Heritability, correlation and selection response estimates of some traits in fish populations

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Foreword

The material in this dissertation was developed after a presentation at a Fisheries-induced Adaptive Change Workshop coordinated by The International Institute for Applied Systems Analysis, Luxenburg, Austria on March 14-17, 2001, with an intent to publish this dissertation and companion manuscripts in a volume pertaining to that workshop. Although peer review acceptance of this work has been completed, no publication has been forthcoming as of March 2010. Additional commentary on 2009 papers related to this work is included. The paper is now being posted on the Huntsman Marine Science Centre website (www.huntsmanmarine.ca) in order to make the information available, and to serve as a benchmark for the rate of advancement of the field.

1. Introduction

Fishing is a major contributor to adult mortality in commercially important fish stocks. Size at harvest and age at maturation, conventionally considered components of life history traits, a term not conventional in animal and plant breeding but used in fisheries, have shown long-term declines in heavily exploited fish stocks (Ricker 1981, Allendorf *et al.* 1987, Law and Grey 1989, Smith 1994). Changes in life history traits result from genetic changes due to selection, both natural and fishery induced and from non-genetic changes due to shifts in the biotic and physical environment. The genetic change or selection response is a product of the selection differential and heritability. Selection intensity can be estimated in wild populations, but there are few estimates of heritability for traits in such populations. Estimates of heritability for key life-history traits are essential for untangling the genetic and environmental components of observed life-history changes in fish stocks.

Heritability estimates have been used extensively in animal breeding programs (Hofer 1998). The high reproductive potential in many fish species can increase selection differentials because few individuals are needed to replace populations. The increasing number of heritability estimates for fish species under aquaculture provides a background for considering fisheries-induced adaptive changes in natural populations. In this chapter the history of the heritability concept is reviewed, before considering heritability estimates in fishes, and the key phenomena of inbreeding, multiple traits, and genotype x environment interactions.

2. History of the heritability concept

An appreciation of the concept of heritability can be gained from its historical development. Concepts of quantitative variation formed the underlying principles of heritability. Knowledge derived from empirical observations on the existence of variability and its random origin was paramount in the emergence of quantitative genetics (Wearden 1979).

Mendelian principles rediscovered in the late nineteenth century, about thirty years after Mendel's publications on peas, introduced complexities in the understanding of quantitative genetics, where discrete classifications of characteristics were not apparent. The merger of the concept of inheritance with that of continuous variation, expressed by Galton (1897) as the regression of offspring on parents, was not without controversy in the scientific community. The hypothesis that several genes contributed to quantitative traits (Yule 1907) was supported by

observations on colour genes in wheat and oats, recorded by Nillson-Ehle early in the twentieth century (see review by Akerberg 1986). The development of a statistical theory involving correlation between relatives by Fisher (1918) represented a breakthrough in the analyses of quantitative traits, and was enhanced by the publication on systems of mating by Wright (1921). Many of the applications of statistics and matrix algebra in animal breeding stem from the pioneering works of Fisher and Wright (see review by Hofer 1998).

The exact origin of the term "heritability" is obscure, but Wright (1921) used the symbol h^2 to define the proportion of the variance that can be ascribed to heredity in the piebald colour pattern in guinea pigs. The term heritability appears frequently in the animal breeding literature (e.g. Lerner, 1950) where it is defined in a broad sense as "the proportion of the total variance that is directly due to genetic differences". $h^2 = \sigma^2_G/\sigma^2_P$, where σ^2_G = the genetic variance, and σ^2_P = the phenotypic variance of the stock. Heritability is defined in a narrow sense as the fraction of the genetic variation that is due to genes with a simple additive effect, $h^2 = \sigma^2_A/\sigma^2_P$ (σ^2_A = the additive genetic variance). The realized heritability is defined as R/S, where R (the response to selection) is the difference in average phenotype between the unselected stock and the progeny of the selected parents reared under the same conditions, and S (the selection differential), is the difference in average phenotype between parents and the stock from which they were selected (Ricker 1981). However, environmental conditions are not necessarily the same between generations and estimates of R/S often involve control populations (eg Friars *et al.* 1997).

A literature search for the words "heritability" and "fish" found 148 references in Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts in 2000). Growth rate and size, age at maturation, and survival or survival indicator traits were included in the search. Most heritability studies on farmed fish were carried out in the twenty-five years prior to 2001 and in the subsequent nine years through 2009, but the results provide a background for understanding changes in comparable traits in wild fisheries. Developments in molecular biology provide the opportunity for new applications, including heritability estimates and the prediction of genetic gains. The establishment of genetic markers may be feasible in populations mixed during rearing (Ritland 1996).

3. Within and between population variation in traits of fish

The practical estimation of heritability is usually confined to a single population under specific conditions. However more broad heritable variation between species, local populations, stocks and strains also needs to be recognized (see Roff 1992 for an overview).

Variances among river stocks of Atlantic salmon (*Salmo salar)* have been reported for size at return, percent return, day of return, and percent of grilse (Bailey and Saunders 1984). Diallel crosses of four river stocks of salmon revealed larger effects due to the stock of the dams than that of the sires (Friars, Bailey and Saunders 1979). Differences in resistance to the monogean *Gyrodactylus salaris* were found between populations of Atlantic salmon (Bakke *et al.* 1990) and between populations of charr (Bakke *et al.* 1996). However, strain effects accounted for only 1.8 to 7.4 percent of total variance in size, development, and survival traits in several river stocks of Atlantic salmon (Gjedrem *et al.* 1991a), indicating that heritable variation within stocks is of more consequence.

Mixing stocks from different geographical regions may result in shifting gene frequencies. When a large number of Atlantic salmon escape from sea-cages, enter streams and interbreed with wild stocks, they may disturb adapted gene pools (Crozier 1993). An update on the interaction between aquaculture and wild stocks can be found at ICES (2009).

Molecular techniques have been used to measure genetic variation within and between many fish stocks. However the measurement of simple Mendelian inherited characters, detected with allozymes and molecular DNA variation, is not directly amenable to heritability analyses of quantitative variation, although such techniques are being developed (Ritland 1996).

4. Estimation of heritability

Genetic gain or selection response R is predicted by the product of heritability (h^2) and the selection differential S. Various methods of estimating heritability are outlined in Box 1. Estimates of heritability are generally dependent on the assumptions of large random mating populations in the absence of migration, mutation, and selection, and most methods have been developed for diploids with normal meiosis. Sex-specific differences in recombination may also need to be considered (Sakamoto et al 2000).

BOX 1 Methods for estimating heritability

A. Regression between parents and offspring
Regression methods estimate the extent of the transmission of a trait from parent to offspring: y = a + bx where x and y are the mean values of the trait for the parents and offspring respectively, a is the intercept, and b the regression coefficient. When the mean values of a trait, derived from both parents, is used the heritability is equivalent to the regression coefficient, $h^2 = b$, but if the offspring are compared with just one parent the heritability, $h^2 = 2b$.

B. Hierarchal matings
The following model describes the sources of variation in the population:
$Y_{ijk} = \mu + S_i + D_{ij} + e_{ijk}$ where Y_{ijk} is the measurement of a trait on the kth progeny of the jth dam mated to the ith sire, μ is the overall mean of the population, S_i is the effect of the ith sire, D_{ij} is the effect of the jth dam mated to the ith sire, and e_{ijk} is the environmental plus genetic segregation effect on the kth progeny of the jth dam mated to the ith sire.

Heritability is estimated from the sire component (h^2_S), the dam component (h^2_D), and the sire and dam component (h^2_{S+D}):
$h^2_S = 4\,\sigma^2_S / \sigma^2_S + \sigma^2_D + \sigma^2_e$;
$h^2_D = 4\,\sigma^2_D / \sigma^2_S + \sigma^2_D + \sigma^2_e$; and
$h^2_{S+D} = 2(\sigma^2_S + \sigma^2_D) / \sigma^2_S + \sigma^2_D + \sigma^2_e$.

BOX 1 cont'd.

where σ^2_S is the sire component of variance, σ^2_D the dam component of variance, and σ^2_e the environmental plus genetic segregation component of variance. Dam components are inflated by maternal effects, dominance and epistatic variance to a greater extent than sire components where dams are nested within sires. Also where fertilization is in vitro, as in fish, sires can be nested within dams.

C. Factorial matings
Sets of matings where sires from each strain are mated with dams of each strain allow for partitions of variance components where the theoretical expectations of additive and non-additive effects are as below (McKay *et al.* 1986):
σ^2_A = variance due to additive genetic effects;
σ^2_D = variance due to dominance;
σ^2_{AA}, σ^2_{AD}, σ^2_{ADD} = variance due to epistatic interactions of additive-additive, additive-dominance, and dominance-dominance types respectively;
σ^2_{Ec} = variance due to environmental effects between tanks;
σ^2_{EG} = other environmental effects not due to tank effects;
σ^2_M = variance due to maternal effects.

