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## Selection and crossbreeding in Mediterranean cultured marine fish<sup>1</sup>

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**SUMMARY** - As profit margins decline, and gains from husbandry improvement diminish, marine fish farmers around the Mediterranean are considering the development and use of genetically improved fish strains to increase productivity and profitability. To date, published data on the use of crossbreeding (intraspecific hybridization) and selection in marine Mediterranean cultured species are available only for the gilthead seabream (*Sparus aurata*). Crossbreeding: to date, crosses between *S. aurata* strains usually yielded little heterosis. Between strain selection: differences for growth and survival performance in culture were detected among several Eastern Mediterranean strains of gilthead sea bream *S. aurata*. Within strain selection: mass selection rather than family selection, was technically possible for the group spawning *S. aurata*. Single generation up-selection for weight increase yielded -0.4% to 10.9% gain (average gain of 7.3%), and down-selection for weight decrease yielded 8.5% to 16.2% loss at harvest weight. Gain from selection for increase weight was attributed to increased food conversion efficiency.

**Key words:** Genetics, breeding, crossbreeding, selection, strains, marine, fish.

**RESUME** - "Sélection et croisement chez les poissons marins cultivés en Méditerranée". A mesure que les marges de bénéfice se réduisent et que la rentabilité découlant des améliorations de l'élevage diminue, les aquaculteurs marins du pourtour de la Méditerranée sont en train de considérer le développement et l'utilisation de lignées de poissons améliorées génétiquement, afin d'augmenter la productivité et la rentabilité. Actuellement les données publiées sur l'utilisation du croisement (hybridation interspécifique) et la sélection chez les espèces marines cultivées en Méditerranée, ne sont disponibles que pour la daurade (*Sparus aurata*). Croisement : à ce jour, les croisements entre lignées de *S. aurata* n'ont apporté habituellement que peu d'hétérosis. Sélection inter-lignées : des différences quant aux performances de croissance et de survie en élevage ont été détectées entre plusieurs lignées de daurade *S. aurata* de l'Est de la Méditerranée. Sélection intra-lignée : la sélection massale plutôt que la sélection familiale, a été techniquement possible pour la ponte groupée de *S. aurata*. La sélection positive sur une seule génération pour le rendement en poids a donné de 0,4% à 10,9% de gain (un gain moyen de 7,3%) et la sélection négative a amené de 8,5% à 16,2% de perte pour le poids à la récolte. Le gain dû à la sélection positive a été attribué à une plus grande efficacité de la conversion alimentaire.

**Mots-clés :** Génétique, amélioration, croisement, sélection, lignées, marin, poisson.

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## Introduction

In the last decade, and as production volumes increased, convergence of product prices and production costs was noted for Atlantic salmon, *Salmo salar* (Salmonidae), gilthead seabream, *Sparus aurata* (Sparidae), European seabass, *Dicentrarchus labrax* (Moronidae, or Serranidae) and turbot, *Scophthalmus maximus* (Bothidae) (Sweetman, 1993 and Bartley (this volume) for other species groups in the Mediterranean). Similar convergence has been evident for most (land) agriculture commodities, and should be anticipated for new marine species under consideration for captive culture. Accordingly, only highly efficient and competitive companies will tend to survive and remain profitable in the long term and in the inevitably narrow window between profit and loss. The use of genetically improved strains is expected to be a major factor in increasing commercial competitiveness.

Usually, growth is perceived as the trait of primary economic importance for marine fish. For example, market prices for *S. aurata* are based simply on unprocessed whole body weight. *S. aurata* grow relatively slowly, and may take 14-20 months to reach market size of 300-500 g (Gordin, 1990). Increased growth should lead to greater production volumes with existing facilities, earlier returns on capital investment, and reduced exposure of given crops to accidental loss and disease. Also, selection for growth may result in increased survival and disease resistance (Fjalestad *et al.*, 1993), and perhaps food conversion efficiency (Falconer, 1981). Present genetic improvement efforts in marine fish focus on growth improvement.

