

## RELATIONSHIPS BETWEEN GENETIC VARIABILITY AND LIFE-HISTORY FEATURES OF BONY FISHES

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**Abstract.**—Correlations between genetic variation and life-history variables were obtained for 80 species of bony fishes as a means of testing the hypothesis that genetic variation is directly related to 1) opportunity for balancing selection, as indicated by fecundity, and 2) environmental variation, as indicated by capacity for population increase. Genetic data were taken from the literature, and data on longevity, age at maturity, egg size, body size, and lifetime fecundity were taken from the literature where available and were otherwise estimated from other variables. Average heterozygosity does not increase significantly with increasing fecundity. However, heterozygosity is significantly associated with short generation times, quick maturation, small maximum size, and small eggs. Thus, heterozygosity appears to increase on a demographic continuum toward maximum values in species that are most strongly selected for maximizing the intrinsic rate of increase. Such species are associated with less stable environments. Thus, the results indicate a predominate role for environmental variation in controlling genetic variation of bony fishes.

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Electrophoretic surveys of genetic variation have provided estimates of genetic variability for a large number of plants (Brown, 1979; Hamrick et al., 1979) and animals (Powell, 1975; Nevo et al., 1984). These surveys indicate that, for the loci surveyed by electrophoresis, an average species is polymorphic at 33–50% of its loci and that the average individual is heterozygous for 5–10% of the genes in the sample. But the range in genetic variability is more interesting than the mean. For example, the elephant seal, *Mirounga angustirostris*, and the cheetah, *Acinonyx jubatus*, exhibit no electrophoretic variation (Bonnell and Selander, 1974; O'Brien et al., 1985), while quaking aspen, *Populus tremuloides*, is polymorphic at 92% of its loci (Cheliak and Dancik, 1982) and the marine snail *Littorina neritoides* is polymorphic for 100% of the loci that have been surveyed (Lavie and Nevo, 1981).

Many hypotheses have been offered to explain the differences in genetic variation among species; these can be classified either as neutral models or as selection models. The neutral models use neutral mutation, time, effective population size, migration, and genetic drift to make predictions concerning the differentiation of populations and the amounts of genetic variation (Nei, 1975; Kimura, 1983). Selection models have focused on environmental grain as a con-

sequence of animal size and vagility (Levins, 1968; Selander and Kaufman, 1973), on predictability of trophic resources (Ayala et al., 1975; Ayala and Valentine, 1979), on niche variation (Sabath, 1974; Somero and Soulé, 1974; Lavie and Nevo, 1981), and on contrasts of generalists and specialists (Nevo et al., 1984).

Some analyses of genetic variation, such as those contrasting habitat generalists and specialists, construct necessarily qualitative, univariate categories from continuous multivariate data. The lumping of continuous multivariate data into univariate categories not only sacrifices information, but also introduces judgement errors. For example, Nevo (1978) and Smith and Fujio (1982) differ in their categorization of several species of fishes. Quantitative studies of the relationships between life-history features and genetic variation offer a means of minimizing subjective judgments.

The life-history features of organisms reflect a combination of phylogenetic constraints and selection pressures. Consequently, life-history features may be used as indicators of similarity in the operation of certain kinds of selection, even among kinds of organisms that are in many respects very different from each other. For example, unstable environments in which a species seldom approaches equilibrium are considered likely to place a selection premium on abil-

ity to reproduce rapidly ( $r$  selection), whereas environments that are more stable and are more dominated by density-dependent regulation mechanisms are considered more likely to sacrifice capacity for increase to adaptations promoting survival or persistence ( $K$  selection).

Genetic variability within the bony fishes has been relatively well-documented, and the variation within the group is remarkable. Among species for which we have data, heterozygosity varies from 0.000 to 0.181, lifetime fecundity ranges from 69 to more than 30 million, maximum weight varies from 4 to 73,900 g, and egg diameter ranges from 0.5 to 11.59 mm. Thus, the bony fishes are well suited for testing the relationship of heterozygosity to life-history features.

We have chosen four life-history variables for comparison with genetic variation: fecundity, body size, rate of maturation, and egg size. Ideally, we would also have included  $r_{\max}$ , which can be estimated from other data. However, a sensitivity analysis of the data showed that uncertainties in  $r_{\max}$  caused by weak knowledge of the reproductive schedule, particularly for the first year or two of reproduction, are so great that they preclude the calculation of  $r_{\max}$ .

We hypothesize that genetic variation is correlated with life-history variation, and we recognize two possible causes of this correlation. First, lifetime fecundity directly reflects the opportunity for balancing selection, which will be correlated with genetic variation if the opportunity for balancing selection is a major cause of genetic variation. Second, factors that reflect the high capacity for increase necessitated by unstable environments (early maturation, small eggs, small body sizes) will be correlated with genetic variation if environmental variation is a major cause of genetic variation.

#### MATERIALS AND METHODS

Information on genetic variability was obtained from the literature survey by Nevo et al. (1984), which summarized the published data on electrophoretic studies of fish proteins. For each of the species listed by Nevo et al., we recorded the average proportion of loci heterozygous across all individuals and all loci for which information

was available ( $H$ ) and the proportion of the loci that were polymorphic ( $P$ ). For present purposes,  $H$  is most important, although we also use  $P$  in our analysis. The number of loci had a range of 10–49, a mean of 25.1, and a standard deviation of 9.4. There was no relationship between the number of loci and heterozygosity ( $r = -0.05$ ,  $P > 0.05$ ).

For each fish species whose genetic variability was established, we sought published information on fecundity. We define fecundity in three ways. Total lifetime fecundity ( $F_t$ ) for a given fish species is defined as the number of eggs that would be produced by an individual throughout the entire physiological lifespan. A second type of fecundity, which we call weight-specific fecundity ( $F_w$ ), is defined as  $F_t$  per unit body mass and is expressed here as number of eggs per gram fresh weight. The third type of fecundity,  $F_a$ , is  $F_t$  adjusted for mortality to allow for the decreasing probability of survival from one year to the next during the lifetime of a fish. The value of  $F_a$  is defined as  $\sum_{i=f}^{m-1} 2^{-i} E_i$ , where  $E_i$  is the number of eggs laid in the  $i$ th year of maturity,  $f$  is the first year of maturity, and  $m$  is the last year of life. As shown by the equation, we assume that a mature fish will always spawn but that the probability of any individual fish spawning in the  $i$ th year following maturation is equal to  $1/2^i$ . The equation does not take into account species-specific or population-specific variation in the mortality schedule of mature fish. The equation is intended to acknowledge the decrease in the probability of reproduction at increasing age past maturity, but the apportionment of reproduction across age is only a rough approximation of reality.