Variance Component	σ^2_A	σ^2_A	σ^2_{AA}	σ^2_{AD}	σ^2_{DD}	σ^2_{Ec}	σ^2_{EG}	σ^2_M
Between Families	1/2	1/4	1/4	1/8	1/16	1	0	1
Within Families	1/2	3/4	3/4	7/8	15/16	0	1	0

D. Breeding values
The prediction of breeding values in large data sets has been used extensively in animal breeding. The selection criterion has been based on best linear unbiased prediction (BLUP) of additive genetic effects. BLUP requires knowledge about variance components that have been estimated in practice. Restricted maximum likelihood (REML) has become the method of choice for the estimation of variance components of mixed linear models in animal breeding (Hofer 1998).

E. Inbred lines
The use of variance between and within inbred lines can be used to estimate genetic variance and heritability $h^2_t = h^2_0 (1-F_t)/(1- h^2_0 F_t)$
where h^2_0 is the heritability in the base population, h^2_t and F_t are the heritability and inbreeding coefficients at time represented by generations *t*,

F. Linear heritability estimates
Linear estimates are based on selecting prospective parents for which estimates of average genotypic and phenotypic values are obtained from a pedigreed population (Abplanalp 1961). A regression of genotypic on phenotypic values is determined from a straight line fitted through points representing the population mean genotype and phenotype on one hand and the mean genotype and phenotype of selected parents on the other.

G. Clonal lines
Taniguchi *et al.* (1996) produced mitotic gynogenetic diploids, reared them in a common environment, identified lines using DNA fingerprinting and employed a human twin model to separate genetic and environmental variances.

H. Discrete traits
Traits such as mature versus non-mature fall into discrete binomial distributions. Heritability can be estimated from an underlying continuous scale using techniques, which provide a quantification of multiple gene effects (Robertson and Lerner 1949). Also, family means can be considered for such traits, the heritability of which is outlined later in this chapter.

I. Animal model
Personal communication with L.R. Schaeffer resulted in a quotation as follows:
"An animal model incorporates the animal's records, its parents, and its progeny into one overall estimate of the breeding value of each animal. Pedigree information has to be accurate and complete (personal communication with L.R. Schaffer). Details can be found at: www.aps.uoguelph.ca/~Irs/ABModels/ or www.aps.uoguelph.ca/~Irs/ABMethods/"

5. Heritability estimates in fish

A large number of heritability estimates has been made for fish and shellfish - 19 traits in 26 species. Most heritability estimates are for carp and salmonids, which is not surprising given the long history of carp in culture and the more than 100 years of experience with salmonids in enhancement programs.

Three life-history traits in fisheries, growth rate, size at maturation, and survival, were selected from the 19 traits noted in the literature. These traits are relevant to the changes observed in exploited populations of decreases in size and age at maturation, and survival (which bears on the former two traits with respect to the shifts in genetic make-up that relate to the fitness of the stocks). Heritability estimates for the three traits are summarized in Figures 1, 2 and 3; the numbers in the columns relate to the reference list at the end of this chapter. The histograms show wide distributions for each class of traits.

BSH

```
                      58        75        49                    49   58                                      58
        72      49 49        70 70 70    43      49              49 49   58              58         71              58
        56   49 12 34 49 49 56 56    3  43 25    64      49 49 49   56 58   71      58 58    71    58              58
   12 72 49 49 12 12 10 49 49 3  49    3  12 3  58 12 12 12 20 25   25 49      64 10 49 10 58 58 58 58 75        58
```

NSH

```
                                79
                                78              78
        81                      78        78 78
        70                      75        65 78
        70                      42 79 54 54
        70      81           78 30 78 54 54
   80         65      49      65 78 28 78 53 54
   75         49      49      42 49 26 49 49 52 78      73
   74         49      43      35 45 16 46 47 46 78      65                      54
   65         43      40 78 30 42 14 39 42 19 74      65      57 78 78      54      65
   53         15 70 36 53 19 35 12 21 41 12 41 79 54      54 54 46 57 54      54              73              65
   45 38 38 38 8  68 5  40 12 20 12 12 30 12 30 54 12 54 37 54 19 15 54      53      47 12 73 21      34         16         34
```

Heritability

Figure 1. Estimates of heritability of growth, size and related traits in several species of fish. Narrow sense heritabilities (NSH) contain principally additive genetic effects, including realized heritabilities. Broad sense heritabilities (BSH) contain both additive and non-additive genetic effects. Numbers in the histograms represent points that can be traced to references where the respective papers are denoted in bold superscript in front of the authors. The information predates 2002.

BSH   63   56   56   56   56   10   29   2

NSH

                                              68

     69   77   16   69

     69   63   77   68   69   9   69   68   68   14   68   69   16   14   62

0.00-0.025 | 0.025-0.05 | 0.05-0.075 | 0.075-0.1 | 0.1-0.125 | 0.125-0.15 | 0.15-0.175 | 0.175-0.2 | 0.2-0.225 | 0.225-0.25 | 0.25-0.275 | 0.275-0.3 | 0.3-0.325 | 0.325-0.35 | 0.35-0.375 | 0.375-0.4 | 0.4-0.425 | 0.425-0.45 | 0.45-0.475 | 0.475-0.5 | 0.5-0.525 | 0.525-0.55 | 0.55-0.575 | 0.575-0.6 | 0.6-0.625 | 0.625-0.65 | 0.65-0.675 | 0.675-0.7 | 0.7-0.725 | 0.725-0.75 | 0.75-0.775 | 0.775-0.8 | 0.8-0.825 | 0.825-0.85 | 0.85-0.875 | 0.875-0.9 | 0.9-0.925 | 0.925-0.95 | 0.95-0.975

Heritability

Figure 2. Estimates of heritability of age at maturation, age at smolting and traits related to reproduction in several species of fish. Narrow sense heritabilities (NSH) contain principally additive genetic effects, including realized heritabilities. Broad sense heritabilities (BSH) contain both additive and non-additive genetic effects. Numbers in the histograms represent points that can be traced to references where the respective papers are denoted in bold superscript in front of the authors. The information predates 2002.

BSH

25   61
25   48
23   32
23   66 72   24
1   25   55   66 27 66 60 70   24   60   24   60 72
1   25   44 25   10 23 51 31 48 60 4   43   48 60   60   60 1 72 1 11   11   31   60 61   60

NSH

70
13
11   61
6   80 22 61   60
6   61 22 61   67   76   60   60
6   43 6   60   67   67 17 31   60 55   7
6   22 6   20   60 33   61 13 22   50 6   6   59   32   31 18   7   60 13   60   60

0.00-0.025
0.025-0.05
0.05-0.075
0.075-0.1
0.1-0.125
0.125-0.15
0.15-0.175
0.175-0.2
0.2-0.225
0.225-0.25
0.25-0.275
0.275-0.3
0.3-0.325
0.325-0.35
0.35-0.375
0.375-0.4
0.4-0.425
0.425-0.45
0.45-0.475
0.475-0.5
0.5-0.525
0.525-0.55
0.55-0.575
0.575-0.6
0.6-0.625
0.625-0.65
0.65-0.675
0.675-0.7
0.7-0.725
0.725-0.75
0.75-0.775
0.775-0.8
0.8-0.825
0.825-0.85
0.85-0.875
0.875-0.9
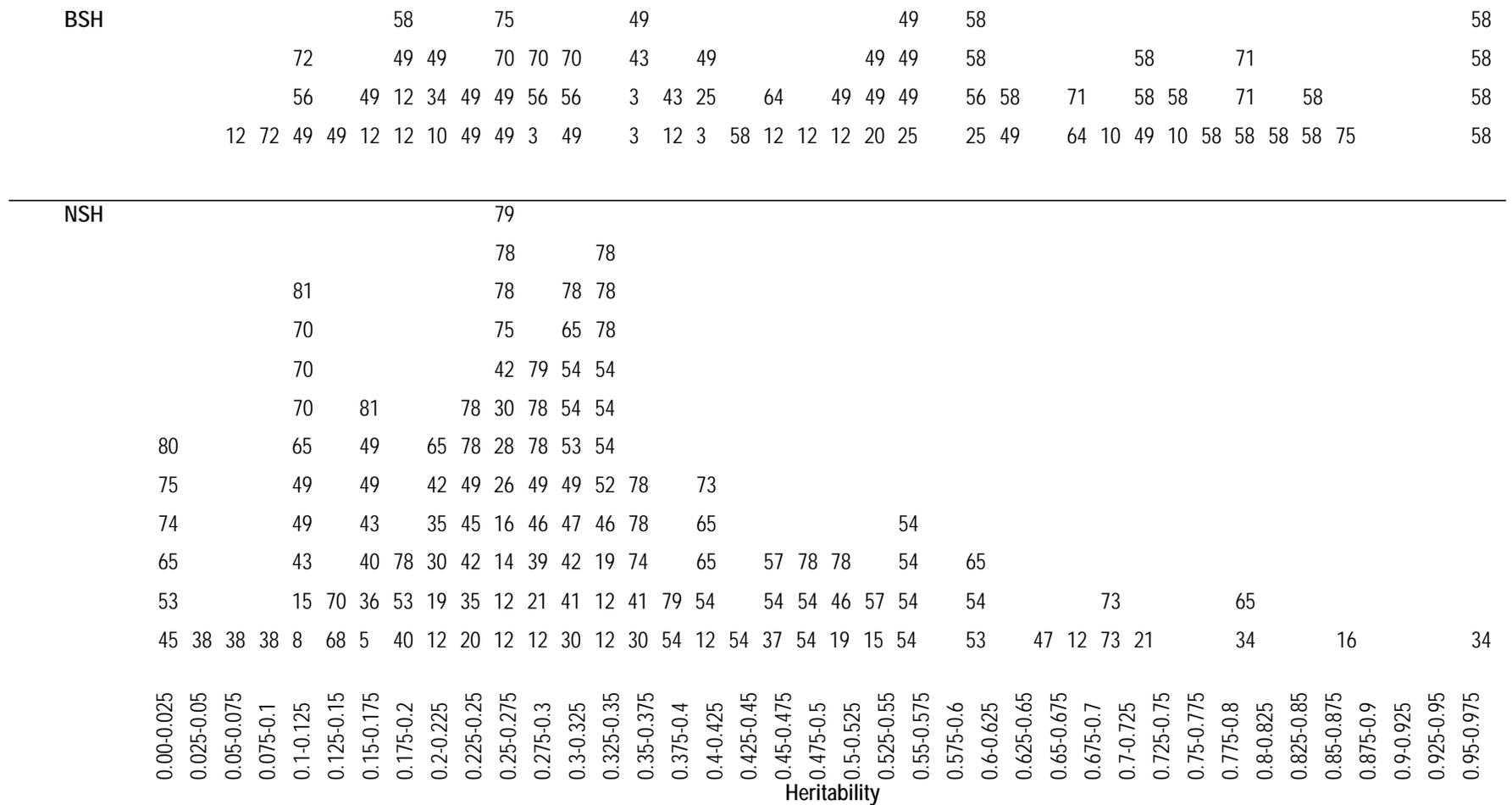0.9-0.925
0.925-0.95
0.95-0.975