## Selection between strains

Wild and cultured fish strains of the same species from different geographic locations may show differences for performance (growth, survival, etc.) in captive culture conditions as was noted for carp, *Cyprinus carpio* (Cyprinidae) (Moav *et al.*, 1975), salmonid species (Gjerde, 1986 for review), channel catfish, *Ictalurus sp.* (Ictaluridae) (Smitherman *et al.*, 1983; Dunham, 1987 for reviews) and tilapia species, *Oreochromis sp.* (Cichlidae) (Hulata, 1995a). Moreover, propagation of fish in captivity over generations may result in genetic changes including unintentional but desirable "domestication" selection and/or undesirable inbreeding. Assessment for potential differences between strains represents a relatively inexpensive investment, and should be conducted prior to within strain selection as choice of the best existing strain/s could equal the genetic gains made by years of selection on inferior strains (Gunnes and Gjedrem, 1978; Kinghorn, 1983).

Additionally, different strains can be crossed and offspring assessed for heterosis (i.e., whether the performance of the offspring exceeds the average of the parents). For freshwater aquacultural teleosts, heterosis was evident in some, but not all, inter-strain crosses of *C. carpio* (Moav *et al.*, 1975) and channel catfish, *I. punctatus* (Dunham and Smitherman, 1983a; Dunham, 1987; Smitherman *et al.*, 1983 for reviews). Only weak heterosis was reported for crossbred *S. salar* (Gjerde and Refstie, 1984).

For *S. aurata*, Francescon *et al.* (1988) observed similar growth for hatchery-bred

and wild-caught *S. aurata* in intensive and extensive systems. A genetic interpretation of these data is problematic without published information on the breeding history of the hatchery fish (including origin, and generations in captivity). Furthermore, genetic, age and rearing effects are confounded in experimental designs using wild-bred fish.

Knibb *et al.* (1996, 1997a) compared several hatchery-raised *S. aurata* strains for growth and survival in separate and communal rearing conditions (Fig. 1). Strains included the Eilat strain (propagated in captivity for more than 20 years and possibly seven generations), first generation offspring of wild-caught fish, and crossbred strains. The ancestors of all strains were wild-caught individuals from the eastern Mediterranean basin.

