differentiation between groups being a measure of the time since they became isolated (Wilson et al., 1977; Clayton, 1981). However, gene flow is a potent force opposing neutral genetic differentiation between groups that are not reproductively isolated. The exchange of a single migrant per generation will prevent different neutral alleles from being nearly fixed in different populations (Wright, 1931), although a higher exchange rate is required to maintain the same allele frequencies between populations (Allendorf and Phelps, 1981; Adkison 1995). Given the sample sizes usually employed in stock identification studies, Carvalho and Hauser (1994) argue that even a small number of migrants per generation is sufficient to prevent detectable heterogeneity in neutral genetic markers.

While neutral genetic markers provide an important tool for identifying the extent of reproductive isolation between groups and for determining phylogenetic relationships among isolated groups, they may not accurately reflect quantitative genetic divergence between groups in adaptive traits (Hard, 1995; Volpe and Ferguson, 1996; Conover, 1998). Genetic divergence in response to natural selection can be rapid (e.g., Reznick et al., 1997; Conover and Munch, 2002; Koskinen et al., 2002) and can occur despite regular gene flow that would prevent the accumulation of neutral genetic differences (Carvalho, 1993; Allendorf, 1995). Reed and Frankham (2001) reported only a weak correlation between molecular and quantitative measures of genetic variation and concluded that molecular markers do not accurately measure differentiation between populations as a result of natural selection. Karhu et al. (1996) found that Finnish Scots pine populations showed a high degree of genetic differentiation in adaptive quantitative traits but little differentiation in molecular markers. Similarly, genetic divergence in quantitative traits tended to be much stronger than molecular genetic (microsatellite) differentiation in recently evolved grayling populations (Koskinen et al., 2002). Finally, there is strong evidence of extensive adaptive genetic divergence among four morphs of sympatric Arctic char, Salvelinus alpinus, in developmental, life history, behavioral, and morphological traits (Skulason et al., 1989,
1993, 1996, 1999; Snorrason et al., 1994), yet there is relatively little variation in neutral molecular traits (Magnusson and Ferguson, 1987; Danzmann et al., 1991; Volpe and Ferguson, 1996).

In some cases, natural selection may also influence the divergence between populations in molecular markers. In cases where greater divergence is indicated by microsatellite DNA than by allozymes, it has been suggested that the allozyme loci are subject to stabilizing selection acting to maintain similar genotypic frequencies in different populations (e.g., Karl and Avise, 1992; Pogson et al., 1995). In other cases, rapid divergence in allozyme loci has been attributed to contrasting selection pressures between populations (e.g., Vuorinen et al., 1991). However, in most cases, molecular genetic markers, in particular noncoding microsatellite DNA variants, are thought to be largely neutral to selection (Carvalho and Hauser, 1994).

Local adaptation and differentiation into genetically distinct populations or stocks are generally thought to be less significant in marine fishes than in freshwater or anadromous fishes (e.g., Blankenship and Leber, 1995; Pawson and Jennings, 1996). This view stems from the lack of obvious physical barriers to migration in the sea and the high vagility of most marine fishes, either as migratory adults or as planktonic eggs or larvae. Consistent with this view, molecular genetic studies suggest lower genetic diversity in marine fishes than in anadromous and freshwater fishes (Gyllensten, 1985; Ward et al., 1994). However, gene flow may be limited despite the absence of physical barriers (e.g., Tallman and Healey, 1994; Wood and Foote, 1996; Skúlason et al., 1999), and genetic differentiation in adaptive traits may occur despite gene flow (e.g., Wood and Foote, 1996; Foote et al., 1997). Genetic differences in phenotypic traits related to fitness have been identified between populations of marine fishes by the few studies that have tested for such differences (e.g., Conover and Present, 1990; Svåsand et al., 1996; Schultz et al., 1996; Puvanendran and Brown, 1998; Purchase and Brown, 2000). Studies of the Atlantic silverside, *Menidia menidia*, provide an example of extensive evidence for local adaptation in a marine fish (Conover, 1998). This species is widely distributed along the east coast of North America, with few physical barriers to gene flow, a neustonic larval stage, and migratory adults. Genetic differentiation in life history and morphological traits has been demonstrated at fine geographic scales even though molecular genetic studies provide little evidence of population subdivision from Florida to Maine (Conover, 1998).

The main advantage in using life history and morphological traits in studies of population structure is that these traits are often related to fitness and respond to selection, and thus may reveal genetic differentiation not evident in neutral genetic traits. Their main disadvantage results from phenotypic plasticity, the ability of a genotype to produce different phenotypes across an environmental gradient (Bradshaw, 1965; Stearns, 1989; Thompson, 1991; Schlichting and Pigliucci, 1998; Debat and David, 2001). Two types of plasticity have been
distinguished (Schmalhausen, 1949). One type involves an environmentally cued switch in developmental programs, producing one phenotype in one set of environmental conditions and a different phenotype in a second set of conditions (Levins, 1963; Smith-Gill, 1983). Usually assumed to be adaptive, examples of this type of plasticity include the predator-induced shell dimorphism of some barnacles (Lively, 1986) and the female “morphotypes” found in some rotifers (Gilbert, 1980). The second type involves an effect of the environment on the rate or degree of expression of a given developmental program, rather than a switch between programs, and has been termed phenotypic modulation (Smith-Gill, 1983). Plasticity in life history and morphological traits of fishes appears to be mostly of this type. Although often considered nonadaptive, reflecting a failure to buffer development against environmental perturbations (Smith-Gill, 1983), recent research has focused on the possibility that this type of plasticity is also an adaptation to environmental heterogeneity in the phenotypes favored by selection (e.g., Thompson, 1991; Via et al., 1995; Schlichting and Pigliucci, 1998).

Phenotypic plasticity can be described as a norm of reaction (Schmalhausen, 1949; Schlichting and Pigliucci, 1998), a function that expresses how the mean phenotypic value of a given genotype changes with the environment (Fig. 4-1). Reaction norms provide information on the magnitude of plasticity in a trait, the presence of genotype × environment (G × E) interactions in the phenotypic expression of a trait, and the extent to which the additive genetic variance or

**FIGURE 4-1.** Hypothetical norms of reaction of two different genotypes to an environmental variable. The reaction norms specify the mean phenotype produced at each level of the environmental variable. Variation about the mean phenotype produced by a particular genotype in a particular environment generally occurs as a result of developmental noise (Waddington, 1957). Genotype × environment interaction is indicated by the intersection of the reaction norms. Common garden experiments conducted only in the vicinity of points A and B would fail to identify the difference between the two genotypes. Reprinted from Swain and Foote (1999) with permission from Elsevier.
heritability changes with the environment. Crossing reaction norms, indicative of G × E interaction, suggest the presence of genetic variation in plasticity. If that genetic variation is additive (i.e., heritable), then selection can produce changes to the shapes of reaction norms, resulting in population differences in responses to environmental change.