The three fecundity indexes are reported directly in the literature only for those few species of fish that spawn only once per lifetime. For other species, we estimated the three fecundity indexes from the following life-history information: age at maturity, maximum age, size at maturity, maximum size, number of eggs at maturity, maximum number of eggs, and egg diameter. Species for which the information base was less than half complete or for which there was no information on either body size or eggs were deleted from the list. Species for which a substantial portion of the information was

TABLE 1. Taxonomic information and sources of information for the 80 species that were used in the data base. Sources: C69 = Carlander (1969), S73 = Scott and Crossman (1973), C77 = Carlander (1977), E74 = Eddy and Underhill (1974), B83 = Becker (1983), N61 = Nikol'skii (1961), B69 = Blaxter (1969), and H73 = Hart (1973).

| Species identification number | Species                             | Family          | Order              | Source             |
|-------------------------------|-------------------------------------|-----------------|--------------------|--------------------|
| 1                             | <i>Alosa sapidissima</i>            | Clupeidae       | Clupeiformes       | C69, S73           |
| 2                             | <i>Ambloplites rupestris</i>        | Centrarchidae   | Perciformes        | C77, S73, E74, B83 |
| 3                             | <i>Amblyopsis rosae</i>             | Amblyopsidae    | Percopsiformes     | C69                |
| 4                             | <i>Amblyopsis spelaea</i>           | Amblyopsidae    | Percopsiformes     | C69                |
| 5                             | <i>Anguilla anguilla</i>            | Anguillidae     | Anguilliformes     | C69                |
| 6                             | <i>Archoplates interruptus</i>      | Centrarchidae   | Perciformes        | C77                |
| 7                             | <i>Atherinops affinis</i>           | Atheridae       | Atheriniformes     | H73                |
| 8                             | <i>Camptostoma anomalum</i>         | Cyprinidae      | Cypriniformes      | C69                |
| 9                             | <i>Carpiodes carpio</i>             | Catostomidae    | Cypriniformes      | C69, B83           |
| 10                            | <i>Carpiodes cyprinus</i>           | Catostomidae    | Cypriniformes      | S73                |
| 11                            | <i>Carpiodes velifer</i>            | Catostomidae    | Cypriniformes      | C69, B83           |
| 12                            | <i>Catostomus catostomus</i>        | Catostomidae    | Cypriniformes      | S73, C69           |
| 13                            | <i>Catostomus columbianus</i>       | Catostomidae    | Cypriniformes      | S73                |
| 14                            | <i>Catostomus commersoni</i>        | Catostomidae    | Cypriniformes      | C69, S73           |
| 15                            | <i>Chologaster agassizi</i>         | Amblyopsidae    | Percopsiformes     | C69                |
| 16                            | <i>Clupea harengus</i>              | Clupeidae       | Clupeiformes       | N61, B69           |
| 17                            | <i>Cololabis saira</i>              | Scomberesocidae | Atheriniformes     | H73                |
| 18                            | <i>Coregonus albula</i>             | Salmonidae      | Salmoniformes      | N61                |
| 19                            | <i>Coregonus clupeiformis</i>       | Salmonidae      | Salmoniformes      | C69                |
| 20                            | <i>Ctenopharyngodon idella</i>      | Cyprinidae      | Cypriniformes      | N61, C69           |
| 21                            | <i>Erimyzon oblongus</i>            | Catostomidae    | Cypriniformes      | C69, B83           |
| 22                            | <i>Erimyzon sucetta</i>             | Catostomidae    | Cypriniformes      | S73, C69, B83      |
| 23                            | <i>Etheostoma microperca</i>        | Percidae        | Perciformes        | S73, B83           |
| 24                            | <i>Fundulus heteroclitus</i>        | Cyprinodontidae | Atheriniformes     | S73                |
| 25                            | <i>Gadus morhua</i>                 | Gadidae         | Gadiformes         | B69, N61           |
| 26                            | <i>Gila bicolor</i>                 | Cyprinidae      | Cypriniformes      | C69, B83           |
| 27                            | <i>Hesperoleucus symmetricus</i>    | Cyprinidae      | Cypriniformes      | C69                |
| 28                            | <i>Hippoglossoides platessoides</i> | Pleuronectidae  | Pleuronectiformes  | N61                |
| 29                            | <i>Hypentelium nigricans</i>        | Catostomidae    | Cypriniformes      | C69                |
| 30                            | <i>Ictiobus bubalus</i>             | Catostomidae    | Cypriniformes      | C69, B83           |
| 31                            | <i>Ictiobus cyprinellus</i>         | Catostomidae    | Cypriniformes      | C69, S73           |
| 32                            | <i>Lampetra planeri</i>             | Petromyzontidae | Petromyzontiformes | C69                |
| 33                            | <i>Lavinia exilicauda</i>           | Cyprinidae      | Cypriniformes      | C69                |
| 34                            | <i>Lepomis auritus</i>              | Centrarchidae   | Perciformes        | C77                |
| 35                            | <i>Lepomis gibbosus</i>             | Centrarchidae   | Perciformes        | C77, B83           |
| 36                            | <i>Lepomis gulosus</i>              | Centrarchidae   | Perciformes        | C77                |
| 37                            | <i>Lepomis humilis</i>              | Centrarchidae   | Perciformes        | C77, B83           |
| 38                            | <i>Lepomis macrochirus</i>          | Centrarchidae   | Perciformes        | C77                |
| 39                            | <i>Lepomis megalotis</i>            | Centrarchidae   | Perciformes        | C77, S73           |
| 40                            | <i>Lepomis microlophus</i>          | Centrarchidae   | Perciformes        | C77                |
| 41                            | <i>Micropterus salmoides</i>        | Centrarchidae   | Perciformes        | C77, S73, E74      |
| 42                            | <i>Moxostoma duquesnei</i>          | Catostomidae    | Cypriniformes      | C69                |
| 43                            | <i>Moxostoma erythrurum</i>         | Catostomidae    | Cypriniformes      | C69, B83           |
| 44                            | <i>Moxostoma macrolepidotum</i>     | Catostomidae    | Cypriniformes      | C69, B83           |
| 45                            | <i>Mylopharodon conocephalus</i>    | Cyprinidae      | Cypriniformes      | C69                |
| 46                            | <i>Notemigonus crysoleucas</i>      | Cyprinidae      | Cypriniformes      | C69, B83           |
| 47                            | <i>Notropis cerasinus</i>           | Cyprinidae      | Cypriniformes      | C69                |
| 48                            | <i>Notropis chrysocephalus</i>      | Cyprinidae      | Cypriniformes      | C69, B83           |
| 49                            | <i>Notropis coccogenis</i>          | Cyprinidae      | Cypriniformes      | C69                |
| 50                            | <i>Notropis cornutus</i>            | Cyprinidae      | Cypriniformes      | S73, E74, B83      |
| 51                            | <i>Notropis lutrensis</i>           | Cyprinidae      | Cypriniformes      | B83                |
| 52                            | <i>Oncorhynchus gorbusha</i>        | Salmonidae      | Salmoniformes      | S73                |
| 53                            | <i>Oncorhynchus keta</i>            | Salmonidae      | Salmoniformes      | S73                |
| 54                            | <i>Oncorhynchus kisutch</i>         | Salmonidae      | Salmoniformes      | S73                |
| 55                            | <i>Oncorhynchus nerka</i>           | Salmonidae      | Salmoniformes      | S73                |
| 56                            | <i>Oncorhynchus tshawytscha</i>     | Salmonidae      | Salmoniformes      | S73, N61           |