Heritability

Figure 3. Estimates of heritability of survival, disease resistance and related traits in several species of fish. Narrow sense heritabilities (NSH) contain principally additive genetic effects, including realized heritabilities. Broad sense heritabilities (BSH) contain both additive and non-additive genetic effects. Numbers in the histograms represent points that can be traced to references where the respective papers are denoted in bold superscript in front of the authors. The information predates 2002.
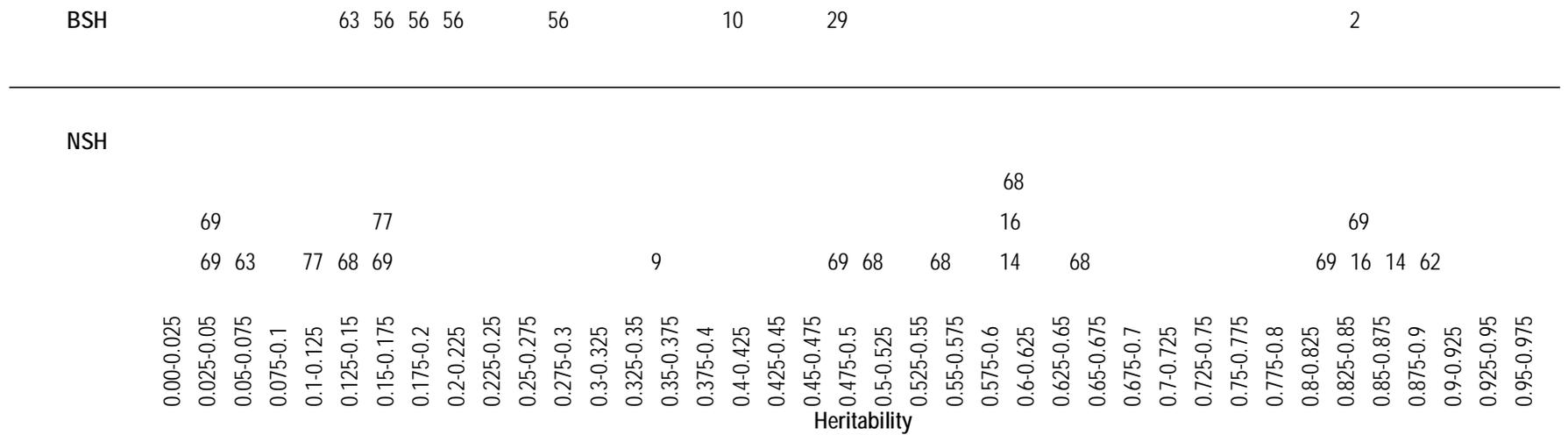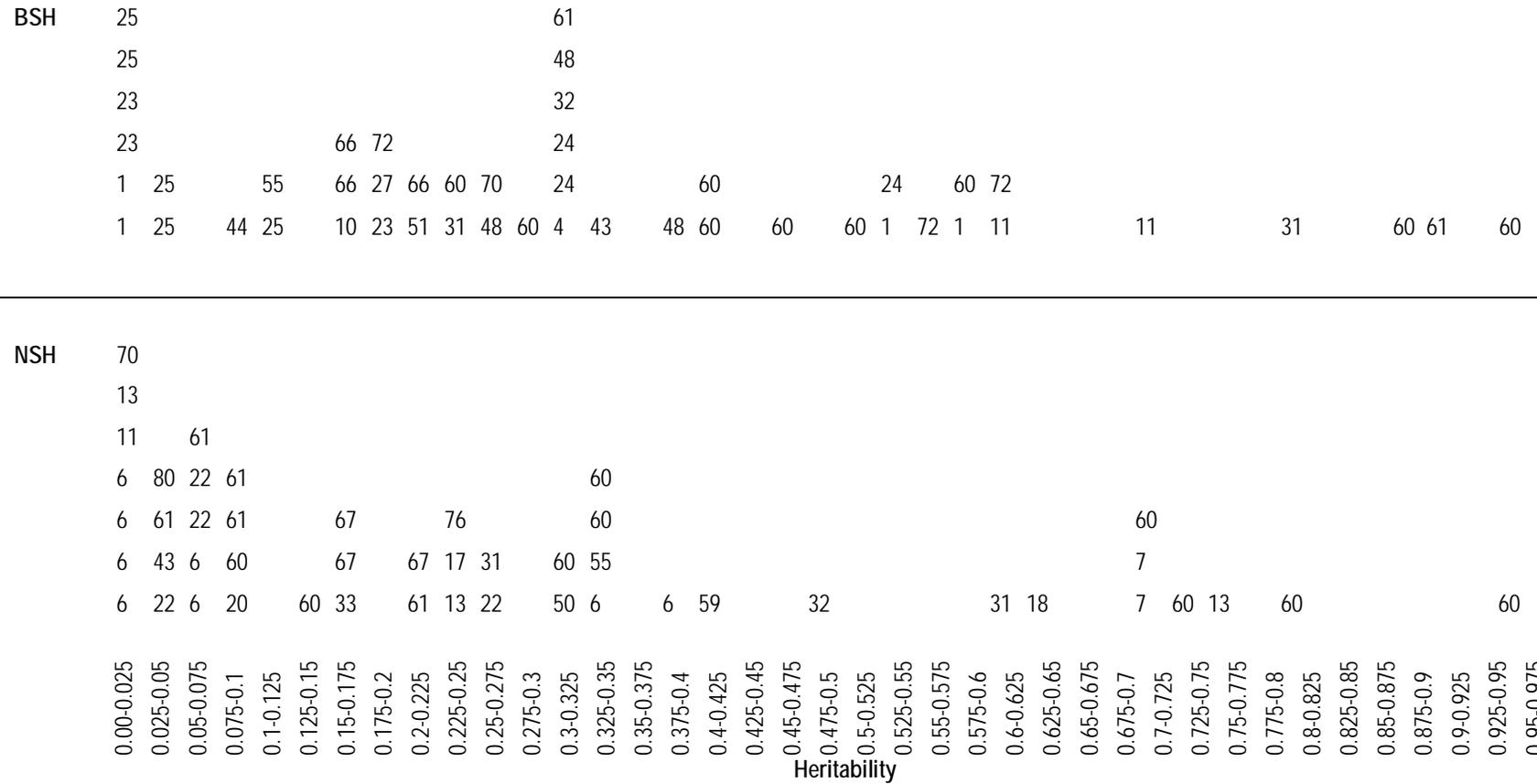
5.1 *Comparisons of heritability estimates for traits related to growth and size, age at maturation, and survival*

There are more references for growth and size than for age at maturation or survival- related traits (Figures 1, 2, and 3). The wide range in heritability estimates for these traits emphasizes the fact that inferences are to populations with a specific genetic make-up in a specific environment. Small sample sizes and biases in estimation procedures also contribute to the wide distributions of estimates. Tests of differences between medians (Table 1) were performed using procedures outlined by Siegel (1956). The probabilities of type 1 errors (rejecting the null hypothesis when true) are generally high, with the exception of the test for narrow- versus broad-sense heritability estimates for growth related traits, because of the large number of estimates. Consequently, statements about the relative levels of heritability of traits must be interpreted with caution. Furthermore, expression of quantitative traits can be highly dependent upon the environment and is likely to be more complex under natural than experimental conditions (Ritland 1996, *Merilä* and Sheldon 2000, Hermida *et al.* 2002). Thus heritabilities of traits in wild fish populations are needed for estimating the selective effects of fisheries. While few data exist for wild populations, with the exception of returning salmonids (Jonasson, 1997), the use of molecular markers to infer relatedness may provide a tool for studying quantitative variation in natural populations (Ritland 1996).