Phenotypic differences between groups in the wild may reflect genetic differentiation, environmental differences, or a combination of the two (Thompson, 1991). Differences that are consistent with expected or known differences in selection pressure are sometimes taken as evidence for genetic differentiation (e.g., Fleming and Gross, 1989). However, these patterns may be entirely environmentally induced (e.g., Swain et al., 1991), reflecting adaptive phenotypic plasticity (e.g., Bradshaw, 1965; Meyer, 1987; Schlichting and Pigliucci, 1998; Robinson and Parsons, 2002) rather than genetic divergence. An experimental approach is needed to disentangle the genetic and environmental components of phenotypic variation (Thompson, 1991; Conover and Schultz, 1995). Two approaches have been used: “common garden” experiments and reciprocal transplants. In common garden experiments, individuals from the different areas or populations are reared in the same controlled environments (e.g., Tallman, 1986; Kinnison et al., 2001; Koskinen et al., 2002). Ideally, a series of environments, spanning the range of conditions experienced in the wild, are used to delineate reaction norms and test for genetic differences in plasticity between groups. The use of a number of levels for the controlled environmental factors also reduces the chances that a genetic difference is overlooked because experiments are conducted at the intersection of reaction norms (e.g., points A and B in Fig. 4-1). In reciprocal transplant experiments, individuals from each population are placed together in each of their natural habitats (e.g., Robinson and Wilson, 1996). This approach has the advantage that genotypes are tested in each of the environments experienced in the wild, but has the disadvantage that care must be taken to avoid the escape of transplanted genotypes. Maternal effects and other preexperimental environmental influences pose a difficulty for both approaches. Differences due to these effects can be avoided by using offspring of parents that have themselves been reared in common environments (Conover and Schultz, 1995), though this will not be possible for many fishes. Alternatively, reciprocal hybrids (e.g., Hatfield, 1997; Craig and Foote, 2001) or quantitative genetic analyses (e.g., Koskinen et al., 2002) can be used to distinguish between genetic and maternal effects.

The possibility that phenotypic similarity reflects genetic differentiation is rarely considered in stock identification studies. However, this situation is likely to exist when phenotypic expression depends on environmental conditions and stabilizing selection favors the same phenotype in groups developing in different environments (e.g., Bervan et al., 1979; Bervan and Gill, 1983; Conover and Present, 1990; Tallman and Healey, 1991; Billerbeck et al., 2001). In this
situation, selection will favor genetic differentiation between the groups to counteract the differing environmental influences. This geographic pattern, in which differences between areas in the genetic influences on a trait oppose the differences in environmental influences, has been termed *countergradient variation* (Levins, 1968; Conover and Shultz, 1995). The alternative pattern, in which genetic and environmental differences reinforce each other, has been termed *cogradient variation*. Numerous examples of cogradient have been identified (see below), perhaps because the phenotypic differences produced by cogradient variation have tended to attract the attention of ecologists and evolutionary biologists. Even though countergradient variation may often be overlooked because of the phenotypic similarity that it produces, a growing number of cases have been demonstrated in marine, anadromous, and freshwater fishes (Conover and Present, 1990; Wood and Foote, 1990; Tallman and Healey, 1991; Present and Conover, 1992; Niciela et al., 1994; Schultz et al., 1996; Schultz and Conover, 1997; Conover et al., 1997; Arendt and Wilson, 1999; Purchase and Brown, 2000; Lankford et al., 2001; Craig and Foote, 2001).

### III. MERISTIC CHARACTERS

#### A. ENVIRONMENTAL INFLUENCES

Meristic characters are the numbers of discrete, serially repeated, countable characters such as vertebrae, gill rakers, and fin rays (e.g., Waldman, this volume). Phenotypic plasticity of meristic characters has been studied extensively (reviewed by Lindsey, 1988). The developmental environment can have a great effect on the number of parts formed in fish. However, early in ontogeny, the number of parts is fixed and remains unchanged regardless of subsequent changes in the environment. Some meristic characters (such as the number of vertebrae) are fixed relatively early in development, usually well before hatching, while others (such as median fin rays counts) may remain labile to environmental influences even well after hatching. The number of parts may be fixed well before the final number is visible and countable (cf. Lindsey et al., 1984).

Meristic characters are influenced by a wide variety of environmental factors including salinity, light, and dissolved oxygen (see review by Lindsey, 1988), but the influence of temperature has been the most widely studied (e.g., Heuts, 1949; Tåning, 1952; Lindsey, 1962; Lindsey and Harrington, 1972; Ali and Lindsey, 1974). Norms of reaction to temperature are most commonly negative (i.e., more parts produced at colder temperatures) for both vertebrae and fin rays, though U-shaped responses (i.e., minimum number at an intermediate temperature) are also common for vertebrae while positive or arched responses are frequent for fin rays (Lindsey, 1988).
Attempts have been made to delimit the developmental period when meristic characters are labile to environmental influences by transferring embryos between temperatures at various developmental stages (e.g., Tåning, 1944; Ali and Lindsey, 1974). This work has led to the definition of "sensitive" periods before and after which meristic counts are not labile, and "supersensitive" periods when a sudden temperature change produces a "shock effect" on meristic counts (e.g., Tåning, 1952). However, subsequent work has cast doubt on the ideas of shock effects and of sensitive periods before which meristic count is unaffected by environmental influences. Instead, meristic number appears to be continuously labile to environmental influences from fertilization to the final fixation of count, with no special periods of supersensitivity (Lindsey, 1988).

Meristic characters can also be affected by environmental influences acting on gametes before fertilization. The temperatures experienced by parents prior to fertilization affected the numbers of vertebrae and fin rays formed in offspring in the zebrafish *Brachydanio rerio* (Denty and Lindsey, 1978) and in the cyprinodont fish *Rivulus marmoratus* (Swain and Lindsey, 1986a). Likewise, the number of parts formed in *R. marmoratus* differed between offspring produced soon or long after the onset of oviposition in parents (Swain and Lindsey, 1986b). These prefertilization influences need to be considered when interpreting the results of common garden experiments. Meristic differences between groups of fish reared in the same environment may not indicate genetic differences, but instead reflect different prefertilization environmental influences acting on genetically similar parents.

**B. Genetic Influences**

Despite the strong environmental influences on meristic traits, there appears to be a strong genetic component to meristic variation within populations. High heritabilities (0.4–0.9) have been reported for a variety of meristic characters, including the numbers of vertebrae, fin rays, spines, and gill rakers (e.g., Hagen, 1973; Kirpichnikov, 1981; Hagen and Blouw, 1983; Tave, 1984; Leary et al., 1985; Beacham, 1990; Foote et al., 1999). Although polygenically controlled, usually by many genes (Kirpichnikov, 1981; Hatfield, 1997), these characters may in some cases be influenced by relatively few loci with major effects (Hagen and Blouw, 1983; Leary et al., 1984). Hagen (1973), Leary et al. (1985), and Foote et al. (1999) found no evidence for maternal or sex-linked effects on meristic traits. A number of common environment experiments have also revealed genetic variation in phenotypic plasticity of meristic characters (e.g., Ali and Lindsey, 1974).

The high heritabilities reported for meristic characters indicate a large store of additive genetic variation within populations available for response to selection. Because natural selection is expected to deplete additive genetic variation, high
heritability in a trait is sometimes assumed to indicate that the trait is not closely related to fitness. However, a link with fitness has been demonstrated for many meristic characters (e.g., Hagen and Gilbertson, 1973; Blouw and Hagen, 1984b; Swain, 1992b; Day and McPhail, 1996). Additive genetic variance in meristic characters appears to be maintained within populations by spatial, temporal, and ontogenetic heterogeneity in selection pressures (e.g., Reimchen, 1980; Swain, 1992b; Foote et al., 1999; Reimchen and Nosil, 2002).