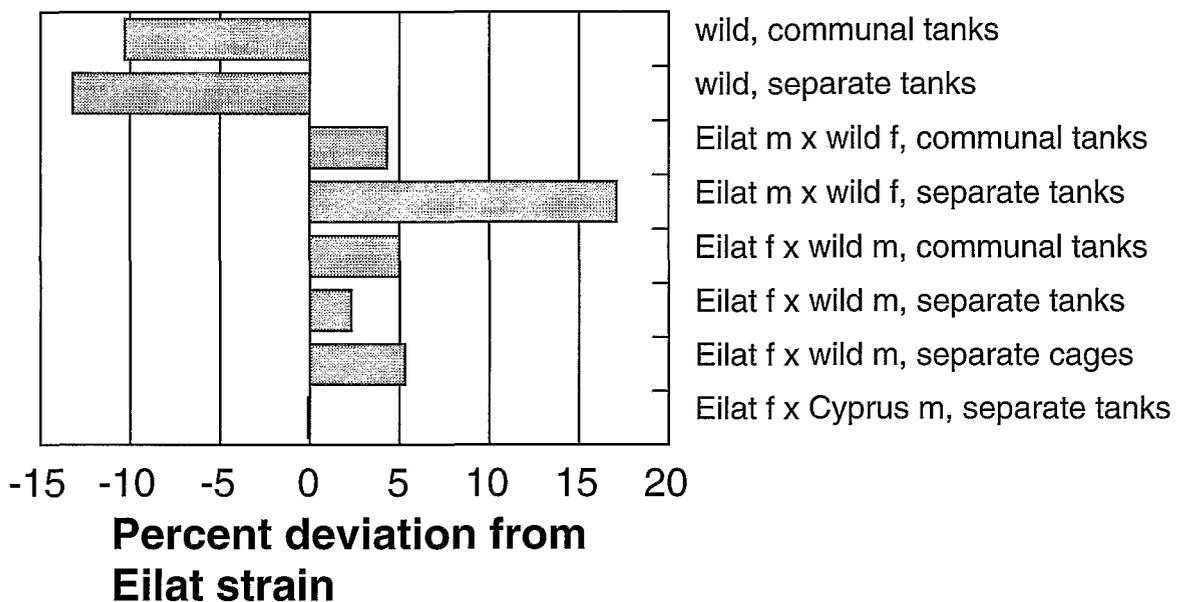


Fig. 1. Final weight differences among strains (as percent deviation from the "reference" Eilat strain). Wild = hatchery reared offspring of wild-caught individuals; Eilat = reference Eilat strain; Cyprus = offspring of Cyprus broodstock; m = male; f = female. Note: *S. aurata* is a protandrous hermaphrodite, and most fish at slaughter size are still male. Genetic complications arising from sexual dimorphism, and variable sex ratios, are not considered in this review for between or within strain assessments (see Falconer, 1981).

Even though few *S. aurata* strains were compared, growth differences under captive culture conditions were detected. Most evident was the inferior performance of the first generation wild fish relative to the long-term captive Eilat strain. Possibly, these differences resulted from "natural/ domestication" selection for performance in culture conditions as has been suspected in channel catfish, *C. carpio* and salmonid species (Doyle, 1983). Another possibility is that genetic differences existed among the ancestral wild populations. The magnitude of the differences is not great, but can be significant when profit margins are narrow.

Inter-strain *S. aurata* crosses tended to show only minor heterosis for growth, which may imply only negligible inbreeding in the long-term captive Eilat strain. More strains require testing, but it might be that little intraspecific heterosis will be a common finding in marine fish. Few impediments to gene flow among wild populations, and relatively short histories of captive propagation, might retard intraspecific genetic differentiation for marine fish, at least in comparison with those freshwater species with geographically isolated populations or with long histories of domestication (see Macaranas and Fujio, 1990). Conflicting data are provided from population genetic surveys of allozyme, mitochondrial DNA, DNA fingerprinting and DNA microsatellite polymorphisms among wild (and farmed) marine populations. Whereas little variation (fixed and frequency allele differences) is evident among tuna and flatfish populations and strains (Purdom, 1993), some variation is evident for *D. labrax* (Martinez *et al.*, 1991; Patarnello *et al.*, 1993), *P. major* (Taniguchi and Sugama, 1990; Takagi *et al.*, 1995) and barramundi or giant sea perch, *Lates calcarifer* (Centropomidae) (Shaklee and Salini, 1985; Salini and Shaklee, 1988; Keenan, 1994). Moreover, it is unknown whether the genetic differences observed using electrophoresis, etc. are indicators of the genetic variation responsible for commercially desirable heterosis and strain differences in culture (Kinghorn, 1983, Bentsen, 1991, 1994).

Presently there are too few data from marine fish strains to assess the importance of genotype x environment interactions, and whether it will be necessary to choose different strains for different production environments.

## **Selection within strains and heritability estimates**

The concept of artificial selection is straight forward: should "offspring tend to resemble their parents", then selection of superior performing individuals or families as parents should yield superior offspring. Historically in early land agricultural, this simple approach presumably was used to produce improved animals and plants strains. The major precondition for genetic improvement by within strain selection is that "offspring resemble parents", or, more formally, at least part of the total phenotypic variation for a particular trait is due to additive genetic variance. Knowledge of this proportion, or heritability, is necessary to predict whether selection for a particular trait will result in genetic change.

Various mating designs, from family to individual or mass selection, were used to estimate heritability for growth, and achieve genetic gain for growth, in freshwater and anadromous species including salmonids (Kincaid *et al.*, 1977; Gjedrem, 1983; Kinghorn, 1983; Gjerde and Gjedrem, 1984; Gjerde, 1986; Hershberger *et al.*, 1990), *I. punctatus* (Bondari, 1983; Dunham and Smitherman, 1983b; Klar *et al.*, 1988), *C. carpio* (Hulata, 1995b for review), and tilapias (Wohlfarth and Hulata, 1989 for review). Relatively few selection experiments failed to achieve genetic gain (Gjerde, 1986; Wohlfarth and Hulata, 1989 for review). For terrestrial animals, Falconer (1981) summarized theoretical efficiencies of different mating designs, the relationship between generation interval and rate of genetic improvement, the use of unselected control lines to distinguish genetic and environmental improvement, and issues concerning variable performance in different environments or genotype x environment interactions. These concepts were restated for fish (e.g., Gall, 1990).