Table 1.Tests of differences in estimates of heritability (both narrow (N) and broad (B) sense) of growth and size (G) from Figure 1, age at maturation (A) from Figure 2, and survival and survival related traits (S) from Figure 3.

	Trait					
	G	**G**	**A**	**A**	**S**	**S**
	N	B	N	B	N	B
Number of estimates	120	75	20	8	49	48
Median	0.28	0.43	0.51	0.21	0.16	0.28
Contrast*	GN-GB	AN-AB	SA-SB	GN-AN	GN-SN	AN-SN
χ^2	8.33	0.04	0.51	1.00	2.10	1.20
P type 1 error	<0.01	<0.95	<0.50	<0.28	<0.20	<0.20

*The contrasts are between narrow and broad sense heritability estimates and between traits.

5.2 *Growth-related traits*

Most estimates for growth related traits fell within the range 0.10 to 0.60 for narrow sense heritabilities (Fig 1); the spikes in frequencies below 0.175 are mostly for salmonids in sea cages, and may indicate lower heritabilities for marine than for land-based aquaculture populations. The heritabilities in the upper Figure 1, include maternal effects and non-additive genetic effects, namely dominance and epistasis, and generally result in a slightly higher mean than that for only additive effects. The lower estimates contain largely additive effects together with minor amounts of epistasis. The significant difference ($P < 0.01$; Table 1) reflects this trend where the heritability estimates (Figure 1) have a higher median value in the broad sense than

those in the narrow sense. Nevertheless, these contributions pertain to population phenomena that may have biological significance.

5.3 *Maturation and other age-related traits*

There is a wide distribution of heritability estimates of age at maturation related traits (Figure 2). Some of the estimates are for traits such as the proportion of smolts at certain ages, and others for proportions exhibiting sexual maturity at specified ages. In general, heritabilities for age at maturation traits (Figure 2) do not appear to be different to values for growth-related traits (Table 1). The limited number of estimates available from the literature indicates that considerable responses could be realized through selection for age at maturation. If fishery- selection acts on age-related traits, it is reasonable to expect that changes in age at maturation will occur.

Age at maturation may be related to fitness, based on the relative numbers of offspring surviving from fish maturing at different ages. For instance, Atlantic salmon grilse reproduce one year before two-sea-winter contemporaries, but produce fewer eggs – influencing the number of offspring per year. Consequently the lower heritability of reproductive traits compared with growth traits, due to higher components of environmental variance, may be limited to specific situations (Merilä and Sheldon 2000).

A review of the early literature on sea-age and maturation in Atlantic salmon concluded that heritable factors were involved in maturation after one-sea-winter (grilse) versus two-sea-winters (Gardner 1976). That view is justified where heritability estimates of non-grilse salmon were of 0.19, 0.21 and 0.22 in three populations, based on fullsibs (O'Flynn *et al.* 1992). Also, a heritability estimate of 0.48 was found for a similar trait in rainbow trout by Gjerde (1988), using crosses of parents from different ages at maturation. The findings of Ritter *et al.* (1986), working with wild stock, agree with these results where the phenomenon of 1-sea-winter versus older salmon representing age at maturation is heritable. The wide range of estimates (Figure 2) substantiates the heritable nature of age at maturation across a number of species.

5.4 *Survival-related traits*

Traits relating to survival generally have lower heritabilities than growth rate and age at maturation (Figure 3 and Table 1), possibly due to the complexity of survival traits that include disease resistance and physiological phenomena. However, selection for disease resistance has been successful in developing resistance to furunculosis in Atlantic salmon (Bailey *et al.* 1993). A heritability of 0.24 for swimming stamina, a trait possibly related to survival, was reported in Atlantic salmon (Hurley and Schom 1984), and similar results have been found for the three-spine stickleback (*Gasteosteus aculeatus),* (Garenc *et al.*1998).

Behavioral traits, such as schooling and migratory tendencies (Rose 1993), could affect survival in a fishery. In Atlantic cod, there are differences in migratory behaviours between coastal and north-east Arctic cod (Godo 1995) and differences in activity patterns between cod stocks in the Irish and North Seas (Righton *et al.* 2001). If fisheries impose selective forces on such traits, shifts in characteristics such as growth and/or age at maturation will be realized due to genetic dependencies between traits. These changes will depend not only on

direct selection on the traits, but will be influenced by genetic correlations among behavioral and other traits.

Return rates of Atlantic salmon, released to sea, represent an aspect of survival. Bailey and Saunders (1984) reported differences in the average date of returns between strains of Atlantic salmon. A summary of some of the heritability estimates of return rates of Atlantic salmon from the findings of Jonasson and colleagues is depicted in Box 2. A genetic equilibrium aspect of return rates was reported in Atlantic salmon where such rates for two synthetic gene pools, produced from crosses of river stocks, revealed percentages of 0.60, 0.18 and 0.43 for the first pool, and 0.68, 0.06 and 1.00 for the second pool, over three successive generations (Friars *et al.* 1994), emphasizing the problem when new genes are introduced into populations. In addition, the return rates of the two synthetic gene pools increased after random mating, at a time when many neighbouring Bay of Fundy rivers were experiencing decreased return rates (Friars *et al.* 1994).

BOX 2 Heritability estimates in sea ranching

Sea ranching is an aquaculture operation that uses the homing habits of anadromous fish, in particular, salmon. The juvenile freshwater stages are raised under controlled hatchery conditions, and at smoltification (the physiological changes prior to entering sea water) the salmon are released to sea where they feed as wild fish. After 1-3 years at sea, the sexually mature fish return to the release site and are caught before they can spawn. Fish returning after one year are known as grilse and after two years as two-sea-winter salmon.

Higher estimates of heritability (Box 1) and of weight and survival using dam (female) as opposed to sire (male) components of variance, have been reported in sea-ranched Atlantic salmon. These are consistent with the estimates in Figure 1 for weight and length with respect to narrow-sense versus broad-sense heritability estimates but not for age at maturation (Figure 2) where the contrast (i.e., the statistical test of differences) is nonsignificant (Table 1).
The higher estimates of the heritability of weight in farmed as opposed to sea-ranched fish are not significantly difference in light of the means and standard errors of sea-ranched and farmed grilse (Table in this box; Jonasson and Gjedrem 1997). It has been assumed that environmental variances are higher in wild stocks than in farmed stocks, partly because environmental effects inflate the denominators of heritability estimates and partly because of the higher standard deviations and of factors other than additive genetic effects (Jonasson and Gjedrem 1997).

	Heritability estimates in Atlantic salmon			
Traits	Sire Component Of variance[a]	Dam component of variance[a]	Animal model[b]	Reference
Freshwater (12 weeks after first feeding)				
Survival	0.04$\pm$0.04	0.34$\pm$0.04		Jonasson 1993
Weight	0.16$\pm$0.02	0.36$\pm$0.03		Jonasson 1993
Length	0.10$\pm$0.02	0.39$\pm$0.03		Jonasson 1993
Sea-ranched grilse				
Weight (1989)			0.20$\pm$0.10	Jonasson and Gjedrem 1997[a]

Weight (1991)		0.23±0.12	Jonasson and Gjedrem 1997[a]
Weight (land-based)		0.31±0.11	Jonasson and Gjedrem
Farmed grilse			
Weight (1989)		0.31±0.17	Jonasson 1997
Weight (1991)		0.27±0.10	Jonasson 1997
Return rate			
Grilse	0.12	0.12	Jonasson et al. 1997[a]
2-sea-winter	0.02	0.11	Jonasson et al. 1997[a]

Correlation estimates in Atlantic salmon

Traits	Phenotypic	Genetic	Reference
Eggsize			
Survival	0.23**		Jonasson 1993[a]
Weight	0.233		Jonasson 1993[a]
Length	0.22**		Jonasson 1993[a]
Survival			
Weight		0.31±0.26	Jonasson 1993
Length		0.39±0.26	Jonasson 1993
Weight-length		0.98±0.01	Jonasson 1993
Weight (relatives in sea-ranched			
And farmed environments			
1989	0.14	0.42±0.28	Jonasson 1997
1991	0.09	0.27±0.34	Jonasson 1997

[a]Where dams are nested within sires in the mating system, the dam components of variance contain maternal effects and more nonadditive genetic effects than the sire components of variance.
[b]An animal model optimally combines information on the individual, its parents, sibs, and progeny to estimate the additive genetic merit of each individual. This information allows the estimation of narrow-sense heritability.
**Significance (P) < 0.01.
Other references on Jonasson's work in this area are as follows: Jonasson, J. 1996; Jonasson, J. and T. Gjedrem 1997.