C. VARIATION AMONG POPULATIONS

Widespread patterns in meristic variation occur among populations of related fishes. For example, vertebral number tends to be higher in populations occurring at higher latitudes or in colder waters (Jordan's rule; Jordan, 1892) as well as in those with greater maximum body lengths (pleomerism; Lindsey, 1975). Gill raker number tends to be higher in limnetic forms than in benthic forms (e.g., Lindsey, 1981; McPhail, 1984, 1992; Snorrsason et al., 1994; Hatfield, 1997), with the difference associated with prey size and the efficiency with which prey are handled (Lavin and McPhail, 1986; Schluter, 1993; Day and McPhail, 1996). Differences between areas or populations in spine and lateral plate numbers of sticklebacks appear to be related to differences in the intensity or type of predation (e.g., Hagen and Gilbertson, 1972; Reimchen, 1980; Blouw and Hagen, 1984a). These widespread trends suggest that meristic traits may be subject to natural selection.

Because of their link to fitness through effects on survival under predation (e.g., Hagen and Gilbertson, 1973; Blouw and Hagen, 1984b), meristic differences between populations in traits like spine and lateral plate numbers are usually expected to have a genetic component, and this has been confirmed by common environment experiments (McPhail, 1992). Gill raker number also has clear adaptive significance through effects on feeding efficiency, and controlled rearing experiments have generally confirmed a genetic component to differences between populations or morphs (Sværdson, 1979; McPhail, 1984, 1992; Snorrsason et al., 1994; Hatfield, 1997; Foote et al., 1999).

In contrast to gill raker number and meristic traits related to the body armature of sticklebacks, the adaptive significance of many meristic traits such as the numbers of vertebrae and fin rays has been obscure. For example, Fowler (1970) argued that, within narrow limits, the precise vertebral count is without selective significance, and that, within these limits, it may be more adaptive to let the number of vertebrae vary in response to environmental changes than to fix the number genetically. Concordant with this view, geographic variation in meristic traits is often attributed to environmental differences rather than to genetic differentiation (e.g., Brander, 1979; Templeman, 1981; Beacham, 1984; Shepherd,
1991), particularly when molecular genetic markers suggest genetic homogeneity between areas (Pepin and Carr, 1993). In contrast, Barlow (1961) argued that genetic differences may often underlie the meristic dissimilarities between populations or races of fish. He suggested that these differences may result from selection acting on correlated physiological processes, arguing that it is unlikely that "the addition or subtraction of a few elements would materially affect the probability of the survival of a fish." However, effects of the precise vertebral phenotype on swimming performance and survival under predation have been demonstrated in larval fishes and suggest that the trends observed among populations in this meristic trait reflect local adaptation to contrasting selection pressures acting directly on the number of vertebrae (Swain, 1988, 1992a,b). Common environment experiments have indicated a strong genetic component to geographic variation in the numbers of vertebrae and fin rays in the few cases examined (references in Lindsey, 1988; Taylor and Foote, 1991; Billerbeck et al., 1997). For example, Billerbeck et al. (1997) revealed a genetic basis to latitudinal variation in vertebral number in the Atlantic silverside using common garden experiments. Maternal effects and other prefertilization influences were ruled out by using offspring of parents that had themselves been reared in a common environment. In this case, genetic and environmental influences were cogradient, since there was also a negative relationship between vertebral number and rearing temperature. However, this environmental effect was slight compared to the strong genetic differences between populations. These genetic differences occurred despite little differentiation in molecular genetic traits (Conover, 1998).

IV. MORPHOMETRIC CHARACTERS

A. ENVIRONMENTAL INFLUENCES

Morphometric characters describe aspects of body shape. In contrast to meristic characters, they are continuous variables and depend on body size. Thus, a key step in measuring morphometric characters is disentangling shape from size (e.g., Rohlff and Bookstein, 1987). Morphometric characters also typically show ontogenetic changes associated with allometric growth (Gould, 1966). These ontogenetic changes in body shape may be particularly rapid at key life history stages, such as metamorphosis from larval to juvenile body forms, smoltification in salmon, and sexual maturation.

Unlike meristic characters, which are fixed early in life, morphometric characters may be labile to environmental influences throughout life (e.g., Wainwright et al., 1991). Although environmental influences on morphometric characters have not been as well studied as those on meristic characters, a number of influential factors have been identified. Body shape in fishes can be modified by
rearing temperature (Martin, 1949; Beacham, 1990), water velocity (Imre et al., 2002), quantity of food (Currens et al., 1989) and type of food or feeding mode (Meyer, 1987, 1990; Witte et al., 1990; Wimberger 1991, 1992; Wainwright et al., 1991; Day et al., 1994; Robinson and Wilson, 1995; Day and McPhail, 1996). Structures made of bone remodel and change shape depending on the stresses imposed on them (Lanyon, 1984; Lanyon and Rubin, 1985). These changes are usually considered to be adaptive (Lanyon and Rubin, 1985). Plasticity in trophic morphology induced by diet or feeding mode is usually assumed to result from bone remodeling in response to differences in loading regime. Other environmental influences may involve heterochrony, changes in the relative timing of developmental events (Meyer, 1987) such as switches between growth stanzas (Martin, 1949).

Phenotypic plasticity in morphometric traits may often be adaptive (Robinson and Parsons, 2002). Predator-induced changes in body shape of crucian carp Carassius carassius provide a striking example of adaptive plasticity in morphology. In the presence of northern pike Esox lucius, a predator of carp, crucian carp develop a deeper body (Brönmark and Miner, 1992). This change in body form occurs in response to chemical cues released by piscivores fed a diet of fish (Brönmark and Pettersson, 1994) and reduces the vulnerability of carp to predation by pike, a gape-limited predator (Nilsson et al., 1995). Adaptive plasticity may also contribute to the morphological differences between the benthic and limnetic forms observed in a variety of fish taxa (Robinson and Wilson, 1994; Robinson and Parsons, 2002). Coexisting limnetic and benthic forms of stickleback (Gasterosteus sp.) in Enos and Paxton Lakes, British Columbia, provide an intensively studied example. The limnetic forms have more and longer gill rakers; shallower bodies and heads; longer heads, snouts, and upper jaws; and larger eyes than the benthic forms (McPhail, 1984, 1992). Foraging success is superior for the limnetic forms in open-water habitats feeding on zooplankton and for the benthic forms in benthic habitats feeding on benthic prey (Bentzen and McPhail, 1984; Schluter, 1993). Common environment experiments indicate that the differences in morphology are inherited (McPhail, 1984, 1992; Hatfield, 1997), but the two forms also exhibit morphological plasticity in the adaptive direction (Day et al., 1994). Each species more closely resembled the other when raised on the latter’s diet. Diet-induced plasticity resulted in improved foraging efficiency (Day and McPhail, 1996) and reduced the morphological gap between species by 30% to 60% (Day et al., 1994). Similar diet-induced plasticity has been demonstrated in the cichlids Geophagus brasiliensis and G. steindachneri (Wimberger, 1991, 1992). Fish fed brine shrimp nauplii (a planktonic prey) developed longer snouts, larger eyes, longer and shallower heads, longer paired fins, and shallower bodies and tails than those fed chironomid larvae (a benthic prey). Similarly, changes in feeding orientation induced morphological differences in guppies Poecilia reticulata (Robinson and Wilson, 1995). Guppies feeding on floating food developed
a more fusiform shape than those feeding on food attached to a plate on the bottom. Morphological differentiation associated with trophic specialization has also been extensively studied in Arctic char *Salvelinus alpinus* and involves both genetic differences and phenotypic plasticity (e.g., Skulason et al., 1989, 1993, 1996; Snorason et al., 1994). Finally, Meyer (1987) reported extensive phenotypic plasticity in trophic morphology resulting from differences in diet and feeding mode in the cichlid *Cichlasoma managuense*. This plasticity paralleled the differences in morphology used to divide cichlids into functional groups. Adaptive phenotypic differences between groups of fish may thus reflect plasticity instead of indicating genetic differentiation between the groups.