## Family analysis

Large numbers of family groups (typically half- and full-sib) are required for reliable heritability estimations, and to carry out family selection without severe inbreeding (Falconer, 1981; Kirpichnikov, 1981). Family groups are readily obtained in many freshwater aquacultured species as a) gamete maturation tends to be synchronous, b) manual stripping of sperm and eggs is possible, and c) artificial fertilization is possible. However *S. aurata* displays distinctive reproductive characteristics. For example, *S. aurata* is a protandrous hermaphroditic species which undergoes sex reversal from male into female. Females have asynchronous development of oocytes and are daily sequential spawners for three months during winter (Zohar *et al.*, 1995). In the wild, *S. aurata* are group spawners (Ben-Tuvia, 1979), and social or group environment appears to be important not only for spawning but also for frequency at which males undergo sex reversal (Happe and Zohar, 1988).

For *S. aurata*, Gorshkov *et al.* (1996) estimated effectiveness of creating genetically related offspring groups with a variety of mating designs.

Both artificial stripping and single pair crossing (placing a male and female in a tank for natural spawning) were not efficient methods to simultaneously form genetically related offspring groups (Fig. 2). Possible reasons for low fertility included the failure to synchronize stripping with the exact daily spawning time of specific females (which varies between individual females), and stress created by housing fish as single pairs rather than as a group.

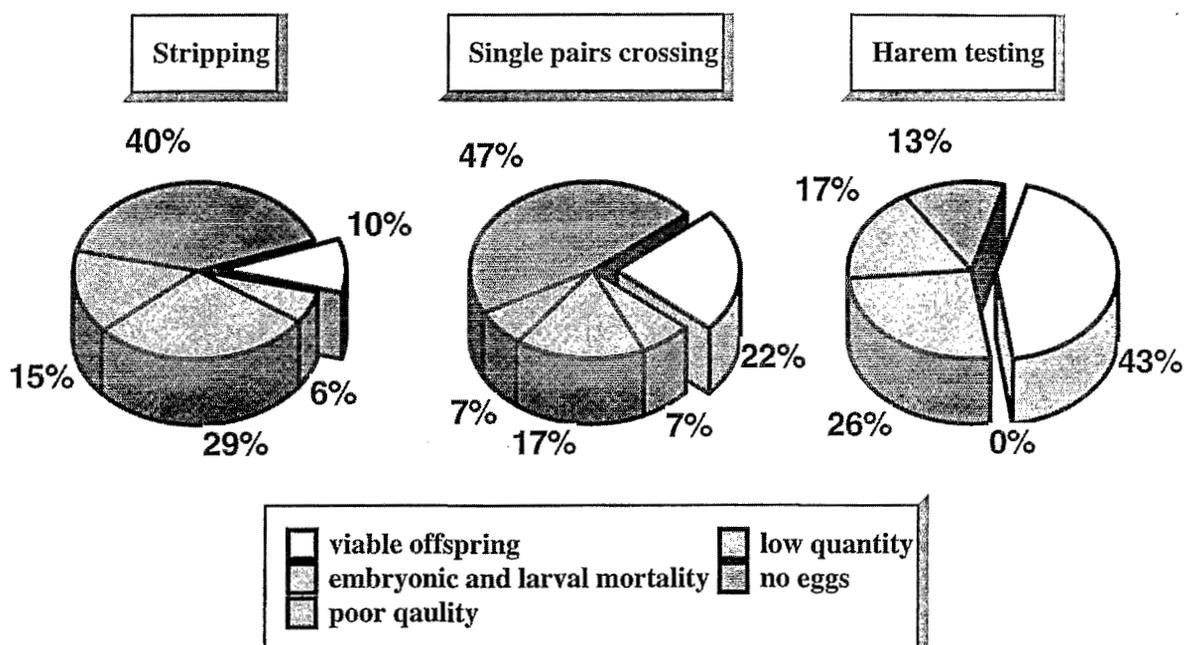


Fig. 2. Success of crossings.