6. Related individuals and inbreeding

Related individuals have genes that are common by descent (Figure 4). This shared inheritance creates correlations between relatives as shown by Fisher (1918). Heritabilities of groups of relatives, such as full or half-sibs, can be estimated by making use of suitable mathematical relationships, and applied in the development of selection and mating programs. Information on relatives has been used extensively in animal breeding:

1. To increase the accuracy of prediction of the breeding value of individuals. An example of this is shown in terms of information from sibs (Figure 5), adapted from Lerner (1958) using an application of path coefficients by Wright, (1921).
2. To establish the breeding value of groups of relatives. One example of the heritability of a group of relatives is depicted in Figure 5. The increased heritability of family means over individual observations is depicted in Figure 6. Caution is needed where the use of information from relatives tends to increase inbreeding during selection.

The use of information on relatives may develop in fisheries as genetic tagging technology evolves (e.g. Herbinger *et al.* 1995; Hansen *et al.* 2001).
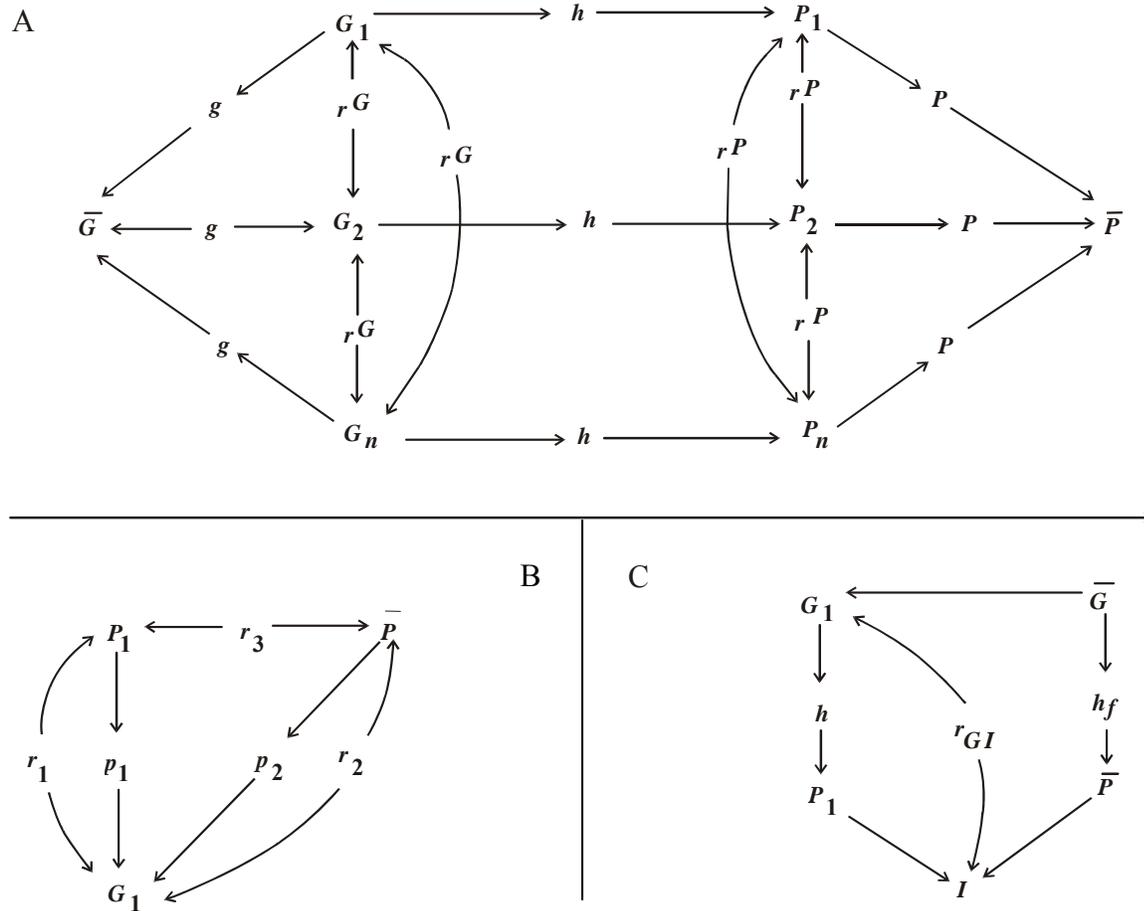

Figure 4. The biometric basis of family selection, adapted from Lerner (1958) using an application of path coefficients by Wright (1921).

A represents the genetic (r^G) and phenotypic (r^P) relationships between n members of a family. The genetic values of each individual are represented by G_1 to G_n; the family average is represented by $\bar{G}$. Individual phenotypic values are represented by P_1 to P_n and the family average by $\bar{P}$.

The path between genotype and phenotype (square root of heritability) is indicated by h. I = selection index, p (with subscripts) = path coefficients and r (with subscripts) = correlation coefficients.

The values of the paths g and p are:
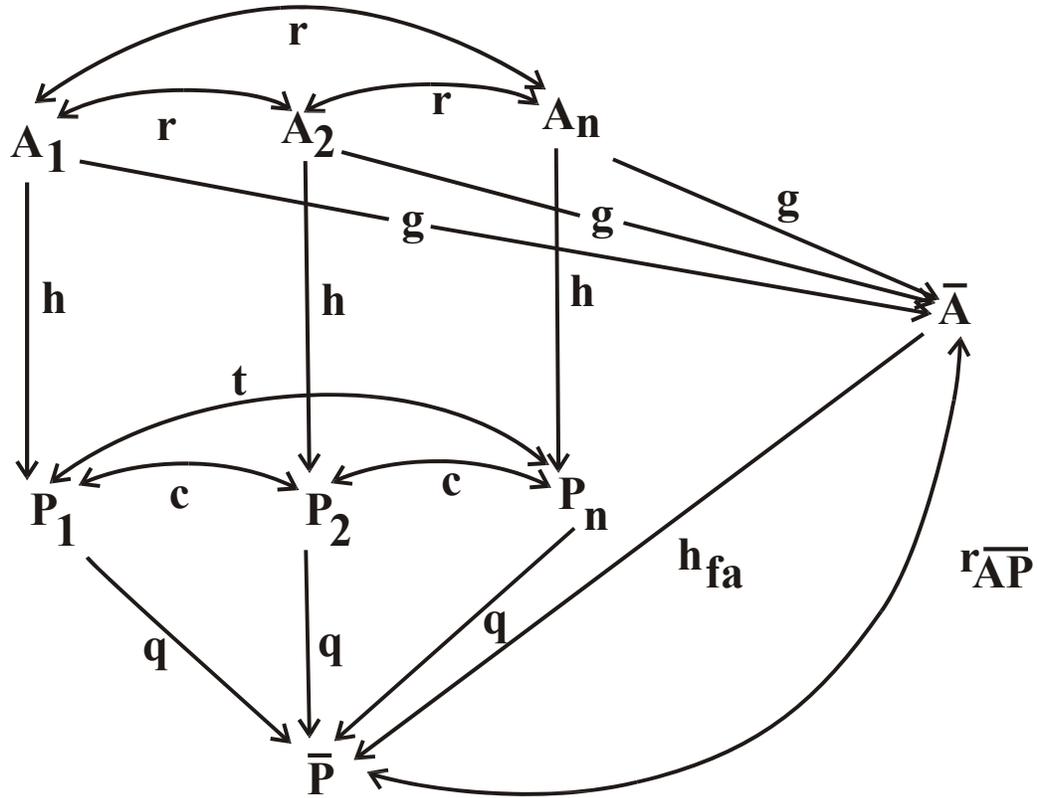$g = 1/\sqrt{n}[1+(n-1)r^G]$ $p = 1/\sqrt{n}[1+(n-1)r^P]$