**B. Genetic Influences**

Like meristic characters, morphometric traits are quantitative genetic characters, generally thought to be influenced by many genes of small individual effect, though some adaptive morphometric differences may be explained by relatively few genes of large effect (Hatfield, 1997). Estimates of the heritability of morphometric characters range between low and moderate values. Riddell et al. (1981) reported heritabilities less than 0.1 for morphometric traits in Atlantic salmon. The average heritability reported for morphometric characters of chum salmon ranged between 0.3 and 0.6, depending on rearing temperature (Beacham, 1990). Lavin and McPhail (1987) reported heritabilities between 0.19 and 0.84 for morphometric characters in the threespine stickleback *G. aculeatus*. Grudzien and Turner (1984) reported a heritability of 0.44 for the mouth width polymorphism in *Ilyodon*. Genetic variation for morphological plasticity has also been demonstrated whenever it has been tested in fishes (Robinson and Parsons, 2002).

**C. Variation Among Populations**

Body shape in fishes is generally thought to reflect adaptation to their ecological niches. Associations between body shape and ecological variables are commonly observed among populations of related fishes. Correlations between body shape and the extent of stream residence in Pacific salmon provide a well-studied example. Body shape and the extent of stream residence are correlated among the species of *Oncorhynchus* (see Scott and Crossman, 1973, p. 145), among life history types of Chinook salmon *O. tshawytscha* (Carl and Healey, 1984), and between ecological types (stream- vs. lake-rearing) of coho salmon *O. kisutch* (Swain and Holtby, 1989). Forms with longer stream residence have deeper bodies with larger, more brightly colored median fins. This pattern presumably
reflects contrasting selection pressures between stream and open-water habitats. In streams, both as territorial juveniles and spawning adults, selection may be predominantly for burst swimming and agonistic performance (e.g., Fleming and Gross, 1989). A deep body with large median fins is advantageous for burst swimming (Webb, 1978, 1984; Taylor and McPhail, 1985b) and during agonistic interactions (Holtby et al., 1993). In open waters (and during migrations to and from the sea), selection may be predominantly for sustained swimming performance, favoring a fusiform or streamlined body shape. Differences in body shape between interior and coastal populations of coho salmon are also consistent with these predictions. Interior coho, which must undertake longer migrations to and from the sea, are more streamlined, with shallower bodies and smaller median fins (Taylor and McPhail, 1985a), and have superior sustained swimming performance and inferior burst swimming performance in comparisons with coastal populations (Taylor and McPhail, 1985b). Similar differences in body shape and swimming performance have been demonstrated between sockeye salmon and kokanee, the anadromous and nonanadromous forms of *O. nerka* (Taylor and Foote, 1991). Body shape also differs between wild and hatchery populations of coho salmon. Both as juveniles (Taylor, 1986; Swain et al., 1991) and as adults (Fleming and Gross, 1989), wild salmon have deeper bodies and larger median fins than do hatchery salmon. These differences are in the direction predicted from the expected differences in selection between wild and hatchery salmon (Fleming and Gross, 1989; Swain et al., 1991).

Numerous other patterns in body shape have been identified between populations of related fishes. As previously noted, predictable differences in trophic morphology and general body shape occur between pelagic and benthic forms of related fishes (e.g., McPhail, 1984, 1992; Robinson and Wilson, 1994). Other examples include associations between body shape and stream velocity in Atlantic salmon *Salmo salar* (Riddell and Leggett, 1981), spawning stream size in chum *O. keta*, pink *O. gorbuscha*, and sockeye salmon *O. nerka* (Beacham, 1984; Beacham et al., 1988; Hamon et al., 2000; Quinn et al., 2001), and predation intensity in *Galaxias platei* (Milano et al., 2002). Such differences among stocks can result in differential exploitation rates, with increased risk of stock extinction, in cases where morphological variation is related to catchability by a fishery (Hamon et al., 2000). Because morphometric differences often result from changes in the timing of developmental events, they can be an indication of life history differences between groups, differences that are central to the assessment and management of exploited fish stocks (Cadrin, 2000).

Differences in body shape between areas, populations, or morphs could reflect genetic differences, phenotypic plasticity, or a combination of both factors. A genetic component to these differences has generally been demonstrated when it has been tested for by controlled rearing in common environments (Riddell et al., 1981; Todd et al., 1981; McPhail, 1984; Taylor and McPhail, 1985a; Taylor
and Foote, 1991; McPhail, 1992; Robinson and Wilson, 1996; Hatfield, 1997). An environmental component has also been found in most cases examined. Genetic differences and phenotypic plasticity both contribute to trophic polymorphism in pumpkinseed sunfish *Lepomis gibbosus* (Robinson and Wilson, 1996) and in stickleback species pairs (Day et al., 1994). In each case, environmental and genetic influences are cogradient, both operating in the adaptive direction. However, morphological differences between groups that appear to be adaptive given known or expected differences in natural selection between the groups are no guarantee that there is a genetic component to the differences. For example, differences in body shape of juvenile coho salmon between hatchery and wild populations, differences that appear to be adaptive given the expected differences in selection between the two types of salmon, are entirely environmentally induced (Swain et al., 1991).

Much of the genetic variation in body shape between fish populations may be overlooked because of the tendency to focus research on the phenotypic differences observed between areas or groups of fish (Tallman and Healey, 1991; Conover and Schultz, 1995). Body shape is similar between early- and late-spawning stocks of *O. keta* in the wild (Tallman and Healey, 1991) but differs distinctly between the stocks when reared in common laboratory environments (Tallman, 1986). Tallman and Healey (1991) suggested that stabilizing selection favored the same body shape in the two populations, resulting in genetic differences between the populations to compensate for the differences in their developmental environments. Given the demonstrated influences of the environment on body shape in fishes (see above), phenotypic similarity between groups of fishes developing in different environments may be more likely to reflect genetic differentiation than genetic homogeneity.

A danger in using multivariate morphometric analyses to discriminate stocks of fishes is that slight differences between groups in individual characters, possibly just sampling artifacts, can result in statistically significant but biologically insignificant differences between groups in multivariate analyses with large sample sizes and many characters (Cadrin, 2000; e.g., Bowering, 1988; Bowering et al., 1998). For example, Bowering et al. (1998) found statistically significant morphometric differences between all 18 samples of American plaice *Hippoglossoides platessoides* that they examined. Sample sizes were large, averaging 241 fish per sample. Bowering et al. (1998) concluded that a large body of additional biological evidence did not support the fine-scale stock separation suggested by the morphometric differences. Morphological differences with clear adaptive significance or ontogenetic causes that are stable over time, persisting between repeat samples taken over a number of years, provide a more meaningful basis for stock separation than differences occurring among a single collection of samples and lacking any evident ecological significance (Cadrin, 2000).
V. LIFE HISTORY CHARACTERS

A. ENVIRONMENTAL INFLUENCES

Life history traits reflect the ways in which individuals vary their stage- or age-specific expenditures of reproductive effort in response to intrinsic and extrinsic factors that influence survival and fecundity. As such, life histories reflect the expression of traits most closely related to fitness, such as age and size at maturity, number and size of offspring, and longevity, and the timing of the expression of those traits throughout an individual's life. Within an evolutionary context, natural selection is predicted to favor those individuals whose age-specific rates of survival and fecundity generate the highest rate of genotypic increase, commonly expressed as either $r$ or $R_0$ (Stearns, 1992; Roff, 2002). When expressed at the individual level, $r$ and $R_0$ represent fitness. When expressed at the population or stock level, they represent rates of population growth, a parameter that reflects a broad range of characteristics of interest to fisheries scientists, including sustainable rates of exploitation, resilience following population collapse, and probability of extinction (Hutchings, 2002).