TABLE 1. Continued.

| Species identification number | Species                             | Family         | Order             | Source        |
|-------------------------------|-------------------------------------|----------------|-------------------|---------------|
| 57                            | <i>Orthodon microlepidotus</i>      | Cyprinidae     | Cypriniformes     | C69           |
| 58                            | <i>Perca flavescens</i>             | Percidae       | Perciformes       | S73, B83      |
| 59                            | <i>Platichthys stellatus</i>        | Pleuronectidae | Pleuronectiformes | H73           |
| 60                            | <i>Pleuronectes platessa</i>        | Pleuronectidae | Pleuronectiformes | B69           |
| 61                            | <i>Polyodon spathula</i>            | Polyodontidae  | Acipenseriformes  | B83           |
| 62                            | <i>Pomoxis nigromaculatus</i>       | Centrarchidae  | Perciformes       | C77, S73      |
| 63                            | <i>Ptychocheilus grande</i>         | Cyprinidae     | Cypriniformes     | C69           |
| 64                            | <i>Rhinichthys cataractae</i>       | Cyprinidae     | Cypriniformes     | C69, S73      |
| 65                            | <i>Salmo clarki</i>                 | Salmonidae     | Salmoniformes     | C69, S73      |
| 66                            | <i>Salmo gairdneri</i>              | Salmonidae     | Salmoniformes     | C69, S73      |
| 67                            | <i>Salmo salar</i>                  | Salmonidae     | Salmoniformes     | C69, N61      |
| 68                            | <i>Salmo trutta</i>                 | Salmonidae     | Salmoniformes     | C69           |
| 69                            | <i>Salvelinus alpinus</i>           | Salmonidae     | Salmoniformes     | C69, S73      |
| 70                            | <i>Salvelinus fontinalis</i>        | Salmonidae     | Salmoniformes     | C69, E74      |
| 71                            | <i>Salvelinus namaycush</i>         | Salmonidae     | Salmoniformes     | C69, S73, E74 |
| 72                            | <i>Scaphirhynchus albus</i>         | Acipenseridae  | Acipenseriformes  | C69, N61      |
| 73                            | <i>Scaphirhynchus platyrhynchus</i> | Acipenseridae  | Acipenseriformes  | C69, N61, B83 |
| 74                            | <i>Sebastes alutus</i>              | Scorpaenidae   | Scorpaeniformes   | H73           |
| 75                            | <i>Sebastes caurinus</i>            | Scorpaenidae   | Scorpaeniformes   | H73           |
| 76                            | <i>Sebastolobus alascanus</i>       | Scorpaenidae   | Scorpaeniformes   | H73           |
| 77                            | <i>Sphyaena argentea</i>            | Sphyaenidae    | Perciformes       | H73           |
| 78                            | <i>Theragra chalcogrammus</i>       | Gadidae        | Gadiformes        | H73           |
| 79                            | <i>Thymallus arcticus</i>           | Salmonidae     | Salmoniformes     | C69, S73      |
| 80                            | <i>Zoarces viviparus</i>            | Zoaridae       | Gadiformes        | N61           |

available were retained on the list, and various methods were developed for quantitatively estimating missing information from other information in the data base, as described below.

The estimation of missing information from quantitative relationships (such as the estimation of maximum weight from maximum length) may introduce additional variance, but is not likely to be a cause of bias and is thus unlikely to be a cause of spurious relationships with genetic variation. Even so, we take the precaution of retesting all significant relationships after the exclusion of values that were not measured directly.

Secondary references were used in preference to the primary literature on life-history variables, because the authors of secondary references have standardized the information in a number of ways and have thus reduced some of the variability in the raw information. For freshwater fishes, the single most important source was Carlander (1969, 1977), whose books are ideal for

present purposes in that extensive life-history information is given in a standardized format for a large number of freshwater taxa. In addition, we relied heavily on Scott and Crossman (1973) and Breder and Rosen (1966). For saltwater taxa, our single most important reference was Hart (1973), but the information on marine taxa was generally more scattered than for freshwater taxa (Table 1).

Lengths corresponding either to maximum size or to size at maturity were much more often available than body masses of fish at these two points in the life history. It was possible to define a close relationship between maximum weight ( $B_m$ ; measured as g wet mass) and maximum length ( $L_m$ ; measured in mm):  $\log(B_m) = 2.726 \log(L_m) - 4.085$  ( $P < 0.001$ ; standard error of slope = 0.12;  $N = 54$ ;  $r = 0.69$ ). This relationship was used to fill in missing weights when lengths were known.