Figure 5. Heritability of a family average. The heritability of a family average h^2_{fa} is analogous to $r^2{}_{\overline{AP}}$. Adapted from Lerner 1958.
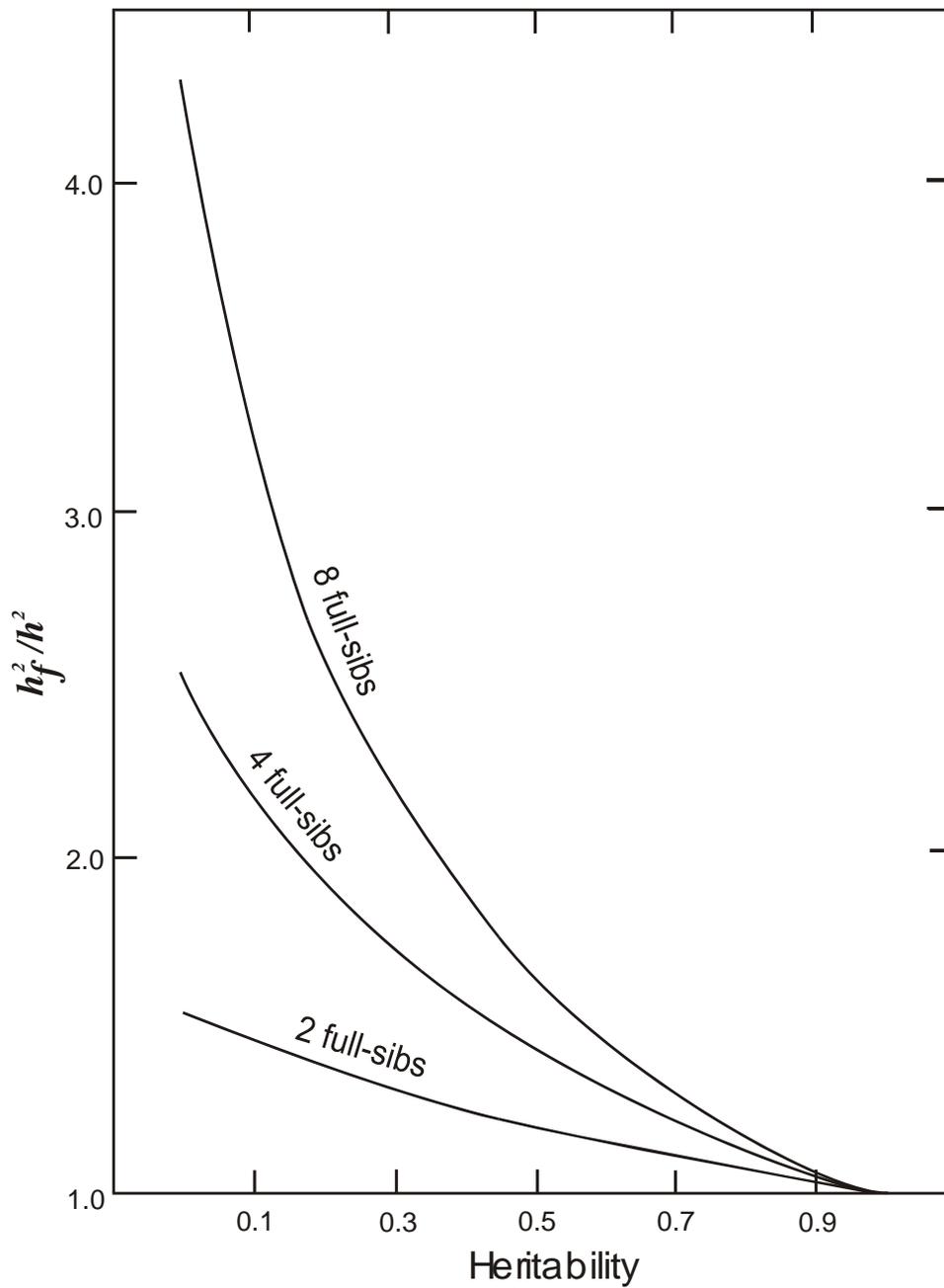
Figure 6. Ratio of family to individual heritability. The curves are based on the assumption that the relationship between full sibs (r^G) is 0.5 and that $r^p = r^G h^2$. (h^2_f = heritability of family averages). The ratio h^2_f /h^2 depends on heritability and on number in a family of full-sibs. Adapted from Lerner 1958.

In aquaculture inbreeding has lead to a decrease in survival and growth related traits in farmed rainbow trout (Gjerde *et al.* 1983) and catfish (Smitherman *et al.* 1996) and similarly in mitotic-gynogenetic diploid fish (Tsujimura and Taniguchi 1996). The development of inbred lines of fish has potential in aquaculture. Heterosis was realized in the crosses of inbred lines of rainbow trout, but the costs and delays in developing inbred lines did not justify the heterotic gains (Gjerde 1988). Large population sizes (N) and effective population sizes (N_e) indicate that inbreeding is not likely to be a problem in most marine fish populations, or in broad samples from the wild for aquaculture.

Bi-directional selection can reveal different rates of progress. For example inbreeding increased the realized heritability more in the downward than in the upward direction in the flour beetle *Tribolium castaneum* (Jui and Friars 1974; McLeod and Friars 1986). In agriculture, goals are usually directed towards increased yields through selection in the upward direction. Conversely fisheries, that preferentially capture larger fish, are directing downward responses in natural populations.

7. Multiple Traits

Several traits such as growth or size, age at maturation, and survival need to be considered simultaneously in fish populations. Heritability estimates pertain to individual traits, and models of multiple traits require the integration of heritabilities with correlations between traits. The yield from a population is influenced by a number of traits, especially more tangible components such as those depicted in Figures 1, 2, and 3. Therefore, in addition to heritability, the genetic, environmental, and phenotypic correlations have to be considered. Figure 7 shows the interrelationships of these phenomena, as they relate to an aggregate or multiple genotype and ultimately an index or collective phenotype.
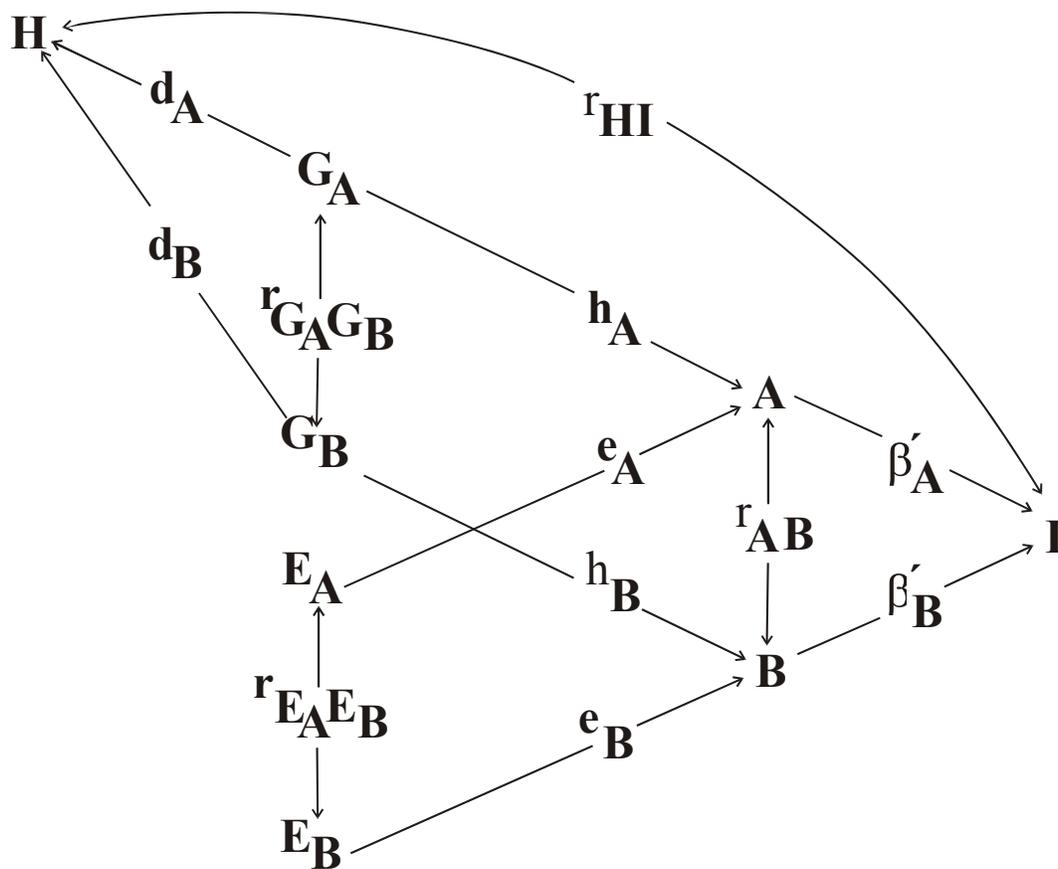
Figure 7. The genetic (*G*), phenotypic, and environmental (*E*) correlations between traits A and B. Adapted from Lerner 1958.

The path diagram (Figure 7) depicts how multiple traits can be combined to form a hypothetical trait in the form of an index. Three types of effects, genetic, environmental, and economic weights, bear on the aggregate index scale. The phenotypic correlation (r_p) can be defined as the sum of the genetic path ($h_A \, r_A \, h_B$) and the environmental path ($e_A \, r_E \, e_B$). The relative economic weights assigned to each trait affect the index to which directional selection can be applied, and are used to provide profit criteria for each trait. In the case of fisheries, size probably receives more emphasis than other traits, such as age at maturation and survival.

An index was developed for Atlantic salmon with a view to increasing the proportion of smolts, developing from hatchery-reared eggs, after 18 months in fresh water and the market size after approximately 70 weeks in seawater, while decreasing the proportion of grilse (O'Flynn *et al.*1992). Such methodology is generally considered to be more efficient than the use of independent culling levels on each trait. Progress from selection using an index that involved market size and non-grilse was realized in Atlantic salmon by Friars *et al.* (1993) where size at market age was increased, while the incidence of grilse was reduced. A reversal of this selection

result appears to take place where large fish are harvested in commercial fisheries. Consequently, earlier sexual maturity and smaller size results (Smith 1994).