Despite this rather clear and fundamental link between individual life histories and population growth rate, life history traits have been underrepresented as means of distinguishing putative stocks. Given that the harvest rates that a stock can sustain are ultimately a function of that stock's maximum rate of increase, it would seem logical to distinguish putative stocks on the basis of their life histories. However, the observation that the environment can affect life history traits appears to have contributed unduly to the relatively infrequent application of life history traits as metrics of stock identity.

In fishes, as with most indeterminately growing organisms, the influence of the environment on life history traits is realized primarily through factors that affect body size and the rate at which body size changes throughout an individual's life. Thus, an environmental factor, such as density, food supply, or temperature, that directly influences size can be expected to have some concomitant impact on several life history traits. A key question is whether these concomitant changes reflect phenotypic or genetic correlations among traits; in many cases, they almost certainly represent both.

Body size has a positive influence on many life history traits. Perhaps most notable among these associations is the observation that larger females produce more eggs than smaller females (Wootton, 1998; Roff, 2002). Larger individuals also tend to produce larger eggs, a correlation that holds for a number of species, such as Atlantic cod (Chambers and Waiwood, 1996), Atlantic herring, Clupea harengus (Hempel and Blaxter, 1967), capelin, Mallotus villosus (Chambers et al., 1989), and striped bass, Morone saxatilis (Zastrow et al., 1989). Increased
body size is also associated with lower mortality in several fishes (Hutchings, 1994; Schluter, 1995; Schultz et al., 1998; Post and Parkinson, 2001).

Reflecting both individual size at age and the rate at which that size is attained, few parameters have greater influence on the life history traits of fishes than growth rate. One of the best-documented associations between growth rate and life history is the observation that fast-growing individuals mature earlier in life than slower growing individuals (Alm, 1959; Hutchings, 1993a; Fox, 1994; Trippel et al., 1995; Godø and Haug, 1999). Independent of its effect on body size, growth rate can also potentially affect fecundity. Scott (1962), for example, reported that rainbow trout (Oncorhynchus mykiss) fed ad libitum produced more eggs per unit body mass than individuals fed a restricted diet. Regarding offspring size, there is evidence that growth rate in early life can both negatively (Jonsson et al., 1996) and positively (Morita et al., 1999) influence egg size in Atlantic salmon and white-spotted char (Salvelinus leucomaenis), respectively.

Although the life history consequences of phenotypic changes to growth rate are reasonably well understood, it is not clear how growth rate affects survival independent of its influence on body size. To some extent, this depends on the scale at which the association is examined. One of the classic life history invariants in fish is that denoted by K/M. Representing the ratio of a metric of growth (from the von Bertalanffy growth equation) to the instantaneous rate of mortality, its invariance across taxa implies that species or populations characterized by rapid individual growth are also characterized by high mortality (Beverton and Holt, 1959; Charnov, 1993). At the proximate level, negative consequences to survival may be effected by physiological, metabolic, and developmental costs associated with compensatory growth, defined as accelerated growth following a period of retarded growth (Metcalfe and Monaghan, 2001). For example, rapid growth during larval development is associated with delays in cranial ossification in pumpkinseed sunfish (Lepomis macrochirus), leading to reduced survival early in life (Arendt and Wilson, 2000). From an ecological perspective, faster growing individuals may place themselves at greater risk of predation if faster growth can only be achieved by riskier foraging behavior (Holtby and Healey, 1990; Werner and Anholt, 1993).

Thus, environmental influences on life history traits are realized primarily through correlated responses to life history generated by environmentally-induced variation in body size and individual growth rate. Indeed, given their heritable basis, their intimate links with fitness, and their manifestation above the level of the individual as population growth rate (r), the utility of using life history characters as metrics of stock identification merits reexamination.
B. GENETIC INFLUENCES

Life history traits are quantitative traits that vary by the expression of many genes, each having a minor influence on a variety of traits. In fishes, studies have consistently revealed strong genetic influences on life history traits, particularly in salmonids (Gjerde et al., 1983; Gjerde, 1984; Le Cren and Saum 1984). Genetic influences on life history traits are realized primarily as the result of differences in individual growth rate. Indeed, given their importance and manifestation above the growth rate (r), the utility of using life history information merits reexamination.

The expression of life history traits in fishes is determined by the interaction of genetic and environmental factors. Genetic differences in life history traits can be demonstrated in laboratory experiments, where progeny of mature male parent is typically killed. However, the incidence of progeny of mature male parent is typically determined by the genetic makeup of the parent, which is in turn determined by the genetic makeup of the parents. This is evident in studies that have compared the genetic makeup of different populations of salmonids, where there is evidence of both genetic and environmental influences on life history traits. For example, genetic differences in salmonid populations have been observed in the expression of life history traits, such as age at maturity, fecundity, and survival. These differences can be attributed to differences in the genetic makeup of the populations, which is in turn determined by the genetic makeup of the parents. This is evident in studies that have compared the genetic makeup of different populations of salmonids, where there is evidence of both genetic and environmental influences on life history traits. For example, genetic differences in salmonid populations have been observed in the expression of life history traits, such as age at maturity, fecundity, and survival. These differences can be attributed to differences in the genetic makeup of the populations, which is in turn determined by the genetic makeup of the parents.
small-male strategy (Myers et al., 1986; Thorpe, 1986; Bohlin et al., 1990; Metcalfe, 1998).

Several authors have suggested that adoption of alternative strategies in male salmonids depends on whether an individual's growth rate in early life exceeds that specified by a growth-rate threshold, that is, that the strategies are conditional upon an individual's state (Leonardsson and Lundberg, 1986; Thorpe, 1986; Hazel et al., 1990; Hutchings and Myers, 1994). In the quantitative genetic sense, threshold traits describe characters that are determined by alleles at multiple loci and that can be assigned to one of two or more distinct classes (Roff, 1998). The loci affecting threshold traits are assumed to each have some small effect on a trait that varies continuously. For alternative strategies in salmonids, the continuously varying trait may be the concentration of a hormone, the amount of lipid deposition, or a metabolic efficiency (Thorpe, 1986; Metcalfe, 1998). Genotypes expressing less than the threshold value of this underlying trait will express one phenotype, while those exceeding the threshold will express the alternative phenotype. Growth-rate thresholds can be modeled as norms of reaction for age at maturity. The existence of substantive differences in the incidence in parr maturity among families reared in a common environment (Glebe and Saunders, 1986; Herbing, 1987) suggests that differences in reaction norms for the probability of parr maturity exist among individuals in the same population.

C. VARIATION AMONG POPULATIONS

Across species, life history traits vary tremendously in fishes. For example, age at maturity ranges from weeks in annual cyprinodonts (Simpson, 1979) to decades in dogfish sharks (Saunders and McFarlane, 1993). Size at maturity varies from less than 1 cm in some gobies (Winterbottom and Emery, 1981) to several meters in whale sharks (Helfman et al., 1997). Fecundity ranges between 2 in some elasmobranchs to millions in many broadcast-spawning marine fish. And egg size differs 100-fold, varying from 0.3 mm in the surffish, *Cymatogaster aggregata* (Kamler, 1992) up to 30 mm in mouth-brooding catfishes (Tyler and Sumpter, 1996).