Maximum age was much more often unknown than maximum size. A method was thus developed for obtaining maximum age

from maximum size. Length was used rather than body mass as an index of size, because length was known for more taxa than mass. Regression analysis based on species for which data were available on both variables indicated the following relationship between maximum age ( $A_m$ ; measured in years) and maximum length ( $L_m$ ):  $\log(A_m) = 0.458 \log(L_m) - 0.256$ . The standard error of the slope for this equation is 0.084, and the relationship is highly significant ( $r = 0.59$ ,  $N = 58$ ,  $P < 0.001$ ). The equation was used in assigning a maximum age when the maximum length was known and the maximum age was not known.

In some instances, neither age at maturity nor size at maturity could be established from the literature. From the data on fish for which such information was available, a relationship was established between age at maturity ( $A_f$ ; measured in years) and maximum length ( $L_m$ ). Both linear and non-linear relationships were tested; the linear relationship fit the data better. The linear fit, as determined by simple regression, is:  $A_f = 0.00231(L_m) + 1.527$ ; standard error of slope = 0.00045;  $r = 0.55$ ,  $N = 63$ ,  $P < 0.001$ .

An attempt was made to establish a relationship between size at maturity and age at maturity, but the relationship contained too much scatter to be useful. Weight at maturity proved to be related to maximum weight, but the raw data base contained insufficient numbers of data points to define the relationship well. Consequently, the relationship was redefined on the basis of a modified data base that contained additional data on maximum weight computed from maximum length by use of the equation described above. This was done after deletion of the salmonids, which cause distortion because of their unusual life history. The result of the analysis is:  $\log(B_f) = 1.170 \log(B_m) - 1.478$ , where  $B_f$  and  $B_m$  are wet mass (g) per individual at first maturity and at maximum age, respectively (standard error of slope = 0.19;  $r = 0.85$ ,  $N = 17$ ,  $P < 0.001$ ).

Calculations of  $F_t$ ,  $F_w$ , and  $F_a$  must be based on the numbers of eggs produced per year throughout an entire lifetime or based on the sizes of the fish through each year of life, from which the numbers of eggs can be estimated. The sizes of fish through each

year of life can be calculated from the duration between maturity and maximum age, the size at maturity, and the maximum size. The rate of change in size with age must also be specified, but fecundity is not very sensitive to variations in this rate of change. An initial attempt was made to establish growth rates ( $G$ ; measured in grams per day) from body mass ( $B$ ) by the equation of Case (1978):  $\log(G) = 0.61 \log(B) - 2.93$ . Although this equation is often cited as an indicator of growth rate in adult fish, it predicts growth rates that are more than an order of magnitude too low to account for the change in size of fish between maturity and maximum size as reported from the literature referenced in Table 1. Consequently, the equation was modified. It was assumed that the exponent used by Case (0.61) would be correct. Although this exponent is lower than the exponent relating body size to basal metabolic rate (0.75; Peters, 1983), it is not unreasonable for somatic growth to increase with size less rapidly than with respiration in adult fish. If the exponent is assumed to be constant at 0.61, the coefficient ( $q$ ) in the equation relating growth rate to size can be obtained separately for each species by solving the growth-rate equation for the growth-rate coefficient. This produces a separate growth equation for each species of fish. Each equation allows growth to proceed at a rate related to the 0.61 power of body mass times a coefficient whose value is exactly as large as necessary to cause the fish to grow from size at maturity to maximum size over the number of years between age at maturity and maximum age. The values of  $q$  computed in this manner are shown in Figure 1. The value of  $q$  from the Case (1978) equation is 0.00117; for our data set, the mean value of  $q$  is 0.013, and the 95% confidence interval for the mean is 0.011–0.015.

For fish species with a span of four years or less between age at maturity and maximum age and for which either the average numbers of eggs per year or the minimum and maximum numbers of eggs per year were available, we assumed that the number of eggs per lifetime was equal to the average number of eggs per year (not necessarily all in one clutch) times the number of years between maturity and maximum age. For

other species, our estimation procedure was more complicated. We used an equation from Blueweiss et al. (1978):  $\log(V) = 0.92(B) - 0.561$ , where  $V$  is the clutch volume in  $\text{mm}^3$  and  $B$  is wet body mass in grams ( $r = 0.93$ ,  $N > 100$ ). This equation was developed for poikilotherms in general, and so we assumed that it applies to fish. The equation was applied to the sizes of each fish species for each year of life between maturity and maximum age; the total volume of eggs was cumulated over this interval. This volume of eggs was converted to mass on the basis of a specific gravity of 1.0. From the egg diameters, the numbers of eggs and the three fecundity indices ( $F_t$ ,  $F_w$ , and  $F_a$ ) were calculated for each species.

The data on egg diameters, which are required for the calculations of total lifetime fecundity for many of the species, are subject to certain known errors. For example, egg diameters vary with the size of the female in some species (Carlander, 1977). In addition, diameters that are measured on eggs removed from the body cavity of a fish rather than from redds or nests are likely to be substantially smaller than diameters measured on eggs that have been released from the female, because of the swelling of fish eggs in water (R. Heidinger, pers. comm.). It was not possible to determine whether egg diameters reported in the literature were for eggs derived from the female body cavity or eggs that had already increased in size due to swelling. For this reason, we ignored this source of error. Because the egg diameters represented in the data base range very greatly with size and because there is no reason to suspect a non-random association of measurements on swollen and unswollen eggs in relation to the other variables of interest, we believe that our inability to correct for the method of egg-diameter measurement results in a tolerable amount of additional random variance around the patterns of interest to us here. For similar reasons, we have ignored the association between body size and egg size, which is relatively minor given the magnitudes of change across species represented in the data base.