7.1 *Selection responses*

The selection response on a trait is determined by the product of the narrow sense heritability and the selection differential. The prediction of such response depends on the reliability of heritability estimates where genetic parameters are subject to change under selection. For instance, Clayton *et al.* (1957a) found fair agreement between early realized selection gains and gains predicted via an estimate of heritability and selection differentials, whereas predictions were poor in the long-term for bristle number in Drosophila (Clayton *et al.* 1957b). However, Enfield (1977) realized 26 genetic standard deviations and 15 phenotypic standard deviations of gain in long-term selection for pupal weight in *Tribolium castaneum*, suggesting that new sources of variation accrue to inhibit the exhaustion of genetic variance. Examples of long-term selection experiments have not been well documented in fish. However, Hershberger *et al.* (1990) found that heritabilities for weight in coho salmon remained high after four generations of selection.

Eight generations of selection in chickens revealed mostly insignificant changes in heritabilities, but changes in genetic correlations were apparent in a study by Friars *et al.* (1962). Larval weight and pupa weight in *Tribolium castaneum*, which would be expected to involve part-whole correlations, showed a positive correlation of 0.55 ± 0.12 and exhibited no detectable change over nine generations of divergent selection (Bell and Burris 1973). Conversely, realized genetic correlations between larva weight and offspring number in *T. castaneum* were positive and decreasing under selection in a wet environment, but in a dry environment, the estimates were near zero and increasing slightly positively under selection (Friars *et al.* 1973). In an optimal environment, such as the wet condition in the *Tribolium* experiments, genetic covariance that positively affects weight and offspring number gets used up under selection. Conversely, depression of the traits in the dry environment probably inhibits the expression of genes that affect both traits positively. Inferences to such a combination of effects could be investigated in a fishery, using data from long-term selection.

Studies by McMillan *et al.* (1995) illustrated that changes in parameters over generations of selection can affect outcomes. Under some simulated conditions, the use of initial genetic parameter values without change could have potentially negative effects on overall genetic gain. Hence, estimation of genetic parameters at varying stages of multiple objective selections is required to attain desired goals. Where selection is being exerted in a fishery, updated estimates of genetic parameters are needed to make decisions related to the multiple traits involved, particularly where evidence in other organisms indicates that changes take place under selection.

A recent high-low controlled selection experiment in Atlantic silversides (*Menidia menidia*) by Conover *et al.* (2009) revealed that "large harvested populations initially produced the highest catch but quickly evolved a lower yield than controls. Small harvested populations did the reverse." In light of these results, Conover *et al.* recommended that management of fishery stocks need reconsideration.

7.2 *Genetic correlations in fish*

Genetic correlations result from pleiotropic effects of genes on multiple traits or from chromosomal linkage of genes affecting different traits. Estimates of genetic correlations between traits have been made for several fishes. Eknath *et al.* (1998) found a full-sib estimate of 0.2 for the genetic correlation between survival and market weight of farmed *Tilapia*. Estimates between different measures of growth and size, were found to be universally positive, from swim-up to four years of age in rainbow trout (McKay *et al.* 1986). Similarly, correlations between measures of growth and smoltification, in fresh water, related to measures of growth in seawater in Atlantic salmon were generally positive, but became progressively weaker the longer the fish were in sea water (Friars *et al.* 1990).

Herbinger and Friars (1991) found a strong positive correlation, between condition factor and total lipid content (an indicator of energy reserves) in immature salmonids. Another study on the same stock revealed a positive relationship, between July and November parr length, but a negative association, between July parr length and incidence of presumptive smolts in February (Bailey and Friars 1994).

Relationships between body weight and age at maturation were reported in rainbow trout, with genetic correlations of 0.67 and 0.58 (Crandell and Gall 1993a). Selection for market size, and related traits, after two sea winters in Atlantic salmon, was associated with a lower proportion of fish maturing after one sea winter (Friars *et al.* 1993). Considering the selection for smaller sized fish to reproduce in a natural fishery, these results would suggest a trend for earlier age at maturation in natural populations where larger fish are harvested.

Survival also relates to reproduction rate where fish die before reproducing. For Atlantic salmon, river stocks differed in their proportion of grilse versus multiple-sea-winter salmon, as noted by Bailey and Saunders (1984). If lower survival is experienced by multiple-sea-winter fish, due to longer exposure at sea, an advantage in reproduction countered by fewer eggs per female is experienced by grilse. Hence, counteracting forces can affect the reproductive output due to later age at maturation versus survival to reproduction at a younger age.

Age at maturation has a wide range of heritability estimates (Figure 2) and if correlated with size, as found in Atlantic salmon and rainbow trout, and then fisheries that selectively harvest larger fish will not only reduce size, due to its heritability, but also decrease age at maturation.

8. Genotype x environment interactions

The differential reaction of genotypes, across different environments, is of concern to agriculturists and aquaculturists. Superior performance of one genotype may not be consistent when genotype x environment interactions occur. Selection for genotypes in a hatchery environment may not produce the optimum genotypes for a production environment. Parallel problems could exist in fisheries where shifts in environments, due to natural causes, could cause similar problems in wild fisheries.

In salmonids, strains reacted differently under two temperature treatments (Figure 8). At the chromosomal level, family differences in relative growth of diploid and triploid Atlantic salmon represented interactions with respect to growth responses, which imply that different genes for growth are involved in diploid and triploid backgrounds (Friars *et al.* 2001). Likewise McKay (1982) observed that families changed rank for gain in fork length and instantaneous growth rate for weight (Table 2). Similar family- environment, but not strain-environment effects were observed in Atlantic salmon (Wild *et al.*1994, Winkelman & Peterson 1994a). The results of Jonassen (1996) with ranched Atlantic salmon were similar for weight, where no significant effect was found for release-site x strain interaction. However, such effects were significant for return rate in two out of three year classes and one out of three for ratio of grilse. Eknath *et al.* (1998), following an extensive study with several strains and farming regimes with Tilapia, also concluded that specialized strains may not be necessary for farming systems in the Philippines.

Table 2. Ranks of families at 7°C and 15°C for growth traits in rainbow trout *Salmo gairdneri*. Source: McKay (1982).

Family[a]	Gain in fork-length				Instantaneous growth rate for weight			
	Period 1		Period 2		Period 1		Period 2	
	7°C	15°C	7°C	15°C	7°C	15°C	7°C	15°C
1	1	8	4	8	3	13	16	18
2	2	12	17	19	1	5	2	31
3	3	11	3	2	2	8	23	19
4	4	30	15	3	6	28	5	10
5	5	7	1	1	4	18	7	6
(Families 6 to 30 not shown)								
31	31	21	35	35	29	9	32	33
32	32	14	29	22	33	24	24	15
33	33	28	23	15	25	23	25	8
34	34	27	28	12	30	20	15	5
35	35	35	22	31	34	35	31	35

[a] Families arbitrarily numbered based on their performance at 7°C in period 1.

LAKE TROUT   F₁ SPLAKE   RAINBOW TROUT   BROOK TROUT

SPECIFIC GROWTH RATE

30

20

10

0

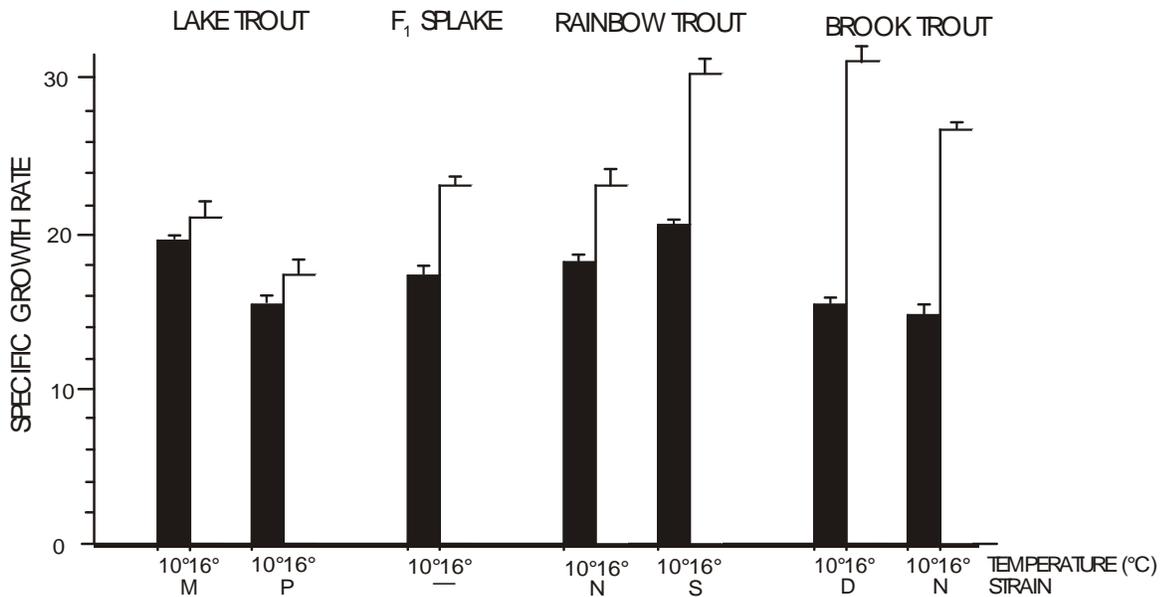| 10°16° | 10°16° | 10°16° | 10°16° | 10°16° | 10°16° | 10°16° | TEMPERATURE (°C) |
| M | P | — | N | S | D | N | STRAIN |

Figure 8. Specific growth rates of strains of three trout species and one hybrid reared at two temperatures (with upper 95% confidence intervals). Brook trout *Salvelinus fontinalis*, lake trout *S. namaycush*, rainbow trout *Salmo gairdneri* and the splake hybrid *S. namaycush* x *S. fontinalis*. Source Sadler *et al.* 1986.