Significant differences in life history traits are not limited to among-species comparisons, and it is this within-species variability upon which stock differentiation could be undertaken (Begg et al., 1999; Begg, this volume, Chapter 6). Among populations of Atlantic salmon (*Salmo salar*), for example, egg size can vary threefold, age at maturity by one order of magnitude, size at maturity can differ 14-fold, and fecundity can vary almost 500-fold (Hutchings and Jones, 1998). Among marine fishes, the Atlantic cod (*Gadus morhua*) can also exhibit wide-ranging differences in age at maturity (2–7 years; Brander, 1994; Trippel et al., 1997), length at maturity (35–85 cm; Patriquin, 1967; Morris and Green,
2002), and size-specific fecundity (Marteinsdottir and Begg, 2002; McIntyre and Hutchings, 2003).

There is considerable evidence to suggest that population variation in life history reflects adaptation by fishes to local environments (see reviews by Hindar et al., 1991; Taylor, 1991; Carvalho, 1993; Conover and Schultz, 1997). Small-scale life history variation among populations of brook trout, Salvelinus fontinalis, on Cape Race, Newfoundland, serves to provide one such example (Ferguson et al., 1991; Hutchings, 1991, 1993a,b, 1994, 1996, 1997). Brook trout inhabiting these rivers are unexploited, do not interbreed, do not differ in density, and are uninfluenced by interspecific competition or predation (Ferguson et al., 1991; Hutchings, 1993a). Comparing the most divergent populations, females in Freshwater River mature, on average, more than a full year earlier than those in Cripple Cove River at a fivefold smaller weight. Regarding reproductive effort, relative to Cripple Cove River females, the smaller Freshwater River females allocate more than twice as much body tissue to gonads, produce significantly more eggs, and produce 40% larger eggs (all comparisons corrected for body size; Hutchings, 1991, 1993a, 1996). These population differences in brook trout life history can be attributed to the consequences of food supply, and possibly habitat, to age-specific rates of survival and fecundity (Hutchings, 1991, 1993a,b, 1994, 1996, 1997), assertions supported by recent genetic evidence of directional selection on body size in response to size-selective overwinter mortality and individual differences in growth (Wilson et al., 2003).

Adaptive population variation in life history is the result of natural selection, acting within populations, favoring those genotypes whose age-specific rates of survival and fecundity generate the highest per capita rate of increase, or fitness. One of the fundamental premises of life history theory is that natural selection acts on age-specific expectations of producing future offspring (Fisher, 1930) in response to environmental and genetic influences on age-specific survival and fecundity. Thus, if population variation in life history is adaptive, one can assume that this is a consequence of differential selection responses to environments that have different effects on survival and/or fecundity.

The potential for fishing to effect significant evolutionary change within a population is no different from that of any other form of predator-induced mortality that differentially affects the survival of individuals of different ages and sizes. The question is not whether fishing represents a primary selective pressure effecting genetic change in exploited fish populations—clearly it must. As Rijnsdorp (1993) put it, fisheries are large-scale experiments on life history evolution.

Irrespective of the causal factors, life history responses to selection are manifested primarily by population differences in (a) age and size at maturity, (b) reproductive effort, and (c) phenotypic responses to environmental change, that is, plasticity.
1. Age at Maturity

Age at maturity reflects an evolutionary compromise between the costs and benefits to fitness of reproducing comparatively early or late in life (Hutchings, 2002; Roff, 2002). Benefits associated with early maturity include increased probability of surviving to reproduce and an increased rate of gene input into the population, resulting in reduced generation time. However, early maturity can also result in reduced fecundity and/or postreproductive survival because of the smaller body size typically associated with earlier maturity within a population. By contrast, the primary cost of delaying one’s initial spawning is the increased risk of death prior to reproduction. The primary fitness advantage to delaying maturity in fishes is the larger initial body size attained by individuals when they first reproduce.

Selection is predicted to favor earlier maturity with reductions in either the ratio of adult to juvenile survival (i.e., survival from birth until age at first reproduction) or with increases in the variance in adult survival relative to the variance in juvenile survival (Cole, 1954; Gadgil and Bossert, 1970; Schaffer, 1974a,b). Intuitively these predictions make sense. As external mortality, that is, that unassociated with reproduction, at potentially reproductive ages increases, selection is expected to favor those individuals (genotypes) that reproduce prior to those ages, thus increasing their probability of contributing genes to future generations. A similar argument can be made for environmental perturbations that increase the variance in survival at potentially reproductive ages, increased variance in survival being associated with increased uncertainty in an individual’s (genotype’s) persistence.

These predictions are generally presumed to hold true for fishes. Leggett and Carscadden (1978) examined population differences in age at maturity among five populations of American shad, *Alosa sapidissima*, from Florida, United States, north to New Brunswick, Canada. They found that males and females in the northern populations, for which they presumed juvenile mortality to be more variable than that in southern populations, matured as much as 11 and 14% older, respectively, than their southernmost counterparts. Similarly, Hutchings and Jones (1998) reported a negative correlation between temporal variance in adult survival and age at maturity in anadromous Atlantic salmon. Reznick et al. (1990), documenting selection responses to predator-induced changes to mortality in guppies, *Pecilia reticulata*, found age at maturity among males and females to be 17 and 7% higher, respectively, in the high juvenile mortality environment relative to that in the environment characterized by comparatively low juvenile mortality. Fox and Keast (1991), comparing life histories of pumpkinseed sunfish, *Lepomis gibbosus*, populations subjected to either high or low overwinter mortality, documented 1- to 2-yr reductions in age at maturity among males and females in the high mortality environments. And age at maturity in
bluegill sunfish, *Lepomis macrochirus*, populations exposed to high juvenile predation is reported greater than that in populations that experience comparatively low juvenile mortality (Belk, 1995).

The predominant changes to life history associated with fishing are reduced age and size at maturity, the latter often being a simple consequence of the former, although increases in both characters might occur under certain circumstances (Heino, 1998; Rochet, 1998). The rapidity with which many of these changes occur within stocks is consistent with the hypothesis of a phenotypically plastic response to exploitation. In theory, reductions in density effected by fishing should lead to reduced competition for resources, resulting in an increase in individual growth rate and possibly body condition. Given the widely documented negative association between individual growth rate and age at maturity in fishes (e.g., Alm, 1959; Roff, 1992; Hutchings, 1993a), a comparatively rapid decline in age at maturity can be explained as a plastic response to increases in individual growth.

However, while some short-term changes in age at maturity appear to be linked to increases in individual growth rate and/or condition and can potentially be explained as plastic responses to fishing, others are not. One example is that of the northern stock of Atlantic cod extending from southeastern Labrador to the northern half of Newfoundland’s Grand Bank. Between the mid-1980s and the mid-1990s, female median age at maturity declined by more than 1 year, a reduction of approximately 17% (Lilly et al., 2001). However, these changes were not associated with either faster individual growth rate or improved condition (Lilly et al., 2001). Hutchings (1999) suggested that the most parsimonious explanation for these changes was an extremely rapid differential reduction of late-maturing genotypes, by severe overfishing, relative to that experienced by early-maturing genotypes. The high exploitation rates experienced by other Northwest Atlantic cod were also sufficiently high to effect genetic selection responses to life history traits, possibly favoring earlier maturity and also slower growth (Sinclair et al., 2002) as a consequence.