Harem testing, where single males were left with many females, more closely simulated the natural group spawning behavior of *S. aurata* and was moderately successful in producing genetically related groups. However, the precise contribution of the different females was unknown and may have varied with assortative mating, differential fecundity and differential fertility (see Taniguchi *et al.*, 1983; Garcia de Leon *et al.*, 1995).

Too few full (n=4) and half-sib (n=4) family groups were produced for reliable estimations of heritability for growth. However, sire components of offspring weight variance were large, suggesting a genetic component for weight differences. At slaughter weight (300-500 g), sire components were statistically significant, and accounted for 29% of total weight variance for the "single pair crossing" family groups, and 14% of total weight variance for the "harem testing" family groups.

It appears that family mating designs, which are technically possible for salmon, are inappropriate for the group spawning *S. aurata*.

### Individual or mass selection

Knibb *et al.* (1996, 1997b) carried out mass selection for growth in *S. aurata* (Fig. 3). Selection objective was defined as "days early to slaughter weight" and selection criterion was defined as "individual weight when the largest fish in a cohort reach slaughter weight".

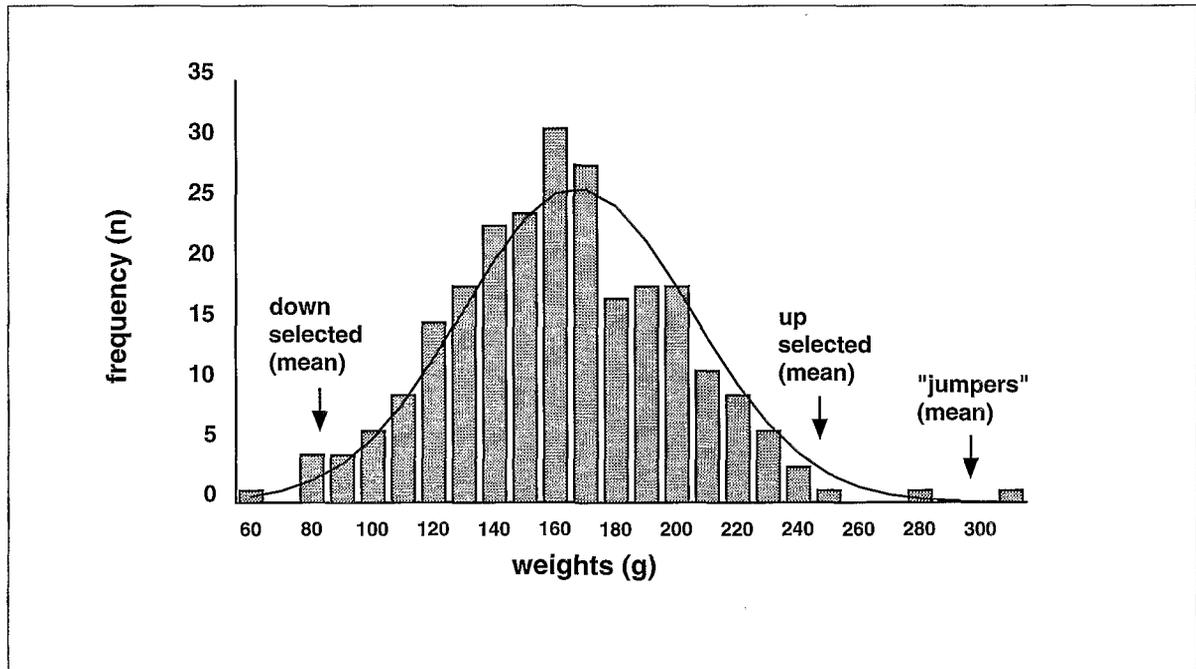


Fig. 3. Parent weights (as frequency histogram with superimposed normal distribution). Slaughter weight was considered to be approximately 300 g. Fish were from the Eilat strain, the same age, and maintained as a distinct group from hatching.

Males and females from the selected and control groups were crossed in various combinations, and progeny growth evaluated under communal and separate tank rearing conditions (Fig. 4). By age 1.5 years (slaughter weight) up-selected (selected for fast growth) progeny were -0.4% to 10.9% heavier (average gain of 7.3%), and down-selected (selected for slow growth) progeny were 8.5% to 16.2% lighter than control unselected groups. Heritability estimates for weight varied among replicates and rearing condition, but overall were positive and of a moderate magnitude (e.g.  $0.34 \pm 0.02$  for communal rearing).