The data base, as modified by the inclusion of estimates derived as described above, is summarized in Table 2. By use of the

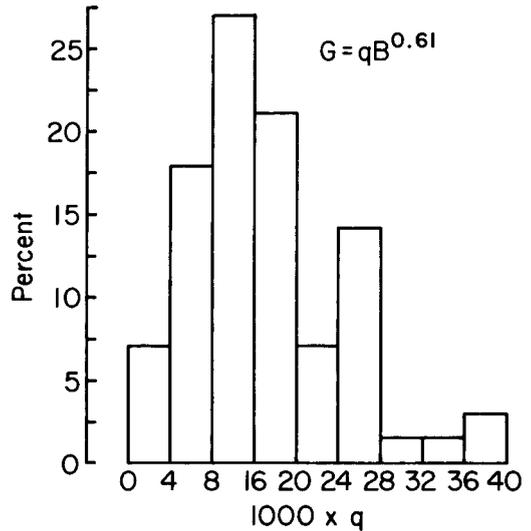


FIG. 1. Frequency distribution of the growth-rate coefficients for the fish species included in the data base.

estimation procedures, data sets were obtained for a total of 80 species. Values added by estimation were as follows: maximum weight from maximum length (24 out of 78), maximum age from maximum length (21 out of 79), age at first reproduction from maximum length (36 out of 79), and mass at maturity from maximum mass (61 out of 78).

## RESULTS

Table 3 summarizes some of the characteristics of the data on fecundity and genetic variability. The frequency distributions of most variables deviated significantly from normality (Kolmogorov-Smirnov test,  $P < 0.05$ ), and standard transformations were only marginally successful in normalizing some variables. Consequently, relationships of genetic variability ( $H$  or  $P$ ) with fecundity were tested nonparametrically (Spearman rank-correlation coefficient). Table 3 shows the correlations of life-history characteristics with  $H$ . Correlations with  $P$  were very similar to or somewhat weaker than correlations with  $H$ .

Table 3 shows that genetic variability, expressed as  $H$ , is negatively related to indicators of the rate of maturation (length at maturity and mass at maturity), to indicators of size (maximum length and maxi-

TABLE 2. Information on fecundity and genetic variability used in the analysis. Species identification numbers correspond to those in Table 1.

| Species identification number | Maximum size (g; wet weight) | Egg diameter (mm) | Number of eggs ( $F_i$ ) | Eggs per gram ( $F_w$ ) | Adjusted number of eggs ( $F_a$ ) | $H$   | $P$   |
|-------------------------------|------------------------------|-------------------|--------------------------|-------------------------|-----------------------------------|-------|-------|
| 1                             | 6,350                        | 3.50              | 239,923                  | 37.78                   | 33,383                            | 0.005 | 0.063 |
| 2                             | 1,656                        | 1.80              | 431,560                  | 260.60                  | 26,126                            | 0.114 | 0.460 |
| 3                             | 4                            | 11.59             | 69                       | 17.25                   | 40                                | 0.006 | —     |
| 4                             | 12                           | 8.00              | 350                      | 29.17                   | 134                               | 0.000 | —     |
| 5                             | —                            | 1.00              | 10,000,000               | —                       | 10,000,000                        | 0.181 | 0.650 |
| 6                             | 1,360                        | 1.41              | 505,071                  | 371.38                  | 54,402                            | 0.038 | 0.000 |
| 7                             | 800                          | 1.70              | 200,248                  | 250.31                  | 28,654                            | —     | 0.160 |
| 8                             | 130                          | 2.40              | 6,563                    | 50.48                   | 1,863                             | 0.070 | 0.351 |
| 9                             | 3,442                        | 1.50              | 1,265,203                | 367.58                  | 114,414                           | 0.089 | 0.449 |
| 10                            | 5,483                        | 1.40              | 3,375,365                | 615.61                  | 442,814                           | 0.083 | 0.409 |
| 11                            | 1,720                        | 1.20              | 259,998                  | 151.16                  | 99,839                            | 0.081 | 0.396 |
| 12                            | 3,312                        | 3.00              | 398,116                  | 120.20                  | 10,601                            | 0.038 | 0.236 |
| 13                            | 892                          | 2.80              | 51,932                   | 58.22                   | 4,653                             | 0.048 | 0.190 |
| 14                            | 3,198                        | 2.04              | 822,448                  | 257.18                  | 46,297                            | 0.024 | 0.153 |
| 15                            | 6                            | 2.70              | 456                      | 76.00                   | 266                               | 0.026 | —     |
| 16                            | 283                          | 1.50              | 213,792                  | 755.45                  | 5,823                             | 0.070 | 0.362 |
| 17                            | 765                          | 2.00              | 117,002                  | 152.94                  | 13,566                            | 0.174 | 0.544 |
| 18                            | 1,492                        | 4.68              | 17,765                   | 11.91                   | 1,786                             | 0.080 | 0.552 |
| 19                            | 4,536                        | 2.04              | 1,952,140                | 430.37                  | 43,113                            | —     | 0.260 |
| 20                            | 32,000                       | —                 | —                        | —                       | —                                 | 0.022 | 0.062 |
| 21                            | 1,814                        | 1.84              | 320,278                  | 176.56                  | 48,389                            | 0.043 | 0.236 |
| 22                            | 914                          | 1.00              | 811,731                  | 888.11                  | 129,454                           | 0.058 | 0.273 |
| 23                            | 5                            | 1.00              | 1,500                    | 300.00                  | 1,125                             | 0.010 | 0.055 |
| 24                            | 48                           | 2.00              | 1,840                    | 38.33                   | 863                               | 0.180 | 0.560 |
| 25                            | 40,000                       | 1.30              | 30,519,399               | 762.98                  | 2,011,131                         | 0.082 | 0.300 |
| 26                            | 207                          | 1.70              | 61,950                   | 299.28                  | 5,396                             | 0.059 | 0.277 |
| 27                            | 465                          | 5.38              | 4,500                    | 9.68                    | 1,728                             | 0.068 | 0.330 |
| 28                            | 680                          | 0.51              | 7,792,865                | 11,460.10               | 428,644                           | 0.083 | 0.400 |
| 29                            | 1,889                        | —                 | —                        | —                       | —                                 | 0.016 | 0.127 |
| 30                            | 15,900                       | 2.22              | 2,544,779                | 160.05                  | 147,011                           | 0.103 | 0.395 |
| 31                            | 36,760                       | 1.80              | 15,044,341               | 409.26                  | 608,306                           | 0.102 | 0.371 |
| 32                            | 160                          | 2.88              | 3,000                    | 18.75                   | 2,250                             | 0.076 | 0.300 |
| 33                            | 539                          | 1.10              | 235,271                  | 436.50                  | 70,817                            | 0.053 | 0.330 |
| 34                            | 312                          | 2.61              | 19,304                   | 61.87                   | 2,277                             | 0.062 | 0.277 |
| 35                            | 482                          | 1.00              | 715,759                  | 1,484.98                | 41,562                            | 0.066 | 0.192 |
| 36                            | 387                          | 1.01              | 402,824                  | 1,040.89                | 41,031                            | 0.030 | 0.151 |
| 37                            | 59                           | 0.50              | 9,500                    | 161.02                  | 4,453                             | 0.049 | 0.192 |
| 38                            | 2,056                        | 1.09              | 1,718,831                | 836.01                  | 40,188                            | 0.041 | 0.149 |
| 39                            | 227                          | 1.00              | 239,248                  | 1,053.96                | 24,136                            | 0.114 | 0.443 |
| 40                            | 1,270                        | 1.60              | 339,254                  | 267.13                  | 35,624                            | 0.037 | 0.114 |
| 41                            | 10,280                       | 1.80              | 2,461,913                | 239.49                  | 49,646                            | 0.073 | 0.250 |
| 42                            | 2,404                        | 5.25              | 17,664                   | 7.35                    | 1,922                             | 0.015 | 0.153 |
| 43                            | 2,211                        | 2.40              | 227,738                  | 103.00                  | 32,076                            | 0.034 | 0.203 |
| 44                            | 4,540                        | 1.90              | 1,061,340                | 233.78                  | 87,196                            | 0.075 | 0.293 |
| 45                            | 900                          | 2.20              | 127,681                  | 141.87                  | 11,527                            | 0.006 | 0.064 |
| 46                            | 340                          | 1.10              | 355,499                  | 1,045.59                | 18,324                            | 0.068 | 0.277 |
| 47                            | 11                           | —                 | —                        | —                       | —                                 | —     | 0.137 |
| 48                            | 242                          | 1.60              | 4,100                    | 16.94                   | 1,922                             | —     | 0.117 |
| 49                            | 27                           | —                 | —                        | —                       | —                                 | —     | 0.071 |
| 50                            | 482                          | 1.50              | 184,831                  | 383.47                  | 17,451                            | —     | 0.138 |
| 51                            | 11                           | 3.95              | 1,169                    | 106.27                  | 877                               | 0.080 | —     |
| 52                            | 1,828                        | 6.00              | 1,750                    | 0.96                    | 1,750                             | 0.032 | 0.151 |
| 53                            | 5,483                        | 9.00              | 5,500                    | 1.00                    | 4,125                             | 0.034 | 0.079 |
| 54                            | 5,483                        | 5.25              | 7,100                    | 1.29                    | 5,325                             | 0.016 | 0.129 |
| 55                            | 1,828                        | 4.75              | 1,066                    | 0.58                    | 1,066                             | 0.017 | 0.100 |
| 56                            | 15,991                       | 6.50              | 18,900                   | 1.18                    | 14,175                            | 0.028 | 0.196 |
| 57                            | 1,620                        | 1.13              | 1,167,550                | 720.71                  | 147,167                           | 0.015 | 0.064 |
| 58                            | 1,028                        | 1.60              | 251,053                  | 244.21                  | 34,931                            | —     | 0.136 |
| 59                            | 9,100                        | —                 | —                        | —                       | —                                 | 0.047 | 0.700 |