Thus, as a life history metric of stock identification, age at maturity would be a useful trait to consider, given its heritable basis, its responsiveness to selection, and its close correspondence with individual fitness and population growth rate.

### 2. Reproductive Effort, Fecundity, and Egg Size

Metrics of reproductive effort may also be useful as tools for distinguishing stocks, particularly if used in conjunction with other life history traits. Reproductive effort can be defined as the proportion of total energy devoted to the physiological and behavioral aspects of reproduction, measured across a biologically meaningful time period (Hirshfield and Tinkle, 1975) such as gonad development, movement/migration to spawning grounds, reduction of feeding prior to and
concomitant with reproduction, mate competition, nest construction, or parental care.

A common surrogate of reproductive effort is the gonadosomatic index, or GSI, that is, the weight of an individual's gonads relative to that individual's body weight. Among species, GSI ranges from as little as 0.2% in male *Tilapia* spp. (Helfman et al., 1997) and 0.5% in male white sticklebacks, *Gasterosteus* sp. (C-A. Smith and J. A. Hutchings, unpublished data) to as much as 47% in female European eels, *Anguilla* (Kamler, 1992). Among populations, GSI in females has been reported to differ 1.5 times in brook trout (Hutchings, 1993a) and twofold among Northwest stocks of Atlantic cod (McIntyre and Hutchings, 2003). Population differences in GSI will be reflected by differences in size-specific fecundity (number of eggs per unit of body mass), differences in absolute or size-specific egg size, or both. Regarding the former, there are surprisingly few comparisons among populations, although one recent study of Atlantic cod reported that size-specific fecundity can differ several-fold among stocks, depending on maternal size (Martinsdottir and Begg, 2002). Population differences in average egg size have often been considered a proxy for adaptive variation. But, as noted elsewhere (Hutchings, 1991; Reznick and Yang, 1993), the relationship between offspring size and offspring survival must differ among environments, or among populations, for environment- or population-specific egg size optima to exist.

Various hypotheses have been proposed to explain population variation in egg size and fecundity in fishes. Many of these center on proposed selection responses to species- and age-specific differences in the quality of parental care (Sargent et al., 1987) and to seasonal (Rijnsdorp and Vingerhoed, 1994; Trippel, 1998), population (Kaplan and Cooper, 1984; Hutchings, 1991, 1997), and individual (Jonsson et al., 1996) differences in access to food resources. Quinn et al. (1995) suggested that among-population variation in sockeye salmon, *Oncorhynchus nerka*, egg size can be explained as adaptive responses to differences in the size composition of incubation gravel, arguing that the positive association between egg size and substrate size may be related to the latter's influence on dissolved oxygen supplies relative to the surface-to-volume ratio constraints of eggs. Although somewhat more problematic to compare among populations, it has recently been shown that within-female variability in egg size can differ significantly among populations, and that there is good reason to believe that these differences are adaptive. In a study of 10 brook trout populations, Koops et al. (2003) found that there is less egg size variability, both within and among females, when environments are more predictable, and hypothesised that females use variability in egg size to offset the cost of imperfect information about their environment when producing smaller eggs.

Population differences in reproductive effort are thought to be associated with adaptive responses to age at maturity. For example, a decline in survival during
potentially reproductive ages (adult survival), relative to that during prereproductive ages (juvenile survival), is predicted to favor genotypes that increase reproductive effort, in addition to maturing earlier in life (Gadgil and Bossert, 1970; Law, 1979). Evidence of such a direct response to selection has been forthcoming from Reznick et al.'s (1990) work on Trinidad guppies. From 30 to 60 generations after a shift in predator-induced mortality from adults to juveniles, guppies responded to the presumed increase in the ratio of adult to juvenile survival by reducing reproductive allotment and by increasing age at maturity. Life history comparisons among populations have also supported these predictions concerning effort and maturity. Comparing pumpkinseed sunfish from five populations that experienced either high or low levels of overwinter mortality, Fox and Keast (1991) found males and females inhabiting high-mortality environments to mature earlier and to have significantly higher GSIs than those inhabiting low-mortality environments. Among brook trout populations in Newfoundland, declines in the ratio of adult to juvenile survival are associated with earlier maturity and increase in reproductive effort, as approximated by GSI (Hutchings, 1993a). A negative association between age at maturity and reproductive effort (GSI and size-specific fecundity) has also been reported for yellow perch, *Perca flavescens* (Jansen, 1996).

Reductions in adult survival attributable to fishing should also, in theory, be predicted to increase reproductive effort. Although there has been considerably less attention directed to such changes, there is evidence that temporal changes in size-specific fecundity in the orange roughy, *Hoplostethus atlanticus*, may reflect a life history response in reproductive effort to fishing. Between 1987 and 1992, when the roughy stock off east Tasmania was reduced by 50%, individual fecundity increased 20% on average (Koslow et al., 1995). Law (1979) reported a 60% increase in the fecundity of 3-year-old northern pike, *Esox lucius*, 12 years after an experimental harvest in Lake Windermere, U.K.

### 3. Phenotypic Plasticity and Norms of Reaction

When life history trait optima differ among environments inhabited largely at random with respect to genotype within and among generations, selection can be expected to act on the way in which a genotype alters its life history in response to environmental change; that is, selection will act on a genotype’s norm of reaction (Schmalhausen, 1949; Via and Lande, 1985; Schlichting and Pigliucci, 1998). Such adaptive phenotypic plasticity may underlie many life history responses by fish to environmental change, notably to nongenetic variation in individual growth rate, but also to differences in temperature, habitat quality, and food supply.

Experimental studies have revealed how reaction norms for juvenile growth rate (a proxy for environmental change) in brown trout (*Salmo trutta*) (Einum
and Fleming, 1999) and juvenile survival in brook trout (Hutchings, 1991) can be influenced by egg size, and there is corresponding evidence that growth rate in early life can negatively (Jonsson et al., 1996; Morita, et al., 1999) and positively (Morita et al., 1999) influence egg size as an adult in Atlantic salmon and white-spotted char (Salvelinus leucomaenis), respectively. By modeling reaction norms as threshold traits, researchers have been able to account for the influence of both environmental and genetic influences on age and size at maturity when explaining the maintenance of conditional alternative mating strategies in Atlantic salmon (Salmo salar) (Hutchings and Myers, 1994) and coho salmon (Oncorhynchus kisutch) (Hazel et al., 1990).

Comparatively few studies have examined population variation in the plasticity of life history traits, that is, population differences in the ways in which individuals alter their life history in response to environmental change. Using optimality theory, Hutchings (1996) predicted the fitness consequences associated with different ages at maturity and different rates of juvenile growth (a proxy for environmental change), permitting the construction of norms of reaction for age at maturity for different populations of brook trout in southeastern Newfoundland. In one population (Freshwater River), age at maturity was invariant with growth rate (individuals being favored to mature as early in life as possible), while in the other populations age at maturity was inversely related to growth. The adaptive basis for these population differences in reaction norms underscores the point that the fitness advantages of delaying maturity (increased fecundity and higher overwinter survival because of larger body size) are inevitably balanced by the probability of realizing those benefits. Thus, Freshwater River females appear to be favored to mature early in life, regardless of growth rate, because the survival costs of delaying maturity are too high relative to the apparently marginal benefits of increased fecundity.