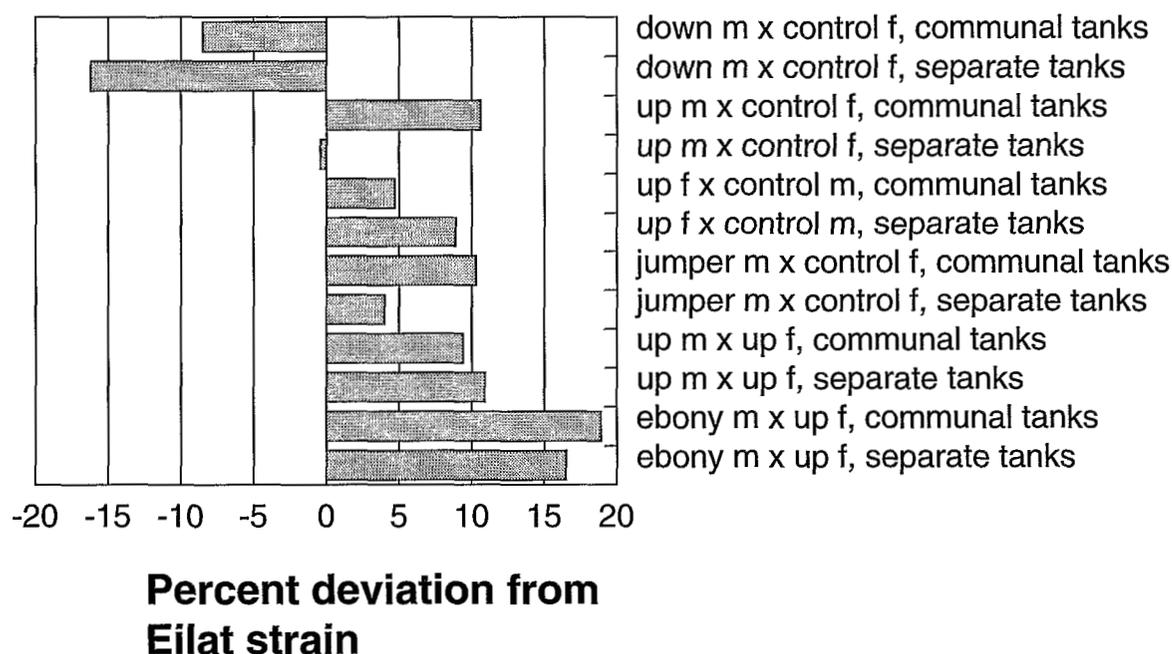


Fig. 4. Offspring weights (expressed as percent deviations from control unselected Eilat strain). Down = down selected, up = up selected, jumper = extreme up selected, ebony = *ebony* mutation strain, M = males, f = female.

There can be several potential unintentional consequences of selection.

First, selection for one trait, may result in genetic and phenotypic changes in other traits. *S. aurata* offspring of heavy (up-selected) parents showed several phenotypic differences from offspring of unselected parents (Table 1). Potentially desirable changes included improved food conversion efficiency, while undesirable changes included increased gonadal somatic index.

Second, propagation of closed finite-sized populations over generations (as usually required for selection) can lead to substantial inbreeding and genetic drift (Falconer, 1981). Genetic bottlenecks and inbreeding result from using few founders. Continued use of few parents for successive generations, as can occur with high selection intensity, will cause further inbreeding. Also, selected parents may contribute disproportionately to the next generation because of differential fertility and offspring survival. Some marine species are highly fecund, and so fertility and survival differences can be large. For example, a single *S. aurata* female can

produce thousands of eggs per day, and several million eggs per season (Zohar *et al.*, 1995). Thus effective population sizes in marine fish may be substantially smaller than total numbers of broodstock as concluded from monitoring allozyme frequencies during mass mating in the black seabream, *Acanthopagrus schlegeli* (Sparidae) (Taniguchi *et al.*, 1983), in *P. major* (Sugama *et al.*, 1988), and from monitoring microsatellite DNA variation in family crosses of *D. labrax* (García de León *et al.*, 1995). Consequences of inbreeding, especially high levels, include reductions in survival and growth (Kincaid, 1983, for review).