TABLE 2. Continued.

| Species identification number | Maximum size (g, wet weight) | Egg diameter (mm) | Number of eggs ( $F_t$ ) | Eggs per gram ( $F_w$ ) | Adjusted number of eggs ( $F_a$ ) | $H$   | $P$   |
|-------------------------------|------------------------------|-------------------|--------------------------|-------------------------|-----------------------------------|-------|-------|
| 60                            | —                            | 2.00              | —                        | —                       | —                                 | 0.102 | 0.480 |
| 61                            | 73,900                       | 2.00              | 8,692,521                | 117.63                  | 1,132,509                         | 0.013 | 0.060 |
| 62                            | 1,315                        | 0.93              | 2,043,746                | 1,554.18                | 217,882                           | 0.009 | 0.129 |
| 63                            | 14,500                       | 5.22              | 106,791                  | 7.36                    | 12,449                            | 0.011 | 0.064 |
| 64                            | 112                          | 3.76              | 2,720                    | 24.29                   | 1,275                             | 0.057 | 0.215 |
| 65                            | 3,400                        | 4.70              | 26,678                   | 7.85                    | 4,537                             | 0.040 | 0.109 |
| 66                            | 23,000                       | 4.00              | 431,960                  | 18.78                   | 39,030                            | 0.060 | 0.272 |
| 67                            | 45,690                       | 6.00              | 249,308                  | 5.46                    | 23,465                            | 0.023 | 0.101 |
| 68                            | 17,123                       | 4.90              | 321,169                  | 18.76                   | 13,578                            | 0.022 | 0.092 |
| 69                            | 11,793                       | 4.50              | 398,812                  | 33.82                   | 13,931                            | 0.006 | 0.016 |
| 70                            | 6,625                        | 5.00              | 87,343                   | 13.18                   | 3,867                             | 0.077 | 0.252 |
| 71                            | 46,267                       | 5.50              | 1,368,624                | 29.58                   | 24,548                            | 0.015 | 0.142 |
| 72                            | 30,800                       | —                 | —                        | —                       | —                                 | 0.010 | 0.098 |
| 73                            | 4,536                        | 2.30              | 416,849                  | 91.90                   | 45,241                            | 0.017 | 0.098 |
| 74                            | 1,976                        | 1.29              | 3,939,459                | 1,993.65                | 70,501                            | 0.038 | —     |
| 75                            | 2,428                        | 1.17              | 1,591,990                | 655.68                  | 173,869                           | 0.014 | —     |
| 76                            | 5,655                        | 1.30              | 3,189,316                | 563.98                  | 294,018                           | 0.049 | 0.200 |
| 77                            | 21,301                       | 1.40              | 8,580,046                | 402.80                  | 884,175                           | —     | 0.160 |
| 78                            | 9,579                        | 1.40              | 3,994,291                | 416.98                  | 1,095,224                         | 0.006 | 0.084 |
| 79                            | 2,270                        | 2.70              | 204,718                  | 90.18                   | 26,361                            | 0.033 | 0.110 |
| 80                            | 465                          | 3.00              | 25,321                   | 54.45                   | 2,708                             | 0.089 | 0.290 |

imum mass), and to egg size. There is no significant relationship between heterozygosity and two of the fecundity indicators ( $F_t$  and  $F_a$ ). However, there is a positive relationship between  $F_w$  (eggs per gram of body mass) and heterozygosity. The 12 species with the highest  $F_w$  ( $H = 0.056$ ,  $F_w = 720$  eggs per g of body weight) have genetic variability about 50% higher than the 12 species with lowest  $F_w$  ( $H = 0.037$ ,  $F_w = 13.2$  eggs per g of body weight). Figure 2 illustrates some of the key relationships among variables. When retested without the use of estimates to fill in missing data, these relationships were not significantly changed.

The correlation between heterozygosity and length at maturity suggests a relationship between rapid maturation and high heterozygosity. However, this correlation is not reflected in the relationship between age at maturity and heterozygosity, probably because of the low precision in determinations of age at maturity. For practical reasons, it is not possible to resolve the age at maturity for intervals of less than approximately one year, even though fish show considerable variation in time to maturity over time scales much shorter than this. Consequently, length at maturity provides a much more sensitive indicator of the speed of maturation than does age at maturity.

## DISCUSSION

### *Predictions of Genetic Variability from Neutral Theory*

Implicit in the search for relationships between genetic variability and life-history characteristics is the hypothesis that levels of genetic variation reflect intensities of balancing selection, i.e., forms of selection that maintain genetic variation. It is also possible, however, that all or part of the genetic variation evident among fishes is irrelevant to adaptation and, hence, is unaffected by natural selection. If the genetic variation is predominantly neutral, then its levels would be best explained by 1) time since the last bottleneck (or perhaps since speciation), 2) the neutral-mutation rate, and 3) the effective population size. Neutral-mutation theory (Kimura and Ohta, 1971) describes the equilibrium value of heterozygosity,  $H$ , as

$$H = \frac{4N_e u}{1 + 4N_e u}$$

where  $N_e$  represents the effective population size and  $u$  is the neutral mutation rate.

Several surveys of genetic variation have reported relationships between population size and genetic variation. For example, heterozygosity increased with a rough estimate of population size, i.e., the number of in-

TABLE 3. Characteristics of the data set that was used in testing the relationship between fecundity and genetic variability.

| Variable  | Mean      | N  | SD        | Range   |            | Relationship to $H$<br>( $r_s$ ) |
|---|-----------|----|-----------|---------|------------|----------------------------------|
|   |           |    |           | Minimum | Maximum    |                                  |
| <b>Indexes of genetic variability:</b>          |           |    |           |         |            |                                  |
| $H$   | 0.052     | 72 | 0.040     | 0       | 0.181      | —                                |
| $P$   | 0.230     | 72 | 0.155     | 0       | 0.700      | —                                |
| <b>Life-history traits:</b>                     |           |    |           |         |            |                                  |
| Age at maturity (years)                         | 3.08      | 79 | 2.43      | 1       | 20         | -0.12                            |
| Maximum age (years)                             | 10.8      | 79 | 6.82      | 2       | 41         | 0.12                             |
| Length at maturity (mm)                         | 366       | 21 | 250       | 61      | 968        | -0.55**                          |
| Maximum length (mm)                             | 579       | 78 | 379       | 46      | 1,650      | -0.24*                           |
| Mass at maturity (g)                            | 1,710     | 78 | 3,330     | 0.153   | 16,800     | -0.24*                           |
| Maximum mass (g)                                | 7,160     | 78 | 13,200    | 4       | 73,900     | -0.22*                           |
| Egg diameter                                    | 2.79      | 74 | 2.10      | 0.50    | 11.6       | -0.30**                          |
| Eggs per lifetime ( $F_t$ )                     | 1,674,000 | 73 | 4,330,000 | 69      | 30,500,000 | 0.15                             |
| Eggs per lifetime, mortality adjusted ( $F_a$ ) | 260,000   | 73 | 1,200,000 | 40      | 10,000,000 | 0.12                             |
| Eggs per lifetime per gram ( $F_w$ )            | 461       | 72 | 1,380     | 0.58    | 11,460     | 0.25*                            |

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

dividuals within a species, in a broad survey of 717 plants and animals (Nevo et al., 1984 table 11a). Heterozygosity differed among groups ( $P < 0.01$ ) and was estimated to be 0.053, 0.066, 0.077, and 0.090 in groups of species with small ( $10^3$ ), medium ( $10^5$ ), large ( $10^6$ ) and very large ( $10^9$ ) numbers of individuals per species, respectively. The same pattern was evident in fishes; heterozygosity

was estimated to be 0.020, 0.044, 0.046, and 0.068 in fishes with small, medium, large, and very large numbers of individuals per species, respectively. Soulé approximated effective population size from information on population density and dispersal capability and found that heterozygosity increased with population size in a broad group of animals (Soulé, 1976). More recently, Nei

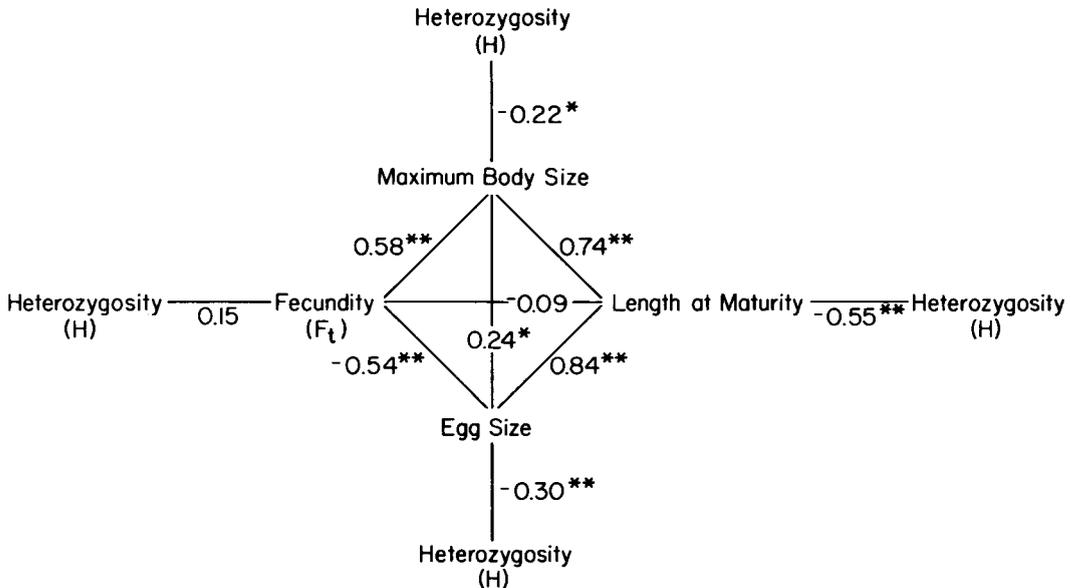
\*  $p < 0.05$ \*\*  $p < 0.01$ 

FIG. 2. Diagram of correlation coefficients for life-history variables and heterozygosity.

and Graur (1984) tested the hypothesis that genetic variation increases with the product of effective population size ( $N_e$ ) and generation time ( $G$ ). In their sample of 77 species, the observed level of heterozygosity was correlated with the product of effective population size and generation time ( $r = 0.65$ ,  $P < 0.001$ ). In both the survey by Nei and Graur and the study by Soulé, however, the observed levels of genetic variation were far below those predicted by neutral-mutation theory. The predicted levels of heterozygosity are for populations at equilibrium, and in each of these two studies, the authors mention the possibility that there has not been sufficient time since speciation or since the last severe bottleneck for genetic variation to rise to its equilibrium level.

We note, however, that an increase in genetic variation with population size is not clear evidence that the genetic variation is adaptively neutral; the same pattern is expected for all genetic variation, whether it be adaptively neutral or maintained by selection. When effective population size is very small, drift will erode the genetic variability at virtually all polymorphic loci.

Our data indicate that fishes that should be selected for rapid population increase have high genetic variability, but we have no means of measuring the relationships between life-history variables and population size. Because we have no reason to suspect that species having high capacities for increase also have greater population sizes, we favor a selective mechanism to explain the high genetic variability in such species.

#### *Interpretations of Correlations among Variables*

Several generalizations concerning genetic variation and life-history variation in the bony fishes can be extracted from the data (Table 3, Fig. 2). Larger fish tend to mature later ( $r = 0.74$ ), to produce larger eggs ( $r = 0.24$ ), and to be more fecund ( $r = 0.58$ ). Fecundity reflects egg size ( $r = -0.54$ ) as well as body size ( $r = 0.58$ ) but is not related to length at maturity. Fish maturing early are not only smaller ( $r = 0.74$ ), but also produce smaller eggs ( $r = 0.84$ ). Heterozygosity is related to body size and to egg size. Heterozygosity decreases with increasing maximum body size ( $r = -0.22$ ), but this

relationship is not strong; the associations of genetic variation with egg size ( $r = -0.30$ ) and with length at maturity ( $r = -0.55$ ) are strongest. Heterozygosity varies inversely with egg size and with length at maturity, which is interpreted here primarily as the length of the prereproductive stage of the life cycle. In general, fishes that mature early and produce small eggs exhibit the highest levels of genetic variation; these fishes have the highest capacity for increase. For convenience, we shall refer to these species as *r*-selected, with due recognition that this term may in some senses be unsatisfactory (Boyce, 1984).

#### *Contrasts between Bony Fishes and Larger Groups of Organisms*

On a grand scale, there is an association between fecundity and genetic variation. For example, the conifers, which have high fecundity, have the highest known genetic variability (Hamrick et al., 1979). Groups of species with relatively low levels of genetic variation are the birds and mammals (Avisé and Aquadro, 1982), and these groups are also characterized by low fecundities. Analyses of fecundity and heterozygosity among diverse species have revealed that these variables are positively correlated in both plants ( $r = 0.37$ ,  $P < 0.001$ ) and animals ( $r = 0.66$ ,  $P < 0.001$ ) (Hamrick et al., 1979). However, heterozygosity is not correlated with estimates of lifetime fecundity ( $F_a$  and  $F_l$ ) in the bony fishes.

The increase of genetic variation with lifetime fecundity in diverse assemblages of organisms is consistent with a parallel trend in the opportunity for balancing selection, which increases with reproductive excess. Fecund organisms have the potential to sustain very high intensities of selection and, therefore, might maintain high levels of genetic variation. Why, then, does genetic variation not increase with fecundity in the fishes?

The data on bony fishes indicate that opportunity for balancing selection (as indicated by fecundity) is secondary to environmental heterogeneity (as indicated by capacity for increase) as a cause of genetic variation. This is not necessarily contradictory to the association between fecundity and genetic variation in broader groups of

organisms. Even if environmental variation is the predominant underlying cause of genetic variation, the life-history associations of genetic variation may still differ among groups. Where environmental variation is primarily spatial and breeding organisms are not motile, selection may place a premium specifically on fecundity. Where environmental variation is primarily temporal and the mature individuals are motile, selection may focus on capacity for increase rather than fecundity. Because life-history associations of environmental variation will vary among groups, fecundity must be evaluated in conjunction with other variables.

The relationship between genetic variation and environmental variation suggested by our data has also been described in a comparative study of gobies (Wallis and Beardmore, 1984). Nine closely related species of gobies were surveyed for genetic variation at 31 gene loci and also ranked for the degree of environmental heterogeneity that they experienced. Environmental variation is postulated to decrease from estuaries to neritic to offshore habitats for this group. Heterozygosity increases with environmental heterogeneity, as measured by position along that gradient ( $r = 0.86$ ,  $P < 0.01$ ).

Our analysis of genetic and life-history variation supports the hypothesis that the primary factor explaining genetic variation in the bony fishes is temporal variation in the environment, which is reflected among these species by a positive relationship between the degree of environmental variation and life-history traits that favor rapid population increase. Further studies of multiple life-history variables in relation to genetic variation offers the prospect of better insight into the factors that control genetic variation in other groups.

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