The existence of genetic variation in the shapes of reaction norms in some taxa (Schlichting and Pigliucci, 1998; Pigliucci, 2001) raises the possibility that plastic responses by individuals to environmental change can be modified by selection. Furthermore, if natural selection can act on reaction norms, it is possible that selection induced by anthropogenic activities, such as fishing, also may be important.

The adaptive significance of interpopulation differences in plasticity, and the possibility that selection is responsible for these differences, has recently been examined for five Norwegian populations of grayling (Haugen, 2000a,b,c; Haugen and Vøllestad, 2000, 2001). Since their introduction from Lesjaskogsvatn into Hårrtjønn and Øvre Mærrabottvatn in 1910, grayling have since dispersed among several other lakes in south-central Norway, including Aursjøen and Osbumagasinet. Over a period of time ranging from 9 to 22 grayling generations, there has been considerable divergence in life history among these
populations, notably with respect to age at maturity, size at maturity, and fecundity (Haugen, 2000a,b,c).

Population differences in life history have manifested themselves as differences in the shapes of reaction norms for age and size at maturity (Haugen, 2000b). Delayed age at maturity is associated with smaller size at maturity for grayling in four populations, with the population-level reaction norms crossing in state space. Interestingly, the reaction norm for grayling in Øvre Mærrabottvatn expresses an invariance in age at maturity with changes to size at maturity, all individuals maturing at age 3. Consistent with the explanation discussed previously for population differences in reaction norms for age at maturity in Newfoundland brook trout, there appears to be a direct association between the steepness of the grayling reaction norms and average adult mortality (Haugen, 2000b). For individuals aged 4 through 8 years, the instantaneous rate of mortality, \( Z \), was highest (0.77) for Øvre Mærrabottvatn grayling, those apparently favored to reproduce as early in life as possible. By contrast, the reaction norms with the shallowest slopes, encompassing the greatest ranges of ages, are those for Hårrtjønn and Aursjøen grayling, which have the lowest rates of mortality (\( Z = 0.36 \) for both).

To test the hypothesis that population differences in reaction norms are a result of selection, acting over a comparatively short period of time (9–22 generations), Haugen and Völlestad (2000) undertook a common garden experiment in which they reared grayling from three different populations under the same experimental conditions in the laboratory. Specifically, they measured survival and specific growth rate during the first 180 degree-days of exogenous feeding at three different temperatures. These temperatures corresponded to the average temperatures experienced by grayling in each of the three populations during this stage of life in the wild.

The common garden experiments revealed significant genetic differences in reaction norms for survival and growth rate among populations. Survival declined with temperature for the “cold” population (Aursjøen), peaked at the intermediate temperature for the “medium” population (Lesjaskogsvatn), and increased with temperature for the “warm” population (Hårrtjønn). Thus, survival was highest at the temperatures typically experienced by these grayling during this phase of their lives in the wild. There were also clear differences in plasticity for growth rates among population, although the fastest growth rates were not always achieved at the temperatures experienced by grayling in the wild (given the existence of life history trade-offs, this need not be unexpected).

Thus, life history research on grayling has revealed genetic differences in reaction norms for life history traits among populations, providing data consistent with the hypothesis that the shapes of at least some reaction norms [temperature-dependent survival in early life] are adaptive and are the product of natural selection (see also the work by Hendry et al. (1998) on sockeye salmon, \( O. \) *nerka*).
The results are also in agreement with research indicating that natural selection can take place over relatively short (10–20 generations) periods of time (Hendry and Kinnison, 1999).

The question of whether fishing can change the shapes of reaction norms by selection has received comparatively little attention. Reznick (1993) hypothesized that the primary effect may be to change the elevation of the reaction norms, assuming that fishing would select against individuals genetically predisposed to mature at large body sizes. Considering how fishing might affect the slopes of reaction norms, Hutchings (1993b, 1997, 2002) used age-specific survival and fecundity data on brook trout populations to predict how reaction norms for age, size, and effort at maturity might change in response to increases in adult mortality. As fishing mortality increased, selection was predicted to favor a flattening of reaction norms, notably for age and effort at maturity, such that individuals would be favored to reproduce as early in life as possible and to expend the maximum amount of effort at that age, irrespective of growth rate. Flattening of the reaction norm for age at maturity would be expected as the probability of realizing the fitness benefits of delayed maturity declines with increases in mortality due to fishing. Similarly, as longevity declines with increased fishing pressure, selection should favor increases in reproductive effort.

It seems reasonable to conclude that fishing can result in selective changes to reaction norms in heavily exploited populations (Hutchings, 2002). These changes may involve changes to both the slopes and the elevations of reaction norms for several life history traits. Detecting such changes, however, will be exceedingly difficult, given the near absence of research on phenotypic plasticity and reaction norms on commercially exploited fishes.

Perhaps the primary reason that life history traits have not formed the primary basis for distinguishing stocks lies in the presumption that life history variability is predominantly environmental in origin. If so, then within the context of establishing management strategies for the purpose of providing protection for genetically distinguishable units, the use of life history variation thus becomes problematic. On the other hand, given their clear links to individual fitness and population rates of increase, one could argue that it would be prudent to assume that life history variation among putative stocks has a genetic basis until demonstrated otherwise.

VI. CONCLUSIONS

Molecular genetic markers and quantitative phenotypic characters both have advantages and disadvantages for delineating fish stocks. The main advantage to molecular markers is that they are direct measures of genetic differences, unaffected by any environmental differences between groups. Thus, a molecular
genetic difference between groups is an unambiguous indication of genetic differentiation. These markers are also usually assumed to be neutral to selection, and are thus useful for identifying reproductively isolated groups and for determining the phylogenetic relationships among groups. However, this selective neutrality is the main drawback of molecular markers for delineating fish stocks. Selection can result in rapid genetic divergence, much more rapid than expected as a result of mutation and genetic drift. Selection can also generate genetic differentiation between groups in the face of gene flow. Thus, adaptive genetic differences between recently diverged groups or between incompletely isolated groups are not likely to be reflected by neutral molecular genetic differences.

The main advantage to quantitative phenotypic characters such as life history and morphological traits is that these traits are generally related to fitness and respond to natural selection. Thus, local adaptation, rapid adaptive divergence between recently separated groups, and genetic differences maintained by selection in the face of gene flow may all be reflected in these traits. The main disadvantage to phenotypic characters is that they are subject to environmental as well as genetic influences. Thus, differences between groups in these characters, even differences that appear to be adaptive, may reflect phenotypic plasticity rather than genetic differentiation. An experimental approach, in which individuals from different areas or groups are reared in common environments, is needed to disentangle these two sources of phenotypic variation.

Common environment experiments to identify the genetic and environmental components of phenotypic variation are not feasible for many fish species, particularly marine fishes. In these cases, a precautionary approach would be to tentatively treat groups characterized by persistent phenotypic differences as separate stocks, recognizing that these differences may be environmentally induced rather than genetically based. This is particularly true when differences are in life history traits affecting productivity and responses to exploitation. A difficulty with this approach is that when countergradient variation occurs, genetic variation among groups will be cryptic, manifest by phenotypic similarity rather than by differences. When common environment experiments cannot be conducted to disentangle genetic and environmental influences and uncover hidden countergradient variation, the best recourse may be to adopt a 'holistic' approach, employing a broad spectrum of complementary techniques (Begg and Waldman, 1999).

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Environmental and Genetic Influences on Stock Identification Characters


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Environmental and Genetic Influences on Stock Identification Characters