Table 1. Means and standard errors of various traits from offspring of control and growth selected *S. aurata*. Genetic correlations were not estimated

Trait	Control	Up-selected
Body weight in g at slaughter (females)	334.2±10.7	370.6±9.4
Body weight in g at slaughter (males)	308.8±7.0	331.03±7.7
GSI of 2 year old females	1.85±0.31	3.58±0.37
GSI of 2 year old males	1.67±0.18	3.44±0.37
Lipid proportion (dry weight)	0.436± 0.001	0.463±0.007
Feed conversion ratio (total feed/ fish weight)	1.92±0.01	1.73±0.02
Time (seconds/ kg fish) to consume fixed food ration	143.321.4	44.2±7.2
Food consumed <i>ad libitum</i> (g food/ kg fish) per day at slaughter size	48.3±1.2	49.2±1.2

Third, high intensity directional selection over generations may leave closely related individuals (showing superior performance), and may reduce total genetic variance and rate of genetic gain for some traits (Bulmer, 1971; Enfield, 1980; Falconer, 1981; Bentsen, 1994). Also, selection may increase the frequency of specific alleles with major phenotypic effects (Jones *et al.*, 1968; Frankham, 1978; Falconer, 1981), including those which have (artificial) selective advantage as heterozygotes, but are deleterious as homozygotes (Hill and Robertson, 1968; Moav and Wohlfarth, 1976). In one *S. aurata* line initiated by Knibb *et al.* (1996, 1997b), and mass selected for growth, the calculated frequencies of a usually rare recessive mutation (*ebony* allele) increased over one generation from 0.08 in the parents to 0.22 in the offspring. Possibly, *ebony* heterozygotes were selected (preferentially) because of heterosis for growth (Fig. 4). If so, continued selection will produce a high incidence, of the semi lethal and commercially undesirable *ebony* homozygote genotype.

Outcrossing to unrelated strains can ameliorate effects of inbreeding. Alternatively, and in order to maintain closed populations, several independent selection lines can be propagated, and crosses between them used for commercial

growout. The latter practice is followed for commercial development of the *S. aurata* mass selection program initiated by Knibb *et al.* (1992, 1996, 1997b) (also see Gjedrem, 1985), although this procedure requires dedicated facilities, and extra expenses beyond normal production costs. One alternative practice, which seems to have been adopted by several commercial Mediterranean farms, is high intensity mass selection (usually based on visual selection of "jumpers") and propagation of relatively few brood stock. However, the latter practice should lead rapidly to substantial inbreeding.

## Conclusions

Differences for growth and survival performance in culture were detected among several Eastern Mediterranean strains of gilthead seabream *Sparus aurata*, even though few strains were tested. This finding should encourage further strain assessment for marine fish. Also, future programs should assess possible genotype x environment interactions (whether different strains are required for different environments), and the importance of competitive and magnification effects (for strain comparisons in communal rearing conditions).

Usually, crosses between *S. aurata* strains yielded little heterosis. Little intraspecific heterosis may be a common finding in those marine fish with relatively short histories of captive propagation, and with few impediments to gene flow among wild populations.

Reproductive constraints dictate present choices of within strain selection methods. Mass selection, rather than family selection, was technically possible for the group spawning *S. aurata*, and usually resulted in genetic gain for growth. Contingent upon advances in husbandry and reproductive technologies, future possibilities for within strain selection include:

(i) Selection for traits other than growth, including carcass quality/ composition and disease resistance (Chevassus and Dorson, 1990).

(ii) Selection for several traits simultaneously, and for overall economic value using index selection and additional performance information from relatives (Falconer, 1981).

(iii) Use of precise methods to quantify selection criteria, including molecular assays for disease incidence (Knibb *et al.*, 1993).

(iv) Use of variable DNA markers to permit pedigree analyses (even from mass matings), and to detect linkage groups of economic importance (Magoulas *et al.*, 1995).

(v) Reduction of generation intervals (through induction of precocious sexual maturation with hormonal therapy) in order to accelerate rate of genetic gain.

(vi) Selection of fish grown under full commercial production conditions to optimize commercial gain.

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