Juvenile Atlantic salmon reared under two photoperiods, natural day length and 16 hours, revealed that families reacted differently to the shift in the light regimes (Hanke *et al.* 1989, and Figure 9). These examples are related to productivity in aquaculture but suggest that similar phenomena may be acting in natural populations of fish.
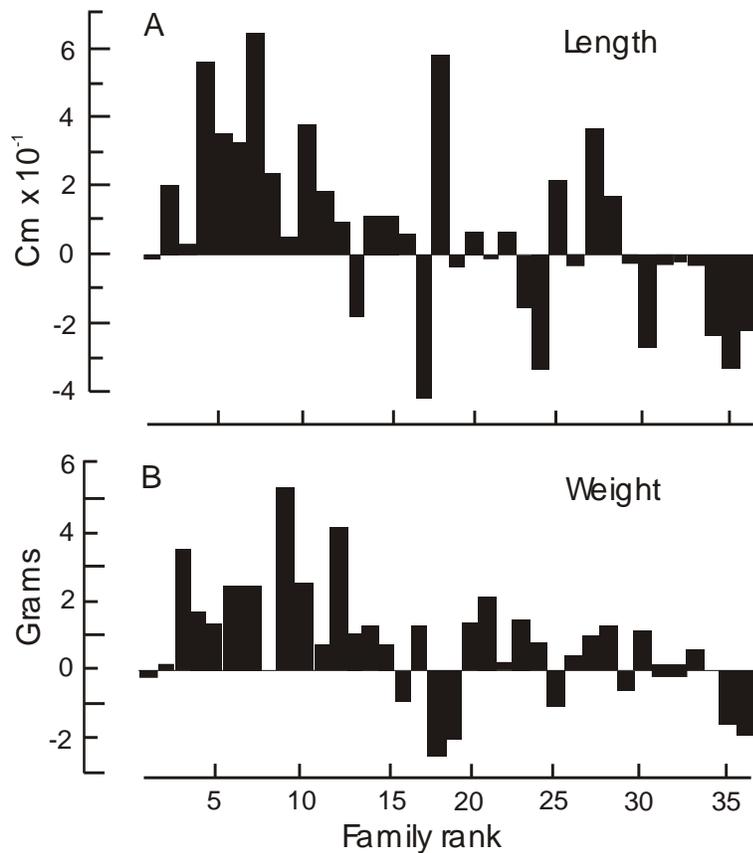
Figure 9. Family rank differences between photoperiod treatments (16 h and natural) for November gains in length and weight, ranked on the basis of increasing initial family means of Atlantic salmon. Source: Hank *et al.* 1989.

The extension of genotype x environment interactions to include several environments has been of concern with terrestrial species. A review of the concepts and biometry of the case of genotype x environment interaction was published by Yamada (1962). A trait, measured in two or more environments, was considered to represent two or more traits and entailed genetic correlations of such traits. That work used random and mixed statistical models. This view of the area relates to the concept of the reaction norm used in ecology and is illustrated in Stearns (1992). Where traits are heritable, as in the case of size at harvest and age at maturation (Figures 1 and 2) the adaptability of gene pools to different environments, including levels of fishing pressure, is relevant to concerns with wild populations, as discussed by Ritter et al (1986).

Interactions are subject to scale. A hypothetical example (Table 3) demonstrates that a log transformation of data can remove an interaction that appears on the untransformed scale. However, the results on a transformed scale often have little practical use. Many of the studies on fish deal with transformed data and do not consider this implication. Observed genotype by environment interactions must be taken into account to be of use in fisheries, where specific gene pools are required for specific environments.

Table 3. Demonstration of log transformation dissipation of an interaction.

Strain	Untransformed weights (gms)		Ln. of weights	
	Environment		Environment	
	E_1	E_2	E_1	E_2
A	10	20	2.3	3.0
B	15	30	2.7	3.4

9. Linking quantitative and qualitative genetics

Molecular or qualitative markers are generally poor indicators of heritable variation in quantitative traits (Mackay and Latta 2002) and their major application in fisheries has been to define genetic population structure. Application of highly variable microsatellite and minisatellite fingerprints of fish enables stock and pedigreed families to be reared in communal ponds and subsequently traced to individual parents (e.g. Herbinger *et al.* 1995; Vandeputte *et al.* 2001). Such techniques have the potential to be extended to natural populations to infer pedigrees allowing the estimation of genetic parameters (Ritland 1996). The construction of detailed genetic maps with molecular markers allows the identification of chromosomal regions influencing quantitative traits in fish (e.g. Sakamoto *et al.* 1999; Peichei *et al.* 2001). Construction of linkage maps based on a large number of DNA markers is necessary to identify quantitative trait loci (QTL) controlling traits of importance in fisheries. Microsatellite markers, which are widely distributed throughout the genome, are ideal for genome mapping and identification of QTL, and are being applied in salmonids (Sakomoto *et al.* 1999, 2000). The application of this technology to other fishes under aquaculture, such as cod and plaice, will allow the identification of QTL controlling traits important in fisheries, and provide new tools for measuring genetic change in natural populations.

10. Recent references

In 2001, a computer search of the literature revealed 148 papers dealing with heritability in fish. A similar search in 2009, covering the period 2000 – 2009, listed 256 papers. A sample of papers in 2009 indicated that heritability studies have been conducted on numerous species of fish dealing with various traits (Table 4).

Table 4. Heritability estimates of certain traits in fish in a sample of papers published in 2009.

Authors	Species	Traits and heritability estimates
Antonello, J. *et al.*	Gilthead sea bream (*Sparus aurata* L.)	Body length post mortem .38 $\pm$ -.07 pasteurellosis resistance; survival post challenge .12 $\pm$ -.04 and .45 $\pm$ -.04 to .18 $\pm$ -.08 binary dead or alive at specific day.
Bardon, A. *et al.*	European sea bass (*Dicentrarchus labrax*)	Spinal deformities – global .21 $\pm$ -.04); lordosis; .13 $\pm$ -.04 scoliosis .13 $\pm$ .04.
Gheyas, A.A. *et al.*	Silver carp	Harvest weight .67 (.42 – .93 conf. lim.)
Guy, D.R. *et al.*	Atlantic salmon (*Salmo salar*)	Infectious pancreatic necrosis percent mortality .07 to .56 $\pm$ <.04.
Khaw, H.L. *et al.*	Nile tilapia (*Oreochromis niloticus*)	Harvest weight .15 – .41 $\pm$ .04
Navarro, A. *et al.*	Gilthead seabream (*Sparus auratus* L.)	Harvest weight .34 $\pm$ -.06; fork length .33 $\pm$ .07; dressing percentage .31 $\pm$ .07; fillet percentage .12 $\pm$ .04.
Taylor R.S. *et al.*	Atlantic salmon (*Salmo salar* L.)	Amoebic gill disease – gill score observed scale .23 to .48; survival challenge .40 to .49; weight .28 to .27; length .27 to .35.

Various methods of estimation, including the animal model were employed in these studies (Table 4). Molecular markers were used in some studies to establish pedigrees – a technique that circumvents the confounding of family and environmental effects such as tank effects, as frequently encountered in older studies. In some of these studies, genetic correlations between traits were also estimated.

11. Summary

The concept of heritability, generally defined as the proportion of phenotypic variation due to genetics, has been widely applied in agricultural fields. Extensions of such developments to fish have been studied principally through aquaculture. A survey of heritability estimates on growth, age at maturation, and survival, and inferences to fisheries were considered in this chapter. Summaries of heritabilities indicate that survival is less heritable than growth or age at maturation even though the probabilities are not strong (Table 1). Consideration of correlations

between traits suggest that multiple traits need simultaneous attention in fisheries. The use of molecular techniques may allow estimations of heritabilities and genetic correlations in wild populations in the near future.

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(Note: the superscripted numbers at the front of some references relate to Figures 1, 2, and 3 for heritability estimates).

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Correct citation for this publication: